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Wave energy and spatial variability in community structure of small cryptic coral reef fishes

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ABSTRACT: The distribution and abundance of small cryptic reef fishes were quantified among microhabitats and reef zones at both exposed and sheltered sites at Lizard Island, Great Barrier Reef. A total of 1042 individuals from 44 species in 8 families were sampled. Marked variation in abundance, species numbers, size-class distribution and species composition were displayed among reef zones at exposed sites; in contrast, comparatively little variation was found in sheltered sites. The exposed, wave-swept front flat reef zone was clearly the most depauperate and species-poor zone with calmer back reef, lagoonal and reef base zones containing the highest numbers of individuals and species. Larger, heavier individuals predominated in exposed wave-swept reef zones whereas smaller, lighter individuals were commonly found in calmer waters. Sheltered sites exhibited little variation among zones. In these sites, microhabitat appeared to play a much greater role in shaping community composition. Overall, 68.5% of all individuals (70.1% at exposed and 65.4% at sheltered sites) were collected from sand/rubble microhabitats as opposed to 31.5% from open reef microhabitats. Assemblages at exposed and sheltered sites exhibited little taxonomic overlap, even of highly abundant species. These results indicate that wave energy plays a significant role in structuring small cryptic coral reef fish communities, with microhabitat type playing a key role in the absence of wave energy.

KEY WORDS: Cryptic · Distribution · Reef fish · Habitat · Community ecology · Gobiidae · Blenniidae · Wave exposure

INTRODUCTION

Of all reef fishes, the community ecology of small cryptic assemblages are least well understood. Difficulties associated with accurately censusing these hidden fishes (see Brock 1982, Willis 2001, Edgar et al. 2004) have limited our overall understanding of the dynamics and role of reef fish communities on coral reefs. Recent studies using anaesthetics and ichthyocides have shown that small cryptic fishes (<10 cm) comprise up to half of the fish numbers on coral reefs (Ackerman & Bellwood 2000, 2002, Greenfield 2003), and constitute a diverse community containing many highly specialised species (e.g. Munday et al. 2002, Depczynski & Bellwood 2004, 2005, Hobbs & Munday 2004). Although occupying the lower end of the size spectrum in reef fishes, this group may provide important insights into the role of fishes in ecosystems, as it is often the smallest organisms that are most abundant, diverse and influential in ecosystem processes (May 1978, Begon et al. 1996). However, we currently lack a detailed description of their distribution and abundance at a reef-wide whole ecosystem scale, an essential pre-requisite in unravelling their contribution to reef ecosystem processes.

Published descriptions of small reef fishes have emphasised that species within this group display marked spatial variation at very small spatial scales of centimetres to metres (Luckhurst & Luckhurst 1978, Townsend & Tibbetts 2000, Wilson 2001). Many also exhibit restricted, and often obligate relationships with particular microhabitat types (Munday 2000, Webster & Hixon 2000, Goncalves et al. 2002, Depczynski & Bellwood 2004). At an individual level, limited home

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and foraging ranges of less than 2 m^2 are consistently reported (Luckhurst & Luckhurst 1978, Reavis 1997, Goncalves & Almada 1998, Depczynski & Bellwood 2004). Despite these studies, nothing is known of the among reef zone variation in small cryptic communities (but see Greenfield & Johnson 1990, 1999 for family-level studies), the level at which most reef fish communities exhibit the greatest variation in composition and abundance (Williams 1982, 1991, Russ 1984). These small-scale observations suggest that the distribution patterns of small cryptic reef fish communities are also likely to display significant variation at larger, among-zone, spatial scales. At these larger among-zone scales, coral reef assemblages are shaped by physical forces acting either directly on individuals, or through indirect influences on habitat or food availability (Fulton et al. 2001, Gust et al. 2001). Given the small size and benthic associations of the small cryptic coral reef fish community, one may hypothesise that these species are highly likely to exhibit marked zonation along these energy gradients. In this study therefore, we describe and quantify the abundance, size composition and community structure of small cryptic coral reef fishes across a gradient of wave exposure to provide a basis for evaluating the role of these fishes in reef processes.

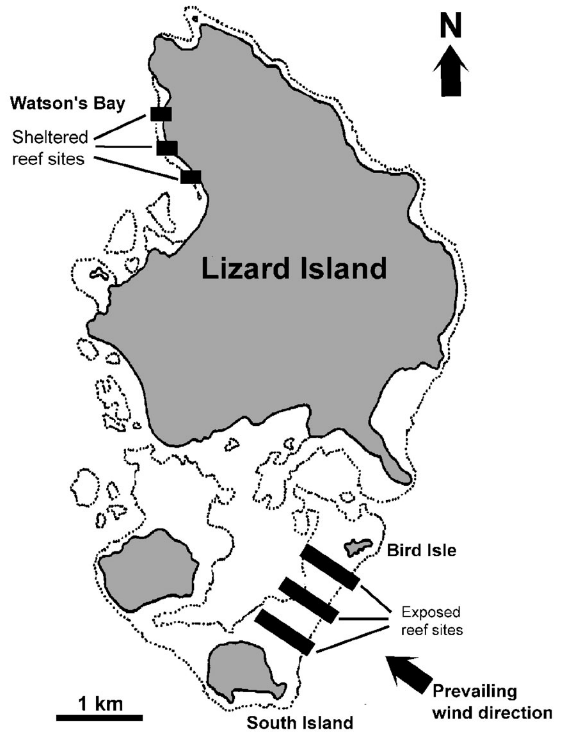

Fig. 1. Exposed and sheltered reef sites where the study was conducted at Lizard Island showing spatial scale and prevailing south-easterly wind direction (modified after Fulton & Bellwood 2005)

