THE RAFFLES BULLETIN OF ZOOLOGY 2007 Supplement No. **14**: 171-176
Date of Publication: 31 Jan.2007
© Academia Sinica and National University of Singapore

DIETARY SELECTION BY CORAL-FEEDING BUTTERFLYFISHES (CHAETODONTIDAE) ON THE GREAT BARRIER REEF, AUSTRALIA

Morgan S. Pratchett
ARC Centre of Excellence for Coral Reef Studies,
James Cook University, Townsville, Q4811, Australia.
Email: morgan.pratchett@jcu.edu.au

***ABSTRACT.* –** This study explored dietary selection among 14 species of coral-feeding butterflyfishes at Lizard Island, in the Northern Great Barrier Reef, Australia. All 14 butterflyfishes studied (*Chaetodon aureofasciatus*, *C. baronessa*, *C. citrinellus*, *C. kleinii*, *C. lunula*, *C. lunulatus*, *C. melannotus*, *C. plebeius*, *C. rafflesii*, *C. rainfordi*, *C. speculum*, *C. trifascialis*, *C. ulietensis* and *C. unimaculatus*) exhibited significant dietary selection, consuming one or more coral species disproportionately to their availability. The most selective of these butterflyfishes was *C. trifascialis*, which selectively consumed *Acropora* corals (especially *A. hyacinthus*) to the exclusion of all other prey corals. There were notable differences in the degree of selectivity exhibited among coral-feeding butterflyfishes, but there was a high degree of concordance in their apparent feeding preferences. Notably, most coral-feeding butterflyfishes predominantly selected *A. hyacinthus* and secondarily *Pocillopora damicornis*. Observed selectivity in the dietary habits of coral-feeding butterflyfishes may influence their spatial and temporal patterns of abundance and is likely to be fundamental in determining their responses to major disturbances (e.g., climate-induced coral bleaching), which alter the availability of different corals.

***KEY WORDS.* –** *Chaetodon*, coral reef fishes, feeding preferences, selectivity.

INTRODUCTION

Butterflyfishes (family Chaetodontidae) are an important component of the ichthyofauna of tropical coral reefs as they are among the few taxa specialised to feed on scleractinian corals (Glynn, 1990). Butterflyfishes, as a whole, consume a wide range of different prey, including algae, scleractinian and alcyonacean corals, hydrozoans, sponges, polychaetes and crustaceans. However, most species feed primarily, if not exclusively, on scleractinian corals (e.g., Anderson et al., 1981; Harmelin-Vivien & Bouchan-Navaro, 1983; Pratchett, 2005). Despite their predilection for scleractinian corals, very few studies have explored specific prey preferences of coral-feeding butterflyfishes. Rather, most studies (e.g., Harmelin-Vivien & Bouchon-Navaro, 1983; Bouchon-Navaro, 1986; Sano, 1989; Pitts, 1991; Zekeria et al., 2002) have treated all scleractinian corals as a single prey category and categorised butterflyfishes as either: 1) obligate coral feeders, which feed exclusively on scleractinian corals; 2) facultative coral feeders, which feed mainly on scleractinian corals, but supplement their diets with other sessile invertebrates (e.g. alcyonaceans) or; 3) non-coral feeders, which never or very rarely consume scleractinian corals.

The few studies that have explored specific prey preferences of coral-feeding butterflyfishes have shown that these fishes may be very selective in their choice of coral prey, consuming only a limited range of different coral species (Gore, 1984; Irons, 1989; Tricas, 1989; Cox, 1994; Berumen et al., 2005; Pratchett, 2005). *Chaetodon trifascialis*, for example, feeds almost exclusively on *Acropora hyacinthus*, even when a wide variety of other coral prey are available (Irons, 1989; Pratchett 2005). Selective consumption of certain corals by coral-feeding butterflyfishes is potentially very important because the availability of preferred prey may determine their distribution and abundance. Further, the specific feeding preferences of coral-feeding butterflyfishes may influence their responses to major disturbance events (e.g., climate-induced coral bleaching) that cause extensive depletion of corals (Pratchett et al., 2004).

The purpose of this study is to test whether coral-feeding butterflyfishes selectively target certain coral species and compare selectivity among co-existing species. The dietary composition of coral-feeding butterflyfishes may be influenced by variation in the relative abundance of different prey species and/or specific prey preferences of individual fishes. Past studies have shown that coral feeding butterflyfishes feed predominantly on highly abundant coral species, such as *A. hyacinthus* and *Pocillopora damicornis* (Pratchett, 2005). This study will compare the proportional

Table 1. Dietary selectivity of 14 species of coral-feeding butterflyfishes. The significance of selectivity (p) was ascertained by comparing overall levels of selectivity (C^2_{L2}) to a chi-square distribution with n(I-1) degrees of freedom, where I was the total number of prey types utilised across all replicate butterflyfish of each species.

