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Influence of resource availability on life-history traits in coral-feeding butterflyfishes (Pisces: Chaetodontidae)

Thesis submitted by
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for the degree of Doctor of Philosophy in Marine Biology
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This thesis includes some collaborative work with my supervisors (Prof. J. Howard Choat, Dr. Morgan Pratchett, and Dr. Geoff Jones) as well as with Dr. Mark McCormick (all of JCU). While undertaking these collaborations, I was responsible for the project concept and design, data collection, analysis and interpretation, and the final synthesis of results into a form suitable for publication. My collaborators provided intellectual guidance, financial support, technical instruction and editorial assistance.

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Abstract

Given the highly stochastic nature of larval supply, coral reef fishes often settle in sub-optimal habitats with limited access to prey or other resources. Variation in the availability and quality of resources among different reef habitats is likely to have significant effects on the physiological condition and subsequent fitness of resident fishes, if not their absolute abundance. The first component of this study compared the abundance, feeding, and condition of two species of coral-feeding butterflyfishes (*Chaetodon baronessa* and *C. lunulatus*) across contrasting habitats with markedly different prey availability. Despite differences in prey availability, densities of *C. baronessa* and *C. lunulatus* were very similar between locations. However, there was significant spatial variation in their feeding and physiological condition. In front-reef locations, where coral prey was highly abundant, *C. baronessa* fed preferentially and almost exclusively on the coral *Acropora hyacinthus*. In contrast, in back-reef locations where coral prey was scarce and *A. hyacinthus* lacking, *C. baronessa* was much less selective and consumed a wider range of different coral prey. *C. lunulatus* was less selective than *C. baronessa*, but the diet of *C. lunulatus* also differed significantly between habitats. *C. lunulatus* consumed mostly *A. hyacinthus* in front-reef locations, but not in greater proportions than it was available. In back-reef locations, *C. lunulatus* preferentially consumed *A. intermedia* and *Porites* spp.. The physiological condition of both *C. baronessa* and *C. lunulatus* was much lower in back-reef locations compared to front-reef locations, which may reflect differences in the quantity and/or quality of prey available in different habitats. This work suggests that small scale (within-reef) differences in prey availability can have significant effects on the physiological condition and subsequent fitness of coral reef fishes.

Having established that resource availability may have a significant influence on physiological condition of fishes, I wanted to explore variation in growth and longevity of butterflyfishes associated with variation in resource availability. However, little basic life-history information on chaetodontids exists, so it was first necessary to establish the best model to describe the growth of these fish. von Bertalanffy growth functions were fitted to size-at-age data for four species of chaetodontids from Lizard Island. Special emphasis on juveniles provided detailed information of the early growth period. All four species demonstrated rapid initial growth achieving an average of 92% of maximum theoretical size in the first 2 years of their life. Within the von Bertalanffy growth function, I used various constraints of the theoretical age at length zero (t_0) in an analysis of both complete data sets and data sets using only adult fish. An unconstrained value of t_0 resulted in the best-fit (maximum r^2) curve when juveniles were included. When excluding juveniles, it was necessary to constrain t_0 to an approximate settlement size to most closely represent the growth of the species.

Several species of corallivorous butterflyfishes are known to have specific feeding preferences. Foraging theory predicts that organisms should specialise on a given resource only if there are tangible fitness benefits, such as increased growth. To assess the influence of different prey types on juvenile growth for two species of highly selective coral-feeding butterflyfish, *C. plebeius* and *C. trifascialis*, individuals were held in tanks for one month on an exclusive diet of only one coral species. The feeding habits of both these species have been well documented in the field, and this study utilised existing data to quantify specific feeding preferences. Selection functions revealed that *C. plebeius* selectively consumes both *Pocillopora damicornis* and *A. hyacinthus*, while *C. trifascialis* selectively consumes *A. hyacinthus*. To test

the fitness consequences of prey preferences, controlled feeding experiments were conducted in which individual butterflyfish were fed exclusively one of three different branching corals (*A. hyacinthus*, *P. damicornis* and *Porites cylindrica*) to compare growth on highly preferred coral species (e.g., *A. hyacinthus* and *P. damicornis*), versus coral prey that was never eaten in the field (*P. cylindrica*). *Chaetodon trifascialis* grew .053mm per day when feeding on *A. hyacinthus*, but actually decreased in total length when feeding on both *P. damicornis* and *P. cylindrica*. *Chaetodon plebeius*, meanwhile, grew at .051mm per day on *P. damicornis*, versus .038mm per day on *A. hyacinthus* and decreased in total length on *P. cylindrica*. This study shows that both *C. trifascialis* and *C. plebeius* selectively consume the coral prey that maximises juvenile growth and probably increases overall fitness. Variation in the early growth of these fish due to resource availability may explain patterns or anomalies in their large-scale population demographics.

Finally, to directly assess the influence of resource availability on life history traits, I quantified large-scale variation in some life history traits of chaetodontids across reefs with marked differences in the abundance of certain coral species. Samples of four species of chaetodontids (*C. citrinellus*, *C. lunulatus*, *C. melannotus*, and *C. trifascialis*) were collected at a northern Great Barrier Reef location (Lizard Island) and at a southern Great Barrier Reef location (One Tree Island). Population characteristics were assessed using a re-parameterised von Bertanlanffy growth function, allowing for better comparisons between populations. Although chaetodontids often had measurable variation between populations in growth rates, longevities, and mean maximum sizes, the variations were not consistent among species. These variations could not be consistently explained by preferred resource availability, temperature/latitude, or conspecific abundance. For, it was expected that

growth rates would be higher where preferred resources are more abundant, but this was not found. It is likely that a combination of resources, latitude (seasonal temperature variation), and conspecific abundance (including behavioural interactions) ultimately determine the large-scale differences in the demographics of butterflyfish populations.

Overall, this study shows that resources play an important role in determining life history characteristics of butterflyfishes. In particular, access to specific resources during the juvenile stage may have significant implications for life-long fitness and will likely effect survivorship and reproductive output. Ultimately, variation in the availability of resources is also likely to directly impact local abundance of butterflyfishes, especially for highly specialised species. While this was not apparent in this study, it is likely that several confounding factors such as competition, predation, and local environmental conditions may obscure the importance of resources in determining population demographics in complex environments, such as coral reefs. Future studies must therefore attempt to isolate the effects of different factors using further experimentation and well-designed sampling programs.

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CHAPTER 1: General Introduction

1.1 Variation in life history characteristics of fishes

Life history parameters (e.g., growth, longevity, reproduction, and mortality rates) and population demographics (e.g., population size- and age-structure) are fundamental characteristics of the biology and ecology of fishes. Importantly, the life history characteristics and population demographics of fishes affect their geographic range, abundance, and persistence (Choat and Robertson 2002), and may also influence habitat associations and biological interactions (Munday and Jones 1998). Despite this, there is very little demographic information available for most coral reef fishes (reviewed by Choat and Robertson 2002). There is an extensive literature on age and growth of commercially exploited fishes, and mostly from non-tropical habitats (e.g., Nakano 1995, Rikardson and Elliot 2000, Yamamoto 2004). Among coral reef fishes however, detailed demographic information is available mainly for the families Acanthuridae and Scaridae, owing to extensive research by J.H. Choat (e.g., Choat and Axe 1996, Choat et al. 1996). There are also good data on significant demographic rates (e.g., growth and mortality) for specific species of commercially exploited reef fishes such as coral trout (*Plectropomus*: Serranidae) (e.g., Russ et al. 1998). However, there are very limited data for most major families of coral reef fishes, including the Chaetodontidae, Pomacanthidae, and Pomacentridae.

Current data that are available on the life histories of coral reef fishes shows that demographic rates can vary greatly among species with significant implications for their ecology. Maximum age, for example, varies by several orders of magnitude among coral reef fishes, ranging from <59 days for the goby *Eviota signillata* (Depczynski and Bellwood 2005) up to >40 years for the surgeonfish *Naso vlamingii*

(Choat and Robertson 2002). Patterns of growth likewise show great variability. For example, *E. signallata* grows at a more or less constant rate throughout its life, and has very limited opportunity to reproduce (Depczynski and Bellwood 2005) while, in contrast, *N. vlamingii* (like other Acanthuridae) grows very rapidly to reach an asymptotic size and then remains at a constant size throughout the extended reproductive period of its life (Choat and Axe 1996). Coral reef fishes are similarly variable in terms of their mean maximum size, and these differences are reflected in their geographic range, abundance and habitat associations (review by Munday and Jones 1998). Moreover, the various life history characteristics of fishes (e.g., longevity and maximum size, longevity, and growth pattern) interact strongly but are not necessarily closely coupled (Choat and Robertson 2002). In general, smaller and shorter-lived fishes tend to have much more restricted geographic ranges, are more abundant, and are more tightly habitat-associated compared to larger and longer-lived fishes (Munday and Jones 1998).

A great deal of variation in the life history of fishes is also associated with reproduction. Most coral reef fishes exhibit little or no parental care, but release gametes into the water column, which are fertilised externally and are then largely at the mercy of ocean currents (Jones 1990). While larval fishes often have exceptional swimming abilities, the distribution and abundance of larvae is largely determined by large-scale processes, such as ocean currents (see Cowen 2002, Leis and McCormick 2002). Moreover, once larval recruits have reached a reef, selection of settlement location and post-settlement migration is very limited (Jones 1991). The end result of this process is often a very stochastic pattern of recruitment. However, the larval duration of fishes is highly variable and may have a major influence on their dispersal ability and population connectivity (Doherty et al. 1995, Jones et al. 1999). On one extreme, there are some species (most notably, *Polyacanthus acanthachromis* (family Pomacentridae)) that lay eggs on benthic substrates and/or lack pelagic larvae (e.g., Robertson 1973). Consequently, the dispersal potential of these species is highly constrained (Doherty et al. 1995). In contrast, some fishes (e.g., *Chlorurus sordidus*) have large well-developed larvae that remain in the plankton for up to 40 days and are very widespread (Bay et al. 2004).

Life history characteristics of fishes (predominantly growth and mortality) also vary among populations within a species (e.g., Gust et al. 2002, Ackerman 2004, Laman-Trip 2004). Spatial variation in life histories for individual species of fishes has been documented at a wide range of scales. For example, Laman-Trip (2004) documented significant variation in the growth rates and reproductive output of *Ctenochaetus striatus* (family Acanthuridae) at both very large (between ocean basins) and very small scales (between habitats). Similarly, Ackerman (2004) documented variation in growth trajectories of *Thallasoma lunare* (family Labridae) between widely separated reefs on Great Barrier Reef, but also among different habitats within each reef. In many cases (e.g., Choat and Axe 1996, Arendt 1997, Meekan et al. 2001, Gust et al. 2002, Ackerman 2004, Laman-Trip 2004), variation in the life histories of fishes is much more pronounced at relatively small spatial scales (within reefs) compared to large-scale differences between widely separated reefs. For example, fish taken from exposed habitats often have very different growth patterns compared to fishes taken from sheltered habitats at the same reef (Gust et al. 2002, Ackerman 2004, Laman-Trip 2004). These small-scale differences in the life histories of fishes are most commonly attributed to variation in the availability of resources (specifically food). Notably, coral reef fishes tend to grow faster and live longer on the exposed sides of reefs (e.g., Ackerman 2004), where planktonic prey, benthic prey, and algae are all much more abundant (Williams 1991).

If the availability of resources is significantly different among habitats, why would fishes occupy sub-optimal habitats with limited resources? As discussed above, the distribution and abundance of most coral reef fishes is ultimately dependent on the distribution and abundance of larvae at the time of settlement, which is known to be highly variable (Sale 1977, Doherty and Williams 1988). Consequently, reef fishes may be distributed across a wide range of habitat types with differing levels of resources (as well as different levels of shelter, competition, and/or predation), and once they have settled, most fishes have very limited opportunity to move (Jones 1991). If fishes settle in extremely unfavorable habitats (e.g., habitats with very limited resources and/or very high rates of predation) they are likely to quickly die (Levin 1998). However, even where fishes do persist they may exhibit considerable variation in life history characteristics (e.g., Gust et al. 2002, Ackerman 2004), probably associated with differences in the structure and composition of different reef habitats (Jones and McCormick 2002).

1.2 Importance of resources in determining life history characteristics

Many different factors may contribute to variation in the life histories of fishes, as observed between oceans (Laman-Trip 2004), between reefs (Ackerman 2004), among habitats (Gust et al. 2002), and with temperature (e.g., Choat and Robertson 2002) and population density (e.g., Warner and Hoffman 1980). To date, variation in demographic rates of fish populations have been variously attributed to predation (e.g., Fraser and Gilliam 1992, Connell 1998), competition (e.g., Levin et al. 1997), resource availability (e.g., Jones 1986), and/or stress (e.g., Billard et al.

1981). As poikilotherms, local environmental factors, such as temperature, must also exert a major influence on life history characteristics (predominantly growth rates and longevity) of fishes (Atkinson 1994). However, resource acquisition has the most immediate impact on individual condition and the energy that individuals have available for allocation to various life history processes (e.g., Kerrigan 1994). Changes in either the quality or quantity of prey resources available to fishes may therefore have significant impacts on their subsequent life history (Jones 1986, Forrester 1990, Holbrook et al. 2000). For example, Jones (1986) and Forrester (1990) demonstrated that increased availability of food led to increased growth rates in newly settled coral reef fishes (see also Kerrigan 1994).

In some instances, fishes are so specialised and dependent upon particular resources that their biology and ecology are closely tied to the abundance of the corresponding resource (Brown 1984, Munday 2001). For obligate coral-dwelling gobies, Munday (2001) showed that occupation of preferred coral species had significant advantages for both growth and survivorship. Although it has not been tested, the consumption of preferred prey may confer similar fitness advantages for fishes with highly specialised diets (e.g., Pratchett 2005). Throughout their geographic ranges, populations of both specialist and generalist fishes will be exposed to differences in the quality and quantity of resources with potential impacts on their fitness (Jones and McCormick 2002). For example, Holbrook et al. (2000) demonstrated that variable access to habitat resources significantly affected survivorship of newly settled *Dascyllus aruanus* (family Pomacentridae).

However, there are very few studies have documented direct effects of resource acquisition on life histories of fishes. Rather, most studies have shown that changes in the availability of resources are temporally or spatially correlated with changes in the abundance of fishes that exploit those resources. For example, McClanahan et al. (2000) showed that the abundance of herbivorous fishes increased rapidly following increases in algal quality (see also Hart and Klumpp 1996). Similarly, for coral-feeding butterflyfishes (*Chaetodon*: Chaetodontidae) the distribution and abundance of fishes is strongly correlated with spatial and temporal variation in the availability of coral prey (e.g., Bouchon-Navaro et al. 1985, Williams 1986, Lewis 1997, Cadoret et al. 1999, Bozec et al. 2005). None of these studies directly measure life history characteristics, but implicitly assume that changes in resource availability affected growth, survivorship, and/or reproductive output of study species, leading to detectable changes in population size (e.g., Hart et al. 1996).

Further evidence for the importance of resources in influencing life histories of fishes has come from studies which documented short-term changes in physiological condition. For example, increased food availability has been shown to lead to improved condition among both larval (Green and McCormick 1999) and adult fishes (Pratchett et al. 2001), measured using estimates of lipid storage in the liver. Declines in food availability also lead to corresponding declines in the condition of fishes (e.g., Pratchett et al 2004 – Appendix 1). Among some blennies (family Chaenopsidae), competitive exclusion of individuals from feeding areas with high resource availability has also been shown to lead to reduced condition (Clarke 1989, 1992). These changes in physiological condition may have subsequent effects on the reproductive success, if not growth and survivorship, of fishes (e.g., Koslow et al. 1995, Ballantyne et al. 1996, Duston and Saunders 1999). The physiological condition of larval fishes directly affects their swimming ability, which may influence their subsequent ability to feed and evade predators and thus affects individual survivorship, population connectivity, and population replenishment (Leis and

McCormick 2002). Moreover, McCormick (2003) showed that fishes with access to high quality prey (provided during mass spawning of corals) produced larvae that were in much better condition compared to larvae produced outside of these periods.

1.3 Life history characteristics and population fitness

Ultimately, an organism's life history is a reflection of their allocation of energy to various essential life processes, such as growth, maintenance and reproduction. Energy (derived from resources) is often limited, so there are inevitable trade-offs in the allocation of energy to different life processes (Begon et al. 1996). For example, excess energy available to fishes may be used to increase somatic growth, but is more often used to increase the quantity or quality of offspring (e.g., Jones 1984, Wootten 1998, Ali and Wootten 1999, McCormick 2003), thereby maximizing reproductive success. The allocation of energy to different life processes varies among populations and among individuals, and also throughout the lifetime of an individual, due to changes in the prioritization of different life processes (Jones and McCormick 2002). In general, the objective of most individuals is to maximise lifetime reproductive success (which is equivalent to individual fitness) (e.g., Caswell 1989), though this may be achieved in a number of ways. Fishes with surplus energy could potentially reproduce sooner, more often, or increase the number and/or quality of offspring produced (see Jones and McCormick 2002).

The importance of energy, and thus resources, in maximizing both individual and population fitness are well known, but the interrelationships between different life-history processes are very complex and poorly understood (Jones and McCormick 2002). Fishes living in sub-optimal locations (e.g., back-reef habitats) are likely to have limited resources and may, therefore, have much lower fitness compared to individuals in optimal locations (e.g., front-reef locations) with surplus resources. Consequently, these two groups of fishes are likely to have very different reproductive strategies, and may contribute different quantities or qualities of offspring to the next generation (sensu McCormick 2003). Conversely, the fishes in sub-optimal habitats may sacrifice longevity for the sake of reproductive output, such that the two meta-populations contribute equally to population-replenishment. Moreover, not all life history traits (e.g., maximum size) always have a clear connection to individual or population fitness. These variables, while plastic, presumably balance other life-history processes to create the optimal usage of available energy in any given situation (Angilleta et al. 2003). For example, growing faster or larger may reduce potential lifespan (Yearsley et al. 2004), or greater gamete production or longer reproductive seasons may reduce reproductive success (Javois and Tammaru 2004). While some studies (e.g., Jones 1987, Kuwamura et al. 1993, Kerrigan 1994, Booth 1995) have made specific connections between certain life history characteristics and overall fitness, considerable work is required to understand the inter-play of different life-history characteristics, and the factors that determine key demographics in coral reef fishes (Choat and Robertson 2002).

1.4 Introduction to butterflyfishes

Fishes in the family Chaetodontidae (commonly referred to as butterflyfishes) represent a significant component of the ichthyofauna of corals reefs, and yet (like many major families of coral reef fishes) little is known about their specific life histories (Allen et al. 1998). Butterflyfishes occur circumtropically in nearly every body of shallow, tropical, marine water, with some species occurring in sub-tropical and/or in deep water (>200m) habitats (Allen et al. 1998). There are 128 species and at least 12 different genera of butterflyfishes (Kuiter 2002), most of which are found exclusively on or near coral reef habitats (Burgess 1978). The family is dominated by fishes of the genus *Chaetodon*, among the most conspicuous inhabitants of coral reef environments (Burgess 1978). These fishes are particularly well known and have been extensively studied because of their tendency to feed on scleractinian corals (e.g., Reese 1977, Harmelin-Vivien and Bouchon-Navaro 1983, Pratchett 2005). In all, butterflyfishes exhibit a great diversity of feeding behaviour, from corallivory to herbivory to planktivory (e.g. Hiatt and Strassburg 1960; Talbot 1965; Hobson 1974; Reese 1981; Harmelin-Vivien and Bouchon-Navaro 1981, 1983). However, scleractinian corals constitute the primary, if not exclusive, prey for most butterflyfishes (e.g., Pratchett 2005).

The distribution patterns of butterflyfishes within different geographical regions are well documented, including Australia's Great Barrier Reef (e.g., Fowler 1990), French Polynesia (e.g., Bouchon-Navaro 1986), New Caledonia (e.g., Bozec et al. 2005), Hawaii (e.g., Cox 1994), Japan (e.g., Cadoret et al. 1999), Sri Lanka (e.g., Öhman and Rajasuriya 1998), and the Red Sea (e.g., Roberts and Ormond 1987). These studies have tended to show close relationships between live coral cover and abundance of butterflyfishes (eg., Harmelin-Vivien and Bouchon-Navaro 1983, Bell and Galzin 1984, Tricas 1989a, Bozec et al. 2005) and others have even described the relationship as "intimate" (e.g., Crosby and Reese 1996), but occasionally this relationship has not been found (Erdman 1997, Kulbicki and Bozec 2005). Moreover, chaetodontids often occur in predictable assemblages at different zones within reefs (e.g. French Polynesia, Harmelin-Vivien and Bouchon-Navaro 1983, Bouchon-Navaro 1986) and on different reefs from inshore to offshore (e.g. Great Barrier Reef, Anderson et al. 1981). Within each of the aforementioned studies, the authors contend that species with greatest dietary overlap occur in spatially separate assemblages, and interpret these patterns as evidence for resource partitioning of food (see also Zekeria et al. 2002).

1.5 Thesis objectives

The overall objectives of this thesis were twofold. The first objective was to quantify key life history characteristics (specifically, age-based growth, asymptotic size, and longevity) for fishes of the genus *Chaetodon* (family Chaetdodontidae). Although there has been considerable research on the ecology of butterflyfishes (focusing mainly on patterns of distribution and abundance, and their feeding ecology), there is surprisingly little known about their life histories. A few authors have touched on specific aspects of their life histories, such as Ralston (1976a, 1976b, 1981), who documented the age and size of maturity in *Chaetodon miliaris*. Suzuki et al. (1980) further investigated the maturational patterns of *C. nippon*, but this was restricted to aquaria-based studies. The primary conclusion of these studies was that the occurrence of sexual maturity depended on size, not age (see also Tricas and Hiramoto 1989). However, none of these studies included an age-based growth analysis over the lifespan of the fish. Fowler (1989, 1991) examined the biology and ecology of three species of butterflyfishes at One Tree Island (*C. rainfordi*, *C. plebius*, and *Chelmon rostratus*). Fowler (1989, 1991) showed that these species were gonochoristic and maturity occurred when the fish achieved adult size, but again this did not include any assessment of age and growth throughout the lifespan of these fishes. This lack of knowledge about the life histories and population demographics severely limits understanding of their basic ecology. For example, it is currently not known how fast butterflyfishes grow, how quickly they mature or how long they live, which limits predictions about how fast butterflyfish populations might recover following major disturbances (e.g. Halford et al. 2004, Berumen and Pratchett in press – Appendix 3).

The second objective of this thesis was to establish the importance of resources in determining life history characteristics of coral-feeding butterflyfishes. Butterflyfishes offer an ideal opportunity to test the role of resources in shaping life history characteristics because they feed mostly on readily measurable resources. For most fishes (e.g., planktivores, piscivores, and herbivores) it is difficult to determine the specific range and types of prey that they consume, let alone to establish the availability of alternate prey types (piscivores, Stewart and Jones 2001; planktivores, Pratchett et al. 2001; herbivores, Wilson and Bellwood 1997). For coral-feeding butterflyfishes, however, the specific range of corals consumed by individual species has been well documented (e.g., Irons 1989, Cox 1994, Pratchett 2005), and it is relatively straightforward to measure the abundance of corals (e.g., Hughes et al. 2000). Further, the abundance of corals is very constant at time scales relevant for sampling (compared to plankton abundance or the abundance of small prey fish).

1.6 Thesis outline

In order to quantify life-history characteristics of *Chaetodon* butterflyfishes and further assess the influence of variation in resources (quality and quantity of resources), I conducted four independent studies, represented by the four main chapters of this thesis. The first of these studies (Chapter 2) represented a preliminary study into the importance of resources (i.e. coral prey) in the biology and ecology of coral feeding butterflyfishes. Both the abundance and composition of scleractinian corals varies greatly within and between coral reefs. Most striking are differences in coral assemblages between exposed (front-reef) versus sheltered (back-reef) habitats (Done 1982). Accordingly, this study measured within-reef variation in the abundance, dietary composition and physiological condition of two species of *Chaetodon* butterflyfishes (*C. baronessa* and *C. lunulatus*) between exposed front-reef locations and sheltered back-reef locations. It was expected that the physiological condition, if not the abundance of butterflyfishes would be significantly higher in front reef locations where coral cover is highest. Although not tested, it was assumed that differences in physiological condition are likely to be further reflected in their life-history characteristics (e.g., Green and McCormick 1999, Pratchett et al. 2001, Pratchett et al. 2004 – Appendix 1). If the effect of a change in resources can be established at a small spatial scale, then there is justification for exploring larger-scale variation in life histories of butterflyfishes associated with marked variation in the abundance and composition of coral assemblages between widely separated reefs.

The ultimate aim of this study was to document spatial variability in the life histories of butterflyfishes, but given the lack of basic data on age-based demographics, it was first necessary to obtain size-at-age data for a range of *Chaetodon* species and establish appropriate models for age-based growth. Studies to date suggest that coral reef fishes exhibit a wide range of growth patterns (Fowler 1995), so it is important to establish taxon-specific (for families, if not genera and species) growth models (Choat and Robertson 2002). There are three critical features to be considered: i) the relationship between size and age, ii) ontogenetic changes in growth rates, and iii) the contribution of early post-settlement growth rates to overall life histories. The second study of this thesis (Chapter 3) presents size-at-age data for four species *Chaetodon* butterflyfishes (*C. baronessa, C. citrinellus, C. lunulatus*, and *C. trifascialis*). All fishes used in this study were collected exclusively from Lizard

Island on the northern Great Barrier Reef. This study fitted von Bertalanffy growth functions to size-at-age data for each the four species to establish their basic growth form and explore species-specific differences in their life-histories. Particular emphasis was placed on including data for juvenile life-stages, following Choat and Axe (1996) and Kritzer et al. (2001). Results of this study are fundamental in establishing the basic growth form before comparing age-based demographic rates between populations in different locations.

The third study of this thesis (Chapter 4) specifically tests whether variation in resource availability impacts individual growth of chaetodontid fishes using feeding experiments conducted under laboratory conditions. Herein, fishes of two species (*C. plebeius* and *C. trifascialis*) were kept in aquaria and fed exclusive diets of one of three different coral species (*Acropora hyacinthus*, *Pocillopora damicornis* and *Porites cylindrica*), which were differentially consumed in the field. Individuals fed different diets were expected to exhibit significant differences in growth rates (based on proportional changes in total length and weight) measured fortnightly for one month. If patterns of prey preference observed in the field constitute optimal foraging, then fishes fed their most preferred prey would be expected to grow faster than fishes fed sub-optimal prey. Therefore, this study would show that variation in coral composition, and not just the abundance of corals, can have a significant influence on the fitness of chaetodontid populations living in different habitats.

If resources are fundamental in determining life history traits of butterflyfishes, this is likely to be most apparent among widespread reefs with measurable differences in coral composition. To determine if there is large-scale variation in the demography of chaetodontids, Chapter 5 compared size-at-age relationships for four species of *Chaetodon* butterflyfishes (*C. citrinellus*, *C.*

lunulatus, *C. melannotus*, and *C. trifascialis*) from Lizard Island and One Tree Island, separated by approximately 1200km on the Great Barrier Reef. This study seeks to determine if measurable large-scale differences in life history characteristics of these species (specifically, growth rates, longevity, and maximum size) exhibit a consistent pattern and whether or not these differences can be related to variation in resource availability.

In addition to the four studies described above, I have also attached three manuscripts (Appendices 1-3), which outline additional studies, at the end of the thesis. While not intended to form part of my PhD research, these manuscripts were all submitted for publication during my PhD candidature. Moreover, each of these publications relate to the biology and ecology of coral-feeding butterflyfishes, and are therefore, directly relevant to the subject of this thesis. The first of these publications (Pratchett et al. 2004 – Appendix 1) explores changes in the abundance, dietary habits and physiological condition of an obligate coral feeding butterflyfish (*C. lunulatus*) associated with temporal declines in the abundance of coral prey. This study was undertaken in response to extensive coral bleaching in the central Great Barrier Reef, and corresponds closely with the aims of Chapter 2.

The second manuscript (Berumen and Pratchett, in press – Appendix 2) details changes in competitive interactions among *Chaetodon* butterflyfishes associated with differences in resource availability. If competitive interactions become more or less intense with decreases in resource availability, then this may drastically alter patterns of energy allocation, leading to differences in growth, survivorship, and/or reproductive success. It was therefore important to consider competitive interactions as a potentially confounding factor in studies considering the effects of resource availability on life history characteristics. Finally, the third manuscript (Berumen and

Pratchett, in press – Appendix 3) explores important issues of recovery (increases in abundance of fishes) and resilience (similarity in species composition to that of the pre-disturbance assemblage) in chaetodontid assemblages at Moorea, French Polynesia, where these assemblages have been subject to a long-history of habitat perturbation (caused by severe tropical storms, climate induced coral bleaching, and infestations of the corallivorous starfish *Acanthaster planci*). If resources are fundamental determining life history traits of butterflyfishes we expected to show that the recovery and resilience of butterflyfish assemblages is strongly dependent upon the recovery and resilience in coral communities.