MATERIALS AND METHODS

Sampling was undertaken in January and February 2003 on reefs around the Lizard Island group (14°40′S, 145°27′E) in the Cairns section of the Great Barrier Reef (GBR). Lizard Island is a granite island in the mid-shelf region of the GBR. Three sites were censused on the exposed reef front between Bird and South Isles at depths of 1 to 15 m, and 3 from the sheltered NW margin of Watsons Bay at depths of 1 to 6 m (Fig. 1). Five reef zones were censused at each site (base, slope, crest, front flat & back flat) at the exposed reef (Fig. 2). The lack of a defined slope at the sheltered reef sites meant that only 4 reef zones could be reliably identified (base, crest, front flat and back flat). Descriptions of reef zones and corresponding wave energy are given (Table 1). In each reef zone, 4 samples were taken in each of 2 microhabitats, open reef and sand/rubble with a total of 120 censuses at the exposed sites and 96 at the sheltered sites. Open reef microhabitats were flat, open areas of live and/or dead coral fully exposed to the surrounding water column from all sides and above; sand/rubble areas of sand and hard coral rubble where >50% of sample area contained visible coral rubble pieces of between 20 to 200 mm.

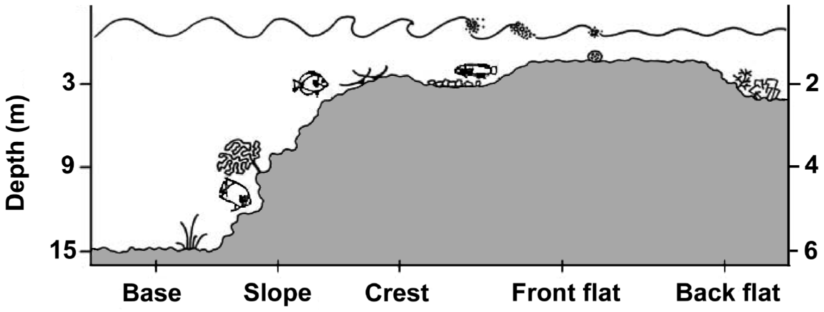

Fig. 2. Reef zones and depth along the reef profile (modified after Fulton & Bellwood 2005). Depths on the left-hand *y*-axis are for exposed reef sites; right-hand *y*-axis for sheltered reef sites

Samples were collected on SCUBA using clove oil and a fine-mesh (2 mm) net covering a basal area of 0.4 m^2. The weighted net was positioned in a circle on the substratum before approximately 125 ml of a 5:1 ethanol:clove oil mixture was sprayed into the netted area and left for 1 min before the search for anaes-

Table 1. Environment description, depth and wave severity of reef zones at exposed and sheltered reef sites. Wave energy estimates follows Fulton & Bellwood (2005) at same location

Reef zone	Environment description			Physical parameters	
	General characteristics	Heterogeneity	Coral cover	Depth (m)	Wave energy
Exposed reef					
Base	Gently sloping fine sand and rubble environment with isolated coral colonies or outcrops	Moderate	Moderate	10–15	Nil
Slope	Variable incline (10 to 90°)/ diverse topography	Highest	High	6–9	Moderate
Crest	High vertical relief	High	Highest	1–3	High
Front flat	Mostly hard flat substrata covered in algal and coarse sand with occasional coral outcrops	Lowest	Low	2–4	Highest
Back flat	Flat, varied environment	Moderate	Moderate	2–4	Moderate
Sheltered reef					
Base	Flat sand and rubble environment with isolated reef outcrops	Lowest	Low	4–6	Nil
Crest	High vertical relief	Highest	High	1–3	Low
Front flat	Mostly flat, hard substrata environment	Moderate	Moderate	2–4	Low
Back flat	Flat, varied environment	Moderate	Moderate	1–3	Low

thetised fish began. Following a 5 min systematic search by 2 divers, fish were put into labelled, clip-seal plastic bags, and placed into an ice-water slurry. Specimens were identified, weighed and measured (total length; TL) at the laboratory, and stored in 70% ethanol. The genus *Eviota* are small and taxonomically challenging to identify (Lachner & Karnela 1980). Thus, identification of highly abundant *Eviota* species were made by H. K. Larson of the Museum and Art Gallery of the Northern Territory. All other *Eviota* species were provisionally identified to Sp. A, Sp. B. etc based on a combination of meristics, their cephalic sensory pore system and readily distinguishable body and facial markings; the key recognised traits for the identification of this genus (see Lachner & Karnella 1980). Already numbering some 70 odd species, the samples probably included several undescribed *Eviota* species.

After initial examination, data were $\log_{10}(x + 1)$ transformed to satisfy requirements for normality and homoscedascity. Following *t*-tests comparing overall numbers of individuals and species at exposed and sheltered reef locations, differences in the abundances of individuals and number of species among sites, zones and microhabitats were analysed using 3-way mixed factorial ANOVAs at exposed and sheltered reef locations separately. Variation in species assemblages among zones were examined using MANOVAs based on the 12 most abundant species (with >10 individuals across all zones) for exposed and sheltered reef locations separately. Bonferroni-corrected multiple comparisons tests were used to identify differences in species assemblages between zones. Canonical discriminant analyses (CDA) based on structure coefficients graphically identified the characteristics of species assemblages in the 4 (sheltered) and 5 (exposed) reef zones. Zone centroids are displayed with 95% confidence clouds. Abundance within each species is displayed by the relative size of species points on the CDA following square root transformation on raw counts. Differences in size (using weight in g) of individuals were investigated among zones at exposed and sheltered reef locations separately using 1-way ANOVAs followed by Tukey's HSD post-hoc tests to identify where differences lay.