Species	Number of Individuals Observed	X^2_{L2}	p
Hard-coral feeders			
Chaetodon aureofasciatus	35	5.53×10^{03}	< 0.001
Chaetodon baronessa	152	6.11×10^{04}	< 0.001
Chaetodon lunulatus	146	2.42×10^{04}	< 0.001
Chaetodon plebeius	105	1.29×10^{04}	< 0.001
Chaetodon rainfordi	33	2.94×10^{03}	< 0.001
Chaetodon trifascialis	71	1.37×10^{05}	< 0.001
Generalists			
Chaetodon citrinellus	114	1.05×10^{04}	< 0.001
Chaetodon kleinii	94	8.07×10^{03}	< 0.001
Chaetodon lunula	28	8.78×10^{02}	< 0.001
Chaetodon rafflesii	30	2.07×10^{03}	< 0.001
Chaetodon speculum	24	1.32×10^{03}	< 0.001
Soft-coral feeders			
Chaetodon melannotus	37	4.46×10^{03}	< 0.001
Chaetodon ulietensis	30	1.91×10^{03}	< 0.001
Chaetodon unimaculatus	31	3.75×10^{03}	< 0.001

consumption of different corals with their relative abundance in the local environment, providing an indication as to whether butterflyfishes actually target or actively avoid particular coral species, following Manly et al. (1993).

MATERIALS AND METHODS

Study site and species. – This study was conducted at North Reef, on the Northern-most tip of Lizard Island (14°40'S 145°27'E) in the far Northern section of the Great Barrier Reef (GBR), Australia. The butterflyfish assemblage at this location comprised a total of 24 species, of which 14 species (*Chaetodon aureofasciatus*, *C. baronessa*, *C. citrinellus*, *C. kleinii*, *C. lunula*, *C. lunulatus*, *C. melannotus*, *C. plebius*, *C. rafflesi*, *C. rainfordi*, *C. speculum*, *C. trifascialis*, *C. ulientensis* and *C. unimaculatus*) consume scleractinian corals (Pratchett, 2005) and will be considered in this study. *Chaetodon aureofasciatus*, *C. baronessa*, *C. lunulatus*, *C. plebius*, *C. rainfordi* and *C. trifascialis* feed almost exclusively on scleractinian corals, while *C. citrinellus*, *C. kleinii*, *C. lunula*, *C. rafflesi* and *C. speculum* are generalist feeders, which feed mainly on scleractinian corals, but also consume other non-coral invertebrates (Pratchett, 2005). *Chaetodon melannotus*, *C. ulientensis* and *C. unimaculatus* feed predominantly on scleractinian corals, but also take a significant proportion of bites from alcyonacean ('soft') corals (Pratchett, 2005).

Feeding observations. – The proportional use of different coral species by each of the 14 species of butterflyfishes was ascertained from field observations of randomly selected individuals. Feeding observations were conducted throughout the day (from 0600 to 1800 hours) and on four separate occasions throughout a 13 month period (from January 1995 to February 1996). During feeding observations, individual butterflyfish were followed for 3 minutes from a distance of 2 - 3 metres, whilst recording the total number of bites taken from each species of scleractinian coral or any other sessile invertebrates, such as alcyonaceans or hydroids. A total of 930 feeding observations were conducted across all 14 species of coral-feeding butterflyfishes, with at least 30 (and up to 152) replicate observations for each species (see Table 1).

To test whether butterflyfishes exhibit significant feeding selectivity, data was pooled across replicate individuals of each species. The proportional use of different coral species was then compared to the proportional availability of different coral species in the local environment. The relative abundance of different coral species was assessed using replicate 10 m line intercept transects, following Hughes et al. (1999). Each transect was orientated parallel to the reef crest and run from an arbitrarily selected starting point within each zone. Thirty replicate transects were run at each of two different depths (3 m and 7 m) at the beginning (January 1995) and end (February 1996) of the study. This is to account for changes in the relative abundance of different corals. However, there was very little change in the overall abundance of corals or relative abundance of specific prey types, so data was pooled across the two sampling periods, giving a total of 120 replicate transects.