Chapter 2: Within-reef differences in diet and body condition of coral-feeding butterflyfishes (Chaetodontidae)[†]

2.1 ABSTRACT

Given the highly stochastic nature of larval supply, coral reef fishes often settle in sub-optimal habitats with limited access to prey or other resources. Variation in the availability and quality of resources among different reef habitats is likely to have significant effects on the physiological condition and subsequent fitness of resident fishes, if not their absolute abundance. This study compared the abundance, feeding and condition of two species of coral-feeding butterflyfishes (*Chaetodon baronessa* and *C. lunulatus*) across contrasting habitats with markedly different prey availability. Despite differences in prey availability, densities of *C. baronessa* and *C. lunulatus* were very similar between locations. However, there was significant spatial variation in their feeding and physiological condition. In front-reef locations, where coral prey was highly abundant, *C. baronessa* fed preferentially and almost exclusively on the coral *Acropora hyacinthus*. In contrast, in back-reef locations where coral prey was scarce and *A. hyacinthus* lacking, *C. baronessa* was much less selective and consumed a wider range of different coral prey. *C. lunulatus* was less selective than *C. baronessa*, but the diet of *C. lunulatus* also differed significantly between habitats. *C. lunulatus* consumed mostly *A. hyacinthus* in front-reef locations, but not in greater proportions than it was available. In back-reef locations, *C.*

[†] This chapter appears as is in the journal *Marine Ecology Progress Series*: Berumen M, M Pratchett, and M McCormick. (2005) Within-reef differences in diet and body condition of coral-feeding butterflyfishes (Chaetodontidae). *MEPS* 287: 217-227

lunulatus preferentially consumed *A. intermedia* and *Porites* spp.. The physiological condition of both *C. baronessa* and *C. lunulatus* was much lower in back-reef locations compared to front-reef locations, which may reflect differences in the quantity and/ or quality of prey available in different habitats. This study suggests that small scale (within-reef) differences in prey availability can have significant effects on the physiological condition and subsequent fitness of coral reef fishes.

2.2 INTRODUCTION

The distribution and abundance of coral reef fishes is ultimately dependent on the distribution and abundance of larvae at the time of settlement, which is known to be highly variable (e.g., Sale 1977, Doherty and Williams 1988, Hixon and Carr 1997). As a consequence, reef fish may be distributed across a wide range of habitat types with differing levels of shelter, prey availability, competition and/ or predation. At all but very small spatial scales (<1km) post-settlement reef fish have limited opportunity to choose among different habitats and are largely restricted to the habitat in which they settle (Jones 1991). In instances where reef fish settle in highly unfavourable habitats (e.g., habitats with limited resources and/ or very high levels of predation) rates of early post-settlement mortality are likely to be very high (Levin 1998). Habitat variability has been shown to exert a major influence on the distribution, abundance and community structure of coral reef fishes (e.g., Shulman 1985, Munday et al. 1997, Holbrook et al. 2000). Even where reef fish do persist, there may be considerable variation in their physiological condition, growth, reproductive output and/or longevity associated with differences in the structure and composition of different reef habitats (Jones and McCormick 2002). However, very few studies (Holbrook and Schmitt 1986, Munday 2001) have considered ecological or fitness consequences for fishes living in different reef habitats.

Habitat requirements of coral reef fish vary greatly among species, but most reef fish are closely associated with the spatial structure of reef substrata and particularly the abundance of scleractinian coral (Bell and Galzin 1984, Munday et al. 1997, Holbrook et al. 2000), and/ or the diversity of corals (Chabanet et al. 1997, Cadoret et al. 1999). These associations arise because scleractinian corals are fundamental in providing living space and shelter for coral reef fishes (Syms and Jones 2000, Holbrook et al. 2000). For butterflyfishes of the genus *Chaetodon* (family Chaetodontidae) scleractinian corals also represent an important food source (e.g., Anderson et al. 1981). Not surprisingly, associations between *Chaetodon* butterflyfishes and scleractinian corals are much stronger than for most other reef fish. Both local and regional scale patterns in the abundance of butterflyfish have been related to variation in live coral cover (Birkeland and Neudecker 1981, Bouchon-Navaro et al. 1985, Findley and Findley 1985, Bouchon-Navaro and Bouchon 1989, Cadoret et al. 1999; but see also Bell et al. 1985, Fowler 1990). Moreover, several studies (e.g., Bouchon-Navaro et al. 1985, Williams 1986) have revealed significant declines in the abundance of butterflyfishes following extensive depletion of scleractinian corals, caused by outbreaks of crown-of-thorns starfish (see also Sano et al. 1984, 1987).

The aim of this study was to explore ecological and fitness consequences for coral feeding butterflyfish living across different reef habitats with marked differences in coral cover. In particular, we wanted to test whether the abundance, feeding rate, or physiological condition is higher for butterflyfishes living in reef habitats with high coral abundance compared to butterflyfishes living in habitats with low coral abundance. Given their strong reliance on scleractinian corals (for food and shelter), variation in the abundance of scleractinian corals would be expected to affect not only the abundance of *Chaetodon* butterflyfishes, but also their physiological condition and individual fitness. Food availability has major effects on growth, maturation and reproductive output in wide variety of fishes (e.g., Green and McCormick 1999, McCormick 2003). Both abundance and composition of scleractinian corals varies greatly within and between coral reefs. Most striking are differences in the abundance (and composition) of scleractinian corals associated with cross-reef gradients in exposure (Done 1982). This study measured within-reef variation in the abundance, feeding habits, and physiological condition of *Chaetodon* butterflyfishes, comparing butterflyfish populations from exposed front-reef locations and sheltered back-reef locations. It is expected that the physiological condition, if not the abundance or feeding rates, of coral feeding butterflyfishes would be higher in front-reef locations where coral cover is highest. A difference in the condition, feeding rates, or abundance could then be attributable to either an increased quantity of corals or an increase in quality of corals.

2.3 METHODS

2.3.1 Sampling locations and study species

This study was conducted between January and April 2000, at Lizard Island (14^{o}40’S, 145^{o}27’E), on the northern Great Barrier Reef, Australia (Figure 2.1). Sampling was conducted at four different locations, representative of two contrasting reef habitats; South Island and Coconut Beach represent front-reef habitats directly exposed to the prevailing South East trade winds, whereas Osprey Islet and Corner Beach represent back-reef and relatively sheltered habitats. In front-reef locations (South Island and Coconut Beach) the reef is comprised of contiguous fringing reef with distinct zonation of the reef flat, crest, slope and base. At front-reef locations, sampling was conducted along the shallow reef crest (2-5 metres depth). In back-reef locations (Osprey Islet and Corner Beach) the reef was comprised of large patch reefs (200-300 metres diameter), separated by wide expanses of open sand. Here, sampling was conducted on the tops of patch reefs (3-6 metres depth).

This study considered two of the most common and widespread butterflyfish species (*Chaetodon baronessa* and *C. lunulatus*), both of which feed almost exclusively on scleractinian corals (Allen et al. 1998). To compare the abundance of *Chaetodon* butterflyfishes among locations, we used 50 × 4m visual belt transects. Ten replicate

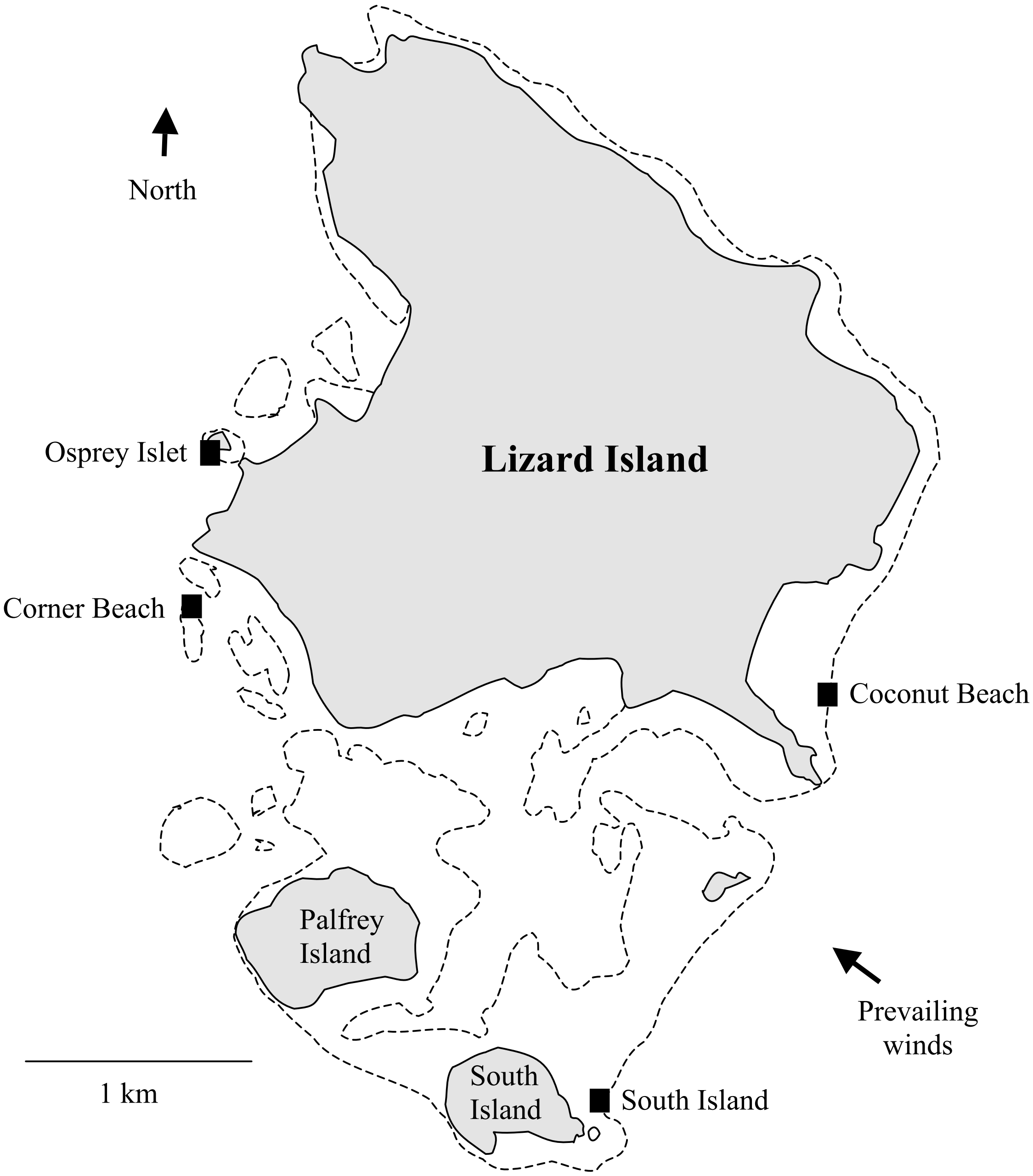


Figure 1. Locations used for the study of *Chaetodon* abundance patterns and physiological condition at Lizard Island, Great Barrier Reef. South Island and Coconut Beach represent front-reef habitats directly exposed to the prevailing southeast trade winds, whereas Corner Beach and Osprey Islet represent back-reef and relatively sheltered habitats. Dashed lines indicate the approximate reef outline.

transects were orientated parallel to the reef crest, and were run from haphazardly selected starting points, within each location. We recorded the abundance of all *Chaetodon* butterflyfishes (19 species in total) on every transect. Spatial variation in the abundance of *C. baronessa* and *C. lunulatus* was analysed using analysis of variance (ANOVA). Raw data was log transformed to meet ANOVA assumption of homogeneity of variances. All statistical procedures were conducted using SPSS 11.0.

2.3.2 Feeding behaviour of butterflyfishes

The range of prey types consumed by *C. baronessa* and *C. lunulatus*, as well as their relative use of different prey types, was ascertained from field observations of the foraging habits of replicate individuals (after Reese 1975). During feeding observations, individual butterflyfish were followed for three minutes, recording the total number of bites taken from each different coral species (see Table 2.1). Feeding observations were conducted throughout the day, from 0600hrs to 1800hrs. However, in order to account for variation that might be attributable to diurnal feeding patterns, approximately equal numbers of observations were conducted in the morning (0600-1000hrs), at mid-day (1000-1400hrs), and in the afternoon (1400-1800hrs), at every location. In all, 50 replicate feeding observations were conducted for each butterflyfish species (*C. baronessa* and *C. lunulatus*) at every location (South Island, Coconut Beach, Osprey Islet and Corner Beach). Most individuals continued to feed despite the presence of divers, but observations were aborted if fish fled from the diver or sought shelter within the reef matrix.

Variation in the dietary composition of butterflyfishes may result from differences in the availability of alternate prey and/or specific differences in feeding preferences. To test whether butterflyfishes exhibited significant feeding selectivity, we used the log-likelihood statistic (X^2_{L2}), calculated using the formula

Table 2.1. Range of prey categories used by *Chaetodon baronessa* and *C. lunulatus* at each location (South Island, Coconut Beach, Osprey Islet and Corner Beach). All prey categories used by each butterflyfish at each location are indicated by "*".

	Chaetodon baronessa				*Chaetodon lunulatus*			
Prey Categories	South Island	Coconut Beach	Osprey Islet	Corner Beach	South Island	Coconut Beach	Osprey Islet	Corner Beach
ACROPORIDAE								
Acropora cytherea	*				*			
Acropora digitifera	*				*	*		
Acropora donei				*		*		
Acropora florida	*	*	*	*	*	*	*	*
Acropora formosa	*	*	*		*	*	*	
Acropora gemmifera	*	*	*		*	*	*	*
Acropora grandis			*	*		*	*	
Acropora humilis	*	*	*	*	*	*		*
Acropora hyacinthus	*	*			*	*		
Acropora intermedia			*	*	*	*	*	*
Acropora loripes				*			*	*
Acropora millepora	*	*	*		*	*	*	*
Acropora monticulosa					*	*		
Acropora nasuta		*	*	*	*	*	*	*
Acropora robusta	*	*	*		*	*		
Acropora sarmentosa			*	*			*	*
Acropora secale		*		*	*	*	*	
Acropora selago			*		*	*		*
Acropora valida	*	*	*	*	*	*		
Astreopora spp.			*		*		*	
Isopora spp.	*	*	*	*	*	*	*	*
Montipora spp.		*	*	*	*	*	*	*
POCILLOPORIDAE								
Pocillopora damicornis	*	*	*	*	*	*	*	*
Pocillopora eydouxi	*	*			*	*		
Pocillopora verrucosa	*	*	*	*	*	*	*	
Seriatopora hystrix			*	*	*		*	*
Stylophora pistillata	*	*	*	*	*	*	*	*

Table 2.1. Continued

	Chaetodon baronessa				*Chaetodon lunulatus*			
Prey Categories	South Island	Coconut Beach	Osprey Islet	Corner Beach	South Island	Coconut Beach	Osprey Islet	Corner Beach
FAVIIDAE								
Cyphastrea seriala					*		*	
Diploastrea heliopora		*		*				
Favia favus			*			*		*
Favia pallida		*		*				*
Favia speciosa						*	*	
Favia stelligera					*			
Favites abdita	*	*	*		*	*		*
Favites halicora					*	*	*	
Goniastrea retiformes		*	*	*	*	*	*	*
Leptastrea transversa			*				*	
Leptoria phrygia	*		*			*		*
Montastrea spp.				*				*
Platygyra daedalea				*			*	*
Platygyra sinensis			*					
Platygyra verweyi							*	
MUSSIDAE								
Lobophyllia spp.			*	*				*
Symphyllia recta		*	*	*		*	*	*
Other Scleractinian corals								
Fungiidae		*	*	*			*	*
Coeloseris mayeri			*	*	*	*	*	*
Pavona varians							*	
Psammacora spp.			*				*	
Galaxea spp.		*	*	*	*	*	*	*
Hydnophora spp.					*	*		*
Porites spp.	*	*	*	*	*	*	*	*
Turbinaria spp.								*
No. categories used	**18**	**24**	**32**	**27**	**32**	**33**	**31**	**29**

$$X^2_{L2} = 2\sum_{j=1}^{n}\sum_{i=1}^{I} u_{ij} Ln\{u_{ij} / E(u_{ij})\}$$

where u_{ij} is the proportional use of each prey type (i) by each individual (j), and $E(u_{ij})$ is the expected number of bites taken from prey type i by the jth individual if use is proportional to availability (Manly et al. 1993). The resulting value of X^2_{L2} was compared to the chi-squared distribution with n(I-1) degrees of freedom (where I is the total number of prey categories) to determine the significance of selectivity exhibited by each butterflyfish species (*C. baronessa* and *C. lunulatus*) at each location (South Island, Coconut Beach, Osprey Islet and Corner Beach). Where log-likelihood statistics revealed that butterflyfishes were feeding selectively, we then used resource selection functions (Manly et al. 1993) to determine which prey categories were used more or less frequently than expected.

Resource selection functions (w_i) were calculated for all coral species (i) used by each species of butterflyfish, using the formula:

$$w_i = u_i / \pi_i$$

which compares the proportional use (u_i) of each prey category (i) with the proportional availability of that prey category (π_i) within the local area (Manly et al. 1993). We also calculated Bonferroni corrected 95% confidence intervals around each selection function, whereby the use of a particular resource was only deemed to be disproportionate to its availability if the 95% confidence interval did not encompass 1. Selection functions significantly greater than 1 indicated that corals were consumed more than expected from their availability (i.e. selected), while selection functions significantly less than 1 indicated that corals were consumed significantly less than expected (i.e. avoided).

To assess variation in the availability of coral prey, we measured the abundance of corals and composition of coral communities at each location (South Island, Coconut Beach, Osprey Islet and Corner Beach). Coral cover and composition were quantified using ten replicate 10-metre line intercept transects at each location. Every colony underlying each transect was identified to species, and the intercept length for each coral species was measured to the nearest centimetre. Variation in total coral abundance among locations was analysed using ANOVA, while variation in the relative abundance of major prey corals (10 taxa) was analysed using multivariate analyses of variance (MANOVA). Univariate homogeneity was tested using Cochran's test and residual plots were examined to confirm MANOVA assumptions of multivariate homogeneity and normality. Pillai's Trace statistic was used to determine the significance of MANOVA results, following Olsen (1976). Where there were significant differences in the relative abundance of major prey corals, we used canonical discriminant analysis (CDA) to show the relative similarity of coral communities among locations.

2.3.3 Physiological condition of butterflyfishes

To test for spatial variation in the physiological condition of *C. baronessa* and *C. lunulatus*, we collected 20 individuals of both species at every location (South Island, Coconut Beach, Corner Beach and Osprey Islet). All fish were speared between 1000hrs and 1400hrs and kept on ice for 1-3 hours before processing. The physiological condition of individual butterflyfish was assessed using estimates of hepatocyte vacuolation (the proportion of hepatic tissues occupied by intra-cellular vacuoles), which is an indirect measure of total liver lipid stores (Pratchett et al. 2004). Lipid (rather than carbohydrate) is the favored energy reserve of fishes and the liver is the first site of lipid deposition. Therefore, liver lipid content provides a very sensitive measure of the physiological condition and subsequent fitness of individual fish (Green and McCormick 1999, Pratchett et al. 2004).

To measure hepatocyte vacuolation in *C. baronessa* and *C. lunulatus*, the entire liver from each fish was removed and placed into 10% calcium buffered formalin (FAACC) for 4 days. After fixing, hepatic tissues were dehydrated in a graded ethanol series and embedded in paraffin wax. Wax blocks of hepatic tissues were sectioned at 5μm, and stained using Mayer's haematoxylin and eosin to emphasise hepatocyte vacuoles. The proportion of vacuoles in hepatic tissues was then quantified using a Weibel eyepiece, recording the proportion of points (out of 121) that intersected hepatocyte vacuoles viewed at ×400 magnification (following Pratchett et al. 2001). Three replicate counts of hepatocyte vacuoles were recorded for three different sections through the different parts of the liver of each fish, giving a total of nine counts for each fish. Hepatocyte vacuolation was then compared between species (*C. baronessa* and *C. lunulatus*) and among locations (South Island, Coconut Beach, Corner Beach and Osprey Islet) using ANOVA.

2.4 RESULTS

2.4.1 Coral cover and composition

The abundance and composition of scleractinian corals varied greatly among the four locations considered during this study. Most notably, coral cover at front-reef locations (South Island and Coconut Beach) was more than double that of back-reef locations (Osprey Islet and Corner Beach). Coral cover was highest at South Island, where scleractinian corals occupied 45.7% (± 3.3 SE) of hard substrata, followed closely by Coconut Beach where scleractinian coral cover was 40.6% (± 4.1 SE). In contrast, scleractinian corals occupied less than 20% of hard substrata at both Osprey Islet (19.5% ± 3.3 SE) and Corner Beach (17.8% ± 2.8 SE). Variation in coral cover among locations was highly significant (ANOVA, F = 17.5, df = 3/39, P < 0.01), as were differences in coral composition (MANOVA, Pillai's trace = 47.2, df = 14, P < 0.001). Variation in the composition of coral communities was very apparent between front-reef locations and back-reef locations (Figure 2.2). However, there were also large differences in the coral communities between the two back-reef locations. Many of the corals surveyed (32/56 species) were found at all four locations, but the abundance of these taxa varied greatly among locations. Coral communities at the front reef locations were dominated by *Acropora hyacinthus*, which accounted for 45.2% and 35.3% of coral cover at South Island and Coconut Beach, respectively. In contrast, *A. hyacinthus* was virtually absent at back reef locations. At Osprey Islet, the coral community was dominated by *A. formosa* and *Montipora* spp., whereas at Corner Beach, the dominant corals were *A. florida* and *Porites* spp.. The one coral species that was reasonably abundant at all four locations was *Pocillopora damicornis*.

2.4.2 Abundance of butterflyfishes

Despite significant differences in the abundance and composition of prey corals, mean densities of *C. baronessa* and *C. lunulatus* varied very little among the four locations. Overall, the mean density of *C. baronessa* was 1.14 ± 0.67 (SE) individuals per 200m^2, and though they were slightly more abundant at front-reef locations (South Island and Coconut Beach) compared to back-reef locations (Osprey Islet and Corner Beach), spatial variation in their abundance was not significant (ANOVA, F = 0.36, df = 3/76, P = 0.09). *C. lunulatus* was twice as abundant as *C. baronessa* at all locations, with a mean density of 2.42 ± 0.67 (SE) individuals per 200m^2 across all locations. Like *C. baronessa*,

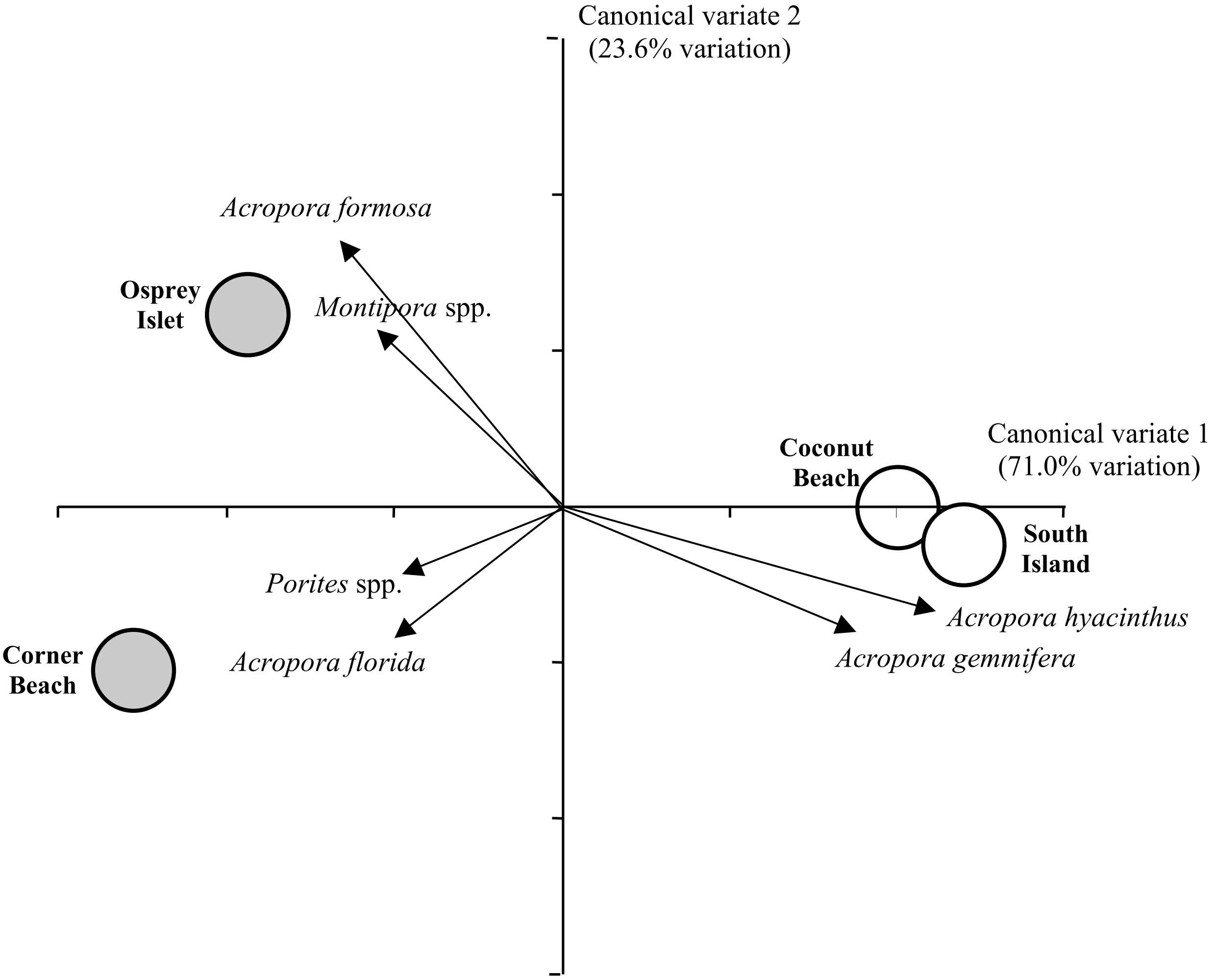


Figure 2.2. Comparison of community structure of scleractinian corals among locations (South Island, Coconut Beach, Osprey Islet, Corner Beach). Results show a canonical discriminant analysis comparing mean coral assemblages. Circles plotted represent 95% confidence limits around centroids for each location. White circles indicate front-reef locations and dark circles indicate back-reef locations. Vectors are structural coefficients of response variables, indicating the relative abundance of main coral species among the four locations.

there was no significant variation in the abundance of *C. lunulatus* among locations (ANOVA, F = 0.34, df = 3/76, P = 0.21).

Although there was no spatial variation in the abundance of the two study species (*C. baronessa* and *C. lunulatus*), the abundance of congeners varied greatly among the four locations. Mean densities of butterflyfishes were very similar for the two front-reef locations, South Island (17.2 ± 2.3 SE fish per $200m^2$) and Coconut Beach (18.7 ± 2.2 SE fish per $200m^2$). However, densities of butterflyfishes at the front-reef locations were more than double that at the back-reef locations, Osprey Islet (8.0 ± 0.9 SE fish per $200m^2$) and Corner Beach (8.5 ± 1.4 SE fish per $200m^2$). Spatial variation in the total densities of butterflyfishes resulted primarily from differences in the abundance of *C. citrinellus*, which was 5-6 times more abundant at exposed locations than at back-reef locations. Moreover, there were three species (*C. kleinii*, *C. rafflesii* and *C. trifascialis*) that were found only at front-reef locations, whereas all other species (*C. aureofasciatus*, *C. auriga*, *C. citrinellus*, *C. ephippium*, *C. lineolatus*, *C. lunula*, *C. melannotus*, *C. pelewensis*, *C. plebius*, *C. rainfordi*, *C. speculum*, *C. ulietensis*, *C. unimaculatus* and C. *vagabundus*) were recorded at all locations.