RESULTS

Patterns of individual and species abundance

A total of 1042 individuals from 44 species in 8 families were sampled over a combined area of 86.4 m^2 (216×0.4 m^2) (Table 2). Of these, the top 19 species (>10 individuals sampled) represented 92.5% of all individuals, with the Gobiidae making up 87.1% of all individuals, and tripterygiids, blenniids and pseudochromids contributing most of the remaining 12.9%. While the Gobiidae dominated all reef zones at sheltered and exposed reef sites, differences in the proportional contribution of non-gobiid families among reef zones varied considerably, particularly at exposed reef sites (Fig. 3).

Table 2. Families (8 total), species, numbers of individuals and numerical and biomass contribution (%) of each species to the entire assemblage sampled at exposed (n = 120) and sheltered (n = 96) reef sites. The 19 most abundant species (in **bold**) represent 92.5 % of all individuals sampled and were chosen for further analyses based on their presence (>10 individuals across all reef zones) at either exposed and/or sheltered reef sites

Family	Species	Abundance				Biomass (g)			
		Exposed	Sheltered	Total (T)	% of T	Exposed	Sheltered	T biomass	% of T biomass
Gobiidae	***Eviota sigillata***	**192**	**24**	**216**	**20.73**	**6.12**	**0.69**	**6.81**	**4.54**
	Eviota queenslandica	**99**	**41**	**140**	**13.44**	**3.88**	**1.34**	**5.22**	**3.48**
	Eviota melasma	**60**	**21**	**81**	**7.77**	**3.14**	**1.59**	**4.73**	**3.15**
	Asterropteryx semipunctatus	**2**	**72**	**74**	**7.1**	**0.15**	**9.08**	**9.23**	**6.15**
	Istigobius goldmanni	**31**	**33**	**64**	**6.14**	**5**	**5.04**	**10.04**	**6.69**
	***Eviota* sp. Q**	**5**	**34**	**39**	**3.74**	**0.36**	**2.76**	**3.12**	**2.08**
	***Eviota* sp. J**	**32**	**0**	**32**	**3.07**	**0.78**	**0**	**0.78**	**0.52**
	***Eviota* sp. K**	**26**	**6**	**32**	**3.07**	**0.87**	**0.18**	**1.05**	**0.7**
	***Amblyeleotris* sp. A**	**8**	**17**	**25**	**2.4**	**2.7**	**0.39**	**3.09**	**2.06**
	Eviota pellicuda	**25**	**0**	**25**	**2.4**	**0.95**	**0**	**0.95**	**0.63**
	***Eviota* sp. O**	**21**	**3**	**24**	**2.3**	**1.45**	**0.29**	**1.74**	**1.16**
	***Callogobius* sp. A**	**0**	**20**	**20**	**1.92**	**0**	**1.48**	**1.48**	**0.99**
	Ctenogobiops feroculus	**0**	**19**	**19**	**1.82**	**0**	**2.22**	**2.22**	**1.48**
	Fusigobius signipinnis	**15**	**2**	**17**	**1.63**	**0**	**1.13**	**0.21**	**0.14**
	Amblygobius phaelena	**4**	**12**	**16**	**1.54**	**2.6**	**4.04**	**6.64**	**4.42**
	Valenciennea muralis	**7**	**9**	**16**	**1.54**	**10.59**	**2.98**	**13.57**	**9.04**
	Callogobius sclateri	3	4	7	0.67	1.7	1.31	3.01	2.01
	Eviota sp. S	1	5	6	0.58	0.01	0.39	0.4	0.27
	Istigobius rigilius	2	3	5	0.48	0.84	0.46	1.3	0.87
	Amblygobius rainfordi	2	1	3	0.29	1.53	0.39	1.92	1.28
	Ctenogobiops pomastictus	0	3	3	0.29	0	0.56	0.56	0.37
	Eviota sp. N	0	3	3	0.29	0	0.16	0.16	0.11
	Eviota sp. P	0	3	3	0.29	0	0.08	0.08	0.05
	Signigobius biocellatus	1	2	3	0.29	0.03	0.34	0.37	0.25
	Trimma striata	3	0	3	0.29	0.29	0	0.29	0.19
	Amblygobius nocturnis	0	2	2	0.19	0	0.59	0.59	0.39
	Coryphopterus neophytus	0	2	2	0.19	0	1.75	2.88	1.92
	Gobiodon quinquistregatus	0	2	2	0.19	0	1.09	1.09	0.73
	Eviota sp. F	1	0	1	0.1	0.04	0	0.04	0.03
Blenniidae	***Salarias patzneri***	**30**	**24**	**54**	**5.18**	**13.78**	**16.45**	**30.23**	**20.14**
	Ecsenius stictus	5	3	8	0.77	3.37	2.67	6.04	4.02
	Salarias guttatus	2	3	5	0.48	3.8	2.65	6.45	4.3
	Entomacrodus sp. A	0	4	4	0.38	0	0.92	0.92	0.61
	Ecsenius bicolour	2	2	4	0.38	1.89	4.27	6.16	4.1
	Crossalarias macrospilus	1	1	2	0.19	0.54	1.02	0.54	0.36
	Salarias fasciatus	1	1	2	0.19	0.14	0.41	0.55	0.37
	Istiblennius sp. A	0	1	1	0.1	0	0.31	0.31	0.21
Apogonidae	*Apogon cooki*	3	0	3	0.29	1.82	0	1.82	1.21
	Apogon doederleini	0	1	1	0.1	0	0.16	0.16	0.11
Pseudochromidae	***Pseudochromis fuscus***	**10**	**2**	**12**	**1.15**	**3.74**	**0.91**	**4.65**	**3.1**
Tripterygiidae	***Enneapterygius tutuilae***	**27**	**31**	**58**	**5.57**	**3.27**	**1.84**	**5.11**	**3.4**
Syngnathidae	*Corythoichthys flavofasciatus*	2	0	2	0.19	0.16	0	0.16	0.11
Pinguipedidae	*Parapercis xanthozona*	2	0	2	0.19	3.2	0	3.2	2.13
Muraenidae	Sp. A	1	0	1	0.1	0.24	0	0.24	0.16
Total		**626**	**416**	**1042**	**100**	**78.98**	**71.94**	**150.11**	**100**