Dietary selectivity of coral-feeding butterflyfishes was analysed using the log-likelihood statistic (C^2_{L2}), calculated using the formula:

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

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). Resource selection functions (Manly et al., 1993) were then used to determine which coral species were used more or less frequently than expected (from their availability) by each species of butterflyfish. To aid in

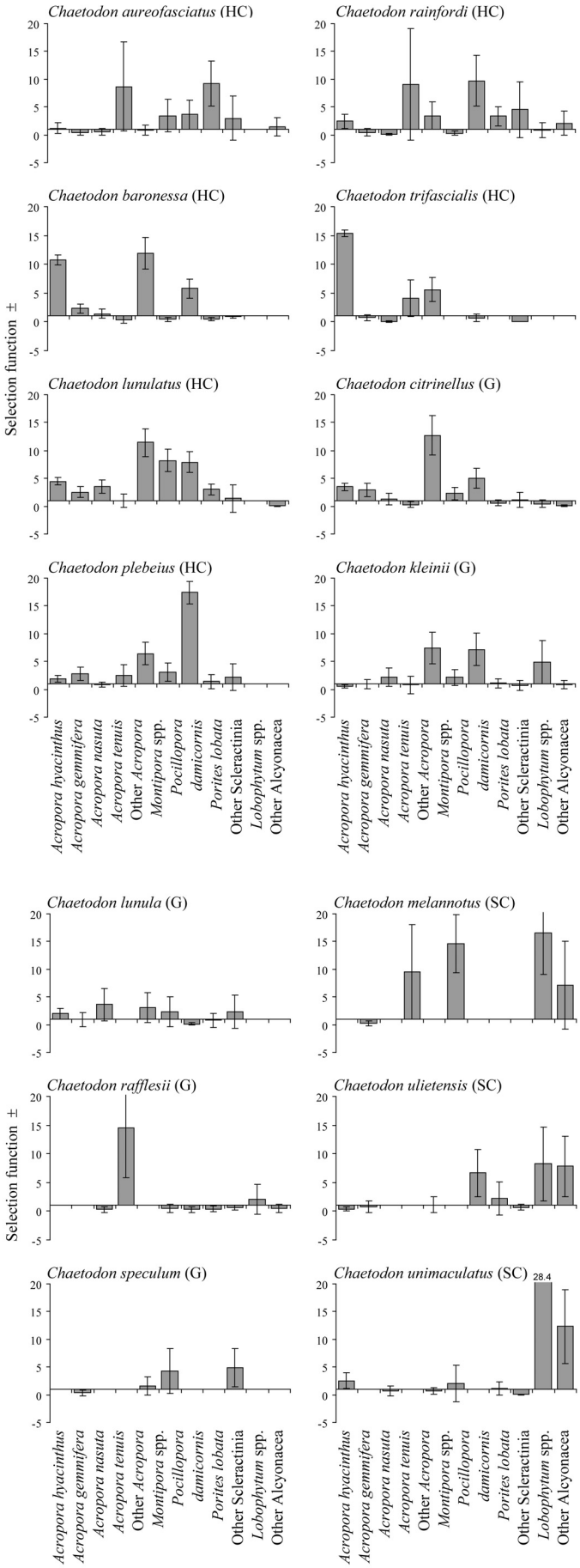

Fig. 1. Dietary selection by 14 species of coral-feeding butterflyfishes. Selection functions significantly greater than 1 indicated that corals were used more than expected from their availability (i.e. selected), while selection functions less than 1 indicated that corals were used less than expected (i.e. avoided). HC = hard-coral feeders; G = generalists; SC = soft-coral feeders.

interpretation of selection functions, Bonferroni corrected 95% confidence intervals were calculated around each selection function and the use of each coral species was only deemed to be disproportionate to its availability if the 95% confidence interval did not encompass 1 (Manly et al., 1993).

RESULTS

The 14 species of butterflyfishes considered in this study (*Chaetodon aureofasciatus*, *C. baronessa*, *C. citrinellus*, *C. kleinii*, *C. lunula*, *C. lunulatus*, *C. melannotus*, *C. plebeius*, *C. rafflesi*, *C. rainfordi*, *C. speculum*, *C. trifascialis*, *C. ulientensis* and *C. unimaculatus*) were seen to consume a total of 89 prey types, including more than 72 species of scleractinian corals. Log-likelihood statistics revealed that all 14 species of butterflyfishes exhibited significant selectivity in their patterns of feeding. *Chaetodon trifascialis* exhibited the greatest feeding selectivity (Table 1), consuming *Acropora hyacinthus* to the exclusion of almost all other scleractinian corals (Fig. 1). *Chaetodon baronessa* also exhibited very high feeding selectivity and selectively consumed *Acropora* corals (especially *A. hyacinthus*) and *Pocillopora damicornis*. In all, most of the exclusive hard-coral feeders (all except *C. aureofasciatus*) consumed *A. hyacinthus* and *P. damicornis* disproportionately to their availability (Table 1 & Fig. 1).