2.4.3 Feeding behaviour of butterflyfishes

C. baronessa and *C. lunulatus* fed exclusively on scleractinian corals and consumed a wide variety of different coral species, including at least 56 species from 11 different families (Table 2.1). However, both butterflyfish species exhibited significant selectivity in their patterns of feeding, using some coral species disproportionately more or less than predicted by their availability (Table 2.2). *C. baronessa* exhibited particularly strong selectivity (especially at front-reef locations), and tended to feed predominantly on just one or two different coral species at each location (Figure 2.3). At South Island, *C.*

baronessa consumed 18 different coral species (Table 2.1), but 87.6% of all bites were taken from *A. hyacinthus*. At Coconut Beach, *C. baronessa* consumed a 24 different coral species, but still 75.7% of bites were taken from *A. hyacinthus* (Figure 2.3). The predominance

Table 2.2. Patterns of feeding selectivity for *Chaetodon baronessa* and *C. lunulatus*. Both species of butterflyfish exhibited significant feeding selectivity (X^2_{L2}) at all locations ($P < 0.01$). "+" indicates corals used significantly more than expected, "-" indicates corals used significantly less than expected, and "0" indicates corals that were used in approximate accordance with their availability. Other corals were not used (NU) or not available (NA).

		Prey Categories									
	X^2_{L2}	*Acropora florida*	*Acropora formosa*	*Acropora gemmifera*	*Acropora hyacinthus*	*Acropora intermedia*	*Pocillopora damicornis*	*Isopora* spp.	*Montipora* spp.	*Galaxea* spp.	*Porites* spp.
Chaetodon baronessa											
South Island	6.9×10^3	0	0	-	+	NU	0	0	NU	NA	NU
Coconut Beach	$6.3.\times 10^3$	0	-	0	+	NU	0	0	-	0	0
Osprey Islet	4.5×10^3	0	0	0	NU	0	+	0	-	0	-
Corner Beach	3.5×10^3	+	NA	-	NA	0	+	0	-	+	-
Chaetodon lunulatus											
South Island	3.2×10^3	0	0	0	0	0	0	+	0	NA	+
Coconut Beach	$2.9.\times 10^3$	-	NU	+	-	0	+	+	-	0	+
Osprey Islet	1.9×10^3	0	0	0	NU	+	0	0	-	0	+
Corner Beach	2.5×10^3	0	NA	0	NA	+	0	0	0	0	+

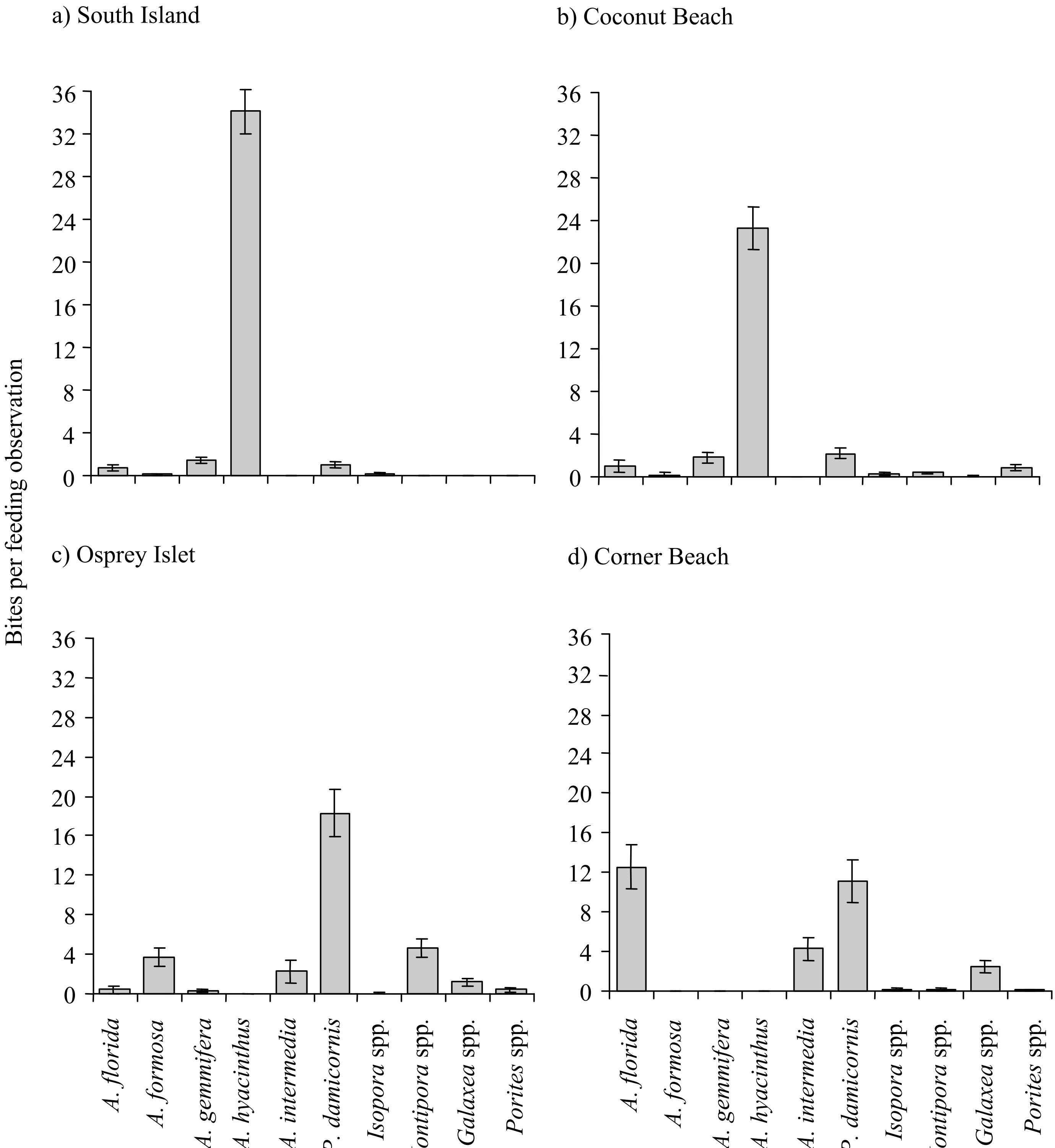


Figure 2.3. Comparison of dietary composition of *Chaetodon baronessa* among four locations: South Island and Coconut Beach (front-reef) and Osprey Islet and Corner Beach (back-reef). Data presented are the mean number of bites (± SE) per three-minute observation on each of 10 dominant coral species, including 5 *Acropora* species and 1 *Pocillopora* species (n = 50 observations per location).

of *A. hyacinthus* in the diet of *C. baronessa* at South Island and Coconut Beach is not surprising given that *A. hyacinthus* was the dominant coral at both these front-reef locations. However, *C. baronessa* consumed *A. hyacinthus* in far greater proportions than would be expected from its availability (Table 2.2).

Compared to front-reef locations, at back-reef locations (where *A. hyacinthus* was scarce) *C. baronessa* consumed a wider range of different coral species (Table 2.1) and was less selective in its choice of prey (Table 2.2). Even so, *C. baronessa* tended to feed predominantly on just one or two different coral species. At Osprey Islet, *C. baronessa* consumed 32 different coral species, but 44% of bites were taken from *P. damicornis* (Figure 2.3). In the absence of *A. hyacinthus*, *C. baronessa* selectively consumed *P. damicornis* over most other coral species (Table 2.2). At Corner Beach, *C. baronessa* consumed both *P. damicornis* and *A. florida* in approximately equal proportions (Figure 2.3). Both these coral species were consumed in greater proportions than expected from their availability, as were *Galaxea* spp. (Table 2.2).

The dietary composition of *C. lunulatus* also differed among locations, but *C. lunulatus* used many different coral species (between 29-33 species) at every location (Table 2.1), and was less selective than *C. baronessa* (Table 2.2). At South Island, *C. lunulatus* consumed mainly *A. hyacinthus*, taking 38% of bites from this one coral species (Figure 2.4). However, electivity indices revealed that *C. lunulatus* was not eating *A. hyacinthus* in greater proportions than it was available (Table 2.2). At Coconut Beach, *C. lunulatus* consumed *A. hyacinthus* in lower proportions than expected from its relative abundance (Table 2.2), taking less than 15% of bites from this abundant coral species. The only coral taxa that *C. lunulatus* consumed more than expected at all locations (i.e. seemingly selected at all locations) was massive *Porites* spp. (Table 2.2). At back reef

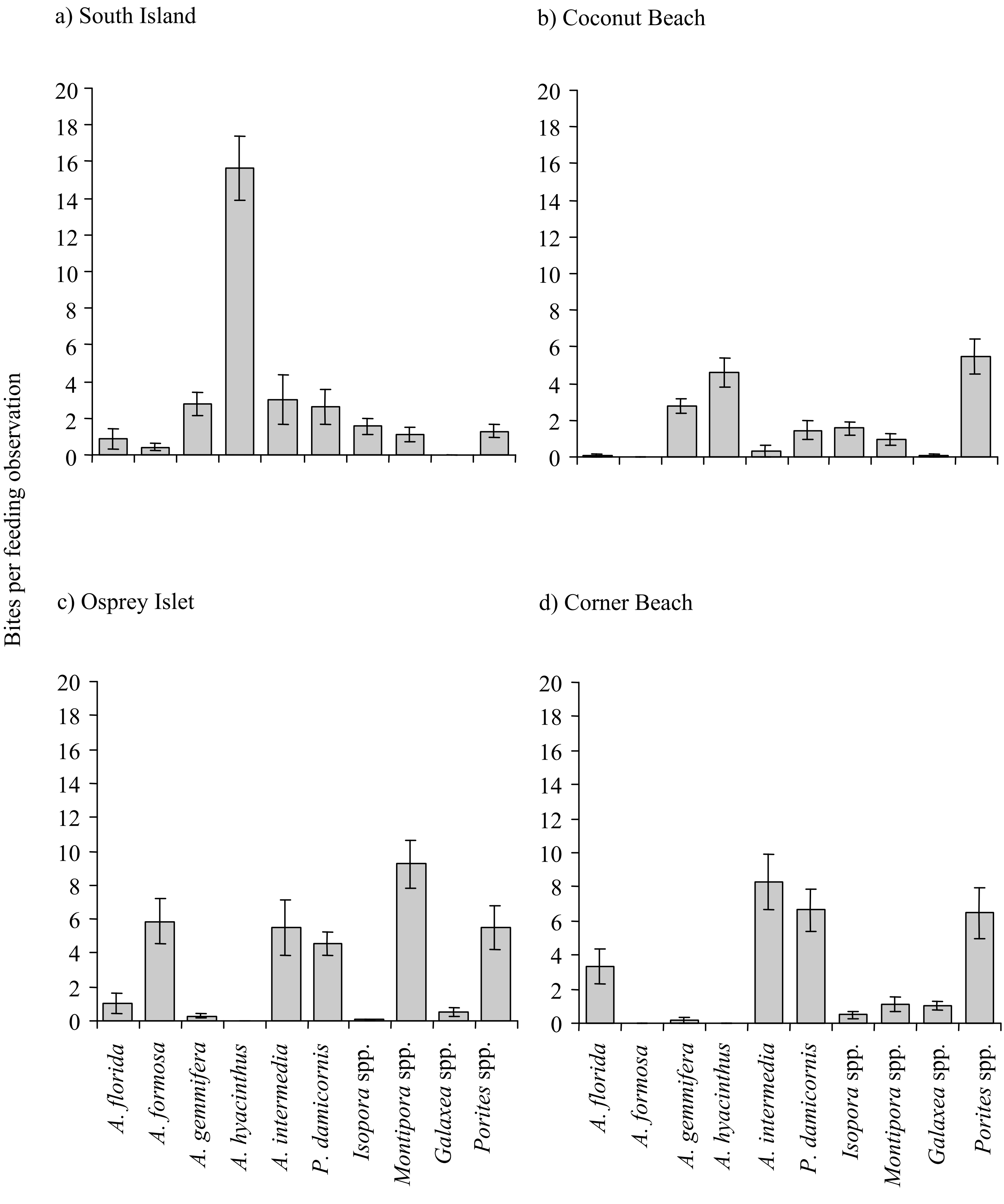


Figure 2.4. Comparison of dietary composition of *Chaetodon lunulatus* among four locations: South Island and Coconut Beach (front-reef) and Osprey Islet and Corner Beach (back-reef). Data presented are the mean number of bites (± SE) per three-minute observation on each of 10 dominant coral species, including 5 *Acropora* species and 1 *Pocillopora* species (n = 50 observations per location).

locations (Osprey Islet and Coconut Beach), *C. lunulatus* consumed several different coral species (*A. intermedia*, *P. damicornis* and *Porites* spp.) in approximately equal proportions. There were however, slight differences in dietary composition between Osprey Islet and Coconut Beach, which were associated with variation in the availability of different coral species. Most notably, *Montipora* was particularly abundant at Osprey Islet (Figure 2.2) and was the main coral eaten by *C. lunulatus* at this location (Figure 2.4).

Despite differences in dietary composition, the mean rate of feeding for both *C. baronessa* and *C. lunulatus* was remarkably constant among locations. Bite rates were highly variable among individuals. For example, the bite rates of *C. baronessa* ranged from 81 bites to a low of just 11 bites during the three-minute observation periods. The mean bite rates of *C. baronessa* were slightly higher at South Island (41.29 bites.3min^{-1} ± 2.1 SE) and at Osprey Islet (40.47 bites.3min^{-1} ± 2.0 SE) compared to Coconut Beach (34.42 bites.3min^{-1} ± 1.9 SE) and Corner Beach (34.72 bites.3min^{-1} ± 1.9 SE). However, there was no significant difference in mean bite rates for *C. baronessa* among locations (ANOVA, $F = 2.20$, df = 3/196, $P = 0.08$), nor was there any significant difference among times of day (ANOVA, $F = 0.97$, df = 2/196, $P = 0.42$). In comparing between butterflyfish species, *C. baronessa* tended to feed at a higher rate (34.12 bites.3min^{-1} ± 1.1 SE) than *C. lunulatus* (28.73 bites.3min^{-1} ± 1.2 SE) and feeding rates of *C. lunulatus* were also more variable. Bite rates for *C. lunulatus* ranged from 97 bites to just one bite during the three-minute observation periods. Bite rates of *C. lunulatus* did not differ with time of day (ANOVA, $F = 0.94$, df = 2/196, $P = 0.43$), but did differ among locations (ANOVA, $F = 6.83$, df = 3/196, $P < 0.01$). Notably, mean bite rates for *C. lunulatus* were much lower at Coconut Beach (22.86 bites.3min^{-1} ± 1.7 SE) than at South Island (40.88 bites.3min^{-1} ± 2.7 SE), Osprey Islet (38.86 bites.3min^{-1} ± 2.6 SE) and Corner Beach (31.46 bites.3min^{-1} ± 2.0 SE).

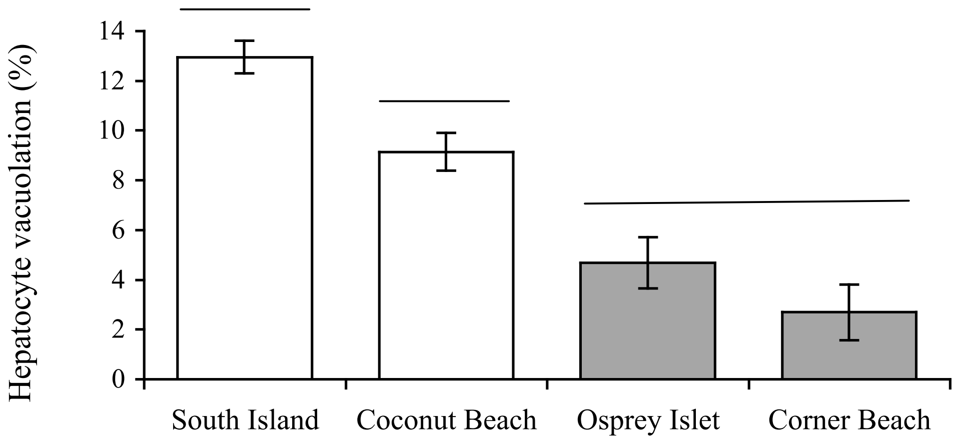
2.4.4 Physiological condition

In accordance with differences in dietary composition, physiological condition, as measured by hepatocyte vacuolation, differed significantly among locations for both *C. baronessa* (ANOVA, F = 13.34, df = 3/76, P < 0.01) and *C. lunulatus* (ANOVA, F = 3.72, df = 3/76, P < 0.05). For *C. baronessa*, the mean proportion of hepatocyte vacuoles in cross-sections through the liver ranged from 12.94% (± 0.67 SE) for individuals collected from South Island to 2.67% (± 1.12 SE) for individuals from Corner Beach. Overall, hepatocyte vacuolation was much higher for individuals collected from front-reef locations (South Island and Coconut Beach) compared to back-reef locations (Figure 2.5). However, there was also a difference between the two front-reef locations, with *C. baronessa* collected from South Island having a greater proportion of hepatocyte vacuoles than individuals from Coconut Beach (Figure 2.5). There was no consistent pattern of variation in hepatocyte vacuolation between front-reef and back-reef habitats for *C. lunulatus* (Figure 2.5). Rather, at South Island, *C. lunulatus* had much higher levels of hepatocyte vacuolations compared to individuals collected from all other locations (Figure 2.5).

2.5 DISCUSSION

The size of reef fish populations often varies in accordance with spatial variation in coral abundance and composition (e.g., Bell and Gazlin 1984, Bouchon-Navaro et al. 1985, Munday et al. 1997, Holbrook et al. 2000), particularly for coral-feeding butterflyfish (e.g., Sano et al. 1984, 1987, Bouchon-Navaro et al. 1985, Williams 1986, Lewis 1997, Cadoret et al. 1999). However, at Lizard Island, densities of *C. baronessa* and *C. lunulatus* did not vary between front-reef and back-reef locations, despite a two-fold difference in the abundance of scleractinian coral, as well as significant variation in the composition of coral

a) *Chaetodon baronessa*



b) *Chaetodon lunulatus*

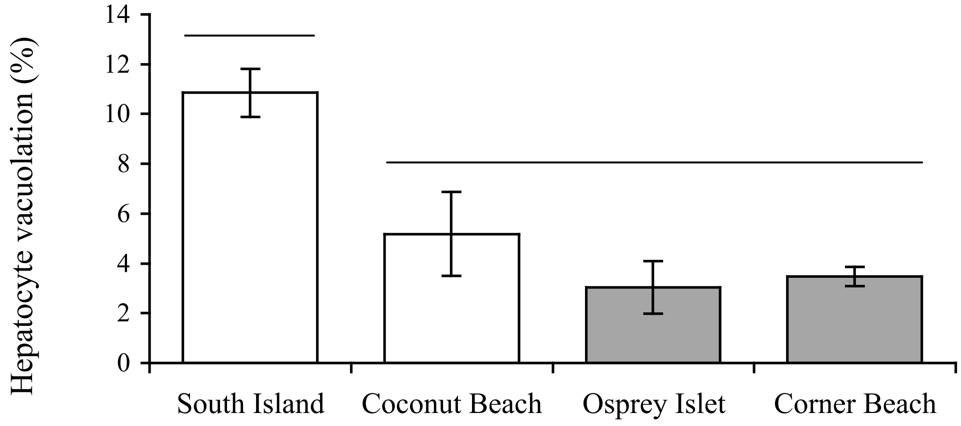


Figure 2.5. Comparison of hepatocyte vacuolation for a) *Chaetodon baronessa* and b) *C. lunulatus* among four different locations. Data presented is the mean proportion of hepatocyte vacuoles in cross-sections through the liver of 20 replicate fish (± SE). White bars indicate front-reef locations and dark bars indicate back-reef locations. Horizontal lines represent homogeneous subsets identified by Tukey's HSD *post-hoc* test.

communities (see also Bell et al. 1985, Roberts and Ormond 1987). The strength of relationships between butterflyfish abundance and scleractinian coral cover vary greatly among different studies. These differences may relate to differences in sampling and scale between studies (Bell et al. 1985, Syms 1995), or from real differences in the recruitment history and demographic parameters of individual species (Jones 1990, 1991). Also, different processes (e.g., recruitment versus resource availability) may regulate the size of reef fish populations in different locations or at different times (Bell et al. 1985). Where fish populations are regulated by recruitment (e.g., Wellington and Victor 1985, Doherty and Fowler 1994) their abundance could vary independently of differences in prey availability, competition or predation.

Although there was no difference in the abundance of butterflyfishes (*C. baronessa* and *C. lunulatus*) between contrasting reef habitats, there were significant differences in their physiological condition. Similarly, Pratchett et al. (2004) documented significant declines in the condition of *C. lunulatus* during extensive coral depletion caused by bleaching in the central Great Barrier Reef. This study, conducted over two years (2000-2002), showed that there was no change in the abundance of *C. lunulatus*, but hepatocyte vacuolation was 50% lower in fish collected after the bleaching event compared to fish collected before the bleaching (Pratchett et al. 2004). These data, along with the findings of the present study, suggest that variation in the abundance and/ or composition of scleractinian corals can have significant effects on the physiological condition (specifically, liver lipid storage) of coral-feeding butterflyfishes.

Physiological condition is major determinant of individual fitness in fishes, affecting growth, survivorship, and reproductive success (Jones and McCormick 2002). Therefore, variation in coral abundance and composition could have a significant influence on the structure and dynamics of butterflyfish populations, and could even have long-term effects on population abundance. The amount of food available to gravid females has been shown to be directly related to individual fecundity (Wootton 1990), and also affects to the viability of offspring (McCormick 2003). The quality and quantity of prey resources is also fundamental to the growth of fishes (e.g., Clifton 1995). Limited availability of prey rarely causes mortality directly, but fishes living in habitats with limited prey may have much lower survivorship, which could result in lagged effects on population size (Jones and McCormick 2002).

Variation in the physiological condition of *C. baronessa* and *C. lunulatus* (among locations) appeared to be related to differences in the composition of coral communities, more than differences in mean coral abundance. Feeding rates of *C. baronessa* and *C. lunulatus* varied very little among the four locations, suggesting that there must have been sufficient coral at every location to meet basic dietary requirements (sensu Tricas 1989a). However, differences in dietary composition are likely to have had major effects on the energetic intake of butterflyfishes in different locations (Birkeland and Neudecker 1981, Tricas 1989a). Both *C. baronessa* and *C. lunulatus* were 'generalist' coral feeders, foraging on a wide variety of different coral species (cf. *C. trifascialis*, Irons 1989), but preferentially consumed a few different species which may represent coral species of highest nutritional quality (Tricas 1989a). For both *C. baronessa* and *C. lunulatus*, physiological condition increased with increased consumption of *A. hyacinthus*. Although the nutritional quality of this coral species has never been tested, these findings suggests that *A. hyacinthus* may be the most profitable prey species for both *C. baronessa* and *C. lunulatus* (see also Irons 1988, 1989). Further, the feeding behaviour of *C. baronessa* is consistent with expectations for a fish foraging on an optimal prey (sensu Hughes 1980), specialising on *A. hyacinthus* when it is abundant (in front-reef locations), but becoming more generalist when *A. hyacinthus* is scarce (in back-reef locations). *A. hyacinthus* was recorded at Osprey Islet on in very low quantities (one small colony in 10 replicate 10m transects) and we did not observe any individuals of either *C. baronessa* or *C. lunulatus* feeding on this colony. Where *A. hyacinthus* was unavailable, both butterflyfish species tended to make use of the most abundant coral species. For example, large stands of *A. florida* at Corner Beach were heavily exploited by both *C. baronessa* and *C. lunulatus*.

Variation in dietary composition and patterns of feeding are known to influence physiological condition in fishes (Pulliam 1974, Charnov 1976, Stephens and Krebs 1986, Bruggemann et al. 1994, Green and McCormick 1999). However, variation in the condition of butterflyfishes may also be attributable to factors other than prey availability (e.g., disease, predation, or competition). Importantly, inter-specific competition can modify access to available resources. Holbrook and Schmitt (1986) showed that the physiological condition of the black surfperch (*Embiotoca jacksoni*) is reduced in the presence of the striped surfperch (*Embiotoca lateralis*), which restrict their access to profitable shallow water feeding grounds. Inter-specific competition is also important for *Chaetodon* butterflyfishes, affecting fine-scale distributions of individual species and restricting access to certain prey resources (Anderson et al. 1981, Bouchon-Navaro and Bouchon 1989). At Lizard Island, densities of *Chaetodon* butterflyfishes and also the intensity of inter-specific competition among *Chaetodon* species have been shown to be highest at front-reef locations (Berumen and Pratchett in press – Appendix 2). Therefore, if competition did have an important influence on the condition of butterflyfish populations in the two different habitat types it would counter the observed trends in physiological condition, affecting individuals at front-reef locations far more than at back reef locations.

Inter-specific competition may be important in explaining differences in the diet and condition of butterflyfishes between front-reef locations (South Island and Coconut Beach), where coral cover and composition were very similar. At South Island, both *C.*

baronessa and *C. lunulatus* fed mainly on the tabulate coral, *A. hyacinthus*. This concurs with several other studies (Reese 1975, Irons 1989), indicating that *A. hyacinthus* might be the most preferred coral species for a variety of different *Chaetodon* species. However, at Coconut Beach, *C. lunulatus* consumed *A. hyacinthus* in much lower proportions than expected from its relative abundance. *C. baronessa* also consumed much less *A. hyacinthus* at Coconut Beach than at South Island. These differences may be related to differences in the abundance of *C. trifascialis*, which might exclude *C. lunulatus* (and to a much lesser extent, *C. baronessa*) from feeding on *A. hyacinthus*. *C. baronessa* and *C. trifascialis* are the dominant butterflyfish competitors at Lizard Island (Beurmen and Pratchett in press – Appendix 2), forming well defended territories in the vicinity of *A. hyacinthus* colonies (see also Reese 1975). Therefore, *C. lunulatus* would have limited access to colonies of *A. hyacinthus*, and may feed very little on this coral even though *A. hyacinthus* may be its preferred prey. Interference competition by *C. trifascialis* may also explain the unusually low feeding rate of *C. lunulatus* at Coconut Beach. *Chaetodon trifascialis* feeds almost exclusively on *A. hyacinthus*, and maintains heavily defended territories around patches of *A. hyacinthus* (Irons 1988, 1989). Reese (1981) showed that densities of *C. trifascialis* and *C. baronessa* are inversely correlated on reefs in Papua New Guinea, which may be evidence of strong inter-specific competition between these species (Bell et al. 1985). At Lizard Island, densities of *C. trifascialis* were much higher at Coconut Beach (1.9 fish per $200m^2$ ± 0.4 SE), compared to South Island (0.6 fish per $200m^2$ ± 0.3 SE), corresponding with lower consumption of *A. hyacinthus* by both *C. lunulatus* and *C. baronessa.* We suggest, therefore, that *C. baronessa*, *C. lunulatus* and *C. trifascialis* all compete for access to *A. hyacinthus* and observed feeding preferences may be confounded by competition. Conclusive evidence for the influence of inter-specific competition on dietary composition of *Chaetodon* butterflyfishes requires the removal of dominant competitors (*C. baronessa* and/ or *C. trifascialis*), followed by the assessment of whether there is a subsequent shift in dietary composition of sub-ordinate species (e.g., *C. lunulatus*).

In conclusion, this study strongly suggests that differences in prey availability can have significant effects on the physiological condition of fishes living in different habitats. These differences in physiological condition may also have ramifications for reproduction, growth and long-term survivorship (sensu Jones and McCormick 2002). In this study, we show significant variation in the physiological condition of coral-feeding butterflyfish among habitats with varying coral composition and cover. Diet alone may not be responsible for such variation in the energetics of coral-feeding butterflyfish populations, but whatever the reason, there are clear differences in the condition of butterflyfishes living in these different habitats. Importantly, these differences occurred over very small spatial scales (within reefs), and must be considered when comparing reef fish populations within and between coral reefs. In previous studies (e.g. Eckert 1985, Shulman 1985), population size of reef fish has been used to infer habitat quality. However, this study has shown that dramatic differences in the condition of reef fish may exist as a consequence of differences in habitat, and these differences are not necessarily reflected in population size.

Chapter 3: The importance of juveniles in modelling growth: butterflyfish at Lizard Island[†]

3.1 ABSTRACT

I established and fitted von Bertalanffy growth functions to size-at-age data for four species of chaetodontids at Lizard Island. Special emphasis on juveniles provided detailed information of the early growth period. All four species demonstrated rapid initial growth achieving an average of 92% of maximum theoretical size in the first 2 years. I used various constraints of the theoretical age at length zero (t_0) in an analysis of both complete data sets and data sets using only adult fish. An unconstrained value of t_0 resulted in the best-fit (maximum r^2) curve when juveniles were included. When excluding juveniles, it was necessary to constrain t_0 to an approximate settling size to most closely represent the growth of the species.

