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

Michael L. BERUMEN [1, 2 *] **and Morgan S. PRATCHETT** [1]

[1]Centre for Coral Reef Biodiversity, School of Marine Biology and Aquacultur, James Cook University, Townsville, Queensland 4811, Australia
[2]Honors College, University of Arkansas, Fayetteville, Arkansas 72701 USA

[*]Corresponding author: M Berumen
FAX: (+61) 7 4725 1570, email: michaelb@uark.edu

Abstract Coral reefs throughout the world are highly degraded and subject to an increasing prevalence of disturbances. Degradation of coral reef habitats is likely to lead to a decline in resource availability for many reef fishes. To assess whether coral-feeding butterflyfishes (Chaetodontidae) would demonstrate increased competition for reduced prey following habitat degradation, the competitive behaviours of several species of butterflyfishes were quantified at Lizard Island, Great Barrier Reef, Australia. We compared the aggressive interactions of butterflyfishes in two reef habitats with very different resource availability during timed visual observations. Home range sizes of two species (*Chaetodon baronessa* and *C. lunulatus*) were measured at four sites with varying coral availability. The dominant butterflyfishes at Lizard Island appear to be *C. baronessa* and *C. trifascialis*, which show aggression towards many other species of butterflyfishes. At exposed locations where its preferred prey was highly abundant, *C. baronessa* aggressively defended small territories. In back-reef locations where food was more limited, *C. baronessa* had larger territories and was less aggressive towards other butterflyfish. Territory size varied little between habitats for *C. lunulatus*, and it rarely showed aggression towards other butterflyfish. As its territory size was a decreasing function of the abundance of high-quality preferred prey resources, *C. baronessa* appears to be an optimal forager. Meanwhile, *C. lunulatus* appears to be a subordinate competitor, restricted from accessing high-quality coral prey, and consequently it utilises a different optimal foraging strategy.

Key words aggression; competition; coral reef fish; foraging theory; habitat degradation; territoriality; resource depletion

Introduction

Coral reefs are being highly degraded by many types of disturbance (such as cyclones or outbreaks of crown-of-thorns starfish) that can vary in their effect at small scales (<1km) and further increase spatial variability in benthic habitats (Brown 1997). The increasing prevalence of disturbances on coral reefs, such as coral bleaching (Hoegh-Guldberg 1999), is leading to worldwide degradation of habitats for reef organisms. This degradation, when combined with naturally occurring habitat variation at small scales (reviewed by Done 1982), is likely to affect fishes with close links to their habitat, especially fishes with obligate coral feeding requirements, such as butterflyfishes (Hourigan et al. 1988).

Butterflyfishes are among the most common and conspicuous fishes in coral reef communities (Burgess 1978), with more than 125 species distributed worldwide in tropical and temperate waters (Kuiter 2002). The distribution patterns of butterflyfishes are often closely related to the distribution of their particular prey resources (eg. Birkeland and Neudecker 1981; Carpenter et al. 1981). For coral-feeding fishes, the composition and quantity of prey resources varies greatly across a range of different spatial and temporal scales. It has been well documented that butterflyfish abundances often vary in accordance with coral cover and often decline following extensive coral depletion (e.g., Bouchon-Navaro et al. 1985; Hourigan et al. 1988; Cadoret et al.

M Berumen & M Pratchett (2006) Effects of resource availability on the competitive behaviour of butterflyfishes (Chaetodontidae). Proc 10th Int Coral Reef Symp (Okinawa, Japan): 644-650

1995; Halford et al. 2004; Berumen and Pratchett, unpublished), even prompting the notion that this family may be useful as an indicator of environmental quality on coral reefs (Hourigan et al. 1988; Crosby & Reese 1996). Degradation of coral resources may also lead to sublethal stresses in butterflyfishes (e.g., Pratchett et al. 2004), however, there has been no work done on the behavioural responses of butterflyfishes to a decline in coral cover. Variation in the availability of prey amongst habitats may lead to differences in competitive aggression and territoriality (Vincent et al. 1996; Ritchie 1998; Robinson and Wilson 1998). As a consequence, feeding selectivity, territory size, and aggression vary even among individuals occupying adjacent territories (Irons 1989). When prey is highly abundant it may be profitable for individuals to defend a particular resource from competitors. However, in some habitats it may not be viable for an animal to defend a territory aggressively (Brown 1964; Hixon 1980; Tricas 1989). If resources are limited and the animal must cover a wide area to forage, the energetic cost of defending this area may outweigh the benefits (Ritchie 1998). By forsaking the maintenance of territories, individuals can spend more time feeding and may thereby compensate for the lack of optimal prey resources (Hughes 1980).

