Within-reef differences in diet and body condition of coral-feeding butterflyfishes (Chaetodontidae)

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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. This study compared the abundance, feeding and condition of 2 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 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 worse 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.

KEY WORDS: Competition · Coral reef fish · Feeding preferences · Hepatocyte vacuolation · Physiological body condition · Prey selection

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 & Williams 1988, Hixon & 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 (<1 km), 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 & McCormick 2002). However, very few studies (Holbrook & Schmitt 1986, Munday 2001) have considered

ecological or fitness consequences for fishes living in different reef habitats.

Habitat requirements of coral reef fishes 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 & Galzin 1984, Munday et al. 1997, Holbrook et al. 2000), and/or the diversity of corals (Chabanet et al. 1997, Cadoret et al. 1999). Such associations arise because scleractinian corals are fundamental in providing living space and shelter for coral reef fishes (Holbrook et al. 2000, Syms & Jones 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 fishes. Both local and regional scale patterns in the abundance of butterflyfishes have been related to variation in live coral cover (Birkeland & Neudecker 1981, Bouchon-Navaro et al. 1985, Findley & Findley 1985, Bouchon-Navaro & 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 butterflyfishes 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 a wide variety of fishes (e.g. Green & 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 was 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 was 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.

MATERIALS AND METHODS

Sampling locations and study species. This study was conducted between January and April 2000 at Lizard Island (14° 40' S, 145° 27' E) on the northern Great Barrier Reef, Australia (Fig. 1). Sampling was conducted at 4 different locations, representative of 2 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. Front-reef locations comprise
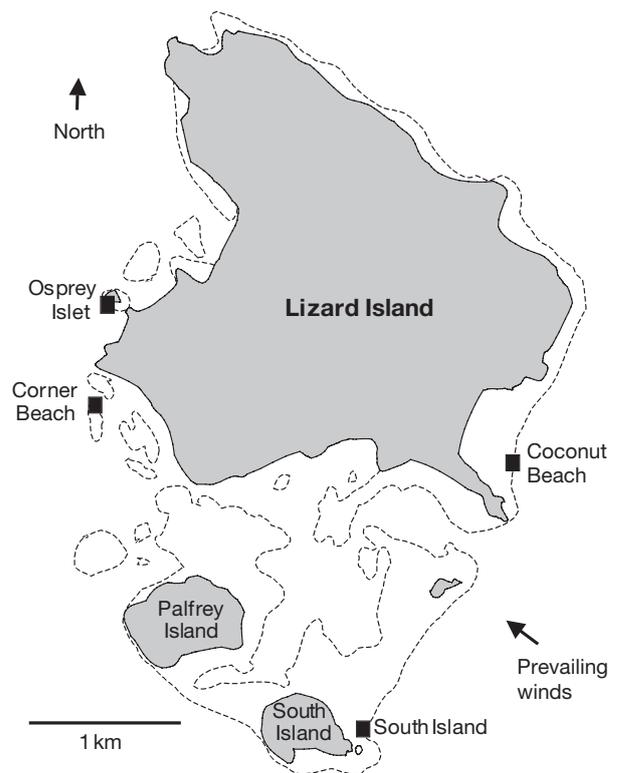
Fig. 1. *Chaetodon* species. Locations used for the study of abundance patterns and physiological condition at Lizard Island, Great Barrier Reef. South Island and Coconut Beach represent front-reef habitats directly exposed to the prevailing southeast trade winds, whereas Corner Beach and Osprey Islet represent back-reef and relatively sheltered habitats. ---- indicate the approximate reef outline

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 to 5 m depth). In back-reef locations, the reef was comprised of large patch reefs (200 to 300 m in diameter), separated by wide expanses of open sand. Here, sampling was conducted on the tops of patch reefs (3 to 6 m depth).

This study considered 2 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* spp. butterflyfishes among locations, we used 50×4 m visual belt transects. Ten replicate 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 spp. 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 the ANOVA assumption of homogeneity of variances. All statistical procedures were conducted using SPSS 11.0.