The generalist feeders (*C. citrinellus*, *C. kleinii*, *C. lunula*, *C. rafflesi* and *C. speculum*) and soft-coral feeders (*C. melannotus*, *C. ulientensis* and *C. unimaculatus*) were much less selective compared to those species which fed exclusively on scleractinian corals, but they still exhibited significant feeding selectivity (Table 1). *Chaetodon citrinellus* consumed *A. hyacinthus*, *A. gemmifera*, other *Acropora* spp. and *P. damicornis* disproportionately more than expected from their availability, while *C. kleinii* consumed several species of *Acropora* as well as *P. damicornis* much more than expected (Fig. 1). *Chaetodon rafflesi* exhibited very high selectivity for *A. tenuis* (Fig. 1). Not unexpectedly, the soft-coral feeders, *C. melannotus*, *C. ulietensis* and *C. unimaculatus*, consumed the soft coral, *Lobophytum* spp. and/or other alcyonaceans in much higher proportions than they were available (Fig. 1). For example, *C. unimaculatus* took > 49% of bites from the soft-coral, *Lobophytum* spp., though it accounted for < 2% of coral cover at North Reef.

DISCUSSION

Many previous studies on the feeding habits of coral-feeding butterflyfishes (Harmelin-Vivien & Bouchon-Navaro, 1983; Bouchon-Navaro, 1986; Sano, 1989; Pitts, 1991; Zekeria et al., 2002) have lumped all corals into a single dietary category, implicitly assuming that butterflyfishes do not discriminate between different coral species. In contrast, this study has shown that coral-feeding butterflyfishes are highly selective in their feeding, using prey corals disproportionately to their availability. Interestingly, this study showed that some species are highly specialised, while others are much more generalist. *Chaetodon trifascialis* was the most specialised species, selectively targeting *Acropora hyacinthus* and some other *Acropora* spp. Meanwhile, *C. lunula* was the least selective and consumed a wide range of different coral prey, mostly in accordance with their availability (Fig. 1). These differences in feeding selectivity may reflect individualistic responses of butterflyfishes, whereby certain butterflyfishes are morphologically adapted to feed on a narrower range of different prey corals (Motta, 1988). It also implies that inter-specific competition among butterflyfishes may determine accessibility to preferred prey corals, whereby specialisation is related to competitive dominance, as was suggested by Pratchett (2005).

Coral-feeding organisms (including butterflyfishes, *Acanthaster planci* and *Drupella* spp.) often exhibit significant feeding selectivity (e.g., Irons, 1989; Tricas, 1989; Keesing, 1990), but the underlying basis of these prey preferences is still not known. Similarities in dietary preferences among coral-feeding butterflyfishes may suggest that most preferred coral species, such as *A. hyacinthus* and *Pocillopora damicornis*, have the highest nutritional quality or provide the greatest energetic return. However, previous studies (e.g., Tricas, 1985; Keesing, 1990; Pratchett, 1995) have failed to relate the feeding preferences of coral-feeding butterflyfishes to the nutritional value of different prey corals. Tricas (1985) examined the calorific content of different coral species in Hawaii and found little correlation between prey preferences of coral-feeding butterflyfishes and the nutritional content of different coral species. Similarly, Keesing (1990) found that feeding preferences of *Acanthaster planci* were not consistent with differences in the nutritional value of different prey corals.

Aside from nutritional quality, patterns of prey preferences exhibited by coral-feeding butterflyfishes may be structured by: 1) differences in the morphology of corals, with certain corals being easier to feed upon (Tricas, 1989); 2) variation in the physical defences of corals, such as the size and density of nematocysts (Tricas, 1989; Gochfeld, 2004) or; 3) the presence of feeding deterrents in less preferred coral species (Alino et al., 1988). The restricted range of prey types consumed by butterflyfishes may also reflect niche contraction, which has occurred over evolutionary time to reduce inter-specific competition and promote coexistence among sympatric species (sensu Schoener, 1974). In Hawaii, Cox (1994) showed that patterns of resource use of butterflyfishes in the field were different from those observed in the laboratory (in the absence of congeners), suggesting that normal patterns of prey use may be constrained by inter-specific competition. Further, Cox (1994) showed that sympatric butterflyfishes often exhibit highly complementary patterns of dietary selectivity. For example, in Kaneohe Bay, Hawaii, the two most abundant coral-feeding butterflyfishes (*C. unimaculatus* and *C. lunulatus*) each fed on a different coral species (*Montipora verrucosa* and *Porites compressa*, respectively) (Cox, 1994).