In this study, we examine the competitive behaviours of butterflyfishes at Lizard Island. We further compare the territorial behaviour of two butterflyfishes to explore how differences in the availability of resources affect territoriality. At Lizard Island, *Chaetodon baronessa* Cuvier 1931 has been shown to be highly selective when its preferred coral prey, *Acropora hyacinthus*, is available, and a generalist when *A. hyacinthus* is rare (Berumen et al. 2005). At Lizard Island, *C. lunulatus* Quoy and Gaimard 1824 (previously referred to as *C. trifasciatus*) is a generalist corallivore, consuming many types of available corals in all habitats (Berumen et al. 2005). Three basic predictions arise: 1) Assuming that fish will only dedicate the minimum energy necessary to defend a territory, we predict that territory size will be a decreasing function of prey abundance. 2) As the value of a resource increases, an animal should accordingly increase the amount of energy dedicated to securing that resource. Therefore, we predict that butterflyfishes will more aggressively defend territories where preferred prey is most abundant. 3) Similarly, as specialist fish are predicted to specialize on that resource providing the maximum energetic return (Hughes 1980), we predict that specialists will be more aggressive than generalists in areas where this optimal resource is most abundant.

Methods

Study Location

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). The competitive behaviours of butterflyfishes were observed at each of four locations: South Island, Coconut Beach, Osprey Islet, and Corner Beach. South Island and Coconut Beach were situated on the southeast side of Lizard Island and directly exposed to the prevailing southeast trade winds, whereas Osprey Islet and Corner Beach are relatively sheltered habitats (Fig. 1). At Osprey Islet and Corner Beach the reef was comprised of isolated reef patches in 3-6m depth, which did not exhibit any obvious patterns of depth zonation. At these locations, observations were conducted throughout larger reef patches, avoiding areas of sand separating the reef patches. At South Island and Coconut Beach the reef was comprised of contiguous fringing reef with distinct zonation of the reef flat, crest, slope and base. Here, sampling was confined to the reef crest, providing a depth range similar to the isolated reef patches at sheltered locations. At exposed locations (South Island and Coconut Beach) hard coral cover was in excess of 50% and dominated by the tabular coral *A. hyacinthus*, while hard coral cover at sheltered locations (Corner Beach and Osprey Islet) was typically less than 15% and soft corals (family Alcyonacea) dominated the reef benthos (Berumen et al. 2005).