Feeding behaviour of butterflyfishes. The range of prey types consumed by *Chaetodon 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 3 min, recording the total number of bites taken from each different coral species (see Table 1). Feeding observations were conducted throughout the day, from 06:00 to 18:00 h. 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 (06:00 to 10:00 h), at mid-day (10:00 to 14:00 h) and in the afternoon (14:00 to 18:00 h) 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 (χ^2_{L2}), calculated using the formula:

$$\sum\nolimits^2_{L2} = 2 \sum_{j=1}^{n} \sum_{i=1}^{I} u_{ij} \ln [u_{ij} / \mathrm{E}(u_{ij})]$$

where u_{ij} is the proportional use of each prey type (i) by each individual (j) and $\mathrm{E}(u_{ij})$ 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 χ^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 (*Chaetodon 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 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:

$$w_i = u_i / p_i$$

which compares the proportional use (u_i) of each prey category (i) with the proportional availability of that prey category (p_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 10 replicate 10 m 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.

Physiological condition of butterflyfishes. To test for spatial variation in the physiological condition of *Chaetodon 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 10:00 and 14:00 h and kept on ice for 1 to 3 h before processing. The physiological condition of individual butterflyfishes 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 favoured 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 & McCormick 1999, Pratchett et al. 2004).

To measure hepatocyte vacuolation in *Chaetodon baronessa* and *C. lunulatus*, the entire liver from each fish was removed and placed into 10% calcium-buffered formalin (FAACC) for 4 d. After fixing, hepatic tissues were dehydrated in a graded ethanol series and embedded in paraffin wax. Wax blocks of hepatic tissues were sectioned at 5 μm, 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 3 different sections through the different parts of the liver of each fish, giving a total of 9 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.

RESULTS

Coral cover and composition

The abundance and composition of scleractinian corals varied greatly among the 4 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 (Fig. 2). However, there were also large differences in the coral communities between the 2 back-reef locations. Many of the corals surveyed (32/56 species) were found at all 4 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 1 coral species that was reasonably abundant at all 4 locations was *Pocillopora damicornis*.

Abundance of butterflyfishes

Despite significant differences in the abundance and composition of prey corals, mean densities of *Chae-*
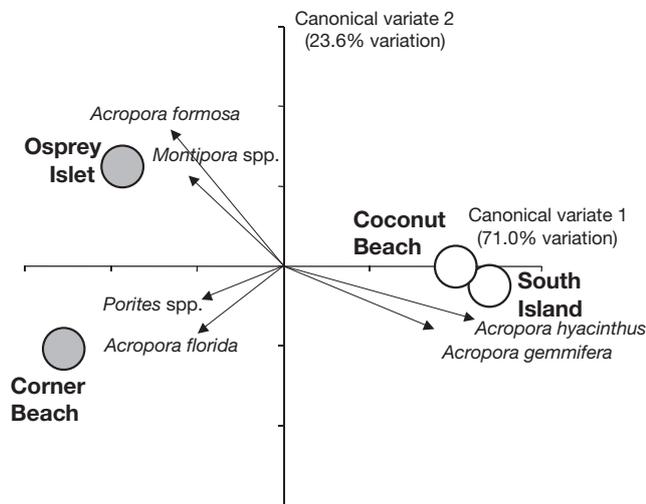
Fig. 2. Scleractinian corals. Comparison of community structure among locations (South Island, Coconut Beach, Osprey Islet, Corner Beach). Results show a canonical discriminant analysis comparing mean coral assemblages. Circles plotted represent 95% confidence limits around centroids for each location. ○: front-reef locations; ◐: back-reef locations. Vectors are structural coefficients of response variables, indicating the relative abundance of main coral species among the 4 locations

todon baronessa and *C. lunulatus* varied very little among the 4 locations. Overall, the mean density of *C. baronessa* was 1.14 ± 0.67 SE ind. 200 m^{-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 ind. 200 m^{-2} across all locations. As for *C. baronessa*, 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 2 study species (*Chaetodon baronessa* and *C. lunulatus*), the abundance of congeners varied greatly among the 4 locations. Mean densities of butterflyfishes were very similar for the 2 front-reef locations, South Island (17.2 ± 2.3 SE fish 200 m^{-2}) and Coconut Beach (18.7 ± 2.2 SE fish 200 m^{-2}). However, densities of butterflyfishes at the front-reef locations were more than double those at the back-reef locations; Osprey Islet (8.0 ± 0.9 SE fish 200 m^{-2}) and Corner Beach (8.5 ± 1.4 SE fish 200 m^{-2}). Spatial variation in the total densities of butterflyfishes resulted primarily from differences in the abundance of *C. citrinellus*, which was 5 to 6 times more abundant at exposed locations than at back-reef locations. Moreover, there were 3 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.