[†] This chapter appears as is in the journal *Environmental Biology of Fishes*: Berumen ML (2005) The importance of juveniles in modeling growth: butterflyfish at Lizard Island. *Env Biol Fishes* 72: 409-413

3.2 INTRODUCTION

Most studies involving the analysis of age-structure and growth in fishes have focused on temperate, pelagic, or deep-water groups and have made substantial contributions to the management of these groups (Choat and Robertson 2002). In comparison, the age-based demography of coral reef fishes is poorly studied and understood. The effective management and conservation of fish stocks requires better information on demography and life history features. This is particularly true in the case of coral reef fish where increasing evidence of extended life spans and the decoupling of size and age (e.g., Hart and Russ 1996, Choat and Robertson 2002) argues against the use of size-based analyses (Hilborn and Walters 1992). Given the diversity of coral reef fishes, more comprehensive demographic sampling of the major groups is required before useful generalisations of life histories can be developed (Caley 1998). Studies to date suggest that coral reef fishes demonstrate a wide range of growth patterns and life history traits (Fowler 1995). There are three critical features to be considered: i) the form of the growth curve and the distribution of somatic growth rates in the life history; ii) the relationship between size and age; and iii) the consequences of inadequate sampling of early life history stages. This study examines these issues in four species of chaetodontid fish.

Chaetodontids (butterflyfish) are highly conspicuous and abundant on coral reefs, with more than 120 species in 12 genera throughout the world (Kuiter 2002). Abundances and distributions of butterflyfish have been frequently studied in the context of coral associations (Cadoret et al. 1999, Findley and Findley 2001) and additionally as potential “indicator species” of the general state or health of a coral reef (e.g. Crosby and Reese 1996). However, very little work has been done on the basic growth and life history of these fish (but see Ralston 1976a, Fowler 1991). As many chaetodontids have obligate feeding associations with coral (Findley and Findley 2001), understanding age-based growth rates and longevity will aid in predicting the impacts of resource variation for butterflyfish (Pratchett et al. 2004, Berumen et al. 2005 – Chapter 2). The current study was conducted because of the importance of understanding how quickly juveniles can become established and grow to reproductive size.

This study examined growth characteristics of four common species of butterflyfish occurring on tropical coral reefs. The aim of the study was to establish fundamental parameters of growth in the context of an age-based model. Size-at-age data was used to establish the basic form of the growth curve. Previous studies have shown that a lack of data in the earliest growth period of reef fish can lead to greater variability in growth model parameter estimations (Kritzer et al. 2001) and consequently, a special emphasis was placed on including information on juvenile life-stages.

3.3 METHODS

I collected samples of *Chaetodon baronessa*, *C. citrinellus*, *C. lunulatus*, and *C. trifascialis* from reefs around Lizard Island (14° 40′S, 145° 28′E) in February 2003. Divers on scuba or snorkel collected fish by spearing or netting. Some of the smallest individuals had recently settled into coral colonies and were sheltering within the branches. Divers used a clove oil mixture to anaesthetise these fish and then collected them with hand nets following Munday and Wilson (1997). I recorded the total length of each fish collected to the nearest mm; removed sagittal otoliths, cleaned them in fresh water, and stored them dry.

I prepared otoliths following Choat and Axe (1996). I viewed sectioned otoliths using a dissecting microscope (10x) using transmitted light. I counted opaque bands and presumed them to be annular growth deposits (Fowler 1995). I viewed otoliths not clearly displaying two or more rings using a high-power microscope (400x) and counted daily increments following Ralston (1976a).

I then plotted total length against age for each species. I fitted von Bertalanffy (1938) growth functions and estimated parameters L_∞ (theoretical asymptotic length) and K (the index of curvature) by minimising the sum of squares of deviations for a given data set. I examined three values of the parameter t_0 (age at theoretical length 0) for all species. I first constrained t_0 to '0,' resulting in a growth curve passing through the origin (indicative that the fish is a length of 0 at age 0). I also constrained t_0 to pass through the y-axis at the approximate size of settlement for a given species based on light-trapped sizes and recruit sizes observed on the reef (Stobutzki 1998, Berumen and Pratchett, unpublished data). Finally, t_0 was not constrained and I optimised the parameters K and L_∞ to produce the best-fit curve for the data, maximizing r^2. Changing the value of t_0 inherently changes the parameters L_∞ and K as the predicted size-at-age trajectory must be altered to cross the y-axis at the appropriate size of settlement (L_0) (Kritzer et al. 2001).

To assess the importance of juveniles in the growth analysis, von Bertalanffy functions were again fitted to the data with all juveniles (*C. baronessa* < 70mm total length TL, *C. citrinellus* < 70mm TL, *C. lunulatus* < 90mm TL, *C. trifascialis* < 75mm TL) removed from the data set. The various methods of constraint were also again applied as described above.

3.4 RESULTS AND DISCUSSION

When analysing size at age data for all individuals (including juveniles) of a species, I found that the von Bertalanffy growth functions for all four species had the highest r^2 values when t_0 was left unconstrained (Table 3.1). Kritzer et al. (2001) found that the parameters L_∞

Table 3.1 Parameters and associated values of von Bertalanffy growth functions used to describe growth of four chaetodontid species from Lizard Island. Key: n = number of individuals in sample; L_∞ = theoretical asymptotic length in mm; K = index of curvature; t_0 = theoretical age in years at length 0 (x-intercept); r^2 = Pearson's product coefficient of momentum; $L_{0\,c}$ = constrained settlement size in mm (length at time 0) (constrained y-intercept).

Species		n	L_∞	K	t_o	r^2	$L_{0\,c}$
Chaetodon baronessa	(All individuals)	36	108.2	1.104	0	0.909	0
			108.5	1.024	-0.066	0.912	14
			108.6	0.999	-0.092	0.912	N/A
	(Adults only)	33	108.2	1.094	0	0.677	0
			108.6	0.975	-0.142	0.705	14
			112.4	0.325	-3.133	0.839	N/A
C. citrinellus	(All individuals)	27	90.4	2.704	0	0.921	0
			90.6	2.163	-0.072	0.923	13
			90.7	2.150	-0.074	0.923	N/A
	(Adults only)	19	93.5	1.097	0	0.283	0
			93.8	1.002	-0.149	0.300	13
			126.0	0.083	-11.482	0.471	N/A
C. lunulatus	(All individuals)	41	104.2	3.787	0	0.828	0
			105.1	3.054	-0.05	0.858	15
			106.9	1.941	-0.241	0.882	N/A
	(Adults only)	28	106.4	2.550	0	0.427	0
			106.7	2.283	-0.066	0.459	15
			112.8	0.308	-5.127	0.823	N/A
C. trifascialis	(All individuals)	37	101.8	1.974	0	0.855	0
			105.0	1.301	-0.102	0.892	13
			111.3	0.693	-0.464	0.914	N/A
	(Adults only)	21	110.4	0.853	0	0.535	0
			111.4	0.754	-0.165	0.559	13
			134.2	0.158	-4.956	0.676	N/A

and *K* were always more precise when parameters are constrained, but this was for samples of large reef fish in which early growth information is not well known. In analyses using all individuals, I found that constraining t_0 to 0 always produced the lowest r^2 values (Table 3.1).

When excluding juveniles from the analysis, I found that r^2 values were again highest when t_0 was unconstrained. It is important to note, however, the wide deviation that occurs in these models from the best-fit models (Figure 3.1). The resultant curves do not produce biologically realistic growth information for any of these species. Of the two constraints for t_0 that I tested, using an approximate settlement size produced the highest r^2 values (Table 3.1).

The patterns of highly asymptotic growth with rapid initial growth I found in butterflyfish (Figure 3.1) follow a general acanthuroid growth pattern found in many reef fish (Choat and Robertson 2002). For example, Choat and Axe (1996) found acanthurid fishes achieving 80% of their growth in 15% of their lifespan. The species in this study on average attain 92% of their maximum size within the first two years of their life. This suggests that many age classes would accumulate in a narrow size range, limiting the informative value of size frequencies in demographic analyses (Choat and Axe 1996) and further emphasising the need for age-based demographic studies suggested by Hilborn and Walters (1992). Inadequate sampling during the juvenile stage will lead to several complications in analysing the life history of these species. The recruitment process will be difficult to interpret as demographic data will be lacking for the early life stages. Establishing critical aspects of the maturation process will be impossible if reproduction is size based, as is common in reef fish (e.g. Ralston 1981). Finally, using the widely accepted von Bertalanffy growth function analysis of growth, inadequate sampling of juveniles leads to substantial error in parameter estimates.

Ralston (1981) found that *C. miliaris* attained sexual maturity only at or near maximum size (90% of maximum length). Given the rapid initial growth seen in these four species, it is

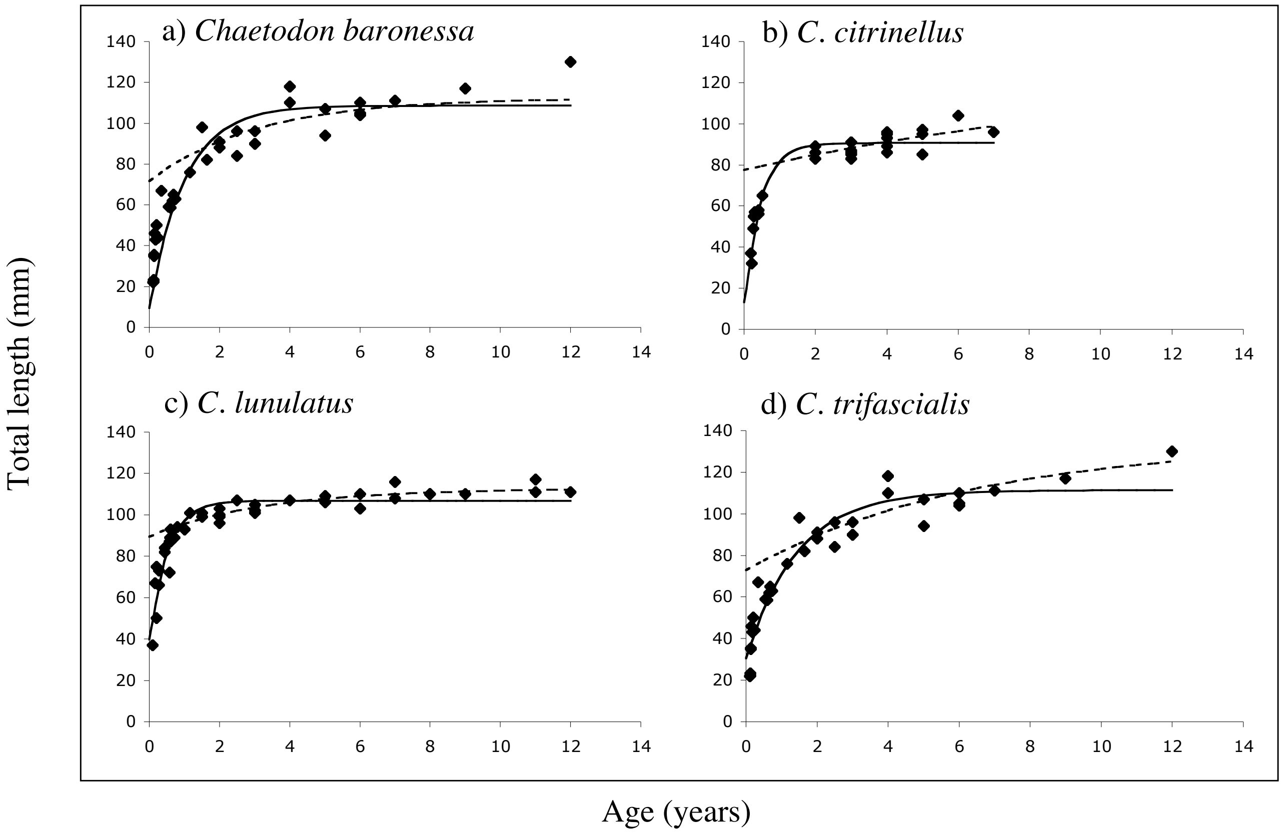


Figure 3.1 Size-at-age plots for four species of chaetodontids from Lizard Island; a) *Chaetodon baronessa*, b) *C. citrinellus*, c.) *C. lunulatus*, d) *C. trifascialis*. Solid line represents the best-fit von Bertalanffy growth function using unconstrained parameters of L_∞, K, and t_0 for all individuals. Dashed line represents unconstrained parameters when excluding juveniles from the analysis.

suspected that chaetodontids attain sexual maturity very early in life. Environmental factors during this rapid initial growth phase may be critical in determining how quickly these fish can establish themselves on a reef and attain maturity (e.g., following a disturbance). In particular, quality or abundance of coral resources may influence this early phase of growth for obligate corallivores (Berumen et al. 2005 – Chapter 2).

All four of these butterflyfish feed on coral (Randall et al. 1997). *C. baronessa* and *C. trifascialis* are extremely specialised and prefer to exclusively eat *Acropora hyacinthus* when it is available (Pratchett 2002, Pratchett et. al 2004 – Appendix 1). Optimal foraging theory predicts that an animal should only specialise on a resource that conveys the largest overall net gain of energy (Hughes 1980). It could then be predicted that for these specialists, this energy would translate into more rapid growth as a juvenile when compared to a generalist coral feeder such as *C. citrinellus* and *C. lunulatus*. Figure 3.1 and the respective K-values (Table 3.1) indicate that this prediction does not hold. It is possible that juveniles of these species do not fully realise the benefit of the specialisation until reaching adult size. Alternatively, the higher energy intake may result in a greater level of lipid storage. It seems unlikely that the specialisation is an ontogenetic shift in resource usage as all juveniles observed feeding followed the same preferences as adult fish (Berumen and Pratchett, unpublished data). Further investigations into the impacts of feeding on juvenile growth will begin to resolve these questions during this critical period of growth.

Constraining t_0 to 0 always produced the lowest r^2 values in analyses using all individuals. When ample data exists during the early growth of fish rapidly attaining maximum size, it is suggested that constraining t_0 is not appropriate. When juvenile data is not available, however, constraints are useful to most closely represent a population with rapidly growing juveniles. The most appropriate constraint would be to use a known settlement size. Where this settlement size is not available, constraining settlement size to 0 seems to be the best alternative to approximate the characteristics in the later stages of life, consistent with the findings of Kritzer et al. (2001). Although constraining settlement to a size of 0 is biologically inaccurate, the later stages of life are more accurately represented while the early pattern of growth is also more closely represented despite the lack of sampling during this period.

Chapter 4. Influence of prey availability on the growth of coral-feeding chaetodontids

4.1 ABSTRACT

Several species of corallivorous butterflyfishes (Chaetodontidae) are known to have specific feeding preferences. While the reasons for these preferences are not well understood, foraging theory predicts that individuals should specialise on a given resource only if there are tangible fitness benefits, such as increased growth. The purpose of this study was to assess the influence of different prey on juvenile growth for two species of highly selective coral-feeding butterflyfish, *Chaetodon plebeius* and *C. trifascialis*. The feeding habits of both these species have been well documented in the field, and this study utilised existing data to quantify specific feeding preferences. Selection functions revealed that *C. plebeius* selectively consumes both *Pocillopora damicornis* and *Acropora hyacinthus*, while *C. trifascialis* selectively consumes *A. hyacinthus*. To test the fitness consequences of prey preferences, controlled feeding experiments were conducted in which individual butterflyfish were fed exclusively one of three different branching corals (*A. hyacinthus*, *P. damicornis* and *Porites cylindrica*) to compare growth on highly preferred coral species (e.g., *A. hyacinthus* and *P. damicornis*), versus strongly avoided coral prey (*P. cylindrica*). Over a period of approximately one month, an exclusive diet of the coral most preferred in field observations resulted in the highest growth rate in both fishes, while an exclusive diet of avoided corals resulted in little or no growth. *Chaetodon trifascialis* grew 0.053mm per day when feeding on *A. hyacinthus*, but actually decreased in total length when feeding on both *P. damicornis* and *P. cylindrica*. *Chaetodon plebeius*, meanwhile, grew at 0.051mm per day on *P. damicornis*, versus 0.038mm per day on *A. hyacinthus* and decreased in total length on *Porites cylindrica*. This study shows that both

C. trifascialis and *C. plebeius* selectively consume the coral prey that maximises juvenile growth and probably increases overall fitness. Variation in the early growth of these fish due to resource availability may explain patterns or anomalies in their large-scale population demographics.

4.2 INTRODUCTION

4.2.1 Foraging behaviour

Prey acquisition is fundamental to the biology and ecology of all living organisms. However, prey acquisition is often constrained by the quantity of food resources, competition and/or predation (Hughes 1980). These constraints are likely to vary in their intensity amongst habitats, and thereby affect the energetic intake of reef fish (e.g., Holbrook and Schmitt 1986). Due to patchy resources and limited access to preferred prey, consumers may be forced to occupy larger feeding areas, spend more time foraging at various patches, and/or be forced to utilise non-preferred prey. Despite constraints on prey acquisition, reef fish are rarely limited to one prey type or a single foraging location and must therefore make specific choices regarding prey acquisition (Krebs 1978, Pyke 1984, Vincent et al. 1996).

In general, most organisms use a much narrower range of prey types than are actually available (Fox and Morrow 1981). Foraging theory predicts that selectivity should occur where there is a tangible fitness benefit derived from feeding on a specific subset of available prey (Stephens and Krebs 1986). Although some species have been shown to be very specialised in their use of available prey (e.g., Bean et al. 2002), few studies have shown that the specific range of prey used by specialised species contributes directly to greater fitness. Ultimately, measuring fitness is often infeasible (Perry and Pianka 1997), but further understanding why animals forage the way they do will advance our understanding of processes underlying biodiversity (Smith 1979). To maximise their net gain, “optimal foragers” should demonstrate territorial and defensive behaviours when given sufficient access to preferred resources (Schoener 1971). Foraging theory suggests that the energetic cost of resource defence must be compensated by an increased energetic return from that resource; resources not providing such a benefit would not warrant defence (Pyke 1984). Some species may even further increase this benefit by developing an observable, if not a testable, preference or specialisation.

4.2.2 Foraging specialisations

Selectivity may alternatively arise as a mechanism of reproductive isolation (Bristow 1988) or as a result of niche contraction through competition induced resource partitioning (Pratchett 2005). In some communities, specialisation is typical of the dominant competitor (e.g., Irons 1988, 1989), consistent with suggestions that priority in prey selection may further be dictated by access to resources (MacArthur and Pianka 1966). Specialists presumably gain an increased benefit from consumption of the prey on which they specialise. Generalists, however, may fare better than specialists in the case of locally unpredictable variation in resource availability (Schoener 1971, Dill 1983, Jones et al. 2002, Munday 2004).

Within the family of butterflyfishes (Chaetodontidae), there are several species considered to be “specialists” as they primarily consume scleractinian corals (e.g., Burgess 1978) compared to the “generalists”, which may eat hard or soft corals as well as polychaetes and other non-coralline macroinvertebrates (e.g., Pratchett 2005). Subsequent and more detailed investigations of species’ diets have revealed specific feeding preferences, especially within the genus *Chaetodon* (e.g., Gore 1984, Cox 1994, Irons 1989, Tricas 1989b, Berumen et al. 2005, Pratchett 2005). Well-documented among these and perhaps the most widely known is *C. trifascialis*, an extreme specialist that feeds almost exclusively on the tabular coral *Acropora hyacinthus* (Irons 1989) and may exclude other fish from access to this coral (Berumen and Pratchett in press – Appendix 2). Attempts to explain the mechanism or reasons for these preferences have had mixed success. Most commonly cited are defense mechanisms of corals or physical access to polyps (e.g., Alino et al. 1988, Gochfeld 2004). Investigations into the possible nutritional content bases for these preferences (lipids, carbohydrates, etc.) have not supported field-based preferences (Keesing 1990, Pratchett 1995). Nutrition alone may not dictate preferences, however, as micronutrients that are difficult to assess may be a factor (Bozinovic and Martinez del Rio 1996). Analysis of fishes' diets can further be complicated if nutritional needs are not readily apparent in dietary selection (Anderson et al. 2004, Raubenheimer and Simpson 2004). Fish may consume an excess of one nutrient in the process of satisfying a minimum need of another nutrient from the same resource (Anderson et al. 2004, Raubenheimer and Simpson 2004).

4.2.3 Study species and objectives

This study seeks to investigate the impacts of exclusive diets of the preferred versus non-preferred prey on the growth rates of two species of coral-feeding butterflyfishes. The two species considered in this study are *C. trifascialis* Quoy and Gaimard, 1825, and *C. plebeius* Cuvier, 1831. The pronounced preference of *C. trifascialis* for *A. hyacinthus* is conspicuous and well documented (Irons 1989, Pratchett 2005). It is widespread throughout the Indo-West Pacific, ranging from the Red Sea to French Polynesia (Allen et al. 1998, Kuiter 2002). *Chaetodon plebeius* is an exclusive coral-feeder, consuming mostly corals of the genera *Acropora* and *Pocillopora* with a preference for *P. damicornis* (Pratchett 2005). It is common throughout the South Pacific, ranging from Western Australia to French Polynesia and from southern Japan to New South Wales (Randall 2005). Based on feeding observations, both *C. plebeius* and *C. trifascialis* avoid consuming corals in the genus *Porites* when feeding (Pratchett 2005). In this study, the corals *A. hyacinthus*, *Poc. damicornis*, and *Por. cylindrica* are used to represent the preferred prey of each species as well as a non-preferred prey. This study was conducted using juvenile (newly settled) fishes because growth in chaetodontids asymptotes within 1-2 years after settlement (Berumen 2005 – Chapter 3) and most measurable growth will occur during the juvenile phase.

If the prey preference or specialisation observed in the field is an "optimal" choice of prey, then an exclusive diet of this prey would be expected to confer the greatest growth benefits. If, however, the observed preference or specialisation is a result of competitive exclusion, then both fishes may be expected to benefit from the consumption of the single most profitable prey type.

4.3 METHODS

4.3.1 Dietary selectivity

Dietary selectivity of *C. trifascialis* and *C. plebeius* was quantified using existing data on patterns of prey use collected at Lizard Island from 1995 until 2002 (Pratchett 2005). Pratchett (2005) documented the range and proportional consumption of different coral species during *in situ* feeding observations of replicate individuals for a total of 19 *Chaetodon* species, including both *C. trifascialis* and *C. plebeius*. During feeding observations individual fishes were followed for three minutes whilst recording the total number of bites taken from each species of hard (scleractinian) coral, soft (alcyonarian) coral, or any other sessile invertebrate. Feeding observations were conducted for a total of 105 individuals of *C. plebeius* and 71 individuals of *C. trifascialis* (Pratchett 2005).

Dietary selectivity was determined by comparing the proportional use of different prey types with the proportional availability of different coral prey in the local environment. Data on dietary availability was collected using 10-m line intercept transects (n = 40), along which the relative abundance of all hard- and soft-corals, as well as other sessile invertebrates was recorded. The degree of dietary selectivity exhibited by *C.*

plebeius and *C. trifascialis* was quantified using log-likelihood statistics, following Berumen et al. (2005) The resulting value of X^2_{L2} was then compared to the chi-squared distribution with n(I-1) degrees of freedom to determine the significance of selectivity exhibited by *C. plebeius* and *C. trifascialis*.

Having shown that *C. plebeius* and *C. trifascialis* exhibit highly selective feeding, resource selection functions (Manly et al. 1993) were used to determine which coral species were used more or less frequently than expected based on their relative abundance (Manly et al. 1993). Selection functions significantly greater than 1 indicated that corals were consumed more than expected from their availability, indicating prey types that are preferred, while selection functions significantly less than 1 indicated that corals were consumed significantly less than expected, indicating prey types that are avoided.

4.3.2 Feeding Experiments

To evaluate the underlying basis of prey preferences, controlled feeding experiments were conducted in which individual butterflyfish were fed exclusively on a single coral species. The growth of fishes fed on different diets was then compared to assess whether fishes' highest growth was realised on the most preferred coral prey. Juveniles (fishes < 5mm total length) of both *C. plebeius* and *C. trifascialis* were collected from reefs around Lizard Island in January-February 2004 using clove oil and hand nets following Munday and Wilson (1997). A total of 34 fish were caught over three days. Following capture, total length (mm) and weight (g) of each individual were recorded before the fish were placed into aquaria. Total length was measured to the nearest 0.01 mm using digital callipers; weight was measured to the nearest 0.01g using the water displacement method.

Fishes were held in a large plastic aquarium with plastic piping "shelters" for a period of 2-3 hours prior to their introduction to experimental treatments. During the experiment, fishes were maintained in individual aquaria (32 x 20 x 16cm), with a continuous flow (2L/min) of filtered seawater. Fishes were then fed one of three different species of branching coral (*A. hyacinthus, P. damicornis,* or *P. cylindrica*) and provided with a minimum of 100cm^2 of live coral. Fishes were randomly placed in tanks to ensure random distribution and random allocation of fishes to each treatment. Five replicate fish of each species (*C. plebeius* and *C. trifascialis*) were maintained on each of the three different coral diets, resulting in a total of 30 aquaria. Corals within each aquarium were replaced every 3-7 days throughout the experiment to ensure coral tissues remained healthy.

To ensure that fishes were feeding on available corals, feeding observations of each fish were conducted daily for the first three days and every 5 days thereafter. The number of bites taken on coral prey was quantified during 3-minute observations for all fishes. Fish typically began feeding within a few hours of settlement in the experimental aquaria. However, there were a small number of fishes (4) that were not observed feeding even 2 days after introduction to the experimental aquaria. These fishes were replaced with newly caught individuals.

Individual fishes were subject to experimental conditions for a maximum of 33 days, although in some cases, the fish died before the conclusion of the experiment. At the conclusion of the experiment or upon death, each fish was remeasured and weighed. The average growth of each fish was calculated as a percentage change from initial length and weight. Estimates of time-averaged growth were then compared among treatments (*A. hyacinthus*, *P. damicornis*, and *P. cylindrica*) for each fish species using ANOVA.

4.4 RESULTS

4.4.1 Feeding Preferences and Selectivity

Both *C. plebeius* and *C. trifascialis* exhibited significant selectivity in their patterns of feeding in field observations (Table 4.1). *Chaetodon plebeius* selectively consumed a total of 8 different corals, including *P. damicornis*, *A. hyacinthus*, *Montipora* spp., and others (Table 4.1) but was never seen to consume *Porites* spp. *Chaetodon trifascialis*, meanwhile, was an order of magnitude more selective than *C. plebeius* (Table 4.1), consuming *A. hyacinthus* to the exclusion of almost all other scleractinian corals. Like *C. plebeius*, *C. trifascialis* was never seen to consume *Porites* spp. even though these corals were the third most abundant of the scleractinian coral groups used in this analysis (Table 4.1). Similarly, juveniles of *C. plebeius* and *C. trifascialis* were found in close association with *P. damicornis* and A. *hyacinthus*, respectively.

4.4.2 Feeding rates

Fish typically began feeding within a few hours of settlement in the experimental tanks. In rare instances where fishes did not feed within 48 hours after introduction to the experimental tanks (one individual *C. trifascialis* from each treatment and one individual *C. plebeius* from *P. damicornis*), these fishes were replaced. Two individual *C. plebeius* and three individual *C. trifascialis* fed diets of *P, cylindrica* died before the conclusion of the experiment despite normal feeding. Feeding rates of fishes in experimental tanks were 3.19 bites per minutes (± 0.65 SE) for *C. plebeius* and 3.78 bites per minute (± 0.63 SE) for *C. trifascialis*. There was no significant difference in feeding rates among fishes on the different coral diets (*C. plebeius*: ANOVA, P = .566, F = .600, df = 2/11; *C. trifascialis*: ANOVA, P = .100, F = 2.76, df = 2/13) (Figure 4.1).

Table 4.I. Dietary selectivity and prey preferences of butterflyfish. The significance of selectivity was ascertained using the chi-square statistic (X^2_{L2}), while selection function were used to test whether certain prey types were used more or less than expected. "+" indicates prey that were used disproportionately more than expected from their availability (ie. selected); "-" indicates prey that were used less than expected (avoided); "u" indicates prey that were never used (strongly avoided); blank cells indicate prey that were used in approximate accordance with their availability and neither selected or avoided.