However, at Lizard Island, all coral-feeding butterflyfishes exhibited highly convergent patterns of prey preference,

selecting *A. hyacinthus* and/or *P. damicornis*, which is contrary to expectations of niche partitioning (Pratchett, 2005). In this situation, the high diversity and heterogeneous distribution of prey corals may prevent dominant species from monopolising access to preferred prey types, resulting in incomplete competitive exclusion and enabling coexistence of coral-feeding butterflyfishes with highly convergent prey preferences (Pratchett, 2005).

Given very strong and highly convergent patterns of prey preferences observed among coral-feeding butterflyfishes, it is possible that butterflyfishes may significantly affect the condition, growth, survivorship and/or reproductive output of preferred prey corals. In the past, it was believed that feeding by coral-feeding butterflyfishes was spread over a sufficiently large number of different coral colonies from many different species, such that effects of feeding on individual colonies would be virtually negligible (Harmelin-Vivien & Bouchon-Navaro, 1981). However, Cox (1986), demonstrated that selective predation by *C. unimaculatus* had a significant influence on the growth, competitive ability and zonation of *Montipora verrucosa* in Kaneohe Bay, Hawaii (see also Neudecker, 1979). Similarly, chronic predation by butterflyfishes in the Western Pacific may adversely affect the growth and reproductive output, if not the distribution and survivorship, of *A. hyacinthus* and *P. damicornis*. The next step in this research will involve quantification of the energetic cost of chronic predation by butterflyfishes on scleractinian corals, with controlled removals of coral-feeding butterflyfishes from replicate patch reefs to compare the growth, reproductive output and survivorship of corals on patch reefs with and without coral-feeding butterflyfishes.

In conclusion, this study has demonstrated that coral-feeding butterflyfishes exhibit a high level of discrimination among different coral species and selectively consume certain coral species (e.g., *A. hyacinthus*) and avoid others (e.g., *Porites lobata*). Further research is required to ascertain the underlying basis of dietary preferences in coral-feeding butterflyfishes, but these findings have significant implications for the ecology of these fishes. Importantly, specific dietary preferences of different butterflyfishes may provide much greater resolution in relating patterns of abundance to prey availability and also facilitate much better predictions regarding species-specific responses following significant disturbance events, such as widespread coral bleaching (e.g., Berumen and Pratchett, 2006; Pratchett et al., 2006).

ACKNOWLEDGEMENTS

This research was funded by a Merit Research Grant from James Cook University. Field assistance was provided by Andrew Baird, Ross Thomas and Stuart Watson. Comments by G. P. Jones, M. I. McCormick, P. L. Munday and two anonymous reviewers greatly improved the manuscript.

LITERATURE CITED

Alino, P. M., P. W. Sammarco & J. C. Coll, 1988. Studies of the feeding preferences of *Chaetodon melannotus* (Pisces) for soft corals (Coelenterata; Octocorallia). *Proceedings of the 6th International Coral Reef Symposium,* **3**: 31-36.

Anderson, G. R. V., A. H. Ehrlich, P. R. Ehrlich, J. D. Roughgarden, B. C. Russell & F. H. Talbot, 1981. The community structure of coral reef fishes. *The American Naturalist,* **117**: 476-495.

Berumen, M. L., M. S. Pratchett & M. I. McCormick, 2005. Within reef variation in the diet and condition of two coral feeding butterflyfish (Pisces: Chaetodontidae). *Marine Ecology Progress Series,* **287**: 217-227.

Berumen, M. L. & M. S. Pratchett, 2006. Recovery without resilience: persistent disturbance and long-term shifts in the structure of fish and coral communities at Tiahura Reef, Moorea. *Coral Reefs*, **25**: 647-653.

Bouchon-Navaro, Y., 1986. Partitioning of food and space resources by chaetodontid fishes on coral reefs. *Journal of Experimental Marine Biology and Ecology,* **103**: 21-40.