Feeding behaviour of butterflyfishes

Chaetodon 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 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). *C. baronessa* exhibited particularly strong selectivity (especially at front-reef locations) and tended to feed predominantly on just 1 or 2 different coral species at each location (Fig. 3). At South Island, *C. baronessa* consumed 18 different coral species (Table 1), but 87.6% of all bites were taken from *Acropora hyacinthus*. At Coconut Beach, *C. baronessa* consumed 24 different coral species; nevertheless, 75.7% of bites were still taken from *A. hyacinthus*

(Fig. 3). The predominance 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).

Compared to front-reef locations, at back-reef locations (where *Acropora hyacinthus* was scarce), *Chaetodon baronessa* consumed a wider range of different coral species (Table 1) and was less selective in its choice of prey (Table 2). Even so, *C. baronessa* tended to feed predominantly on just 1 or 2 different coral species. At Osprey Islet, *C. baronessa* consumed 32 different coral species, but 44% of bites were taken from *Pocillopora damicornis* (Fig. 3). In the absence of *A. hyacinthus*, *C. baronessa* selectively consumed *P. damicornis* over most other coral species (Table 2). At Corner Beach, *C. baronessa* consumed both *P. damicornis* and *A. florida* in approximately equal proportions (Fig. 3). Both these coral species were consumed in greater proportions than expected from their availability, as were *Galaxea* spp. (Table 2).

The dietary composition of *Chaetodon lunulatus* also differed among locations, but *C. lunulatus* used many different coral species (between 29 and 33 species) at every location (Table 1) and was less selective than *C. baronessa* (Table 2). At South Island, *C. lunulatus* consumed mainly *Acropora hyacinthus*, taking 38% of all bites from this 1 coral species (Fig. 4). However, electivity indices revealed that *C. lunulatus* was not feeding on *A. hyacinthus* in greater proportions than it was available (Table 2). At Coconut Beach, *C. lunulatus* consumed *A. hyacinthus* in lower proportions than expected from its relative abundance (Table 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) were massive *Porites* spp. (Table 2). At back-reef locations (Osprey Islet and Coconut Beach), *C. lunulatus* consumed several different coral species (*A. intermedia, Pocillopora 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 (Fig. 2) and was the main coral eaten by *C. lunulatus* at this location (Fig. 4).

Despite differences in dietary composition, the mean rate of feeding for both *Chaetodon baronessa* and *C. lunulatus* was remarkably constant among locations. Bite rates were highly variable among individuals. For example, the bite rates of *C. baronessa*

Table 1. *Chaetodon baronessa* and *C. lunulatus*. Range of prey categories used by the 2 butterflyfish species at each location (South Island, Coconut Beach, Osprey Islet and Corner Beach). Prey categories used by each butterflyfish at each location are indicated by +