Butterflyfish	X^2_{L2}	P	Carbonate Pavement	*Acropora digitifera*	*Acropora hyacinthus*	*Acropora intermedia*	*Acropora millepora*	*Acropora tenuis*	Other *Acropora*	*Montipora* spp.	*Pocillopora damicornis*	*Goniastrea retiformis*	*Porites lobata*	Other Scleractinia	*Lobophytum* spp.	Other Alcyonaria	Non-coral Invertebrates
Availability (% cover) of different prey categories			70.56	1.43	5.64	0.21	0.15	0.22	1.03	1.16	1.36	0.62	1.36	9.58	0.44	1.39	0.46
Chaetodon plebeius	1.29×10^{04}	<0.001	-	+	+	+	+		+	+	+	+	U		U	U	U
Chaetodon trifascialis	1.37×10^{05}	<0.001	-		+	+			+	U		U	U	-	U	U	U

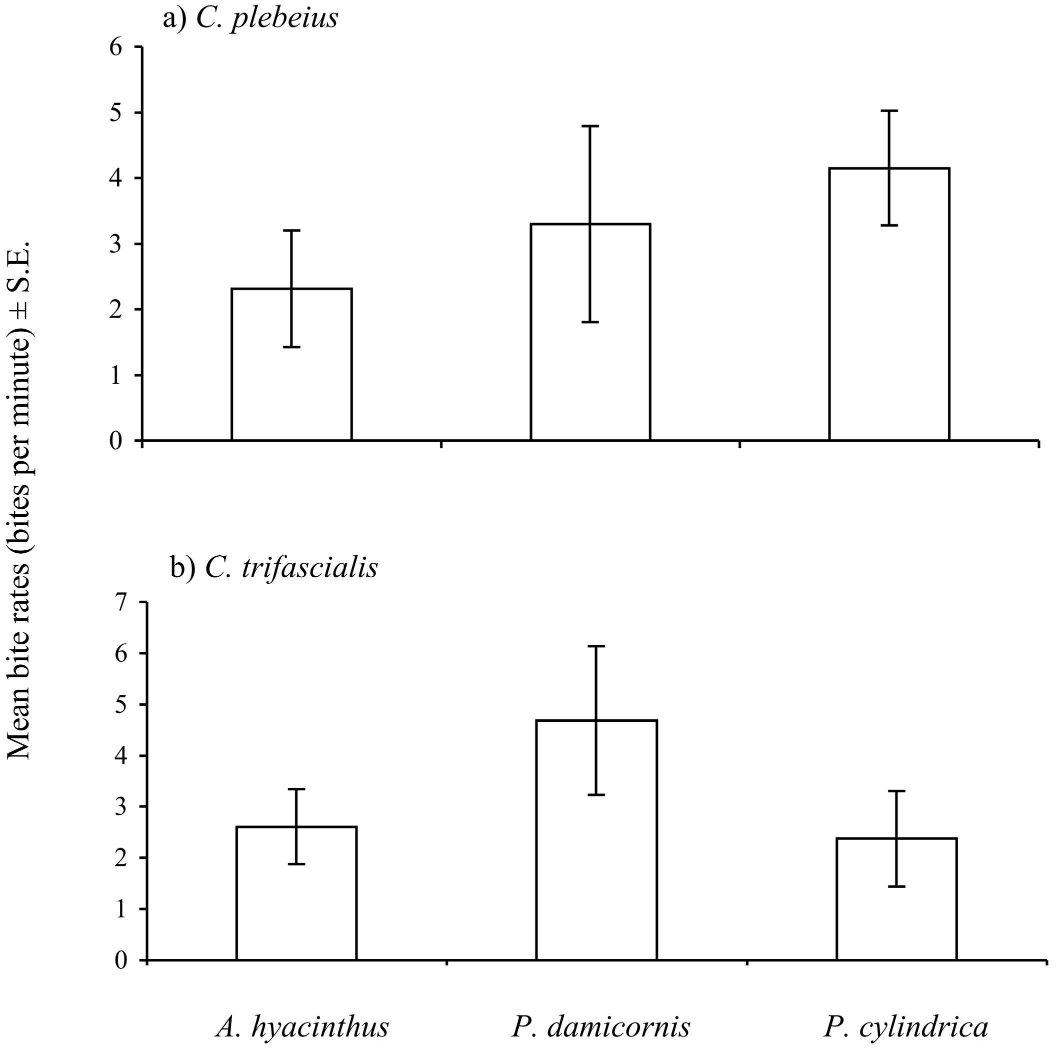


Figure 4.1. Mean bite rates of two *Chaetodon* species of butterflyfish in a feeding experiment. Bars represent the mean number of bites per minute (± S.E.) of fish while being fed one of three coral diets (category axis).

4.4.3 Change in length

Fishes fed exclusive diets of 1 of 3 different corals exhibited markedly different growth rates. In terms of total length, there was a significant difference in the change in length of *C. plebeius* among treatments (ANOVA, F= 8.72, df = 2/13, P = 0.004). When feeding on *P. damicornis*, *C. plebeius* had an average daily percent change in total length of 1.88 X 10^{-3} (± 1.29 X 10^{-3} SE) (Figure 4.2). Fish feeding on *P. cylindrica* fared poorly, and were found to have negative growth rates (-4.15 X 10^{-3} ± 2.61 X 10^{-4} SE). This was also apparent in the visible condition of the fish, as many of the fish feeding on *P. cylindrica* developed tattered fins and a generally lethargic swimming behaviour.

There was also a significant difference in the change in length of *C. trifascialis* among treatments (ANOVA, F = 15.88, df = 2/17, P < 0.001). When feeding on *A. hyacinthus*, *C. trifascialis* had an average daily percent change in total length of 1.75 X 10^{-3} (± 5.40 X 10^{-4} SE) (Figure 4.2), significantly higher than mean daily growth rates when feeding on *P. damicornis.* As with *C. plebeius*, fish feeding on *P. cylindrica* fared poorly, and were found to have negative growth rates (-4.21 X 10^{-3} ± 6.40 X 10^{-4} SE).

4.4.4 Change in weight

The pattern of change in percent weight matched that of change in percent length for both species of fish though differences among treatments were less pronounced (Figure 4.3). There was a significant difference in the change in weight of *C. plebeius* among treatments (ANOVA, F= 16.47, df = 2/10, P < 0.001). When feeding on *P. damicornis*, *C. plebeius* had an average daily percent change in weight of 4.33 X 10^{-2} (± 3.70 X 10^{-3} SE) (Figure 4.3). Fish feeding on *P. cylindrica* fared poorly, and were found to have negative changes in weight (-6.13 X 10^{-3} ± 5.79 X 10^{-3} SE).

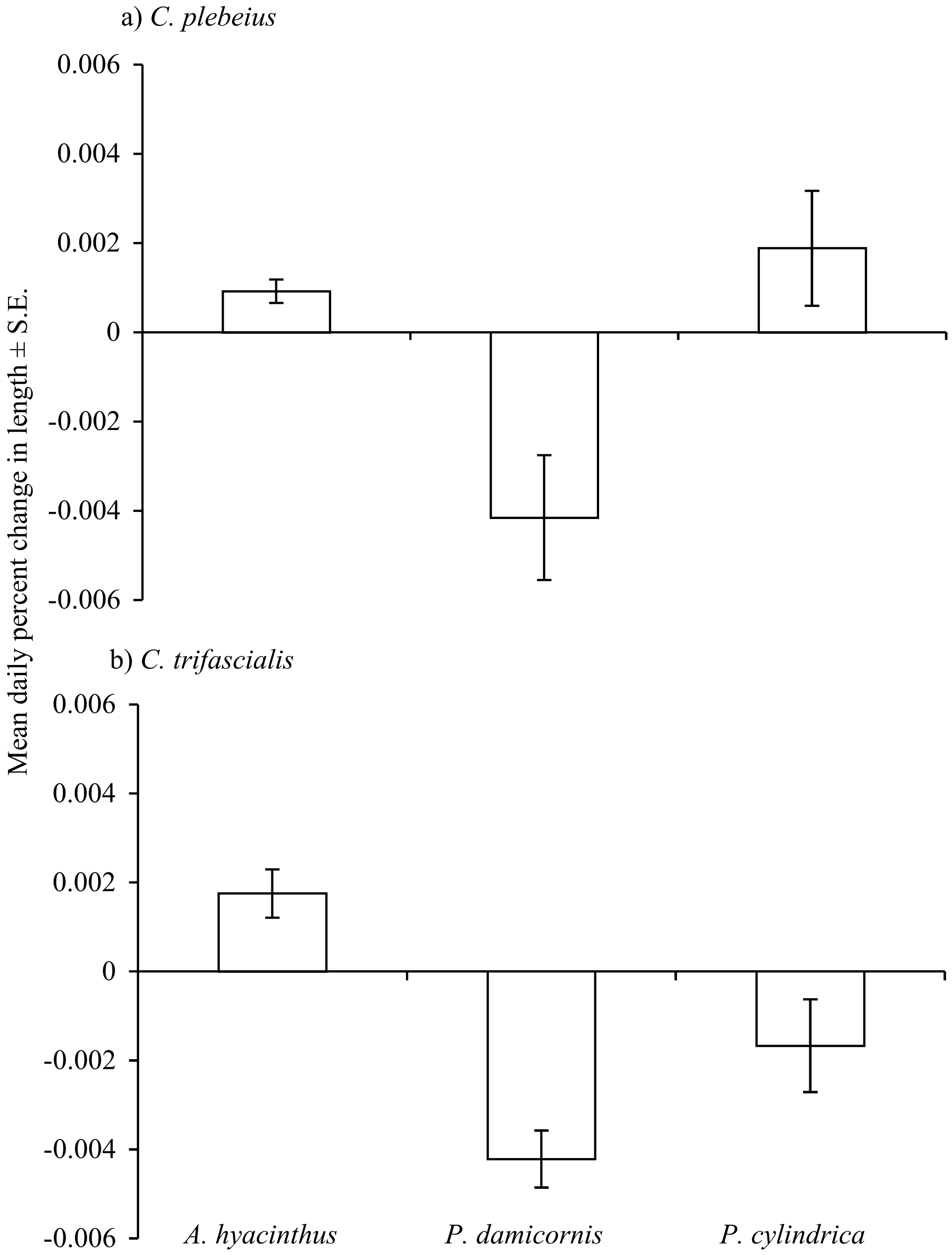


Figure 4.2. Mean percent change in length of two *Chaetodon* species of butterflyfish in a feeding experiment. Bars represent the percent change per day in total length (± S.E.) of fish while being fed one of three coral diets (category axis).

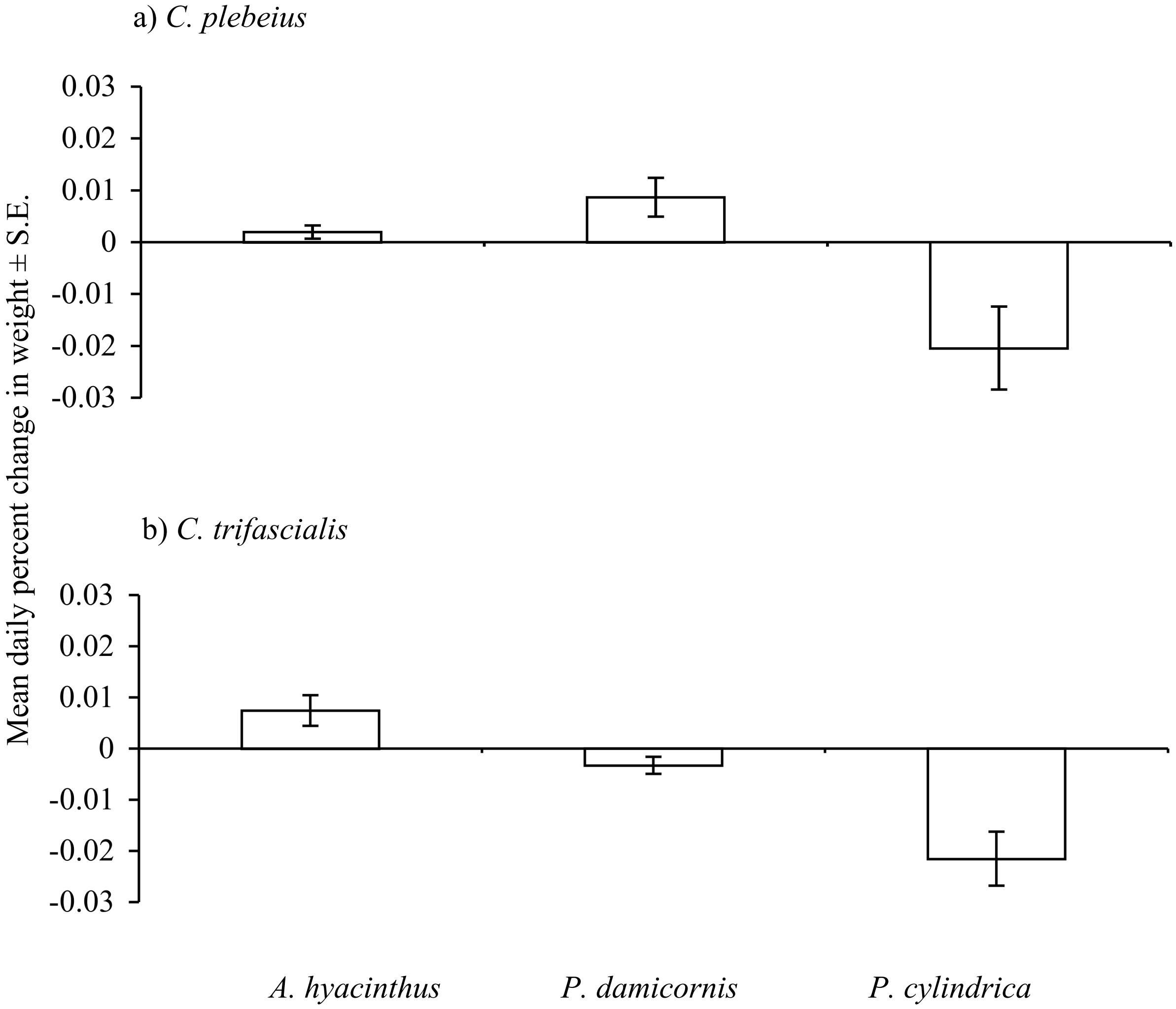


Figure 4.3. Mean percent change in weight of two *Chaetodon* species of butterflyfish in a feeding experiment. Bars represent the percent change per day in weight (± S.E.) of fish while being fed one of three coral diets (category axis).

There was also a significant difference in the change in weight of *C. trifascialis* among treatments (ANOVA, $F = 18.17$, $df = 2/14$, $P < 0.001$). When feeding on *A. hyacinthus*, *C. trifascialis* had an average daily percent change in weight of 7.43×10^{-3} ($\pm 2.90 \times 10^{-3}$ SE) (Figure 4.3), significantly higher than mean daily percent change in weight when feeding on *P. damicornis.* As with *C. plebeius*, fish feeding on *P. cylindrica* fared poorly, and were found to have negative growth rates ($-2.12 \times 10^{-2} \pm 4.78 \times 10^{-3}$ SE).

4.5 DISCUSSION

In this experiment, both *C. plebeius* and *C. trifascialis* gained maximum benefit from consumption of the corals that they preferred based on field observations. While this study does not resolve which of the mechanisms underlies the preferences (e.g., coral morphology, Tricas 1989b; defenses of corals, Alino et al. 1988, Gochfeld 2004; competition, Berumen and Pratchett in press – Appendix 2; nutritional ecology, Anderson et al. 2004, Raubenheimer and Simpson 2004), it provides empirical evidence that these fishes may be selecting optimal prey in the field. During the juvenile phase of chaetodontid life histories, growth is likely the most important energy investment (Berumen 2005 – Chapter 3). Optimising prey choice during this growth phase could therefore be fundamental to increasing fitness. Growth of juveniles is particularly critical in determining life histories (Berumen 2005 – Chapter 3) and chaetodontids must rapidly reach adult size to reduce the threat of predation (see Webster 2002, Almany 2003). Moreover, as reproductive maturity is most likely size-dependent in chaetodontids (Ralston 1981), maximising growth will reduce time to maturation. This does not preclude the possibility that chaetodontids have an ontogenetic shift in preference or nutritional requirements, but in these two species, patterns of prey use appears to be the same for both juvenile and adult individuals (Irons 1989, Pratchett 2005). It is likely that these specialists continue to gain maximum benefit from these corals throughout their adult life.

Exclusive diets of their most preferred prey resulted in maximum growth for both *C. plebeius* and *C. trifascialis*, although this pattern was most pronounced in *C. trifascialis*. Several previous studies have identified *C. trifascialis* as a highly specialised coral-feeder which feeds primarily or almost exclusively on the tabular corals *A. hyacinthus* or *A. cytherea* (e.g., Irons 1988, 1989, Alwany et al. 2003, Pratchett 2005), but this has not previously been linked to any physiological benefit. At Lizard Island, *C. trifascialis* was found to be an order of magnitude more specialized than *C. plebeius*. While *C. plebeius* generally used more species of coral, both fishes avoided *Porites* corals in field observations. Optimal foraging theory would predict that a specialist gets a greater benefit from its preferred prey than a generalist would (Stephens and Krebs 1986), and this appears to be the case with *C. trifascialis*. *Chaetodon trifascialis* may in fact be so specialised that it is hard for it to survive without its preferred prey. It is rarely observed feeding on any other prey (Irons 1989, Pratchett 2005) and, despite its willingness to feed on other corals in this experiment, this study seems to indicate that it gains very little nutritional value from other prey species. However, both fish gained the greatest benefit from the coral they preferred in the natural environment, supporting the idea that that these butterflyfishes are foraging in an optimal manner. As such, chaetodontids may be an ideal subject for further testing various aspects of foraging theory (sensu Perry and Pianka 1997).

While other studies have suggested that *A. hyacinthus* is an optimal prey for coral-feeders (e.g., Pratchett 2002, Berumen et al. 2005 – Chapter 2, Berumen and Pratchett in press –Appendix 2), it appears that *C. plebeius* has specialised on a different coral (*P. damicornis*) which leads to much higher juvenile growth. Competitive exclusion (Berumen and Pratchett in press – Appendix 2) or resource partitioning (see Pratchett 2005) are two possible causes of this specialisation, but in either case, fish are observed to consume optimal prey in field observations (Pratchett 2005). This conforms to predictions that specialist species should gain significant benefit from feeding on their preferred prey.

Specialisation and generalisation, however, are extremes along a continuum of ecological versatility and there are significant trade-offs in being specialist versus generalist (MacNally 1995). While gaining greater benefit from a resource specialisation, a species may sacrifice some degree of resilience to changes in resource availability if it becomes dependent on a given resource (Munday 2004). The results of feeding selectivity analyses in this study show that *C. plebeius* is less specialised than *C. trifascialis* and selectively consumes several different corals (including several *Acropora* spp, *Montipora* spp, *P. damicornis*, and several other coral species). Because of its ability to utilise many different resources, *C. plebeius* may be more “ecologically versatile” (see MacNally 1995). Accordingly, *C. trifascialis* appears much more sensitive to depletion of coral resources, particularly *A. hyacinthus*, compared to *C. plebeius* and other more generalist corallivores (e.g., Pratchett 2002, Berumen and Pratchett in press – Appendix 3).

In a more general context, access to particular resources may structure other population characteristics, such as survivorship or reproduction, as suggested in Chapter 2. Diet may directly affect the health of the juvenile population and will thus influence later population characteristics. Diet can affect the condition of fishes (Berumen et al. 2005 – Chapter 2) and physiological condition is major determinant of individual fitness for fishes, affecting growth, survivorship, and reproductive success (Jones and McCormick 2002). The quality and quantity of prey resources is also fundamental to the growth of fishes (e.g., Clifton 1995). Overall, variation in coral abundance and composition could have a significant influence on the structure and dynamics of butterflyfish populations as populations with greater access to preferred corals may be more productive. Limited availability of prey rarely causes mortality directly, though in the case of extreme specialists the distribution of essential resources will necessarily constrain their distribution and abundance. This experiment clearly shows that a lack of prey for specialists can lead to rapid mortality, which may explain why *C. trifascialis* is always found in close association with *A. hyacinthus* (e.g., Irons 1989). Fishes living in habitats with limited or poor quality prey may have much lower survivorship, which could result in lagged effects on population size (Jones and McCormick 2002). Populations with differing access to preferred prey may thus vary in their structure and dynamics, which will be further explored in Chapter 5.

In conclusion, this study shows that the different feeding preferences of *Chaetodon* butterflyfishes (at least for *C. plebeius* and *C. trifascialis*) are not simply a consequence of concerted resource partitioning (see also Pratchett 2005) but have an more important energetic basis. Fishes fed exclusively on their preferred prey grew faster and were in much better condition compared to conspecifics fed on sub-optimal diets. Accessibility to these preferred prey types is therefore likely to have a significant influence on the growth, survivorship, and overall fitness of individuals in the field (e.g. Berumen et al. 2005 – Chapter 2). This is likely to have further ramifications for patterns of distribution and abundance of reef fishes. Importantly, this may be the mechanism promoting strong associations between coral-feeding butterflyfishes and their preferred prey resources (e.g., Pratchett 2002). Resources can thus have a major influence on the life history traits of these fishes.

Chapter 5: Large-scale variations in some life-history features of chaetodontids.

5.1 ABSTRACT

If resources are fundamental in determining life history traits of chaetodontids, this is likely to be apparent among widespread reefs with measurable differences in coral composition. To determine the pattern of large-scale variation in the demography of chaetodontids, up to 50 individuals of each of four species of chaetodontids (*Chaetodon citrinellus*, *C. lunulatus*, *C. melannotus*, and *C. trifascialis*) were collected at two locations on the Great Barrier Reef, Lizard Island and One Tree Island, separated by approximately 1200km. Size and age of all individuals were determined, and age-based demographic characteristics were assessed using re-parameterised von Bertanlanffy growth functions that allowed for highly specific comparisons among populations. The study species displayed measurable variation in growth rates, longevities, and mean maximum sizes, but the variations were not consistent among species and could not be consistently explained by preferred resource availability, temperature or latitude, or intra- or interspecific abundance. For *C. citrinellus*, maximum size and growth rate were higher at One Tree Island, but there was no significant difference in longevity. For *C. lunulatus*, longevity was higher at Lizard Island though maximum size and growth rate did not vary between reefs. *Chaetodon melannotus* had a greater maximum size and growth rate at One Tree Island, but had a higher longevity at Lizard Island. *Chaetodon trifascialis* had a greater maximum size at One Tree Island, greater longevity at Lizard Island, and no significant difference in the growth rate. Although it would be expected that growth rates would be higher where preferred resources are more abundant, this was not

found. It is likely that a combination of resources, latitude (or seasonal temperature variation), and conspecific abundance (including behavioural interactions) ultimately determine large-scale patterns in the structure and dynamics of chaetodontid populations. Species that have highly specific feeding patterns showed greater demographic variation at broad scales than generalist feeders. Local habitat features may be a greater determinant of demographic variation in generalist as opposed to specialist feeders. Determining the relative importance of these various factors will require extensive experimentation and careful large-scale sampling.

5.2 INTRODUCTION

5.2.1 Variations in reef fish life histories

The study of life histories of coral reef fishes has received considerable attention in recent years. Life history features of reef fishes, including growth rates, reproductive output and success, recruitment patterns, age and/or size at maturity, mortality rates, longevity and maximum size, demographics of population age and/or size structures have been shown to vary among species and also among populations within species (e.g., Atkinson 1994, Pawson et al. 2000) in response to environmental conditions. Some life history characteristics, such as growth, vary at several scales (e.g., Ackerman 2004, Laman-Trip 2004), although the patterns are not always consistent.

Robertson et al. (2005) and Laman-Trip (2004) documented variations in size structure and growth rates at both geographical and habitat scales in acanthurids. In these examples, there were consistent geographical patterns. In contrast, Ackerman (2004) documented variation in the labrid *Thalassoma lunare*, in which habitat variation obscured geographical trends. Gust et al. (2002) documented highly localised variation in growth in two species of scarids. Interestingly, local-scale variation in growth rates appears to be a consistent feature of reef fishes. All four studies cited resources as a potential source of variation in growth rates (see also Berumen et al. 2005 – Chapter 2), but none were able to test for this. Trying to incorporate resource variation into analysis of local populations can be problematic as it has proven difficult to identify and measure resources, especially food (MacNally 1995).

5.2.2 Potential mechanisms of life history variation

Variability in key life history processes has a significant influence on the overall structure and dynamics of fish populations. McCormick and Hoey (2004), for example, found that larval growth history influenced subsequent survivorship and future growth in pomacentrids. Larval growth has also been shown to influence the recruitment success of an acanthurid (Bergenius et al. 2002). Food availability has frequently been shown to affect the growth rate of juvenile fish (e.g., Jones 1986) and amount of feeding has been connected to time to maturity (e.g., Forrester 1990). Therefore, subtle changes in early growth patterns may manifest in subsequent patterns of growth, survivorship, and reproductive output (Jones and McCormick 2002). Further, early life-history stages of many coral reef fishes are highly sensitive to larval density, food availability, water temperature, and predators (Leis and McCormick 2002).

Several factors have been cited or explored as possible agents or mechanisms of life history variation. Importantly, many studies have linked certain life history responses to environmental factors such as depth (Jones 1986) and temperature (Green and Fisher 2004). Temperature must always be considered as a potential factor when studying poikilotherms (such as fishes) as some metabolic functions are sensitive to environmental variation (Atkinson 1994) and numerous studies have documented latitudinal variation in life histories (e.g., Robertson et al. 2005). However, there are likely to be synergistic effects of varying environmental conditions, biological interactions, and resource availability on the energetics and subsequent life history traits of fishes (Jones and McCormick 2002), especially at large spatial scales. Biological interactions (e.g., competition and predation) also influence how energy is allocated in life histories and can affect growth and survivorship (e.g., Warner and Chesson 1985, Warner 1998, Peterson and Warner 2002). Competition (maintenance of territories and defending resources), for example, may require considerable energy expenditure, limiting energy available to other life history processes. Holbrook and Schmitt (1984) demonstrated changes in condition as a result of access to feeding areas in surfperch. Reproductive ontogeny is also likely to influence other life history characteristics as pressures to reach maturational size may be intense in species where size directly influences reproductive success. This is true in many sex-changing species and may have significant connections to growth rate (e.g., Munday et al. 2004). Similarly, predation pressures can influence life history traits. If predation pressure is high, fishes may grow more quickly to attain sufficient size to reduce the risk of predation. These influences may reflect either natural or anthropogenic (fishing) effects (Dulvy et al. 2004), but fishing pressure is of limited interest as there is no fishery for chaetodontids in the study area.

Previous studies of resources in fishes frequently address abundance or condition. Numerous studies have linked the abundance of consumers directly to the abundance and/or distribution of their resources (e.g., McClanahan et al. 2000, Stewart and Jones 2001). Other studies have further linked small-scale differences in physiological traits to resources within a given habitat (growth, Jones 1986, Alofs and Polivka 2004; reproduction, Ali and Wootton 1999; condition, Pratchett et al. 2001, 2004 – Appendix 1, Berumen et al. 2005 – Chapter 2). Very few studies, however, have been able to establish the importance of resources in determining life history variations over large scales (e.g., Gust et al. 2002, Ackerman 2004, Laman-Trip 2004).

5.2.3 Study species and location

This study will focus on four species from the genus *Chaetodon* (family Chaetodontidae): *C. citrinellus*, *C. lunulatus*, *C. melannotus*, and *C. trifascialis*. All four species are widespread with geographic ranges encompassing much of the Pacific Ocean basin (Allen et al. 1998, Kuiter 2002). Further, each species is abundant on Australia's Great Barrier Reef (Randall et al. 1997). Each species varies in their prey preferences (Pratchett 2005). *Chaetodon citrinellus* is a generalist feeder, consuming prey items from several categories, both coral and non-coral, including small invertebrates and even possibly some algal material (Harmelin-Vivien and Bouchon-Navaro 1983, Pratchett 2005). *Chaetodon lunulatus* is a hard-coral feeder, but is a "generalist" hard-coral feeder. It typically consumes more different species of scleractinian corals than any other hard-coral feeder (Pratchett et al. 2004 – Appendix 1, Berumen et al. 2005 – Chapter 2, Pratchett 2005). *Chaetodon melannotus* is a soft-coral feeder, consuming a variety of coral and non-coral prey, but mostly specializing on soft coral species (Alino et al. 1988, Pratchett 2005). *Chaetodon trifascialis* is an extreme hard-coral specialist, preferring and usually only consuming one species of coral, *Acropora hyacinthus* (Reese 1975, Irons 1989, Pratchett 2005). Samples of study species were collected from two locations, Lizard Island (14° 40´S, 145° 28´E), located in the northern section of the Great Barrier Reef, and One Tree Island (23° 30´S, 152° 06´E), located in the southern section of the Great Barrier Reef. These two reefs are separated by approximately 1200km.

5.2.4 Study objectives

The objective of this study is to assess the pattern of demographic variation in the above species of chaetodontids. Two geographic locations that differ in mean annual temperature will be sampled for age-specific demographic rates and abundance patterns in each species. In addition, the abundance of scleractinian corals will be assessed at each location. As juvenile chaetodontid growth rates have been shown to increase when feeding on preferred resources (Chapter 4), one might predict that measured growth rates should be highest where preferred resources (specific to each species) are most available. It is further predicted that specialists are more sensitive to preferred resource availability than are generalists. If prevailing environmental conditions (i.e., temperature regimes) are more important than resources in structuring life history traits, then it may be generally expected that fish will show greater maximum size, longevity, and growth rates at higher latitudes as has been shown for acanthurids (e.g., Robertson et al. 2005).