Exposed versus sheltered reefs

Overall, exposed and sheltered reefs were broadly similar and statistically non-significant in both mean individual abundance (exposed 14.6 ind. m^{-2} [± 1.4 SE], sheltered 12.5 ind. m^{-2} [± 0.9 SE] [$t = 0.84$, df = 214, $p > 0.05$]) (Fig. 4) and mean species numbers (exposed 6.7 ind. m^{-2} [± 0.4 SE], sheltered 7.8 ind. m^{-2} [± 0.5 SE] [$t = -1.83$, df = 214, $p > 0.05$]) (Fig. 5). Species richness tended to mirror individual abundances among reef zones and habitats. A total of 31 species were recorded on exposed and 36 species on sheltered reefs (Table 3).

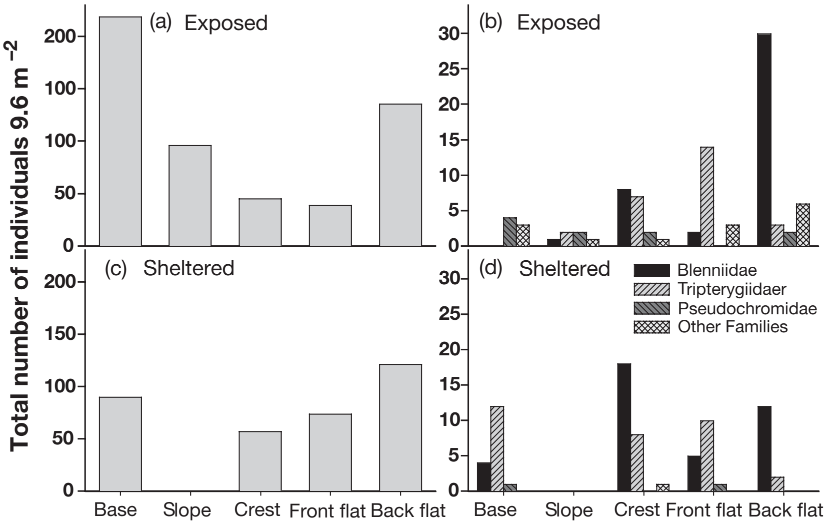

Fig. 3. Familial composition of small cryptic reef fishes across reef zones (n = 24 with a total area of 9.6 m^2 per zone). (a,c) Gobiidae, (b,d) non-gobiid families. No samples were taken from the slope at sheltered reef sites. The identity of 'Other Families' is listed in Table 2

Among reef zones, however, species richness varied considerably at the exposed reef, less so at the sheltered reef. With 2 exceptions, where abundances were at their lowest (front flat at exposed reef and crest at sheltered reef), the influence of microhabitat on number of individuals and species is consistent (Figs. 4 & 5, Table 4) with the sand/rubble microhabitat samples having more individuals and species than open reef microhabitat samples. A total of 68.5% of all individuals were censused from sand/rubble habitats and 41 of 44 species. In contrast, open reef samples contained only 27 species in total.

Exposed reef

Individual abundance and species richness varied significantly at both the zone and microhabitat level (Table 4). The influence of microhabitat on numbers of individuals is apparent for most zones with the exception of the front flat where very low abundances were recorded in both microhabitat types (Fig. 4a). Sand/rubble microhabitats contained 70.1% of all sampled individuals on exposed reefs with distinct differences between zones, whereas open reef microhabitats were roughly equal in fish abundance across reef zones.

For reef zones, front flat areas were clearly the most depauperate in terms of individuals and species with base and back flat areas the most populated. A Tukey's post-hoc test identified the front flat as being statistically different from all others for both numbers of individuals and species (Table 5); all other reef zones shared varying relationships to one another. In total, 58 individuals and 10 species were found in the

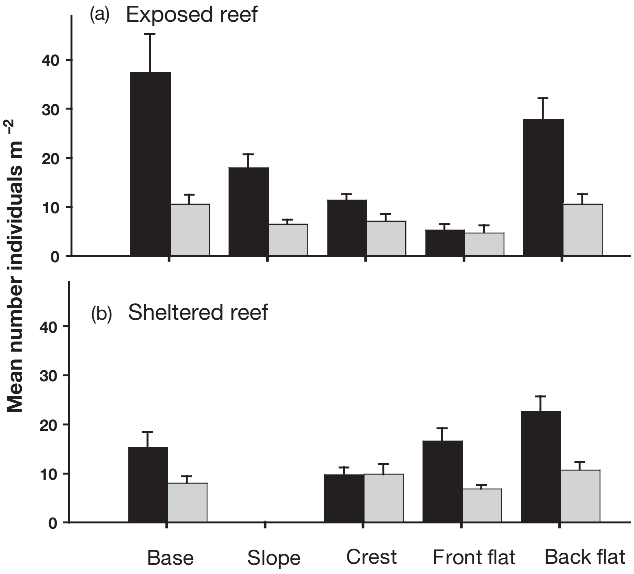

Fig. 4. Mean number of individuals m^{-2} (+SE, n = 12 samples) among the reef zones and microhabitats sampled at (a) exposed and (b) sheltered reefs. Black bars: sand/rubble; gray bars: open reef microhabitats. No samples were taken from the slope at sheltered reef sites