Prey category	*Chaetodon baronessa*				*Chaetodon lunulatus*			
	South Island	Coconut Beach	Osprey Islet	Corner Beach	South Island	Coconut Beach	Osprey Islet	Corner Beach
ACROPORIDAE								
Acropora cytherea	+				+			
A. digitifera	+				+	+		
A. donei				+		+		
A. florida	+	+	+	+	+	+	+	+
A. formosa	+	+	+		+	+	+	
A. gemmifera	+	+	+		+	+	+	+
A. grandis			+	+		+	+	
A. humilis	+	+	+	+	+	+		+
A. hyacinthus	+	+			+	+		
A. intermedia			+	+	+	+	+	+
A. loripes				+			+	+
A. millepora	+	+	+		+	+	+	+
A. monticulosa					+	+		
A. nasuta		+	+	+	+	+	+	+
A. robusta	+	+	+		+	+		
A. sarmentosa			+	+			+	+
A. secale		+		+	+	+	+	
A. selago			+		+	+		+
A. valida	+	+	+	+	+	+		
Astreopora spp.			+		+		+	
Isopora spp.	+	+	+	+	+	+	+	+
Montipora spp.		+	+	+	+	+	+	+
POCILLOPORIDAE								
Pocillopora damicornis	+	+	+	+	+	+	+	+
P. eydouxi	+	+			+	+		
P. verrucosa	+	+	+	+	+	+	+	
Seriatopora hystrix			+	+	+		+	+
Stylophora pistillata	+	+	+	+	+	+	+	+
FAVIIDAE								
Cyphastrea seriala					+		+	
Diploastrea heliopora		+		+				
Favia favus			+			+		+
F. pallida		+		+				+
F. speciosa						+	+	
F. stelligera					+			
Favites abdita	+	+	+		+	+		+
F. halicora					+	+	+	
Goniastrea retiformes		+	+	+	+	+	+	+
Leptastrea transversa			+				+	
Leptoria phrygia	+		+			+		+
Montastrea spp.				+				+
Platygyra daedalea				+			+	+
P. sinensis			+					
P. 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**

Table 2. *Chaetodon baronessa* and *C. lunulatus*. Patterns of feeding selectivity. Both species of butterflyfish exhibited significant feeding selectivity (χ^2_{L2}) at all locations (p < 0.01). +: corals used significantly more than expected; –: corals used significantly less than expected; 0: corals that were used in approximate accordance with their availability; NU: not used; NA: not available

	χ^2_{L2}	Acropora florida	A. formosa	A. gemmifera	A. hyacinthus	A. intermedia	Pocillopora damicornis	Isopora spp.	Montipora spp.	Galaxea spp.	Porites spp.
C. baronessa											
South Island	6.9×10^3	0	0	–	+	NU	0	0	NU	NA	NU
Coconut Beach	6.3×10^3	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	–	+	–
C. lunulatus											
South Island	3.2×10^3	0	0	0	0	0	0	+	0	NA	+
Coconut Beach	2.9×10^3	–	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	+

ranged from 81 bites to a low of just 11 bites during the 3 min observation periods. The mean bite rates of *C. baronessa* were slightly higher at South Island (41.29 ± 2.1 SE bites 3 min⁻¹) and at Osprey Islet (40.47 ± 2.0 SE bites 3 min⁻¹) compared to Coconut Beach (34.42 ± 1.9 SE bites 3 min⁻¹) and Corner Beach (34.72 ± 1.9 SE bites 3 min⁻¹). 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
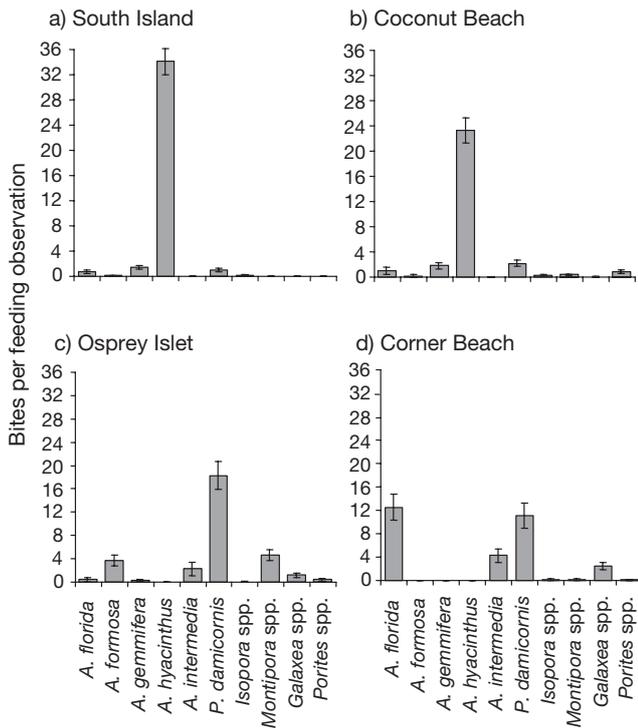
Fig. 3. *Chaetodon baronessa*. Comparison of dietary composition among 4 locations: (a,b) front-reef, (c,d) back-reef. Data presented are the mean number of bites (±SE) per 3 min observation on each of 10 dominant coral species, including 5 *Acropora* species and 1 *Pocillopora* species (n = 50 observations per location)
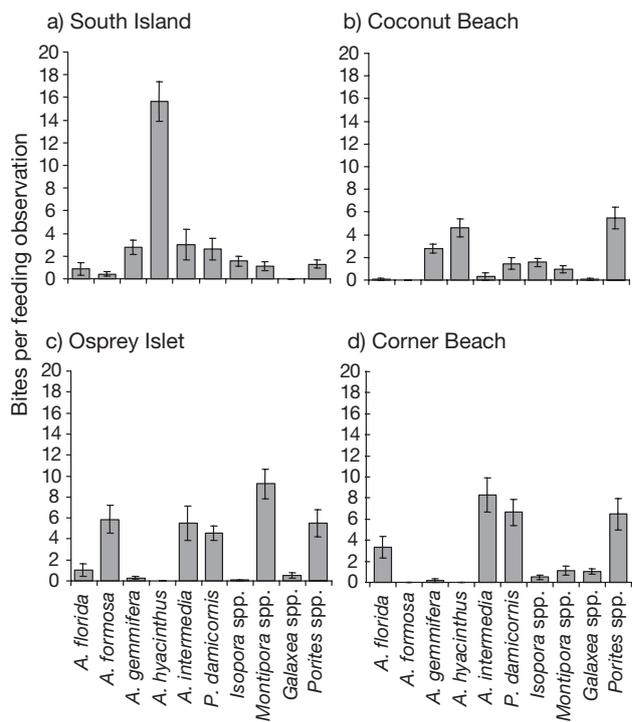
Fig. 4. *Chaetodon lunulatus*. Comparison of dietary composition among 4 locations: (a,b) front-reef, (c,d) back-reef. Data presented are the mean number of bites (±SE) per 3 min observation on each of 10 dominant coral species, including 5 *Acropora* species and 1 *Pocillopora* species (n = 50 observations per location)