Cox, E. F., 1986. The effects of a selective corallivore on growth rates and competition for space between two species of Hawaiian corals. *Journal of Experimental Marine Biology and Ecology,* **101**:161-174

Cox, E. F., 1994. Resource use by corallivorous butterflyfishes (Family Chaetodontidae) in Hawaii. *Bulletin of Marine Science,* **54**: 535-545.

Glynn, P. W., 1990. Feeding ecology of selected macroconsumers: patterns and effects on coral community structure. In: Dubinsky, Z. (ed.), *Ecosystems of the world 25. Coral Reefs*. Elsevier, Amsterdam. Pp. 365-400.

Gochfeld, D. J., 2004. Predation-induced morphological and behavioral defenses in a hard coral: implications for foraging behavior of coral-feeding butterflyfishes. *Marine Ecology Progress Series,* **267**: 145-158.

Gore, M. A., 1984. Factors affecting the feeding behaviour of a coral reef fish, *Chaetodon capistratus. Bulletin of Marine Science,* **35**: 211-220.

Harmelin-Vivien, M. L. & Y. Bouchon-Navaro, 1981. Trophic relationships among chaetodontid fishes in the Gulf of Aqaba (Red Sea). *Proceedings of the 4th International Coral Reef Symposium,* **2**: 537-544.

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

Hughes, T. P., A. H. Baird, E. A. Dinsdale, N. A. Moltschaniwskyj, M. S. Pratchett, J. E. Tanner & B. L. Willis, 1999. Patterns of recruitment and abundance of corals along the Great Barrier Reef. *Nature,* **397**: 59-63.

Irons, D. K., 1989. Temporal and areal feeding behaviour of the butterflyfish, *Chaetodon trifascialis*, at Johnston Atoll. *Environmental Biology of Fishes,* **25**: 187-193.

Keesing, J. K., 1990. *Feeding biology of the crown-of-thorns starfish,* Acanthaster planci *(Linnaeus)*. PhD thesis, James Cook University, Townsville. 197 pp.

Manly, B. F. J., L. L. McDonald & D. L. Thomas, 1993. *Resource selection by animals.* Chapman & Hall, London. 176 pp.

Motta, P. J., 1988. Functional morphology of the feeding apparatus of ten species of Pacific butterflyfishes (Perciformes, Chaetodontidae): an ecomorphological approach. *Environmental Biology of Fishes,* **22**(1): 39-67.

Neudecker, S., 1979. Effects of grazing and browsing fishes on the zonation of corals in Guam. *Ecology,* **60**: 666-672.

Pitts, P. A., 1991. Comparative use of food and space by three Bahamian butterflyfishes. *Bulletin of Marine Science,* **48**: 749-756.

Pratchett, M. S., 1995. *Spatial distribution, abundance and diet selection of butterflyfish (Pisces: Chaetodontidae).* Honours thesis. James Cook University. Townsville. 96 pp.

Pratchett, M. S., 2005. Dietary overlap among coral-feeding butterflyfishes (Chaetodontidae) at Lizard Island, Northern Great Barrier Reef. *Marine Biology,* **148**: 373-382.

Pratchett, M. S., S. K. Wilson, M. L. Berumen & M. I. McCormick, 2004. Sub-lethal effects of coral bleaching on an obligate coral feeding butterflyfish. *Coral Reefs,* **23**: 352-356.

Pratchett, M. S., S. K. Wilson & A. H. Baird, 2006. Declines in the abundance of *Chaetodon* butterflyfishes (Chaetodontidae) following extensive coral depletion. *Journal of Fish Biology*, **69**: 1269-1280.

Schoener, T. W., 1974. Resource partitioning in ecological communities. *Science,* **185**: 27-39.

Sano, M., 1989. Feeding habits of Japanese butterflyfishes (Chaetodontidae). *Environmental Biology of Fishes,* **25**:195-203.

Tricas, T. C., 1985. The economics of foraging in coral-feeding butterflyfishes of Hawaii. *Proceedings of the 5th International Coral Reef Congress,* **5**: 409-414.

Tricas, T. C., 1989. Prey selection by coral-feeding butterflyfishes: strategies to maximize the profit. *Environmental Biology of Fishes,* **25**:171-185.

Zekeria, Z. A., Y. Dawit, S. Ghebremedhin, M. Naser & J. J. Videler, 2002. Resource partitioning among four butterflyfish species in the Red Sea. *Marine and Freshwater Research,* **53**: 163-168.