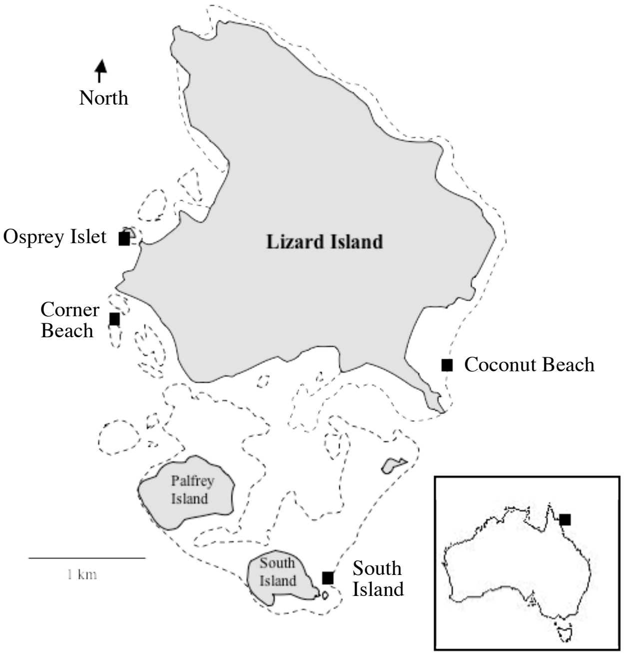

Fig. 1. Sites used for the study of butterflyfish territory sizes at Lizard Island, Great Barrier Reef, Australia. South Island and Coconut Beach represent front-reef habitats with high coral cover (>50%), whereas Corner Beach and Osprey Islet represent back-reef habitats typically dominated by soft corals and with low coral cover (<15%). Dashed lines indicate the approximate reef outline. Inset map of Australia indicates approximate location of Lizard Island.

Territory Size

To assess the territory size of butterflyfishes, individuals of *C. baronessa* and *C. lunulatus* were followed at a discreet distance of 1-3 metres, following Reese (1975). The total time required to obtain accurate estimates of the territory size of butterflyfish was ascertained during a preliminary study in which individuals were observed for 30 minutes. Two transect tapes were laid at right angles within a fish's territory to provide references points on a 50m x 50m grid. The fish was given approximately 15 minutes to acclimatise to the tape. The position of the fish within the grid was then recorded at 45-second intervals as Cartesian coordinates (X, Y) with reference to the two tape measures. A minimum of 10 points was used in the calculation of cumulative home range for observations totaling 7.5, 15, 22.5, and 30 minutes. The area of the smallest convex polygon to contain all the plotted points was calculated. Cumulative territory sizes assessed for 6 individual *Chaetodon baronessa* from each of two different locations (Osprey Islet and South Island) showed that the observed territory sizes were not different after about 15 minutes (Fig. 2). To maximize observations, all subsequent observations to assess territory size were conducted for only 15 minutes.

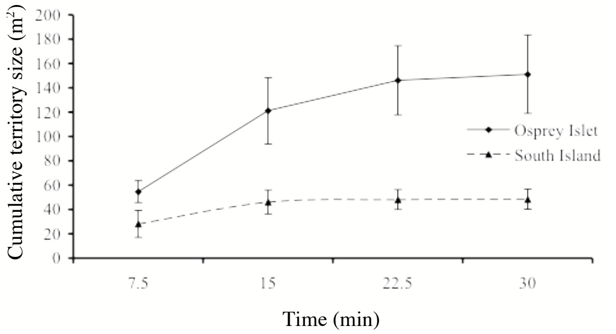

Fig. 2. Mean cumulative territory size (m^2) for *C. baronessa* at two sites at Lizard Island during a pilot study of visual territory observations. Values are means (± standard errors) calculated at 7.5-minute intervals during 30-minute observations. (n = 6 per site).

To compare the territory sizes of *C. baronessa* and *C. lunulatus* amongst the four different locations, we followed 10 individual fish of both species from each location. Strips of flagging tape were fashioned with a heavy stainless steel washer on one end and a small float on the other. These strips were used to mark territory boundaries during timed visual observations. After the 15-minute observation, transect tapes were laid and the position of each strip was recorded as coordinates as above. The area of the territory was then calculated using the smallest convex polygon to fit the recorded boundaries.

Aggressive Behaviours

We also wanted to test whether there was any difference in the frequency of aggressive behaviours demonstrated by butterflyfishes at Lizard Island. To quantify these behaviours, we recorded the number of aggressive interactions involving butterflyfishes during three-minute observations of eight common species of butterflyfishes (*C. auriga*, *C. baronessa*, *C. citrinellus*, *C. kleinii*, *C. plebius*, *C. trifascialis*, *C. lunulatus*, and *C. vagabundus*). Fish were haphazardly within the search areas. Any aggressive behaviours by or towards the focal individual were recorded. The species of the other butterflyfish chased by or chasing the focal individual was also noted. Aggressive interactions were then quantified as the frequency of occurring during a three-minute observation.