a) *Chaetodon baronessa*

b) *Chaetodon lunulatus*
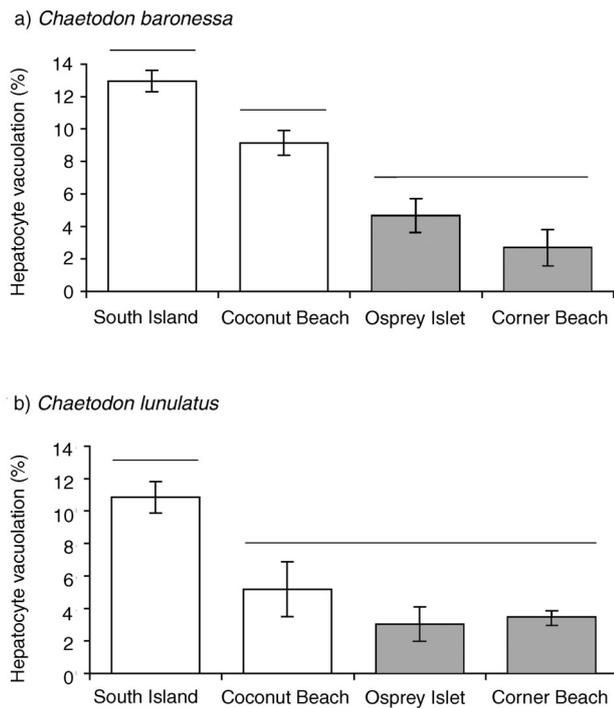
Fig. 5. *Chaetodon baronessa* and *C. lunulatus.* Comparison of hepatocyte vacuolation for (a) *Chaetodon baronessa* and (b) *C. lunulatus* among 4 different locations. Data presented are the mean proportion of hepatocyte vacuoles in cross-sections through the liver of 20 replicate fish (±SE). White bars indicate front-reef locations and grey bars indicate back-reef locations. Horizontal lines represent homogeneous subsets identified by Tukey's HSD post-hoc test