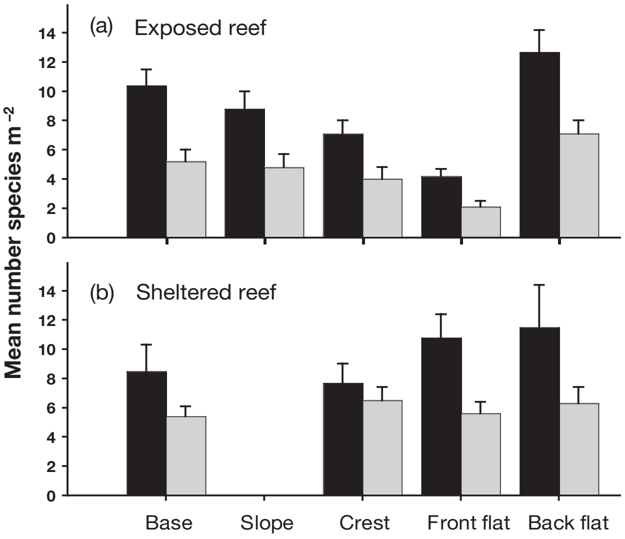

Fig. 5. Mean number of species m^{-2} (+SE; n = 12 samples) among the reef zones and microhabitats sampled at (a) exposed and (b) sheltered reefs. Black bars: sand/rubble; gray bars: open reef microhabitats. No samples were taken from the slope at sheltered reef sites

Table 3. Mean fish density, species richness and mean number of individuals per species (±SE) for exposed and sheltered reefs for each reef zone. Total number of species found at exposed and sheltered reef sites indicated in **bold**

Zone	No. of ind.	Density (m^{-2})	No. of species/zone	Mean no. ind./species
Exposed				
Base	224	23.4	13	16.1 (±9.6)
Slope	105	10.9	14	7.5 (±2.9)
Crest	63	6.5	18	3.5 (±0.9)
Front flat	58	6.0	10	5.8 (±2.1)
Back flat	176	18.3	20	8.8 (±4.0)
Total	**626**		**31**	
Sheltered				
Base	96	10.0	22	4.5 (±1.0)
Crest	80	8.3	27	3.1 (±0.7)
Front flat	99	10.3	17	5.4 (±1.4)
Back flat	141	14.7	17	8.4 (±2.8)
Total	**416**		**36**	

front flat zone compared to 176 individuals and 20 different species in back flat zone (Table 3).

Sheltered reef

Fish abundance and species richness patterns showed comparatively little among-reef zone variation in sheltered reefs (Figs. 4b & 5b). A significant site × zone × microhabitat interaction indicates that patterns of abundance at this sheltered reef may be quite complex in comparison to those found at the exposed reef (Table 4). A more thorough investigation indicated that statistical differences were primarily driven by the microhabitat and, to a lesser extent, reef zone factors. Inconsistent patterns exist among and within the 3 factors aside from a trend towards higher abundances in back flat reef zones and sand/rubble microhabitats. A Tukey's post-hoc test identified differences between the back flat and all other reef zones as the major determinant of statistical differences for abundance at the reef zone level (Table 6).

Table 5. Results of Tukey's post-hoc tests identifying the reef zones that statistically differ from each other in individual and species numbers at the exposed reef location. **Bold** numbers denote significance at $p < 0.05$

	Base	Slope	Crest	Front flat
No. of individuals				
Base				
Slope	**0.024**			
Crest	**0.002**	0.933		
Front flat	**0.000**	**0.000**	**0.001**	
Back flat	1.0	**0.021**	**0.002**	**0.000**
No. of species				
Base				
Slope	0.783			
Crest	0.270	0.909		
Front flat	**0.000**	**0.003**	**0.036**	
Back flat	0.490	0.053	**0.004**	**0.000**

Table 4. Three-way ANOVA results comparing fish abundance and species richness [$\log_{10}(x + 1)$] in exposed and sheltered reefs amongst sites, reef zones and microhabitats (M'habitat). Exposed reef location: n = 120, df = 4; Sheltered: n = 96, df = 3. **Bold** numbers denote significance at $p < 0.05$

Source	Fish abundance			Species richness		
	MS	*F*	p	MS	*F*	p
Exposed reef						
Site	0.14	2.51	0.087	0.02	0.07	0.934
Zone	1.15	21.07	**<0.001**	0.40	11.93	**<0.001**
M'habitat	2.73	50.18	**<0.001**	1.12	33.12	**<0.001**
Site × Zone	0.10	1.74	0.099	0.04	1.07	0.389
Site × M'habitat	0.01	0.25	0.776	0.01	0.40	0.672
Zone × M'habitat	0.08	1.39	0.244	0.01	0.21	0.932
Site × Zone × M'habitat	0.05	0.88	0.540	0.02	0.54	0.821
Error	0.05			0.03		
Sheltered reef						
Site	0.09	2.64	0.078	0.05	1.99	0.144
Zone	0.16	4.96	**0.003**	0.04	1.30	0.283
M'habitat	0.85	25.87	**<0.001**	0.44	16.14	**<0.001**
Site × Zone	0.06	1.71	0.130	0.05	1.66	0.143
Site × M'habitat	0.11	3.22	**0.046**	0.09	3.42	**0.038**
Zone × M'habitat	0.10	3.05	**0.034**	0.05	1.64	0.187
Site × Zone × M'habitat	0.10	2.99	**0.012**	0.06	2.20	0.053
Error	0.03			0.03		