5.3 METHODS

5.3.1 Size-at-age analysis

Samples of *C. citrinellus*, *C. lunulatus*, *C. melannotus*, and *C. trifascialis* were collected from reefs around Lizard Island (14° 40´S, 145° 28´E) in February and August of 2003 and February of 2004. Samples of these species were also collected from reefs around One Tree Island (23° 30´S, 152° 06´E) in August of 2003 and March and November of 2004. Divers on scuba or snorkel collected fish by spearing or netting. Some of the smallest individuals had recently settled into coral colonies and were sheltering within the branches. Divers used a clove oil mixture to anaesthetise these fish and then collected them with hand nets following Munday and Wilson (1997). The total length of each fish collected was recorded to the nearest mm; sagittal otoliths were removed, cleaned in fresh water, and stored dry.

Otoliths were prepared following Choat and Axe (1996). Sectioned otoliths were examined using a dissecting microscope (10x) using transmitted light, counting opaque bands. These were presumed to be annular growth deposits (Fowler 1995, Berumen 2005 – Chapter 3). Otoliths not clearly displaying two or more rings were examined using a high-power microscope (400x) and daily increments were counted following Ralston (1976a).

5.3.2 Habitat/Benthic analysis

At each reef, fish were collected exclusively from sites on the exposed side of the reef at One Tree Island (Longtom, Keyhole, and Wistari) and Lizard Island (Washing Machine, South Island, and Coconut Beach). To assess the availability of coral and non-coral resources, the abundance and composition of benthic communities at both One Tree Island and Lizard Island were measured. Benthic cover and composition were quantified using ten replicate 50-metre transects at each location. 100 random points were placed onto each transect, and each of the 100 points was recorded as one of 55 categories (Table 5.1). Variation in total coral abundance among locations was analysed using ANOVA, while variation in the relative abundance of major benthic categories (10 taxa) was analysed using multivariate analyses of variance (MANOVA). Univariate homogeneity was tested using Cochran's test and residual plots were examined to confirm MANOVA assumptions of multivariate homogeneity and normality. Pillai's Trace statistic was used to determine the significance of MANOVA results, following Olsen (1976). All statistical procedures were conducted using SPSS 11.0.

Table 5.1. Benthic categories used for comparing resource availabilities at One Tree Island and Lizard Island, Great Barrier Reef.

Hard coral categories:		
Acanthastrea spp.	*Favites* spp.	Other *Pocillopora* spp.
Acropora aspera Gp.	*Galaxea* spp.	Branching *Porites* spp.
Acropora florida Gp.	*Goniastrea* spp.	Massive *Porites* spp.
Acropora formosa Gp.	*Goniopora* spp.	*Seriatopora* spp.
Acropora humilis Gp.	*Heliopora* spp.	*Stylophora* spp.
Acropora hyacinthus Gp.	*Hydnophora* spp.	*Symphyllia* spp.
Acropora loripes Gp.	*Isopora* spp.	*Turbinaria* spp.
Acropora nasuta Gp.	*Merulina* spp.	Other Agaricidae
Acropora robusta Gp.	*Montastrea* spp.	Other Faviidae
Other *Acropora* spp.	Branching *Montipora*	Caryophillidae
Astreopora spp.	Encrusting *Montipora*	Fungiidae
Coeloseris spp.	*Pavona* spp.	Pectiniidae
Echinopora spp.	*Platygyra* spp.	Siderastreidae
Favia spp.	*Pocillopora damicornis*	
Other categories:		
Algae	*Millepora* spp.	*Sarcophyton* spp.
Clam	*Palythoa* spp.	*Sinularia* spp.
Hydroid	Pavement	*Xenia* spp.
Lobophyllia spp.	Rubble	Other Alcyonaceans
Lobophytum spp.	Sand	

5.3.3 Chaetodontid abundance

Along the same 50m transects that benthic analysis was conducted, chaetodontid abundances were estimated using 50m x 4m visual belt transects. The abundance of all *Chaetodon* spp. was recorded on each transect. Variation in total chaetodontid abundance among locations was analysed using ANOVA, while variation in the relative abundance of species was analysed using multivariate analyses of variance (MANOVA). Univariate homogeneity was tested using Cochran's test and residual plots were examined to confirm MANOVA assumptions of multivariate homogeneity and normality. Pillai's Trace statistic was used to determine the significance of MANOVA results, following Olsen (1976). All statistical procedures were conducted using SPSS 11.0.

5.3.4 Estimation of growth rate

Growth was modeled separately for each species and from each location using the re-parameterised equation of the Von Bertalanffy Growth Function (rVBGF) (Francis 1988) following Laman-Trip (2004). The rVBGF equation allows for comparison of growth rates at specific ages among populations (Francis 1988, Laman-Trip 2004). The model parameters $L(\tau)$, $L(\omega)$ and $L(\mu)$ are based on average body size at three arbitrary ages τ, ω and μ (with $\omega = \frac{\mu + \tau}{2}$). Age τ was selected as 1-year-old and age μ as 5-years-old. Age ω was calculated to be 3-years-old. The parameters used in this study were thus $L(1)$, $L(3)$ and $L(5)$. For the purpose of this study, only the parameter $L(1)$ will be examined. $L(1)$ is a measure of initial size and in rapidly asymptotically growing species can function as a proxy of growth rate (Francis 1988).

5.3.5 Growth model analysis

For each species, parameters were compared for populations from both locations (One Tree Island and Lizard Island) by minimising the maximum likelihood estimate (Kimura 1980), and location-specific growth trajectories were plotted through observed size-at-age estimates for populations at both locations. Confidence regions were generated around the rVBGF parameters $L(1)$, $L(3)$ and $L(5)$ for all populations using a bootstrapping technique (Manly 1997). While maintaining original sample size and population age structure, for each species, location-specific size-at-age estimates were re-sampled 1000 times with replication (Haddon 2001). This generated 1000 combinations of best-fit parameter values for each population, from which confidence regions around the original parameters *L(1)*, *L(3)* and *L(5)* can be calculated (Laman-Trip 2004). Analysis of variance (ANOVA) was performed on the bootstrap estimates of *L(1)* to compare growth rates of intraspecific populations between locations.

Mean maximum size and age were calculated using a similar bootstrapping technique. For each species, the populations from both locations were sampled 1000 times with replication, maintaining the original sample size and age structure (Haddon 2001). Mean maximum size and age were calculated as the average size (TL, mm) and average age (years) of the largest and oldest 5% of each sample, respectively. Means were then adjusted for bias-correction of the difference between the original parameter value and the mean of the bootstrap estimates of the parameter (Bias-adjusted mean = original value – bias) (Haddon 2001). Confidence intervals (CI) were then calculated as CI = 1.96 * SE of the bootstrapped estimates (Haddon 2001).

5.4 RESULTS

5.4.1 Size-at-age analysis

A total of over 500 fish (across all four species) were collected and aged for life-history character analysis from six sites (3 each at both Lizard Island and One Tree Island) (Table 5.2). 146 individuals under two years of age were aged by counting daily rings. Sample sizes at sites within location (reef) was not large enough to allow for intra-reef comparison. Comparisons between locations are presented in the remainder of this chapte**r.**

Table 5.2 Numbers of chaetodontids of four species aged for size-at-age analysis of life history characters at two Great Barrier Reef locations. Numbers indicate the total numbers aged (both adults and juveniles) while numbers in parentheses indicate the number of juveniles aged (estimated < 2 years old).

Species	Number Aged	
	Lizard Island	One Tree Island
	Total (Juveniles)	Total (Juveniles)
Chaetodon citrinellus	69 (36)	29 (5)
C. lunulatus	123 (45)	56 (0)
C. melannotus	33 (2)	73 (11)
C. trifascialis	67 (35)	56 (12)

5.4.2 Maximum size

The maximum size of all four species varied between locations (Figure 5.1). All four species were consistently larger at One Tree Island compared to Lizard Island, although this difference was significant only for *C. citrinellus*, *C. melannotus*, and *C. trifascialis*, but not for *C. lunulatus* (Figure 5.1). At One Tree Island, *C. lunulatus* had a mean maximum size of 120.6mm (± 1.86mm 95% C.I.) while at Lizard Island its mean maximum size was 116.0mm (± 2.65mm 95% C.I.). The most pronounced difference was found in *C. melannotus*, which had a mean maximum size of 120.6mm (± 11.90mm 95% C.I.) compared to 116.0mm (± 1.63mm 95% C.I.) at Lizard Island.

5.4.3 Longevity

The mean maximum ages of the four species did not show a clear pattern (Figure 5.2). Although one species, *C. citrinellus*, had a greater mean maximum age

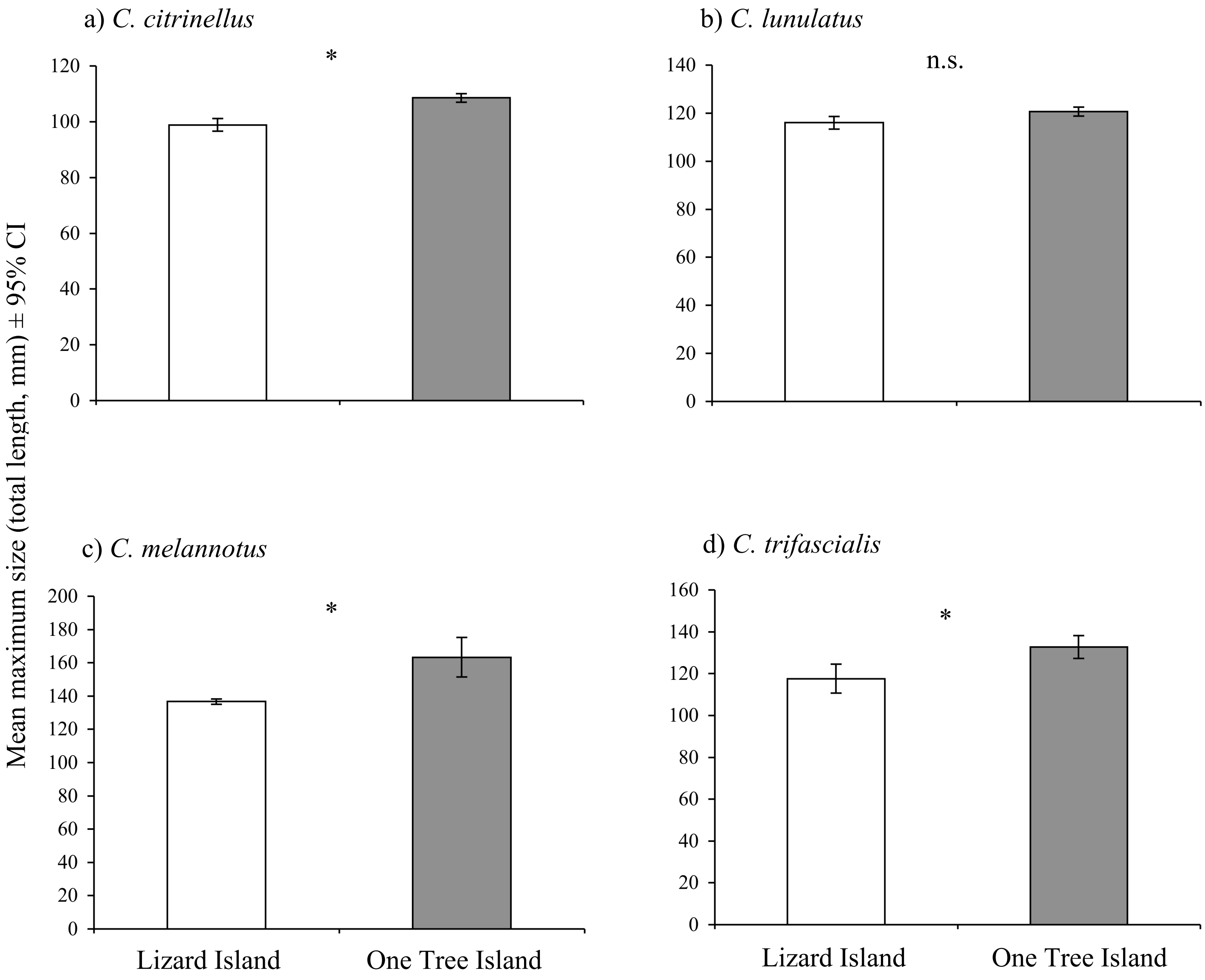
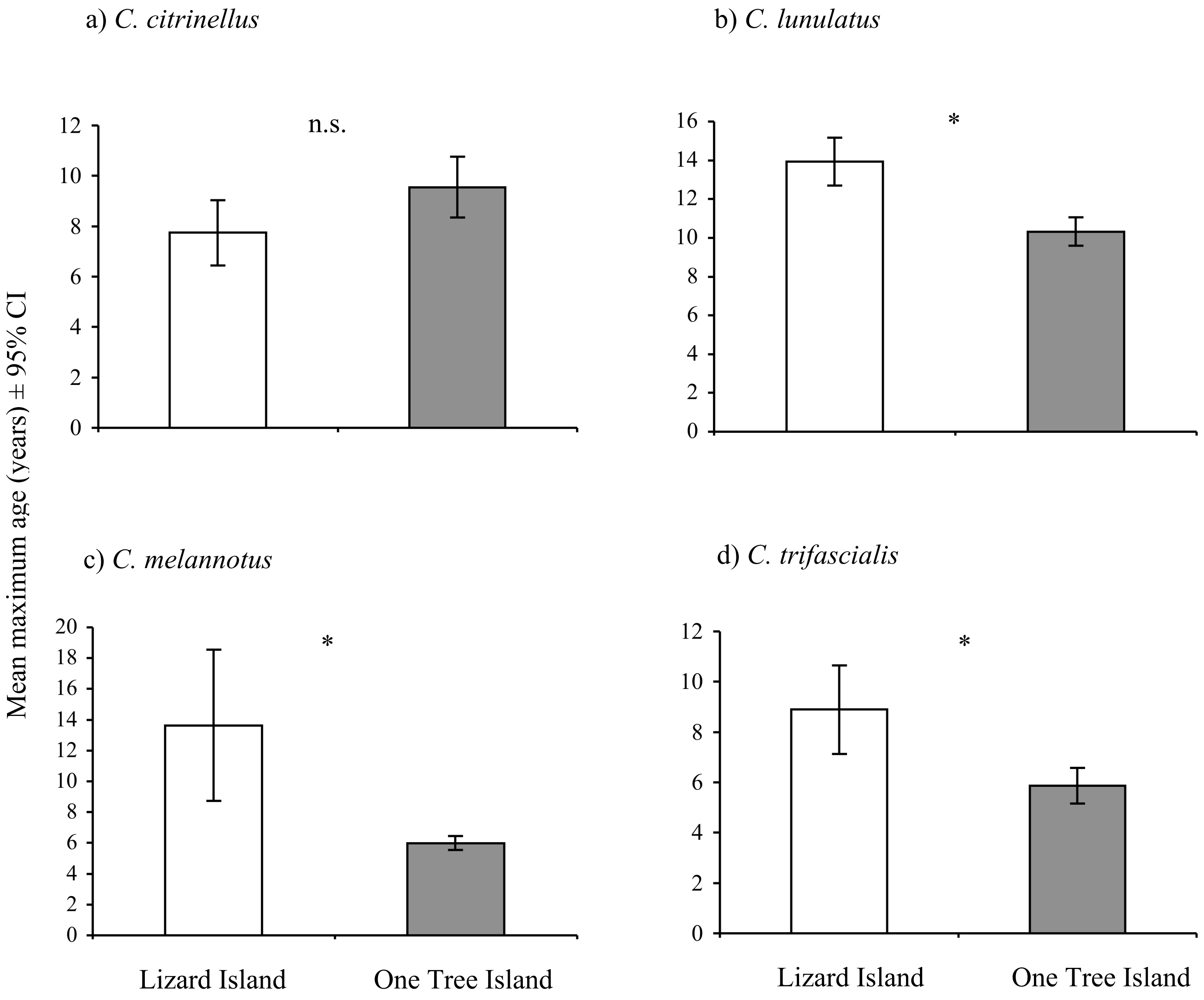


Figure 5.1. Mean maximum size (fork length in mm) for four species of *Chaetodon* butterflyfishes from two locations on the Great Barrier Reef, Lizard Island (open bars) and One Tree Island (shaded bars). Means are bias-adjusted values of bootstrap rVGBF estimates and are presented with 95% confidence intervals. A "*" indicates a significant difference between locations, while "n.s." indicates no significant difference.



a) *C. citrinellus*

b) *C. lunulatus*

c) *C. melannotus*

d) *C. trifascialis*

Figure 5.2. Mean maximum age (years) for four species of *Chaetodon* butterflyfishes from two locations on the Great Barrier Reef, Lizard Island (open bars) and One Tree Island (shaded bars). Means are bias-adjusted values of bootstrap rVGBF estimates and are presented with 95% confidence intervals. A "*" indicates a significant difference between locations, while "n.s." indicates no significant difference.

at One Tree Island than at Lizard Island (9.5yrs ± 1.21yrs 95% C.I. vs. 7.7yrs ± 1.29yrs 95% C.I.), this was insignificant. The other 3 species all showed significantly greater mean maximum ages at Lizard Island than at One Tree Island (Figure 5.2).

5.4.4 Growth rate

The growth rates, by comparison of length at age one, also varied between locations for some species (Figure 5.3). *C. melannotus* grew faster at One Tree Island in the first year, attaining a mean length at age one of 89.0mm (± 5.52mm 95% C.I.) while at Lizard Island its mean size at age one was 56.2mm (± 3.48mm 95% C.I.). Similarly, *C. citrinellus* had a greater growth rate at One Tree Island than at Lizard Island, and *C. lunulatus* and *C. trifascialis* did not show a significant difference between locations (Figure 5.3).

5.4.5 Chaetodontid abundance

A total of 406 fish representing 23 species were recorded at Lizard Island and One Tree Island in the visual surveys. Composition of chaetodontid communities between Lizard Island and One Tree Island was significantly different (MANOVA, Pillai's trace = 0.782, F = 8.07 df = 8/18, P < .001) (Figure 5.4). Data was Log_{10} (x+1) transformed. Total chaetodontid abundance was significantly different between locations (ANOVA, P = .023, F = 5.848, df = 1/25). For each of the four species studied, only one showed significant differences between locations. At One Tree Island, *C. lunulatus* had an average abundance of 3.83 (± 0.56 SE) per 200m^2 while at Lizard Island, it had an average abundance of 1.67 (± 0.89 SE). The other three species did not show significant differences in abundances between locations (Figure 5.4).

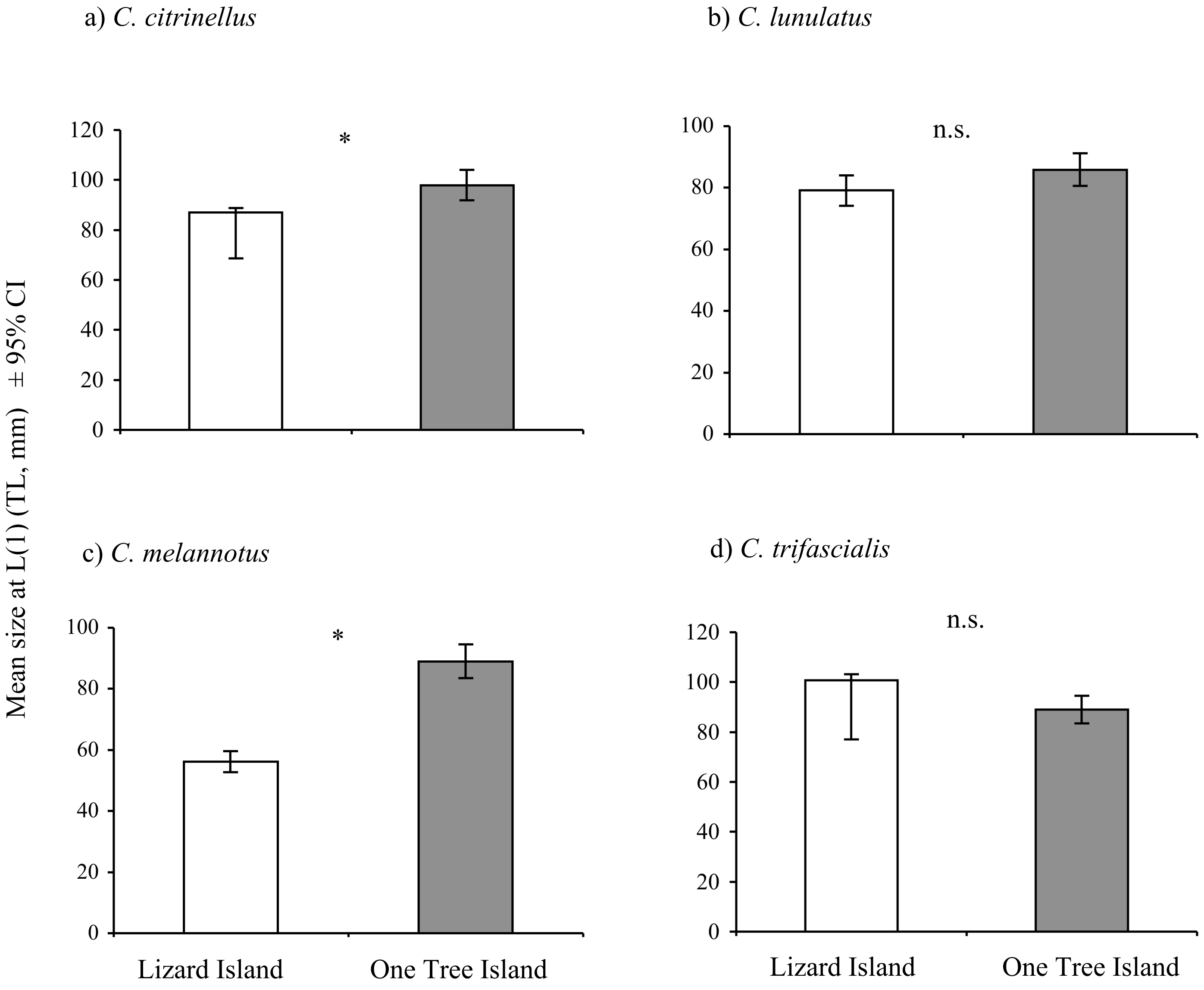


Figure 5.3. Mean initial body size (total length, mm), a proxy for growth rate, for four species of *Chaetodon* butterflyfishes from two locations on the Great Barrier Reef, Lizard Island (open bars) and One Tree Island (shaded bars). Means are bias-adjusted values of bootstrap rVGBF estimates and are presented with 95% confidence intervals. A "*" indicates a significant difference between locations, while "n.s." indicates no significant difference.

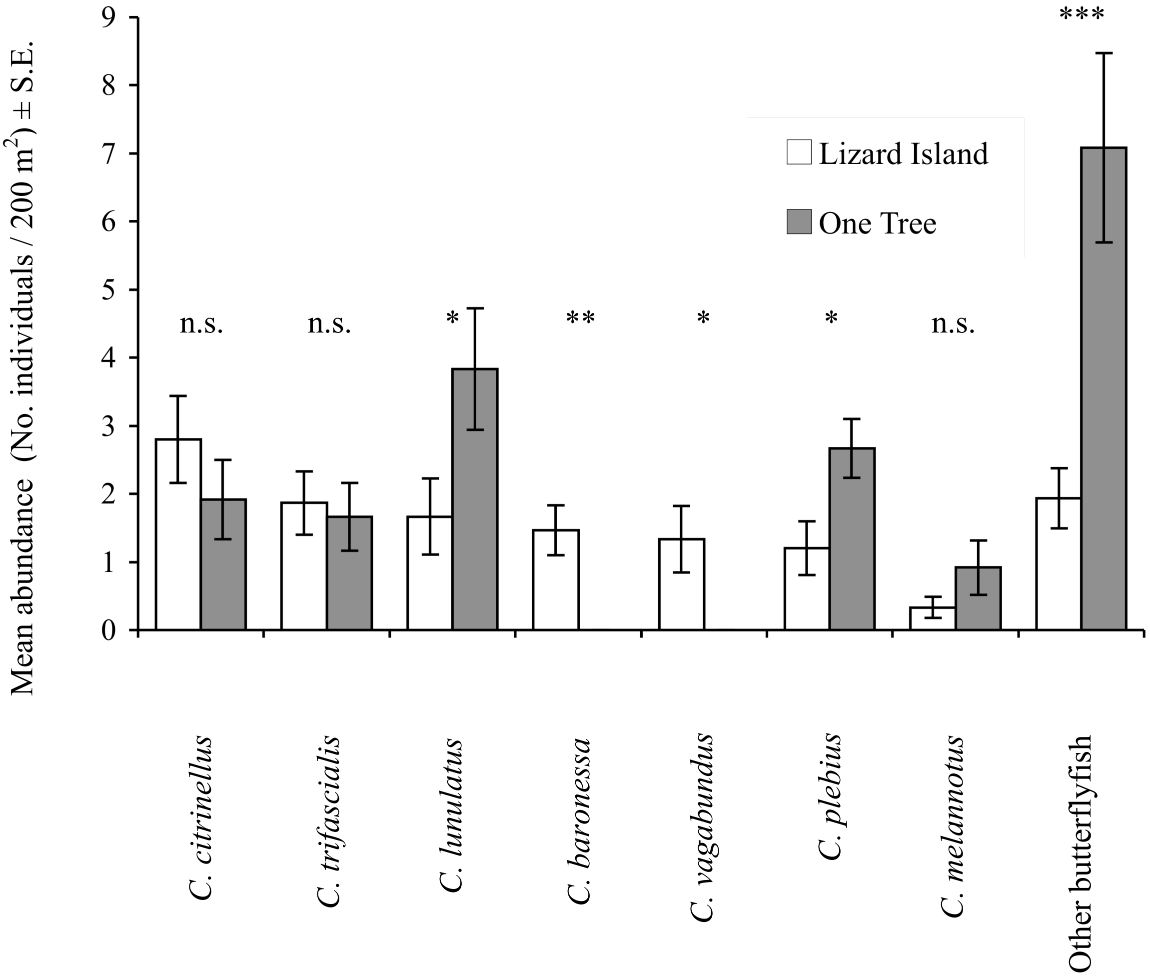


Figure 5.4. Mean abundance of chaetodontids (including 8 species of the genus *Chaetodon*) from exposed sites at two locations on the Great Barrier Reef, Lizard Island (open bars) and One Tree Island (shaded bars). Bars represent the mean number of individuals counted in 200m^2 visual belt transects ± S.E. ANOVA results of significance of difference between locations for each species is indicated: *** = P < .001 ; ** = P < .01 ; * = P < .05 ; n.s. = not significant (P > .05).

5.4.6 Benthic communities

The composition of benthic communities between Lizard Island and One Tree Island was significantly different (MANOVA, Pillai's trace = 0.867, F = 14.64, df = 8/18, P < .001) (Figure 5.5). Data was arcsine ($P_{(x)}$) transformed. Comparisons of important benthic categories between Lizard Island and One Tree Island revealed significant differences between abundances in several categories: *Acropora* spp. (excluding *A. hyacinthus*), *Montipora* spp., and other hard corals were all more abundant at One Tree Island than at Lizard Island, while soft corals and all non-coral prey were more abundant at Lizard Island than at One Tree Island (Figure 5.5). *A. hyacinthus*, *Pocillopora* spp., and *Porites* spp. did not show a significant difference between the two locations (Figure 5.5).