Results

Territory Size

The size (specifically, the total area) of territories varied between *C. baronessa* and *C. lunulatus*, but also varied among different locations (Fig. 3). In general, *C. baronessa* maintained smaller territories than *C. lunulatus*, but the size of *C. baronessa* territories differed significantly among sites (ANOVA, F = 7.34, df = 3/39, $p < 0.001$). The mean size of *C. baronessa* territories was 112.0 ± 17.8 (SE) m^2 at Corner Beach and 125.4 ± 16.3 m^2 at Osprey Islet. At South Island and Coconut Beach, the mean territory sizes for *C. baronessa* were less than half the size (55.3 ± 9.3 m^2 and 53.9 ± 7.7 m^2, respectively) of territories for *C. baronessa* at back-reef locations (Fig. 3). Territories also varied in their shape between sheltered and exposed habitats. At back-reef sites the territories were mostly round, but at exposed sites the territories of *C. baronessa* were mostly elongate and aligned parallel to the reef crest. Mean perimeter distances, however, were still 30-40% lower at South Island and Coconut Beach than at back-reef locations.

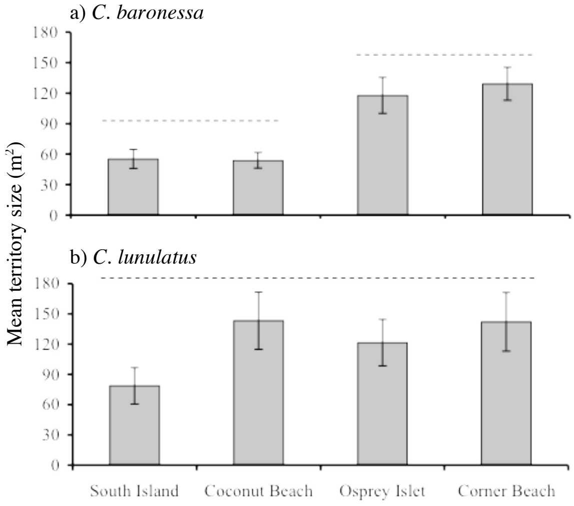

Fig. 3. Mean territory size for a) *C. baronessa* and b) *C. lunulatus* from four sites at Lizard Island. Values are means (± standard errors) of estimates of foraging area (m^2) from 15-minute visual observations. Dotted lines indicate homogenous subsets identified by Tukey's HSD *post hoc* test. (n = 10 per site).

Territories of *C. lunulatus* were larger than the territories of *C. baronessa*, and the mean size of territories was more consistent amongst the four locations (Fig. 3). Although the territories of *C. lunulatus* from South Island averaged only 78.75 ± 17.9 m^2 while the average territory size for *C. lunulatus* at all other locations was greater than 120m^2, there was no significant difference in the size of territories among sites (ANOVA, F = 0.87, df = 3/39, p = 0.47). Territories of *C. lunulatus* were also more circular in shape compared to territories of *C. baronessa* and were not restricted to crest habitat.

Aggressive Behaviour

There were substantial differences in the degree to which butterflyfishes demonstrated aggressive behaviours. The most aggressive butterflyfishes at Lizard Island appeared to be *C. baronessa* and *C. trifascialis*, which frequently chased conspecifics and other corallivorous butterflyfish (Table 1). The overall frequency of *C. baronessa* chasing another butterflyfish was 0.36 in three-minute observations, while *C. trifascialis* had a frequency of 0.61 of chasing another butterflyfish during three-minute observations (Table 1). The most common interactions were aggressions between *C. baronessa* and *C. trifascialis*, closely followed by intraspecific interactions of *C. trifascialis*. Several fish (*C. auriga*, *C. citrinellus*, *C. lunulatus*, and *C. vagabundus*) rarely chased others and *C. plebius* was never observed chasing any butterflyfishes.