Patterns in size

Total lengths of individuals varied from 7.5 to 92.6 mm TL overall, with 91% of all individuals measuring between 7.5 to 29.9 mm (mean 19.1 ± 0.3 SE). Striking differences in the mean weight of individuals were apparent at exposed sites ($F_{4,626} = 13.27$, $p < 0.001$) with the heaviest individuals coming from exposed wave-swept reef zones (crest, front flat and back flat) (Fig. 6a). Individuals present at the front flat reef zone had mean weights of 0.34 g (± 0.13 SE); at the crest of 0.18 g (± 0.04 SE); and at the back flat of 0.14 g (± 0.02 SE). These values are in stark contrast to the 0.07 g (± 0.01 SE) in base and slope reef zones (Fig. 6a). Tukey's post-hoc tests differentiate these 2 groups. While half of all individuals of <15 mm at the exposed reef sites were found at the base, the largest individuals (>45 mm) were predominantly found at crest and

Table 6. Results of Tukey's post-hoc tests identifying the reef zones that statistically differ from each other in individual and species numbers at the sheltered reef location. **Bold** numbers denote significance at $p < 0.05$

	Base	Crest	Front flat
No. of individuals			
Base			
Crest	0.833		
Front flat	0.998	0.742	
Back flat	**0.033**	**0.003**	**0.049**
No. of species			
Base			
Crest	0.987		
Front flat	0.589	0.790	
Back flat	0.313	0.504	0.965

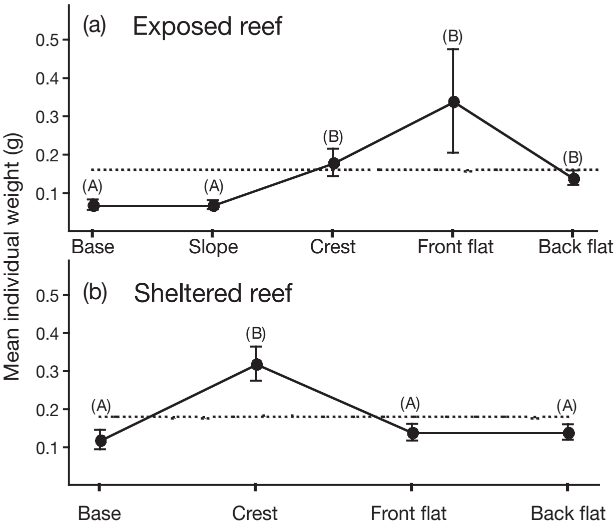

Fig. 6. Mean weight (g) (±SE, n = 24 samples) of all individuals censused at (a) exposed and (b) sheltered reef zones. Dotted line represents the average weight (g) across all reef zones for exposed and sheltered reef sites. Letters denote statistically indistinguishable groupings (same letter)

back flat reef zones. Of these, approximately half were from the family Blenniidae, with larger gobies (*Amblygobius phaelena*, *A. rainfordi*, *Valenciennea muralis* and *Istigobius goldmanni*) making up the remainder. Reef zones at the sheltered sites were less variable, but overall differences were significant ($F_{3,416}$ = 15.11, $p < 0.001$). This pattern is due to the crest zone where mean individual weights (0.32 g ± 0.04 SE) were nearly twice that of the overall mean across all reef zones (0.18 g, ± 0.14 SE) (Fig. 6b). For these sites, the crest contained the highest abundance of the >45 mm size-class, due to the presence of large blenniid species in the crest reef zone. Size-classes were evenly spread across the other 3 sheltered reef zones.

Patterns in species assemblages

Only 6 species (from the 12 selected for analyses) were abundant (with >10 individuals) at both exposed and sheltered reef sites; *Eviota melasma*, *E. sigillata*, *E. queenslandica*, *Istigobius goldmanni*, *Enneapterygius tutuilae* and *Salarias patzneri*. *Callogobius* sp. A and *Ctenogobiops feroculus* were found exclusively at sheltered reef sites; *Eviota* sp. J and *E. pellicuda* were only found on exposed reef sites. MANOVAs based on the 12 most abundant species at exposed and at sheltered reef sites revealed significant differences in species assemblages among reef zones for both exposed and sheltered reefs (Pillai's trace $p < 0.001$). Post-hoc Bonferroni-corrected multiple comparisons indicated that species abundances varied among reef zones in 10 of 12 species at exposed reef sites, and 6 of 12 at sheltered reef sites (Table 7). Canonical discriminant analysis shows the nature of

Table 7. Results of the Bonferroni-corrected multiple comparisons tests identifying the species that differed significantly in abundance among reef zones at exposed and sheltered reef sites. Analyses was based on the 12 most abundant (>10 individuals across all zones) species censused at (1) exposed and, (2) sheltered reef sites. Letters indicate statistical non-significance (same letter) or significant differences (different letter) of each species among relevant reef zones. No samples were taken from the slope at sheltered reef sites

	Base	Slope	Crest	Front flat	Back flat	p
Exposed reef						
Eviota melasma	A	A	B	B	B	<0.001
Eviota sp. J	A	B	B	B	B	<0.001
Eviota sigillata	A	A,B	B	B	B	<0.001
Eviota sp. O	A	A	B	A	A	<0.01
Eviota queenslandica	A	A	A	A	B	<0.001
Eviota pellicuda	A,C	A	B,C	B,C	B,C	<0.05
Istigobius goldmanni	A	A	A	A	B	<0.001
Enneapterygius tutuilae	B	B	A,B	A	A,B	<0.01
Fusigobius signipinnis	A,B	A	A,B	B	B	<0.05
Salarias patzneri	A	A	A	A	B	<0.001
Sheltered reef						
Eviota melasma	A	–	B	B	B	<0.001
Eviota queenslandica	B	–	B	B	A	<0.001
Asterropteryx semipunctatus	A	–	A,C	A,C	B,C	<0.05
Istigobius goldmanni	B	–	B	A,B	A	<0.001
Salarias patzneri	B	–	A	A	B	<0.01
Ctenogobiops feroculus	B	–	A,B	A,B	A	<0.05