5.5 DISCUSSION

This study reveals significant differences in life history characters of butterflyfishes between two reefs (Lizard Island and One Tree Island) separated by 1200km. Between these two reefs, scleractinian corals were as abundant or more abundant at One Tree Island compared to Lizard Island. Therefore, if life-history characteristics of coral-feeding butterflyfishes were influenced primarily by access to prey resources, individuals living at One Tree Island would be expected to grow faster, live longer and/or have higher reproductive output compared to individuals at Lizard Island. This study showed that butterflyfishes at One Tree Island are indeed generally growing larger and growing faster but do not live as long compared to conspecifics at Lizard Island. However, *C. melannotus*, which feeds largely on soft corals (Alino et al. 1988; Pratchett 2005), also grew significantly faster at One

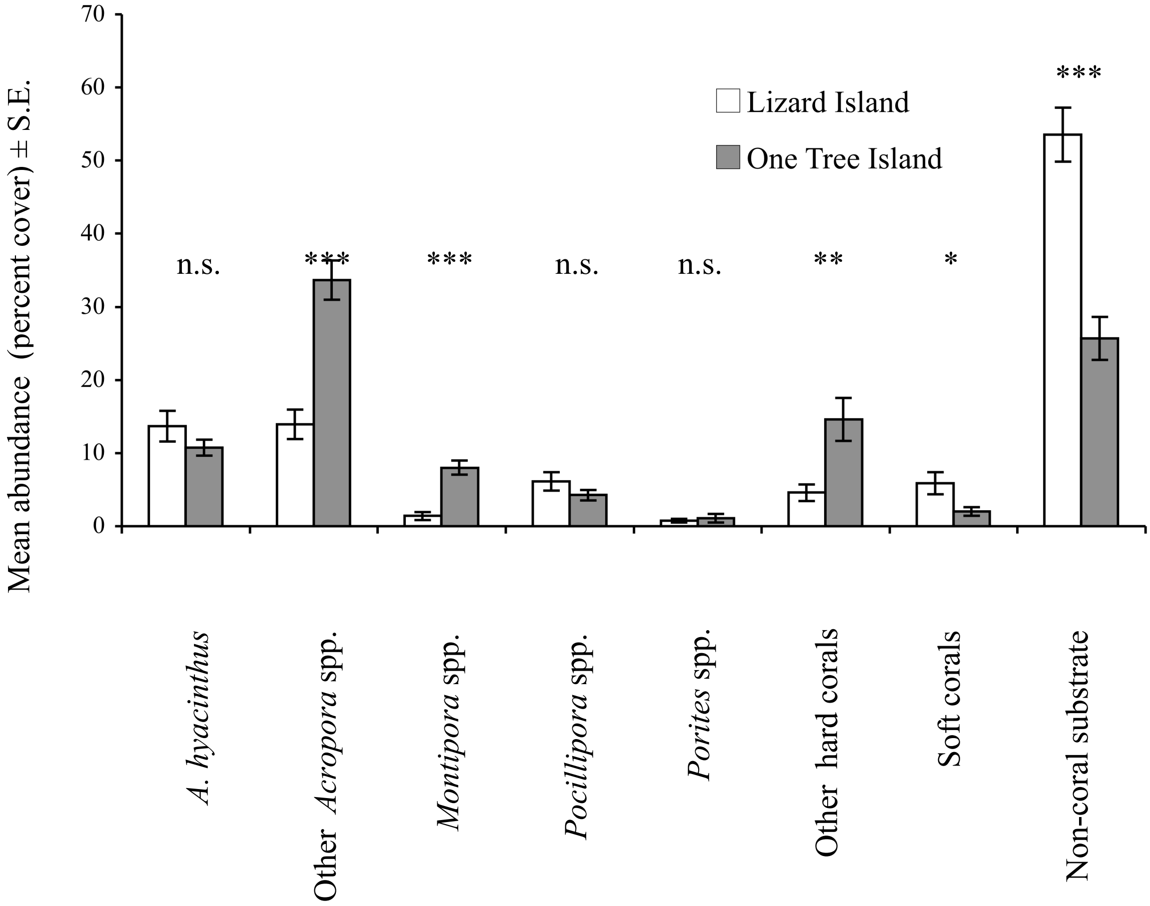


Figure 5.5. Mean abundance of 8 benthic categories (including *Acropora hyacinthus*) from exposed sites at two locations on the Great Barrier Reef, Lizard Island (open bars) and One Tree Island (shaded bars). Bars represent the mean coverage of categories counted in 10m line-intercept transects ± S.E. ANOVA results of significance of difference between locations for each species is indicated: *** = P < .001 ; ** = P < .01 ; * = P < .05 ; n.s. = not significant (P > .05).

Tree Island compared to Lizard Island despite the fact that there was much higher abundance of soft-corals at Lizard Island. It is possible, therefore, that observed differences in life-history characteristics are attributable to differences in environmental conditions as much as they are attributable to differences in resource availability.

If any of these species would be expected to be sensitive to differences in resources, however, it would be expected that *C. trifascialis* should grow faster where there is more of its preferred resource, *A. hyacinthus* (Chapter 4). There was no significant difference of *A. hyacinthus* availability between the two reefs, and accordingly, the growth rates of the two populations showed no significant difference. However, the effect of differences in latitude or temperature may confound differences of resource availability for the other species. As chaetodontids have highly asymptotic growth (Berumen 2005 - Chapter 3), variation in the first two years of life may be critical. Further complicating this analysis, resource availabilities present at the time of this study may not reflect the resources that were available during their juvenile period of growth due to changes in chaetodontid communities (see Berumen and Pratchett in press - Appendix 2) or even changes in coral communities. Availability of resources to juveniles may be determined at a microhabitat scale which is inadequately assessed by the survey method used in this study and would likely require a separate census. Differences in maximum body size would be achieved during this period of rapid growth as well, and so again, resource availabilities at the time that these individuals would be growing would be a critical factor (see also Mulligan and Leaman 1992). Notably, there have been severe episodes of coral depletion, such as reef-wide bleaching of corals on the Great Barrier Reef in 1998 and 2000 (Bellwood et al. 2004), in the lifetime of the fishes studied here. However, given that maximum size was almost always greater in the higher-latitude location (One Tree Island), it may be possible that maximum size is dictated more by temperature regime than by resource availability or population densities.

As care was taken to sample in habitats with equivalent wave exposure, life history variation due to exposure such as that found by Gust et al. (2002) and Robertson et al. (2005) should not be a factor. Although at large scales it is not possible to control for resources, this study is the first field-based attempt to account for the variance in specific resource availability between study sites in the context of life history consequences. Detailed dietary information from every location would be necessary to confirm what prey species consume and prefer at each location. Although Pratchett (2005) provides the most detailed analysis of chaetodontid diets to date, the author acknowledges the limitation of this information coming from only one site. In general, however, the findings are in agreement with other chaetodontid diet studies (e.g., Reese 1981, Berumen et al. 2005) but for some species there is marked discrepancy (e.g., *C. auriga*, Harmelin-Vivien and Bouchon-Navaro et al. 1983; *C. unimaculatus*, Cox 1994). Location-specific differences in consumption or preferences are possible and may further complicate inter-population comparisons of life histories.

There is also the potential for the actual resources to vary in some measure of "quality" between locations. Little is known about the variation in "quality' of corals over environmental gradients. Various attempts to analyse nutritional values of corals have not produced results consistent with observed feeding preferences (Keesing 1990, Pratchett 1995). Exactly what chaetodontids "target" nutritionally is unclear (see Anderson et al. 2004). Until this is established, detecting large-scale patterns in coral "quality" or the nutritional significance of prey preferences will not be feasible.

Future work with respect to the nutritional ecology of chaetodontids will be important to tease apart the relationship between feeding habits and life history consequences, as what chaetodontids eat may not directly reflect their nutritional needs (e.g,, Anderson et al. 2004, Raubenheimer and Simpson 2004). To further complicate the matter, these needs may change over large scales as environmental conditions change (see also MacNally 1995).

Variation in life history traits of chaetodontids may also be attributable to differences in the intensity of competition between locations (see Wootton 1998, Ali and Wootton 1999). For some species of chaetodontids at Lizard Island, Pratchett (2005) found little dietary overlap between species (e.g., *C. melannotus*), and therefore intra-specific competition is more important than inter-specific competition in influencing life histories for these species. Fish abundances do not seem to explain variations in life histories, although competition is likely to be an important factor. *Chaetodon lunulatus* was the only study species with a difference in abundance. This may be responsible for the observed decrease in its longevity at One Tree (where it is more abundant), although this species is arguably unlikely to be impacted by abundances of intra- and inter-specifics as they rarely are subject to aggressive interactions (Berumen and Pratchett in press - Appendix 2). An important possible exception to this may be *C. trifascialis*. Greater abundance of *C. baronessa* at Lizard Island may decrease access to *A. hyacinthus* (Berumen and Pratchett in press – Appendix 2) and subsequently reduce its growth rate. Competition with *C. baronessa* is not likely at One Tree Island as abundance of *C. baronessa* is negligible. Competition at Lizard Island may thus mask an increase in growth rate conferred by the increased availability of highly preferred prey, *A. hyacinthus*.

Variability in the response of species to differences in availability of resources between Lizard Island and One Tree Island may be further influenced by their ecological versatility (see MacNally 1995). The distribution and abundance of specialist species is constrained by the availability of essential resources, though specialist species are not necessarily less abundant than generalist counterparts. Specialists, such as *C. trifascialis*, may be more sensitive to changes in resource availability than generalists (Munday 2004). Chapter 4 demonstrated the greater response of the more specialised *C. trifascialis* to availabilities of preferred coral prey than the more generalised *C. plebeius*. Because of this enhanced response, specialists' life histories may be primarily determined by availability of preferred resources, whereas a generalist is more influenced by prevailing environmental conditions (sensu Robertson et al. 2005). Longevity, maximum size, and growth rates for *C. citrinellus*, the most generalised fish studied, fit the pattern that one would predict if temperature regime influences these features (Robertson et al. 2005). Other studies have found this trend to be consistent at this scale (Choat and Robertson 2002, Ackerman 2004, Laman-Trip 2004), but the pattern is not so clear for chaetodontids. In two species (*C. lunulatus* and *C. trifascialis*) there is no significant difference in growth rates between One Tree and Lizard Islands. This would further indicate that temperature-based counter-gradient variation is not occurring in these species.

There are clearly many competing explanations for the observed variation in chaetodontid life history characteristics, including temperature-based variation (Robertson et al. 2005), congeneric abundance and competition for preferred food resources (Berumen and Pratchett in press – Appendix 2), availability of preferred resources (Chapter 4), and / or fine-scale nutritional ecological processes (sensu Raubenheimer and Simpson 2004). Any of these explanations may compound or confound the effects of the others, and it is unlikely that any single factor is operating over this spatial scale (see MacNally 1995). Assessing the relative importance of these various factors will require carefully designed experiments, such as "common garden" experiments (e.g., Yamahira and Conover 2002, Martin et al. 2004).

At a fundamental level, prey acquisition and the availability of resources limit the distribution and abundance of organisms and also influences the stucture and dynamics of local populations (e.g., Chapter 4). There are, however, many other factors that may impact on the life history traits of fishes, and the importance of resource availability may only be apparent at some scales (e.g., Berumen et al. 2005 – Chapter 2) or under certain conditions. At very large spatial scales, such as between the widely separated reefs studied here, the role of resources in determining life history traits may be obscured by other large scale processes such as major differences in environmental conditions (e.g., Robertson et al. 2005) and adaptation by local populations (e.g., Yamahira and Conover 2002, Åbjörnsson et al. 2004). Still, among reef fishes, chaetodontids present an ideal opportunity to measure and account for the role of resource availability in determining life history traits. Identification or quantification of resources at a reef-scale may not be sufficient, and a finer-scale analysis might address this problem. The final chapter in this thesis will further identify areas of work with promise related to understanding life history theory.

Chapter 6. General Discussion

Resources play a major role in the energetics and overall fitness of animals. Variation in the quantity and/or quality of resources will determine the energy available for key life processes (growth, maintenance and reproduction), which will effect fitness of individuals and populations (Schoener 1971, Jones and McCormick 2002). Allocation of energy to different life processes will however, vary among species, populations, and individuals, and also varies with ontogeny (van Noordwijk & de Jong 1986). Importantly, energy allocation and life histories of organisms are influenced by biological processes (e.g., competition, predation, and disease) and environmental conditions (e.g., temperature). Therefore, predicting and revealing specific effects of varied resources on the life histories of organisms may be very difficult. This study has shown that variation in the availability of certain resources can have an important influence on physiological condition (Berumen et al. 2005 – Chapter 2) and growth rates (Chapter 4) of coral-feeding butterflyfishes. However, the importance of resources in the life-histories of butterflyfishes was not apparent when exploring differences among two geographically separated populations (Chapter 5).

For coral reef fishes, food availability has been shown to have direct and immediate effects on physiological condition (e.g., Green and McCormick 1999, Pratchett et al. 2001, Pratchett et al. 2004 – Appendix 1), which can further influence individual fitness (McCormick 2003). For example, Pratchett et al. (2001) showed that the physiological condition of fishes increased markedly within 2 days following mass-spawning of corals, which provides a large seasonal pulse of high-energy prey. Moreover, McCormick (2003) showed that fishes which fed on the lipid rich coral spawn yielded larvae that had 25% larger yolksacs and 100% larger oil globules than larvae produced by fishes which did not feed on coral spawn, showing that increased food availability increases larval quality (see also Applebaum & Holt 2003). Similarly, this study showed that butterflyfishes (specifically, *Chaetodon lunulatus* and *C. baronessa*) living in back-reef locations with limited access to preferred coral prey had much lower physiological condition (measured using hepatocyte vacuolation) compared to conspecific individuals living in front-reef locations where coral prey (specifically *Acropora hyacinthus*) was much more abundant (Berumen et al. 2005 – Chapter 2). Further, this study showed that accessibility to specific coral prey has significant effects on the growth and survivorship of juvenile butterflyfishes (Chapter 4). In controlled feeding experiments, conducted under laboratory conditions, butterflyfishes (specifically, *C. trifascialis* and *C. plebeius*) grew much faster and survived much better when fed exclusively on their preferred coral prey (*A. hyacinthus* and *Pocillopora damicornis*, respectively) compared to individuals kept on an exclusive diet of *Porites lobabta*, which is rarely eaten in the field. These findings show that the availability of coral prey is critically important in the energetics and fitness of coral-feeding butterflyfishes.

Small-scale (within-reef) differences in the physiological condition of fishes, as shown in Chapter 2, are unlikely to be the result of varying environmental conditions (e.g., temperature) that vary over much larger spatial scales (e.g., Lecchini et al. 2003, Adjeroud et al. 2005). Rather, these differences are likely to reflect variation in the quantity and/or quality of prey available in different reef habitats (sensu Gust et al. 2002, Ackerman 2004), which can have significant effects on the physiological condition of coral reef fishes (Green and McCormick 1999, Pratchett et al. 2001, Pratchett et al. 2004 – Appendix 1). In the case of butterflyfishes, many species appear to have a direct dependence on coral prey (Pratchett 2005) and thus variation in access to live coral or particular species of coral can have a major impact on energy available for allocation to essential life processes. Although it was not considered in this particular study, small-scale differences in the energetics of butterflyfishes among different reef habitats are likely to translate into significant differences in their longevity, growth rates, and/or reproductive success (e.g., McCormick 2003). Butterflyfishes therefore, seem to be an optimal study group for furthering our understanding of the role that resources play in structuring life history characteristics.

6.1 Determinants of life history characteristics

A growing body of evidence suggests that variation in life history characteristics are mostly associated with large-scale gradients in prevailing environmental conditions, such as temperature (e.g., Robertson et al. 2005). In most cases, adaptation to specific temperature regimes or adaptation to seasonality (or a combination) accounts for most, if not all, of the observed variations in growth rates among populations (Yamahira and Conover 2002). The role of adaptation to local environmental conditions in determining life history characteristics may be tested using common garden experiments, following Conover and Schultz (1995), but results of such tests are not yet available for butterflyfishes. Even so, variation in environmental conditions are unlikely to explain differences in life-history characteristics of fishes observed at relatively small spatial scales, such as within reefs (Gust et al. 2002, Ackerman 2004). Due to the absence of confounding influences associated with large-scale environmental gradients, it may be at these smaller spatial scales (e.g., among reef habitats) that the importance of resources is most apparent.

Determining exactly how resources connect to long-term life-histories of fishes is important, but considerable effort will be required to relate variation in feeding behaviour (e.g., the range and proportional consumption of different prey types) and availability of prey to key life-history characteristics (e.g., growth, survivorship, and reproductive output), which probably needs to be done at the level of individual fishes. This study has indicated that there may be major differences in the life histories of butterflyfishes associated with differences in resource availability at very small (e.g., within reefs; Berumen et al. 2005 – Chapter 2) and very large (e.g., among geographically separated reefs; Chapter 4) scales (see also Gust et al. 2002, Ackerman 2004, Laman-Trip 2004). However, considerable research is still required to detect specific effects of resource variation on life histories of these and many other types of fishes. Most notably, this study did not consider potentially significant effects of resource variation on the reproductive output of butterflyfishes (discussed further below in section 6.2).

Chapter 4 provides further evidence that specific resource availabilities influence growth, especially in juveniles. Changes in the growth patterns of juveniles are likely to have significant consequences on overall life histories since it is during this juvenile period that somatic growth seems to be the most significant investment of energy in butterflyfishes (Ralston 1981, Berumen 2005 – Chapter 3). As Chapter 5 demonstrated, however, the availabilities of resources did not explain differences in growth rates as predicted in this manner. There may be several confounding factors at large scales, and it does not mean that resources are not an important part of the explanation. As the critical growth happens during the juvenile stage (Berumen 2005 – Chapter 3), it is access to preferred prey (due to coral abundance and/or conspecific/congeneric competitive interactions) during the juvenile phase that may influence the observed demographic parameters. Careful analysis of individuals' access to prey during their period of rapid growth could allow us to make a firm connection between resources and long-term demographic characters of butterflyfishes.

Measurable differences were documented in maximum size, longevity, and growth rates of butterflyfishes over large scales (>1000km). The exact mechanisms underlying these differences are not clear, however. While several factors could be contributing, including temperature, latitude, anthropogenic pressure, predation, and exposure, resources are likely to be an important factor, and butterflyfishes offer some evidence that resources are important over large scales. Prey availability alone may not be responsible for variation in the energetics of butterflyfish populations, but this study shows that fishes with access to preferred prey gain significant physiological (including growth) benefits. Even if only due to enhanced growth of juveniles, there may be major differences in the structure and dynamics of reef fish populations living in different reef habitats. Importantly, these differences may occur over very small spatial scales (within reefs at the individual level of prey access) and must be considered when comparing reef fish populations within and between coral reefs.

6.2 Future directions

The findings of this thesis provide the framework and background for future avenues of related research. Several promising areas can be identified, and I will discuss below some of the future directions to further resolve the results of this work. With a wide range and degree of specialisations on measurable resources, butterflyfishes present an important opportunity to advance the state of knowledge in a broad set of theories related to the concepts of ecological versatility and foraging theory. Specifically, this family of fishes allow for the simultaneous investigation of foraging and life history theories. It is not within the scope of this study, however, to adequately address every component of life histories. As reproduction arguably carries the greatest long-term fitness significance, I would be remiss not to address this as an area deserving attention in future work.

A rapidly emerging field of research, not only among tropical ichthyologists, is assessing the consequences and trade-offs associated with the level to which species are specialist or generalist in their use of resources (e.g., Munday 2004). Given the variability among butterflyfishes in the degree to which they are specialists or generalists (e.g., Pratchett 2005, Berumen et al. 2005 – Chapter 2, Chapter 4), this group provides a significant opportunity to contribute to this field of research. Importantly, several studies have found variable responses among butterflyfishes to disturbance events that lead to large-scale depletion of corals (e.g., Williams 1986, Sano et al. 1987, Pratchett et al. in press), which may be related to differences in their specific dietary habits. The various feeding selectivity and specialisations of some species may be responsible for differing response to disturbances where certain corals are disproportionately affected (Pratchett et al. 2004 – Appendix 1, Berumen et al. 2005 – Chapter 2, Berumen and Pratchett in press – Appendix 3). Where preferred resources are disturbed and are no longer available to coral-feeding fishes, reduction in condition and/or growth potential may have significant consequences for whole-population characteristics (sensu Munday 2004).

So why should or do organisms specialise? The conventional answer is that through some mechanism of increased efficiency, the specialising organism will increase its overall fitness (Fox and Morrow 1981, Futuyma and Moreno 1988), and MacArthur (1972) even states that it is this increased efficiency through specialisation that has led to the diversity of species worldwide. There are, however, several case studies in which specialists are not found to have an increased efficiency compared to a generalist (e.g., Sutherland 1987). Results from this study (Chapter 4) however, would suggest that specialist butterflyfishes do gain a significant fitness benefit from their specialising on a restricted range of different coral species, growing much faster on their preferred prey compared to more generalist butterflyfishes. Specialisation, however, may be facultative (or at least non-obligatory). While *C. trifascialis*, the most specialised corallivore, was disproportionately affected by coral depletion caused by outbreaks of *Acanthaster planci* at Lizard Island (Pratchett 2002), another seemingly specialised species (*C. baronessa*) was relatively unaffected. This could have been due to the versatility of *C. baronessa* to utilise a more general range of prey (Berumen et al. 2005 – Chapter 2). While abundances of *C. baronessa* may not have changed, its overall fitness may have still been affected, especially if reproductive effort was affected.

Understanding the mechanisms underlying specific feeding preferences of butterflyfishes will also further advance foraging theories, particularly in regard to specialisation. This study presents strong evidence that coral-feeding butterflyfishes target species that contribute to increased fitness, but it remains to be seen whether this is true for other species. Nutritional stoichiometry (following Raubenheimer and Simpson 2004) could reveal that the fish are not seeking one nutrient in particular (Anderson et al. 2004), but rather that they seek a balance of particular nutrients. Alternatively, they may consume an excess of one nutrient in order to achieve a minimum of another nutrient ("non-independence" sensu Raubenheimer and Simpson 2004).

Reproductive output has not been addressed in this study due to the intensive sampling required even to present a relative measure of reproductive effort. Some butterflyfishes are known to spawn monthly for most of the year, probably on a lunar cycle (Yabuta 1997, Yabuta and Kawashima 1997). As in most fish groups, there may further be variation in the output from month-to-month and year-to-year (see Doherty 1991). The detailed sampling required to fully establish reproductive effort between habitats (within-reef) or locations at geographically separated reefs is therefore beyond the scope of this study. Future work assessing reproductive output could explain a critical trade-off in life history characters driven by energy/resource availability (see Jones & McCormick 2002) or environmental conditions (e.g, Pawson et al. 2000). Many of the life history characteristics studied in this thesis could be affected by energy otherwise budgeted to reproductive functions, particularly over large spatial scales.

6.3 Conclusion

Overall, this study has shown that variations in the quality and quantity of resources influence the condition and growth of butterflyfishes. This is strong empirical support for the generalisation that resource availability plays a major role in shaping the life histories of most organisms. Increased amounts of preferred prey should translate into increased energy available for growth, reproduction, or other processes directly contributing to overall fitness. However, many factors (e.g., predation, competition, and temperature) will influence life history traits and resources alone are unlikely to explain all spatial and temporal variation in the allocation of energy to various life processes.

References

Åbjörnsson K, Hansson L-A, Brönmark C (2004) Responses of prey from habitats with different predator regimes: local adaption and heritability. *Ecology* **85**: 1859-1866

Ackerman JL (2004) Geographic variation in size at age of the coral reef fish, *Thalassoma lunare* (family: Labridae): a contribution to life history theory. Ph.D., School of Marine Biology and Aquaculture, James Cook University, Townsville

Adjeroud M, Chancerelle Y, Schrimm M, Perez T, Lecchini D, Galzin R, Salvat B (2005) Detecting the effects of natural disturbances on coral assemblages in French Polynesia: A decade survey at multiple scales. *Aquat Living Resour* **18**: 111-123

Ali M, Wootton RJ (1999) Effect of variable food levels on reproductive performance of breeding female three-spined sticklebacks. *J Fish Biol* **55**: 1040-1053

Alino PM, Sammarco PW, Coll JC (1988) Studies of the feeding preferences of Chaetodon melannotus (Pisces) for soft corals (Coelenterata; Octocorallia). 6th Int Coral Reef Symp **3**: 31-36.

Allen GR, Steene R, Allen M (1998) A guide to angelfishes and butterflyfishes. Odyssey Publishing, Perth 250 pp.

Almany GR (2003) Priority effects in coral reef fish communities. *Ecology* **84**: 1920-1935

Alofs KM, Polivka KM (2004) Microhabitat-scale influences of resources and refuge on habitat selection by an estuarine opportunist fish. *Mar Ecol Prog Ser* **271**: 297-306

Alwany M, Thaler E, Stachowitsch M (2003) Food selection in two corallivorous butterflyfishes, Chaetodon austriacus and C. trifascialis, in the northern Red Sea. *Mar Ecol* **24**: 165-177

Anderson GRV, Ehrlich AH, Ehrlich PR, J.D. R, Russell BC, Talbot FH (1981) The community structure of coral reef fishes. *Am Nat* **117**: 476-495

Anderson T, Boersma M, Raubenheimer D (2004) Stoichiometry: linking elements to biochemicals. *Ecology* **85**: 1193-1202

Angilletta MJ, Wilson RS, Navas CA, James RS (2003) Tradeoffs and the evolution of thermal reaction norms. *Trends Ecol Evol* **18**: 234-140

Applebaum SL, Holt GJ (2003) The digestive protease, chymotrypsin, as an indicator of nutritional condition in larval red drum (*Sciaenops ocellatus*). *Mar Biol* **142**: 1159-1167

Arendt J (1997) Adaptive intrinsic growth rates: an integration across taxa. *Q Rev Biol* **72**: 149-177

Atkinson D (1994) Temperature and organism size - a biological law for ectotherms? *Adv Ecol Res* **25**: 1-58

Ballantyne J, Mercure F, Gerrits M, Van Der Kraak G, McKinley S, Martens D, Hinch S, Diewert R (1996) Plasma nonesterified fatty acid profiles in male and female sockeye salmon, *Oncorhyncus nerka*, during spawning migration. *Can J Fish Aquat Sci* **53**: 1418-1426

Bay LK, Choat JH, van Herwerden L, Robertson DR (2004) High genetic diversities and complex genetic structure in an Indo-Pacific tropical reef fish (*Chlorurus sordidus*): evidence of an unstable evolutionary past? *Mar Biol* **144**: 757-767

Bean K, Jones GP, Caley MJ (2002) Relationships among distribution, abundance and microhabitat specialisation in a guild of coral reef triggerfish (Balistidae). *Mar Ecol Prog Ser* **233**: 263-272

Begon M, Harper JL, Townsend CR (1996) Ecology - Individuals, Populations, and Communities. Blackwell Scientific Publishing, Oxford 1068 pp.

Bell JD, Gazlin R (1984) Influence of live coral cover on coral-reef fish communities. *Mar Ecol Prog Ser s* **15**: 265-274

Bell JD, Harmelin-Vivien M, Galzin R (1985) Large scale spatial variation in abundance in butterflyfishes (Chaetodontidae) on Polynesian reefs. 5th Int Coral Reef Symp **5**: 421-426.

Bellwood DR, Hughes TP, Folke C, Nystrom M (2004) Confronting the coral reef crisis. *Nature* **429**: 827-833

Bergenius MA, Meekan MG, Robertson RD, McCormick MI (2002) Larval growth predicts the recruitment success of a coral reef fish. *Oecologia* **131**: 521-525

Berumen ML (2005) The importance of juveniles in modelling growth: butterflyfish at Lizard Island. *Environ Biol Fish* **72**: 409-413

Berumen ML, Pratchett MS (in press) Effects of resource availability on the competitive behaviour of butterflyfishes (Chaetodontidae). 10th Int Coral Reef Symp **XXX**:xxx

Berumen ML, Pratchett MS (in press) Recovery without resilience: persistent disturbance and long-term shifts in the structure of fish and coral communities at Tiahura Reef, Moorea. *Coral Reefs* **XXX**:xxx

Berumen ML, Pratchett MS, McCormick MI (2005) Within-reef differences in diet and body condition of coral-feeding butterflyfishes (Chaetodontidae). *Mar Ecol Prog Ser* **287**: 217-227

Billard R, Bry C, Gillet C (1981) Stress, environment and reproduction in teleost fish. In: Pickering A (ed.) Stress and Fish. Academic Press, London (pp 185-208)

Birkeland C, Neudecker S (1981) Foraging behaviour of two Caribbean chaetodontids: *Chaetodon capistratus* and *C. aculeatus. Copeia* **1981**: 169-178

Booth DJ (1995) Juvenile groups in a coral-reef damselfish: density-dependent effects on individual fitness and population demography. *Ecology* **76**: 91-106

Bouchon-Navaro Y (1986) Partitioning of food and space resources by chaetodontid fishes on coral reefs. *J Exp Mar Biol Ecol* **103**: 21-40

Bouchon-Navaro Y, Bouchon C, Harmelin-Vivien ML (1985) Impact of coral degradation on a Chaetodontid fish assemblage (Moorea, French Polynesia). 5th Int Coral Reef Symp **5**: 427-432

Bouchon-Navaro Y, Bouchon C (1989) Correlations between chaetodontid fishes and coral communities of the Gulf of Aqaba (Red Sea). *Environ Biol Fish* **25**: 47-60

Bozec Y-M, Dolédec S, Kulbicki M (2005) An analysis of fish-habitat associations on disturbed coral reefs: chaetodontid fishes in New Caledonia. *J Fish Biol* **66**: 966-982

Bozinovic F, Martinez del Rio C (1996) Animals eat what they should not: why do they reject our foraging models? *Rev Chil Hist Nat* **69**: 15-20

Bristow CM (1988) What makes a predator specialize? *Trends Ecol Evol* **3**: 1-2

Brown JH (1984) On the relationship between abundance and distributions of species. *Am Nat* **124**: 255-279

Bruggemann JH, Begeman J, Bosma EM, Verburg P, Breeman AM (1994) Foraging by the stoplight parrotfish *Sparisoma viride*. II. Intake and assimilation of food, protein, and energy. *Mar Ecol Prog Ser* **106**: 57-71

Burgess WE (1978) Butterflyfishes of the world: a monograph of the family Chaetodontidae. T.F.H. Publications, Surrey 832 pp.