day (ANOVA, $F = 0.97$, df = 2,196, p = 0.42). A comparison between butterflyfish species revealed that *C. baronessa* tended to feed at a higher rate (34.12 ± 1.1 SE bites 3 min^{-1}) than *C. lunulatus* (28.73 ± 1.2 SE bites 3 min^{-1}) and feeding rates of *C. lunulatus* were also more variable. Bite rates for *C. lunulatus* ranged from 97 bites to just 1 bite during the 3 min 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 ± 1.7 SE bites 3 min^{-1}) than at South Island (40.88 ± 2.7 SE bites 3 min^{-1}), Osprey Islet (38.86 ± 2.6 SE bites 3 min^{-1}) and Corner Beach (31.46 ± 2.0 SE bites 3 min^{-1}).

Physiological condition

In accordance with differences in dietary composition, physiological condition, as measured by hepatocyte vacuolation, differed significantly among locations for both *Chaetodon 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 (Fig. 5). However, there was also a difference between the 2 front-reef locations, with *C. baronessa* collected from South Island having a greater proportion of hepatocyte vacuoles than individuals from Coconut Beach (Fig. 5). There was no consistent pattern of variation in hepatocyte vacuolation between front-reef and back-reef habitats for *C. lunulatus* (Fig. 5). Rather, at South Island, *C. lunulatus* had much higher levels of hepatocyte vacuolations compared to individuals collected from all other locations (Fig. 5).

DISCUSSION

The size of reef fish populations often varies in accordance with spatial variation in coral abundance and composition (e.g. Bell & Gazlin 1984, Bouchon-Navaro et al. 1985, Munday et al. 1997, Holbrook et al. 2000), particularly for coral-feeding butterflyfishes (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 neither *Chaetodon baronessa* nor *C. lunulatus* varied between front-reef and back-reef locations, despite a 2-fold difference in the abundance of scleractinian coral, as well as significant variation in the composition of coral communities (see also Bell et al. 1985, Roberts & 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). In addition, 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 & Victor 1985, Doherty & 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 *Chaetodon 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 2 yr (2000 to 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, together 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 a major determinant of individual fitness in fishes, affecting growth, survivorship and reproductive success (Jones & 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 (Wooten 1990) and also affects the viability of offspring (McCormick 2003). The quality and quantity of prey resources are 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 & McCormick 2002).

Variation in the physiological condition of *Chaetodon baronessa* and *C. lunulatus* (among locations) appeared to be related to differences in the composition of coral communities, more than to differences in mean coral abundance. Feeding rates of *C. baronessa* and *C. lunulatus* varied very little among the 4 locations, suggesting that there must have been sufficient coral at every location to meet basic dietary requirements (sensu Tricas 1989). However, differences in dietary composition are likely to have had major effects on the energetic intake of butterflyfishes in different locations (Birkeland & Neudecker 1981, Tricas 1989). 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 1989). For both *C. baronessa* and *C. lunulatus*, physiological condition improved with increased consumption of *Acropora hyacinthus*. Although the nutritional quality of this coral species has never been tested, these findings suggest 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 in very low quantities (1 small colony in 10 replicate 10 m 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 & Krebs 1986, Bruggemann et al. 1994, Green & 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 & 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 *E. jacksoni* 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 & Bouchon 1981). At Lizard Island, densities of *Chaetodon* spp. butterflyfishes and also the intensity of inter-specific competition among *Chaetodon* species have been shown to be highest at front-reef locations (M. S. Pratchett & M. L. Berumen unpubl. data). Therefore, if competition did have an important influence on the condition of butterflyfish populations in the 2 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 *Chaetodon baronessa* and *C. lunulatus* fed mainly on the tabulate coral, *Acropora 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 (M. S. Pratchett & M. L. Berumen unpubl. data), 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. *C. 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 ± 0.4 SE fish 200 m^{-2}), compared to South Island (0.6 ± 0.3 SE fish 200 m^{-2}), corresponding with lower consumption of *A. hyacinthus* by both *C. lunulatus* and *C. baronessa*. We, therefore, suggest 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* spp. 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 & McCormick 2002). In this study, we show significant variation in the physiological condition of coral-feeding butterflyfishes 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 fishes may exist as a consequence of differences in habitat and that these differences are not necessarily reflected in population size.

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