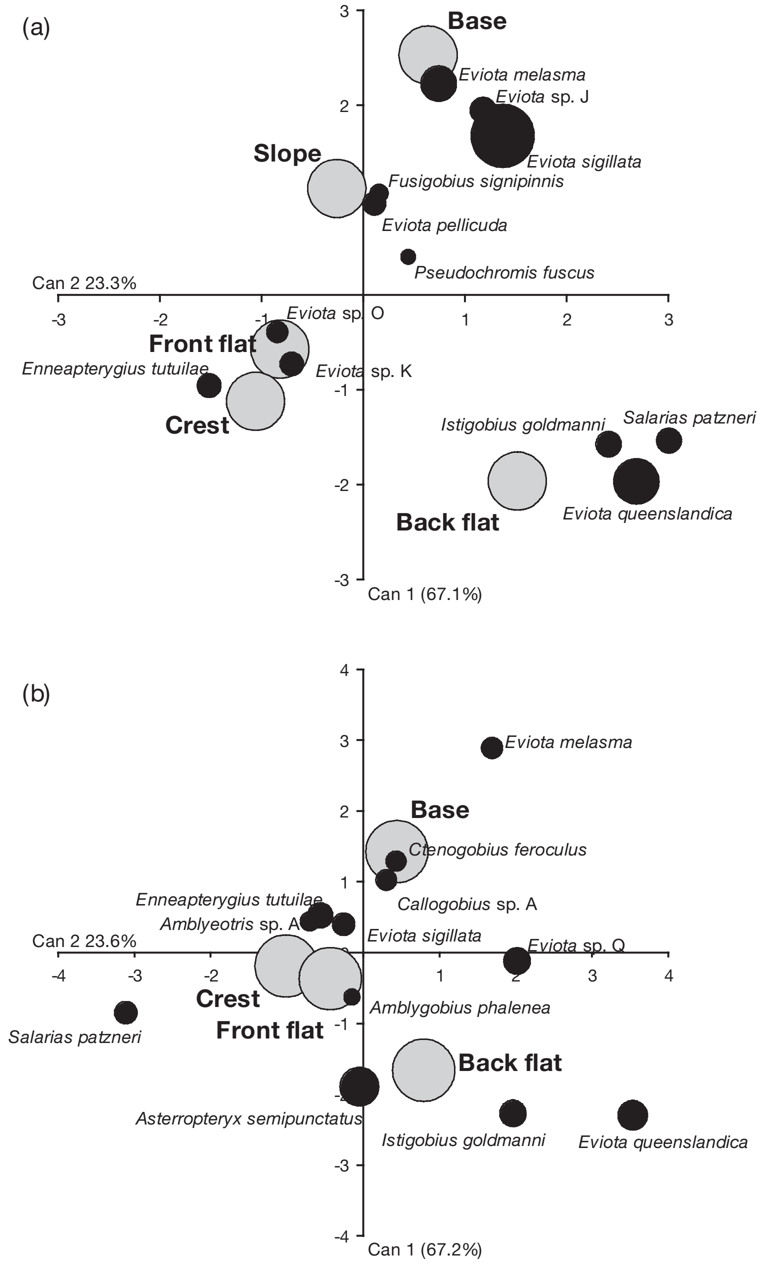

Fig. 7. Canonical discriminant analyses (CDA) displaying the relationship between the small cryptic reef fish community (12 most abundant species) and reef zones at (a) exposed and (b) sheltered reef sites. Confidence clouds (95%) surround reef zone centroids (gray circles). Species bubble sizes reflect total abundance of each species (square root transformation from raw counts)

these differences where centroid means and 95% confidence clouds are plotted for each zone at exposed (Fig. 7a) and sheltered (Fig. 7b) reefs. Except for the front flat and crest, confidence clouds indicate that all other zones have characteristic species assemblages in both exposed and sheltered reef sites. Small, highly abundant species tended to be associated with base and slope zones at exposed reef sites.

DISCUSSION

Our analysis of the small cryptic reef fish community at Lizard Island revealed 3 clear trends. Firstly, sand/rubble microhabitats consistently supported more individuals and species than open reef microhabitats, regardless of the location or spatial scale examined. Secondly, although community patterns of abundance, diversity and size/weight-class distribution varied widely among zones at exposed sites, comparatively little variation was exhibited at sheltered sites. Thirdly, species composition varied considerably along wave energy gradients between exposed and sheltered reef sites and among reef zones.

With the exception of depauperate front flat (exposed sites) and crest (sheltered sites) reef zones, the effect of microhabitat type on the distribution patterns of the small reef fish community at Lizard Island was clear; more than two thirds of individuals and 41 out of a possible 44 species were sampled on sand/rubble microhabitats as opposed to 27 species in open reef samples. Intuitively, the relationship between small substratum-bound fishes and their structural environment is likely to be an intimate one, and it has already been well established that microhabitat type plays a pivital role in the survival, abundance and distribution of these assemblages at small spatial scales (Syms 1995, Prochazka 1998, Munday 2000, Wilson 2001, Willis & Anderson 2003, La Mesa et al. 2004). At this scale, levels of abundance and species richness increase dramatically in more heterogenous environments that offer quality shelter to residents (Caley & St John 1996, Willis & Anderson 2003, Depczynski & Bellwood 2004). Given that microhabit type plays such a key role in structuring small reef fish communities, the question remains, to what extent do larger scale habitat zones influence community distribution structure?