There were marked differences in the aggressive behaviours of the two focal species (*C. baronessa* and *C. lunulatus*) used for territory observations. The frequency of *C. lunulatus* chasing another butterflyfish (0.03 in three-minute observations) was an order of magnitude less than that of *C. baronessa* (Table 1). In addition, *C. lunulatus* was chased by other butterflyfishes more than it chased (Table 1), further highlighting its limited aggression towards other butterflyfishes. This pattern was consistent across all four locations (Table 2), suggesting that *C. lunulatus* has a "home range" as opposed to an actively defended territory. Aggression by *C. baronessa* varied greatly among locations, with far more chases occurring at South Island and Coconut Beach than at back-reef sites (Table 2). The frequency of *C. baronessa* chasing another butterflyfish was 0.63 and 0.46 in three-minute observations at South Island and Coconut Beach, respectively. At Corner Beach and Osprey Islet, the frequency of aggression by *C. baronessa* (0.17 and 0.10 in three-minute observations, respectively) was much less than that seen for the exposed locations.

Discussion

The dominant butterflyfish at Lizard Island seem to be *C. baronessa* and *C. trifascialis* (see also Reese 1975). Aggressive interactions between these two species were common, while aggression towards these two by other species was uncommon. These two fish are known to be highly specialised on *A. hyacinthus* (Irons 1989; Berumen et al. 2005) and aggressively defend territories of this resource where it is common. It is possible that the competitive dominance of these two fishes may restrict access to high-quality resources for other butterflyfishes. Feeding preferences ascertained by visual observations may therefore be influenced by this competitive dominance (*sensu* Berumen et al. 2005).

Table 1. Matrix of aggressive behaviours of butterflyfishes at Lizard Island: a) Frequency of a focal individual (column heading) chasing another butterflyfish (row heading) during three-minute observations. b) Frequency of a focal individual (column heading) being chased by another butterflyfish (row heading) during three-minute observations. n= number of observations.

a)

		Focal Individuals - Aggressors							
		C. auriga	*C. baronessa*	*C. citrinellus*	*C. kleinii*	*C. plebius*	*C. trifascialis*	*C. lunulatus*	*C. vagabundus*
	n=	43	240	44	31	43	121	206	52
Chased	*C. auriga*	0.05	0.01						
	C. baronessa		0.03				0.11		
	C. citrinellus		0.01				0.06		
	C. kleinii		0.01		0.13		0.02		
	C. plebius		0.01	0.02			0.10		
	C. trifascialis		0.18				0.16	0.01	
	C. lunulatus		0.06				0.07	0.02	
	C. vagabundus		0.01				0.02		0.02
	Others		0.04	0.02	0.03		0.07		
	Total	0.05	0.36	0.05	0.16	0.00	0.61	0.03	0.02

b)

		Focal Individuals - Chased							
		C. auriga	*C. baronessa*	*C. citrinellus*	*C. kleinii*	*C. plebius*	*C. trifascialis*	*C. lunulatus*	*C. vagabundus*
	n=	43	240	44	31	43	121	206	52
Aggressors	*C. auriga*								
	C. baronessa		0.01				0.56	0.02	
	C. citrinellus								
	C. kleinii				0.03				
	C. plebius						0.01		
	C. trifascialis		0.06			0.02	0.44	0.07	
	C. lunulatus						0.02		
	C. vagabundus								0.08
	Others			0.11		0.02			
	Total	0.00	0.07	0.11	0.03	0.05	1.03	0.09	0.08

Table 2. Matrix of aggressive behaviours of *C. baronessa* and *C. lunulatus* at four sites at Lizard Island: a) Frequency at a site of a focal individual (column heading) chasing another butterflyfish (row heading) during three-minute observations. b) Frequency at a site of a focal individual (column heading) being chased by another butterflyfish (row heading) during three-minute observations. n= number of observations.

a)

		Focal Individuals - Aggressors							
		C. baronessa				*C. lunulatus*			
		South Island	Coconut Beach	Osprey Islet	Corner Beach	South Island	Coconut Beach	Osprey Islet	Corner Beach
	n=	51	50	51	54	50	50	50	56
Chased	*C. auriga*	0.02	0.02						
	C. baronessa	0.08	0.02	0.02					
	C. citrinellus	0.02	0.02	0.02					
	C. kleinii	0.02							
	C. plebius		0.02		0.02				
	C. trifascialis	0.35	0.26			0.02			
	C. lunulatus	0.04	0.06	0.06	0.06	0.02		0.04	0.02
	C. vagabundus	0.02	0.02		0.02				
	Others	0.08	0.04		0.07				
	Total	0.63	0.46	0.10	0.17	0.04	0.00	0.04	0.02

b)