Cadoret L, Aderjoud M, Tsuchiya M (1999) Spatial distribution of chaetodontid fish in coral reefs of the Ryukyu Islands, southern Japan. *J Mar Biol Ass UK* **79**: 725-735

Caley MJ (1998) Age-specific mortality rates in reef fishes: evidence and implications. *Aust J Ecol* **23**: 241-245

Caswell H (1989) Life-history strategies. In: Cherrett JM (ed.) Ecological Concepts. Blackwell Scientific Publications, Oxford (pp 285-307)

Chabanet P, Ralambondrainy H, Amanieu M, Faure G, Gazlin R (1997) Relationships between coral reef substrata and fish. *Coral Reefs* **16**: 93-102

Charnov EL (1976) Optimal foraging: The marginal value theorem. *Theor Pop Biol* **9**: 129-

136

Choat JH, Axe LM (1996) Growth and longevity in acanthurid fishes: an analysis of otolith increments. *Mar Ecol Prog Ser* **134**: 15-26

Choat JH, Axe LM, Lou DC (1996) Growth and longevity in fishes of the family Scaridae. *Mar Ecol Prog Ser* **145**: 33-41

Choat JH, Robertson DR (2002) Age-Based Studies. In: Sale PF (ed.) Coral Reef Fishes. Academic Press, San Diego (pp 57-80)

Clarke R (1989) Population fluctuation, competition, and microhabitat distribution of two species of tube blennies, *Acanthemblemaria* (Teleostei: Chaenopsidae). *Bull Mar Sci* **44**: 1174-1185

Clarke R (1992) Population shifts in two competing fish species on a degrading coral reef. *Mar Ecol Prog Ser* **137**: 51-58

Clifton KE (1995) Asynchronous food availability on neighboring Caribbean coral reefs determines seasonal patterns of growth and reproduction for the herbivorous parrotfish *Scarus iserti*. *Mar Ecol Prog Ser* **116**: 39-46

Connell S (1998) Effects of predators on growth, mortality, and abundance of a juvenile reef-fish: Evidence from manipulations of predator and prey abundance. *Mar Ecol Prog Ser* **169**: 251-261

Conover DO, Schultz ET (1995) Phenotypic similarity and the evolutionary significance of countergradient variation. *Trends Ecol Evol* **10**: 248-252

Cowen RK (2002) Larval dispersal and retention and consequences for population connectivity. In: Sale PF (ed.) Coral Reef Fishes. Academic Press, San Diego (pp 149-170)

Cox E (1994) Resource use by corallivorous butterflyfishes (Family Chaetodontidae) in Hawaii. *Bull Mar Sci* **54**: 535-545

Crosby MP, Reese ES (1996) A manual for monitoring coral reefs with indicator species: Butterflyfishes as indicators of change on Indo Pacific reefs. Office of Ocean and Coastal Resource Management, National Oceanic and Atmospheric Administration, Silver Spring, MD. 45 pp.

Depczynski M, Bellwood DR (2005) Shortest recorded vertebrate lifespan found in a coral reef fish. *Curr Biol* **15**: R288-R289

Dill L (1983) Adaptive flexibility in the foraging behavior of fishes. *Can J Fish Aquat Sci* **40**: 398-408

Doherty PJ, Williams DM (1988) The replenishment of coral reef fish populations. *Oceanogr Mar Biol Ann Rev* **26**: 487-551

Doherty PJ (1991) Spatial and temporal patterns in recruitment. In: P.F. S (ed.) The ecology of fishes on coral reefs. Academic Press, San Diego (pp 261-293)

Doherty PJ, Fowler A (1994) Demographic consequences of variable recruitment to coral reef fish populations: A congeneric comparison of two damselfishs. *Bull Mar Sci* **54**: 297-313

Doherty PJ, Planes S, Mather P (1995) Gene flow and larval duration in seven species of fish from the Great Barrier Reef. *Ecology* **76**: 2373-2391

Done TJ (1982) Patterns in the distribution of coral communities across the central Great Barrier Reef. *Coral Reefs* **1**: 95-107

Dulvy NK, Ellis JR, Goodwin NB, Grant A, Reynolds JD, Jennings S (2004) Methods of assessing extinction risk in marine fishes. *Fish Fish* **5**: 255-276

Duston J, Saunders R (1999) Effect of winter food deprivation on growth and sexual maturity of Atlantic salmon (*Salmo salar*) in seawater. *Can J Fish Aquat Sci* **56**: 201-207

Eckert GJ (1985) Settlement of coral reef fishes to different natural substrata and at different depths. 5th Int Coral Reef Symp **5**: 385-390

Erdman M (1997) Butterflyfish as bioindicators - a review. *Reef Encounter* **21**: 7-9

Findley JS, Findley MT (1985) A search for pattern in butterflyfish communities. *Am Nat* **126**: 800-816

Findley JS, Findley MT (2001) Global, regional, and local patterns in species richness and abundance of butterflyfishes. *Ecol Monog* **71**: 69-91

Forrester GE (1990) Factors influencing the juvenile demography of a coral reef fish. *Ecology* **71**: 1666-1681

Fowler AJ (1989) Description, interpretation and use of the microstructure of otoliths from juvenile butterflyfishes (family Chaetodontidae). *Mar Biol* **102**: 167-181

Fowler AJ (1990) Spatial and temporal patterns of distribution and abundances of chaetodontid fishes at One Tree Reef, southern GBR. *Mar Ecol Prog Ser* **64**: 39-53

Fowler AJ (1991) Reproductive biology of bisexual and all-female populations of chaetodontid fishes from the southern Great Barrier Reef. *Environ Biol Fish* **31**: 261-274

Fowler AJ (1995) Annulus formation in the otoliths of coral reef fish: a review. In: Secor DH, Dean JM, Campana SE (eds.) Recent developments in fish otolith research. University of South Carolina Press, Columbia (pp 45-63)

Fox LR, Morrow PA (1981) Specialization: species property or local phenomenon? *Science* **211**: 887-893

Francis RICC (1988) Maximum likelihood estimation of growth and growth variability from tagging data. *New Zeal J Mar Fresh* **22**: 42-51

Fraser D, Gilliam J (1992) Nonlethal impacts of predator invasion: Facultative suppression of growth and reproduction. *Ecology* **73**: 959-970

Futuyma DJ, Moreno G (1988) The evolution of ecological specialization. *Ann Rev Ecol Syst* **19**: 207-233

Gochfeld DJ (2004) Predation-induced morphological and behavioral defenses in a hard coral: implications for foraging behavior of coral-feeding butterflyfishes. *Mar Ecol Prog Ser* **267**: 145-158

Gore MA (1984) Factors affecting the feeding behaviour of a coral reef fish, *Chaetodon capistratus. Bull Mar Sci* **35**: 211-220

Green BS, Fisher R (2004) Temperature influences swimming speed, growth, and larval duration in coral reef fishes. *J Exp Mar Biol Ecol* **299**: 115-132

Green BS, McCormick MI (1999) Influence of larval feeding history on the body condition of *Amphiprion melanopus*. *J Fish Biol* **55**: 1273-1289

Gust N, Choat JH, Ackerman JL (2002) Demographic plasticity in tropical reef fishes. *Mar Biol* **140**: 1039-1051

Haddon M (2001) Modelling and quantitative methods in fisheries. Chapman & Hall / CRC, Boca Raton 424 pp.

Halford A, Cheal AJ, Ryan D, Williams DM (2004) Resilience to large-scale disturbance in coral and fish assemblages on the Great Barrier Reef. *Ecology* **85**: 1892-1905

Harmelin-Vivien ML, Bouchon-Navaro Y (1981) Trophic relationships among chaetodontid fishes in the Gulf of Aqaba (Red Sea). 4th Int Coral Reef Symp **2**: 537-544.

Harmelin-Vivien ML, Bouchon-Navaro Y (1983) Feeding diets and significance of coral feeding among Chaetodontid fishes in Moorea (French Polynesia). *Coral Reefs* **2**: 119-127

Hart AM, Klumpp DW (1996) Response of herbivorous fishes to crown-of-thorns starfish *Acanthaster planci* outbreaks. I. Substratum analysis and feeding ecology of *Acanthurus nigrofuscus* and *Scarus frenatus*. *Mar Ecol Prog Ser* **132**: 11-19

Hart AM, Klumpp DW, Russ GR (1996) Response of herbivorous fishes to crown-of-thorns starfish *Acanthaster planci* outbreaks. II. Density and biomass of selected species of herbivorous fish and fish-habitat correlations. *Mar Ecol Prog Ser* **132**: 21-30

Hart AM, Russ GR (1996) Response of herbivorous fishes to crown-of-thorns starfish *Acanthaster planci* outbreaks. III. Age, growth, mortality and maturity indices of *Acanthurus nigrofuscus. Mar Ecol Prog Ser* **136**: 25-35

Hiatt RW, Strassburg DW (1960) Ecological relationships of the fish fauna of coral reefs of the Marshall Islands. *Ecol Monogr* **30**: 65-127

Hilborn R, Walters C (1992) Quantitative fisheries stock assessment: choice, dynamics, and uncertainty. Chapman and Hall, New York 570 pp.

Hixon MA, Carr M (1997) Synergistic predation, density dependence, and population regulation in marine fish. *Science* **277**: 946-949

Hobson ES (1978) Feeding relationships of teleostean fishes on coral reefs in Kona, Haiwaii. *Fish Bull* **72**: 915-1031

Holbrook SJ, Forrester GE, Schmitt RJ (2000) Spatial patterns in abundance of a damselfish reflect availability of suitable habitat. *Oecologia* **122**: 109-120

Holbrook SJ, Schmitt RJ (1984) Experimental analyses of patch selection by foraging black surfperch (*Embiotoca jacksoni* Agazzi). *J Exp Mar Biol Ecol* **79**: 39-64

Holbrook SJ, Schmitt RJ (1986) Seasonally fluctuating resources and temporal variability of interspecifc competition. *Oecologia* **69**: 1-11

Hughes RN (1980) Optimal foraging theory in the marine context. *Oceanogr Mar Biol Ann Rev* **18**: 423-481

Hughes TP, Baird AH, Dinsdale EA, Moltschaniwskyj NA, Pratchett MS, Tanner JE, Willis BL (2000) Supply-side ecology works both ways: the link between benthic adults, fecundity and larval recruits. *Ecology* **81**: 2241-2249

Irons D (1988) Behavioral interactions of the butterflyfish *Chaetodon trifascialis* at Johnston Atoll. *Pac Sci* **42**: 122-123

Irons DK (1989) Temporal and areal feeding behaviour of the butterflyfish, *Chaetodon trifascialis*, at Johnston Atoll. *Environ Biol Fish* **25**: 187-193

Javois J, Tammaru T (2004) Reproductive decisions are sensitive to cues of life expectancy: the case of a moth. *Anim Behav* **68**: 249-255

Jones GP (1984) The influence of habitat and behavioural interactions on the local distribution of the wrasse, *Pseudolabrus celidotus*. *Environ Biol Fish* **10**: 43-58

Jones GP (1986) Food availability affects growth in a coral reef fish. *Oecologia* **70**: 136-139

Jones GP (1987) Competitive interactions among adults and juveniles in a coral reef. *Ecology* **71**: 1691-1698

Jones GP (1990) The importance of recruitment to the dynamics of a coral reef fish population. *Ecology* **71**: 1691-1698

Jones GP (1991) Postrecruitment processes in the ecology of coral reef fish populations: a multifactorial prespective. In: Sale PF (ed.) The ecology of fishes on coral reefs. Academic Press, San Diego (pp 294-237)

Jones GP, Milicich MJ, Emslie MJ, Lunow C (1999) Self-recruitment in a coral reef fish population. *Nature* **402**: 802-804

Jones GP, Caley MJ, Munday PL (2002) Rarity in coral reef fish communities. In: Sale PF (ed.) Coral Reef Fishes. Academic Press, San Diego (pp 81-102)

Jones GP, McCormick MI (2002) Numerical and energetic processes in the ecology of coral reef fishes. In: Sale PF (ed.) Coral Reef Fishes. Academic Press, San Diego (pp 221-238)

Keesing JK (1990) Feeding biology of the Crown-of-Thorns starfish, *Acanthaster planci* (Linnaeus). PHD, Zoology, James Cook University of North Queensland, Townsville

Kerrigan BA (1994) Post-settlement growth and body composition in relation to food availability in a juvenile tropical reef fish. *Mar Ecol Prog Ser* **111**: 7-15

Kimura DK (1980) Likelihood methods for the von Bertalanffy growth curve. *Fish Bull* **77**: 765-776

Koslow J, Bell J, Virtue P, Smith D (1995) Fecundity and its variability in orange roughy: Effects of population density, condition, egg size, and senescence. *J Fish Biol* **47**: 1063-1080

Krebs CJ (1978) Ecology. *The Experimental Analysis of Distributon and Abundance*. Harper and Row, New York 678 pp.

Kritzer JP, Davies CR, Mapstone BD (2001) Characterizing fish populations: effects of sample size and population structure on the precision of demographic parameter estimates. *Can J Fish Aquat Sci* **58**: 1557-1568

Kuiter RH (2002) Butterflyfishes, bannerfishes and their relatives - a comprehensive guide to the Chaetodontidae & Microcanthidae. TMC Publishing, Chorleywood, UK 208 pp.

Kulbicki M, Bozec Y-M (2005) The use of butterflyfish (Chaetodontidae) species richness as a proxyof total species richness of reef fish assemblages in the Western and Central Pacific. *Aquatic Conserv: Mar Freshw Ecosyst* **15**: S127-S141

Kuwamura T, Yogo Y, Nakashima Y (1993) Size-assortative monogamy and parental egg care in a coral goby *Paragobiodon echinocephalus*. *Ethology* **95**: 65-75

Laman-Trip E (2004) A multi-scale analysis of population dynamics and life history features in a widely distributed coral reef fish. M.Sc. thesis, School of Marine Biology and Aquaculture, James Cook University, Townsville

Lecchini D, Adjeroud M, Pratchett MS, Cadoret L, Galzin R (2003) Spatial structure of coral reef fish communities in the Ryukyu Islands, southern Japan. *Oceanol Acta* **26**: 537-547

Leis JM, McCormick MI (2002) The biology, behavior, and ecology of the pelagic, larval stage of coral reef fishes. In: Sale PF (ed.) Coral Reef Fishes. Academic Press, San

Diego (pp 171-199)

Levin P (1998) The significance of variable and density-independent post-recruitment mortality in local populations of reef fishes. *Aust J Ecol* **23**: 246-251

Levin P, Petrik R, Malone J (1997) Interactive effects of habitat selection, food supply, and predation on recruitment of an estuarine fish. *Oecologia* **112**: 55-63

Lewis AR (1997) Recuitment and post-recruitment immigration affect the local populations size of coral reef fishes. *Coral Reefs* **16**: 139-149

MacArthur RH (1972) Geographical Ecology. Harper and Row, New York 269 pp.

MacArthur R, Pianka ER (1966) On optimal use of a patchy environment. *Am Nat* **100**: 603-609

MacNally RC (1995) Ecological Versatility and Community Ecology. Cambridge University Press, Cambridge 453 pp.

Martin LB, Pless M, Svoboda J, Wikelski M (2004) Immune activity in temperate and tropical house sparrows: a common-garden experiment. *Ecology* **85**: 2323-2331

Manly BFJ, McDonald LL, Thomas DL (1993) Resource selection by animals. Chapman & Hall, London 176 pp.

Manly BFJ (1997) Randomizations, bootstrap and Monte Carlo methods in biology. Chapman & Hall, London 424 pp.

McClanahan TR, Bergman K, Huitric M, McField M, Elfwing T, Nyström M, Nordemar I (2000) Response of fishes to algae reduction on Glovers Reef, Belize. *Mar Ecol Prog Ser* **206**: 273-282

McCormick MI (2003) Consumption of coral propagules after mass spawning enhances larval quality of a damselfish through maternal effects. *Oecologia* **136**: 37-45

McCormick MI, Hoey AS (2004) Larval growth history determines juvenile growth and survival in a tropical marine fish. *Oikos* **106**: 225-242

Meekan MG, Ackerman JL, Wellington GM (2001) Demography and age structures of coral reef damselfishes in the tropical eastern Pacific Ocean. *Mar Ecol Prog Ser* **212**: 223-232

Mulligan TJ, Leaman BM (1992) Length-at-age analysis: can you get what you see? *Can J Fish Aquat Sci* **49**: 632-643

Munday PL (2001) Fitness consequences of habitat use and competition among coral-dwelling fishes. *Oecologia* **128**: 585-593

Munday PL (2004) Habitat loss, resource specialization, and extinction on coral reefs. *Global Change Biol* **10**: 1642-1647

Munday PL, Jones GP, Caley MJ (1997) Habitat specialisation and the distribution and abundance of coral-dwelling gobies. *Mar Ecol Prog Ser* **152**: 227-239

Munday PL, Wilson SK (1997) Comparative efficacy of clove oil and other chemicals in anaesthetization of *Pomacentrus amboinensis*, a coral reef fish. *J Fish Biol* **51**: 931-938

Munday PL, Jones GP (1998) The ecological implications of small body size among coral-reef fishes. *Oceanogr Mar Biol Ann Rev* **36**: 373-411

Munday PL, Hodges AL, Choat JH, Gust N (2004) Sex-specific effects in growth of protogynous hermaphrodites. *Can J Fish Aquat Sci* **61**: 323-327

Nakano S (1995) Individual differences in resource use, growth and emigration under the influence of a dominance hierarchy in fluvial red-spotted masu salmon in a natural habitat. *J Anim Ecol* **64**: 75-84

Öhman MC, Rajasuriya A (1998) Relationships between habitat structure and fish communities on coral and sandstone reefs. *Environ Biol Fish* **53**: 19-31

Olsen CL (1976) On choosing a test statistic in multivariate analysis of variance. *Pyschol Bull* **83**: 579-586

Pawson MG, Pickett G, Witthames P (2000) The influence of temperature on the onset of first maturity in sea bass. *J Fish Biol* **56**: 319-327

Perry G, Pianka ER (1997) Animal foraging: past, present, and future. *Trends Ecol Evol* **12**: 360-364

Peterson CW, Warner RR (2002) The ecological context of reproductive behavior. In: Sale PF (ed.) Coral Reef Fishes. Academic Press, San Diego (pp 103-118)

Pratchett MS (1995) Spatial distribution, abundance, and diet of butterflyfish (PISCES: Chaetodontidae). Honours Thesis, Marine Biology, James Cook University, Townsville

Pratchett MS (2002) Dynamics of outbreak populations of crown-of-thorns starfish (*Acanthaster planci* L.), and their impacts on coral reef ecosystems. Ph.D. thesis, School of Marine Biology and Aquaculture, James Cook University, Townsville

Pratchett MS (2005) Dietary overlap among coral-feeding butterflyfishes (Chaetodontidae) at Lizard Island, northern Great Barrier Reef. *Mar Biol* **148**: 373-382

Pratchett MS, Gust G, Goby G, Klanten SO (2001) Consumption of coral propagules represents a significant trophic link between corals and reef fish. *Coral Reefs* **20**: 13-17

Pratchett MS, Wilson SK, Berumen ML, McCormick MI (2004) Sublethal effects of coral bleaching on an obligate coral feeding butterflyfish. *Coral Reefs* **23**: 352-356

Pratchett MS, Wilson SK, Baird AH (in press) Declines in the abundance of *Chaetodon* butterflyfishes (Chaetodontidae) following extensive coral depletion. *J Fish Biol* **XXX**: xxx

Pulliam HR (1974) On the theory of optimal diets. *Am Nat* **108**: 59-75

Pyke GH (1984) Optimal foraging theory: a critical review. *Ann Rev Ecol Syst* **15**: 523-575

Ralston S (1976a) Age determination of a tropical reef butterflyfish utilizing daily growth rings of otiliths. *US Fish Bull* **74**: 990-994

Ralston S (1976b) Anomalous growth and reproductive patterns in populations of *Chaetodon miliaris* from Kaneohe Bay, Oahu, Hawaiin Islands. *Pac Sci* **30**: 395-403

Ralston S (1981) Aspects of the reproductive biology and feeding ecology of *Chaetodon miliaris*, A Hawaiian endemic butterflyfish. *Environ Biol Fish* **6**: 167-176

Randall JE (2005) Reef and shore fishes of the South Pacific: New Caledonia to Tahiti and the Pitcairn Islands. University of Hawaii Press, Honolulu 707 pp.

Randall JE, Allen GR, Steene RC (1997) Fishes of the Great Barrier Reef and Coral Sea. Crawford House, Bathurst, Australia 580 pp.

Raubenheimer D, Simpson S (2004) Organismal stoichiometry: quantifying non-independence among food components. *Ecology* **85**: 1203-1216

Reese ES (1975) A comparative field study of the social behaviour and related ecology of reef fishes of the family Chaetodontidae. *Z Tierpsychol* **37**: 37-61

Reese ES (1977) Coevolution of corals and coral feeding fishes of the family Chaetodontidae. 3rd Int Coral Reef Symp **1**: 268-274

Reese ES (1981) Predation on corals by fishes of the family Chaetodontidae: implications for conservation and management of coral reef ecosystems. *Bull Mar Sci* **31**: 594-604

Rikardson AH, Elliott JM (2000) Variations in juvenile growth, energy allocation and life-history strategies of two populations of Arctic charr in North Norway. *J Fish Biol* **56**: 328-346

Roberts CM, Ormond RFG (1987) Habitat complexity and coral reef fish diversity and abundance on Red Sea fringing reefs. *Mar Ecol Prog Ser* **41**: 1-6

Robertson DR (1973) Field observations on the reproductive behaviour of a pomacentrid fish, *Acanthachromis polyacanthus*. *Z Tierpsychol* **32**: 319-324

Robertson DR, Ackerman JL, Choat JH, Posada JM, Pitt J (2005) Ocean surgeonfish *Acanthurus bahianus*. I. The geography of demography. *Mar Ecol Prog Ser* **295**: 229-

244

Russ GR, Lou DC, Higgs JB, Ferreira BP (1998) Mortality rate of a cohort of the coral trout, *Plectropomus leopardus*, in zones of the Great Barrier Reef Marine Park closed to fishing. *Mar Freshw Res* **49**: 507-511

Sale PF (1977) Maintenance of high diversity in coral reef fish communities. *Am Nat* **111**: 337-359

Sano M, Shimizu M, Nose Y (1984) Changes in the structure of coral reef fish communities by destruction of hermatypic corals: observational and experimental views. *Pac Sci* **38**: 51-79

Sano M, Shimizu M, Nose Y (1987) Long-term effects of destruction of hermatypic corals by *Acanthaster planci* infestation of reef fish communities at Iriomote Island, Japan. *Mar Ecol Prog Ser* **37**: 191-199

Schoener TW (1971) Theory of feeding strategies. *Ann Rev Ecol Syst* **2**: 369-404

Shulman MJ (1985) Recruitment of coral reef fishes: effects of distribution of predators and shelter. *Ecology* **66**: 1056-1066

Smith MJ (1979) Optimization theory in evolution. *Ann Rev Ecol Syst* **9**: 31-56

Stephens DW, Krebs JR (1986) Foraging Theory. Princeton University Press, Princeton 262 pp.

Stewart BD, Jones GP (2001) Associations between the abundance of piscivorous fishes and their prey on coral reefs: implications for prey-fish mortality. *Mar Biol* **138**: 383-397

Stobutzki IC (1998) Interspecific variation in sustained swimming ability of late pelagic stage reef fish from two families (Pomacentridae and Chaetodontidae). *Coral Reefs* **17**: 111-119

Sutherland WJ (1987) Why do animals specialize? *Nature* **325**: 483-484

Suzuki K, Tanaka Y, Hioki S (1980) Spawning behaviour, eggs, and larvae of the butterflyfish, *Chaetodon nippon*, in an aquarium. *Japan J Ichthyol* **26**: 334-341

Syms C (1995) Multi-scale analysis of habitat association in a guild of blennioid fishes. *Mar Ecol Prog Ser* **125**: 31-43

Syms C, Jones GP (2000) Disturbances, habitat structure, and the dynamics of a coral-reef fish community. *Ecology* **81**: 2714-2729

Talbot FH (1965) A description of the coral reef structure of Tutia reef and its fish fauna. *Proc Zool Soc Lond* **145**: 431-470

Tricas TC (1989a) Determinants of feeding territory size in the corallivorous butterflyfish, *Chaetodon multicinctus*. *Anim Behav* **37**: 830-841

Tricas TC (1989b) Prey selection by coral-feeding butterflyfishes: strategies to maximise the profit. *Environ Biol Fishes* **25**: 171-185

Tricas TC, Hiramoto JT (1989) Sexual differentiation, gonad development, and spawning seasonality of the Hawaiian butterflyfish, *Chaetodon multicinctus*. *Environ Biol Fish* **25**: 111-124

van Noordwijk AJ, de Jong G (1986) Acquisition and allocation of resources: their influence on life history tactics. *Am Nat* **128**: 137-142

Vincent TLS, Scheel D, Brown JS, Vincent TL (1996) Trade-offs and coexistence in consumer-resource models: It all depends on what and where you eat. *Am Nat* **148**: 1038-1058

von Bertalanffy L (1938) A quantitative theory of organic growth. II: Inquiries on growth laws. *Hum Biol* **10**: 181-213

Warner RR (1998) The role of extreme iteroparity and risk-avoidance in the evolution of mating systems. *J Fish Biol* **53 (Supp. A)**: 82-93

Warner RR, Chesson PL (1985) Coexistance mediated by recruitment fluctuations: A field guide to the storage effect. *Am Nat* **125**: 769-787

Warner RR, Hoffman S (1980) Population density and the economics of territorial defense in a coral reef fish. *Ecology* **61**: 772-780

Webster MS (2002) Role of predators in the early post-settlement demography of coral-reef fishes. *Oecologia* **131**: 52-60

Wellington GM, Victor BC (1985) El Nino mass coral mortality: a test of resource limitation in a coral reef damselfish population. *Oecologia* **68**: 15-19

Williams DM (1986) Temporal variation in the structure of reef slope fish communities (central Great Barrier Reef): short term effects of *Acanthaster planci* infestation. *Mar Ecol Prog Ser* **28**: 157-164

Williams DM (1991) Patterns and processes in the distribution of coral reef fishes. In: Sale PF (ed.) The ecology of fishes on coral reefs. Academic Press, San Diego (pp 437-474)

Wilson SK, Bellwood DR (1997) Cryptic dietary components of territorial damselfishes (Pomacentridae, Labrodei). *Mar Ecol Prog Ser* **153**: 299-310

Wootton R (1990) Ecology of teleost fishes. Fish and fisheries series 1. Chapman and Hall, London 404 pp.

Wootton R (1998) The ecology of teleost fishes. Kluwer, Dordrecht, The Netherlands 392 pp.

Yabuta S (1997) Spawning migrations in the monogamous butterflyfish, *Chaetodon trifasciatus*. *Ichthyol Res* **44**: 177-182

Yabuta S, Kawashima M (1997) Spawning behavior and haremic mating system in the corallivorous butterflyfish, *Chaetodon trifascialis*, at Kuroshima Island, Okinawa. *Ichthyol Res* **44**: 183-188

Yamahira K, Conover DO (2002) Intra- vs. interspecific latitudinal variation in growth: adaptation to temperature or seasonality? *Ecology* **83**: 1252-1262

Yamamoto T (2004) Sex-specific growth pattern during early life history in masu salmon, *Oncorhynchus masou*. *Ecol Freshw Fish* **13**: 203-207

Yearsley JM, Kyriazakis I, Gordon IJ (2004) Delayed costs of growth and compensatory growth rates. *Funct Ecol* **18**: 563-570

Zekeria ZA, Dawit Y, Ghebremedhin S, Naser M, Videler JJ (2002) Resource partitioning among four butterflyfish species in the Red Sea. *Mar Freshw Res* **53**: 163-168

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"Sublethal effects of coral bleaching on an obligate coral feeding butterflyfish"

Effects of resource availability on the competitive behaviour of butterflyfishes (Chaetodontidae)

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Recovery without resilience: persistent disturbance and long-term shifts in the structure of fish and coral communities at Tiahura Reef, Moorea

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