		Focal Individuals - Chased							
		C. baronessa				*C. lunulatus*			
		South Island	Coconut Beach	Osprey Islet	Corner Beach	South Island	Coconut Beach	Osprey Islet	Corner Beach
	n=	51	50	51	54	50	50	50	56
Aggressors	*C. auriga*								
	C. baronessa	0.04		0.02		0.02			0.09
	C. citrinellus								
	C. kleinii								
	C. plebius								
	C. trifascialis	0.10	0.14			0.09			
	C. lunulatus							0.06	0.02
	C. vagabundus								
	Others								
	Total	0.14	0.14	0.02	0.00	0.11	0.00	0.06	0.11

Territory size as a decreasing function of availability of preferred prey is consistent with predictions of optimal foraging theory (Hixon 1980). The larger size of *C. baronessa* territories at sheltered locations may reflect the limited availability of prey coral at these locations and the consequent need to forage over a larger area in order to obtain sufficient nutrients. Associated with the increase in territory size, it was also evident that *C. baronessa* was less aggressive in defending its territories at sheltered locations. Similarly, Irons (1989) showed that territory size in *C. trifascialis* was inversely related to food density, and the defence of territories declined with increasing territory size. Irons (1989) also suggested that aggressiveness declines with increasing territory size because territories become so large they become impossible to defend effectively (see also Hixon 1980). By forsaking the maintenance of territories, individuals can spend more time feeding and may thereby compensate for the lack of optimal prey resources (Hughes 1980). However, Berumen et al. (2005) reported no increase in the feeding rates of *C. baronessa* in back-reef sites, suggesting that time was spent searching for food as opposed to allocating more time for consuming more food. It is unlikely that variation in fish densities are responsible for differences in territory size or aggressiveness, as densities of *C. baronessa* and *C. lunulatus* do not vary among these locations (Berumen et al. 2005). Overall differences in butterflyfish densities are primarily due to differences in abundance of *C. citrinellus* (Berumen et al. 2005), which is rarely involved in any interspecific interactions (Table 1).

Variation in the aggression and territory sizes of *C. baronessa* may also result from differences in the quality (rather than the quantity) of prey at different locations. The maintenance of feeding territories may be viable only if the resource in question is energetically ‘valuable’ enough to justify the extra energy expenditure necessary to maintain such rigorous territories (eg. Jones and Norman 1986; Nakano 1995; Righton et al. 1998). The preferred prey of *C. baronessa* is *A. hyacinthus*, and consumption of this prey species appears to result in much higher condition for both *C. baronessa* and *C. lunulatus* (Berumen et al. 2005). Aggressively defending small territories may not be a beneficial strategy in sheltered locations because there is no *A. hyacinthus* and available prey is of insufficient quality to warrant defence. Habitat degradation changing pristine habitats to back-reef-like states may therefore result in butterflyfishes eventually forsaking territory defence altogether. The competitive dominance of *C. baronessa* may explain why it is one of the last species affected by coral declines (e.g., Pratchett 2001) as other butterflyfishes may be increasingly excluded from remaining resources when habitat is degraded. A disproportionate sub-lethal impact may arise in butterflyfishes when preferred resources are inaccessible or absent (*sensu* Pratchett et al. 2004; Berumen et al. 2005).

In contrast to *C. baronessa*, *C. lunulatus* did not exhibit any significant variation in the size of its territories among the four sites. Moreover, *C. lunulatus* rarely showed aggression towards other butterflyfishes, which might suggest that this species is a subordinate competitor. As a subordinate competitor, the territory size of *C. lunulatus* could be influenced more by interspecific interactions than the quantity and quality of prey (Hixon 1980, 1981; Irons 1988; Nakano 1995). Although we refer to *C. lunulatus* foraging areas arbitrarily as territories, it appears that *C. lunulatus* is actually just foraging in a home range which may be limited or determined by the competitive dominance of other butterflyfishes.

These findings support the suggestion that *C. baronessa* follows predictions of optimal foraging theory while *C. lunulatus*, as a subordinate competitor, has highly compromised feeding habits in which access to resources is largely determined by the territorial behaviours of other butterflyfishes (see also Kosaki 1991; Yabuta 1997). The full fitness costs or benefits of competitive behaviours (including territoriality) are not known but warrant investigation. Further research into competitive behaviours should address the role that territoriality plays in the observed feeding preferences of other butterflyfishes, while experimental studies could reveal the role that resource availability plays in territoriality.

Acknowledgements

This study was conducted in partial fulfillment of an honours degree from the University of Arkansas under the supervision of R. Kilambi, with research conducted at James Cook University. Research was funded by the Roy and Christine Sturgis Charitable Trust and by the Barry Goldwater Scholarship to M.L.B. Field assistance was provided by M. Kospartov, R. Williams, J. Salmond, and D. deVere. Comments from P. Fong, R. Sandy, and two anonymous reviewers greatly improved the manuscript. This is contribution number 149 of the Centre for Coral Reef Biodiversity at James Cook University.

References

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

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

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

Brown BE (1997) Disturbances to reefs in recent times. In: Birkeland C (ed) Life and death of coral reefs. Chapman & Hall, New York, pp 354-379

Brown JL (1964) The evolution of diversity in avian territorial systems. Wilson Bull 76: 160-169

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

Cadoret L, Legendre P, Adjeroud M, Galzin R (1995) Répartition spatiale des Chaetodontidae dans différents secteurs récifaux de l'île de Moorea, Polynésie française. Ecoscience 2: 129-140

Carpenter KE, Miclat RI, Albaladejo VD, Corpuz VT (1981) The influence of substrate structure on the local abundance and diversity of Philippine reef fishes. Proc 4th Int Coral Reef Symp 2: 497-502

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

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

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

Hixon MA (1980) Food production and competitor density as the determinants of feeding territory size. Am Nat 115: 510-530

Hixon MA (1981) An experimental analysis of territoriality in the Californian reef fish, *Embiotoca jacksoni* (Embiotocidae). Copiea 1981: 653-665

Hoegh-Guldberg O (1999) Climate change, coral bleaching and the future of the world's coral reefs. Mar Freshw Res 50: 839-866

Hourigan TF, Tricas TC, Reese ES (1988) Coral reef fishes as indicators of environmental stress in coral reefs. In: Soule DF, Kleppel GS (eds) Marine organisms as indicators. Springer-Verlag, New York, pp 107-135

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

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

Jones GP, Norman MD (1986) Feeding selectivity in relation to territory size in a herbivorous fish. Oecologia 68: 549-556

Kosaki RK (1991) Patterns of resource use and aggressive interaction among three species of coral-feeding butterflyfish (Chaetodontidae). Pac Sci 45: 94

Kuiter, R. H. 2002. The Marine Fish Families Series:

Butterflyfishes, bannerfishes and their relatives. A comprehensive guide to Chaetodontidae and Microcanthidae. TMC Publishing, Chorleywood, UK. 208 pp

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

Pratchett MS (2001) Dynamics of outbreak populations of crown-of-thorns starfish (*Acanthaster planci* L.), and their impacts on coral reef ecosystems. PhD Thesis, School of Marine Biology and Aquaculture. James Cook University, Townsville, 201 pp

Pratchett, M, Wilson S, Berumen M, McCormick M (2004) Sub-lethal effects of coral bleaching on an obligate coral feeding butterflyfish. Coral Reefs 23: 352-356

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

Righton D, Miller M, Ormond R (1998) Correlates of territory size in the butterflyfish *Chaetodon austriacus (*Rueppell). J Exp Mar Biol Ecol 226: 183-193

Ritchie ME (1998) Scale-dependent foraging and patch choice in fractal environments. Evol Ecol 12: 309-330

Robinson BW, Wilson DS (1998) Optimal Foraging, Specialization, and a Solution to Liem's Paradox. Am Nat 151: 223-235

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

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

Yabuta S (1997) Spawning migrations in the monogamous butterflyfish, *Chaetodon trifasciatus*. Ichthyol Res 44: 177-1