At exposed wave-swept reef zones, we found a dramatic decrease in diversity and abundance, with a corresponding increase in overall fish size. This was most marked in the shallow wave-swept front flat, and to a lesser extent reef crest zones, regardless of microhabitat type. This suggests that microhabitat type plays a minor or secondary role in structuring small reef fish communities under circumstances where incident wave energy is particularly strong. There are 2, non-exclusive factors that may account for these patterns. Firstly, wave-induced water motion may directly affect the distribution of many reef fish species through its interaction with swimming performance. Secondly, wave energy influences their distribution through change to benthic communities and habitat structure.

The swimming abilities of small cryptic coral reef fishes have yet to be quantified. In larger, more mobile species a direct relationship between wave-induced water motion and swimming mode has been identified for a number of reef fish families (Fulton & Bellwood 2005). It appears that wave-swept habitats may have high energetic costs of occupation which may be a barrier for some species based on their swimming mode and efficiency. Fishes with sustained swimming abilities, usually employing energy-efficient lift-based pectoral locomotion, tend to inhabit wave exposed reef environments while slower thrust-based swimmers occupy more sheltered environments (Bellwood & Wainwright 2001, Fulton & Bellwood 2005). Several lines of evidence suggest that small cryptic fishes are comparatively poor swimmers. Unlike larger, more mobile species, most small cryptic species are substratum-bound (many lacking a swim bladder), spending little or none of their time swimming high in the water column where water movement may be greatest (Shashar et al. 1996, Goncalves & Almada 1998). Furthermore, they lead spatially restrictive lives encompassing home ranges of 0.25 to 2 m^2 and many tend to exhibit quite sedentary behaviour (Luckhurst & Luckhurst 1978, Goncalves & Almada 1998, Depczynski & Bellwood 2004). Small cryptic reef fish swimming generally consists of short bursts (1 to 5 s) using body and caudal fin propulsion which may be one of the most energetically expensive modes (Wu 1977, Vogel 1994). Furthermore, their predominantly rounded fins suggest they are suited to powerful short-bursts of speed rather than sustained high speed swimming (Sambilay 1990, Vogel 1994). Overall, it would appear that the swimming ability of small cryptic species are generally unsuitable for high energy wave-swept locations.

Despite these limitations, our results indicate that a few species are able to inhabit even severely wave affected reef areas (i.e. families Blenniidae and Tripterygiidae). Size distributions among exposed reef zones provided some interesting insights into the potential role of wave energy and water motion in structuring size-related spatial patterns in these small reef fish communities. Our data show that, at exposed reef sites, wave-swept reef zones (i.e. front flat) were inhabited by low numbers of larger, heavier (25 to 93 mm TL) individuals including species with high surface area:volume ratios such as blennies, and calm reef zones (i.e. base) by high numbers of very small, lighter (<15 mm TL) ones. These results correlate well with previously described patterns in the Caribbean (Greenfield & Johnson 1981, Greenfield 2003) and at Lizard Island (Wilson 2001) where some species of Blenniidae appear to show preferences for shallow, high energy habitats. Differences in size-class distributions across wave exposure gradients have previously been documented in temperate labrids with smilar results to those presented here (Fulton & Bellwood 2004). Shallow, wave-exposed reef zones were not only poorly inhabited by fewer and larger individuals, but smaller individual size-classes were almost entirely absent. In an earlier paper, Fulton & Bellwood (2002) also demonstrated ontogenetic changes in water column use for coral reef wrasses, with smaller individuals remaining close to the substratum, the authors hypothesising that smaller, less competent swimmers were flow-refuging in near-bottom boundary layers or microhabitat scale eddies. Regardless of the underlying mechanisms, the ability to maintain station in these hostile environments is probably very difficult for small individuals and our data suggests that wave-swept environments may provide a serious challenge to their occupation by smaller-sized individuals.

The role of wave energy in shaping marine environments and marine communities has been well documented for many marine ecosystems (Menge 1976, McQuaid & Branch 1985, Denny 1988, Friedlander & Parrish 1998, Denny & Wethey 2001, Bellwood et al. 2002, Friedlander et al. 2003). Because coral reef ecosystems are biogenic in makeup, presence, absence, type and morphology of reef building organisms are greatly influenced by wave induced water motion (Dineson 1983, Done 1983, Ninio & Meekan 2002), shaping the habitat and living areas of resident biota. Distinct and abrupt changes in reef habitat diversity, complexity and abundance coinciding with changes from one reef zone to another follow depth and corresponding wave energy gradients. The microhabitat at the front flat is essentially level homogenous algal encrusted rock pavement subjected to the highest levels of water motion in our study. Accordingly, open reef microhabitats on exposed wave-swept reef flats theoretically represent the most physically extreme location for small benthic fishes and we found these areas to be poorly inhabited. At our sheltered reef sites where more gradual inter-zone changes take place, we see little overall variation in these community parameters. These differences in habitat topography may be a significant influence on small cryptic reef fish communities.

Trophic resource patterns may also be a significant factor in shaping cryptic reef fish distributions. Most small cryptic reef fishes on the Great Barrier Reef are detritivorous (Depczynski & Bellwood 2003). Despite the higher nutritional value of detritus from exposed reef crests (Purcell & Bellwood 2001), loose detrital aggregates settle and concentrate in habitats and reef areas of low water movement such as lagoonal back reefs (Koop & Larkum 1987, Hansen et al. 1992) where they are easily accessed by benthic feeders. For detritivorous species which are physically able to cope with higher water velocities, such as *Ctenochaetus* species (Acanthuridae), reef crests and flats are highly productive and nutritionally rich reef zones and represent preferred locations (Choat & Bellwood 1985). For small cryptic reef fishes, however, these zones are mainly restricted to larger species.

In summary, we find that small cryptic reef fish taxa show a strong level of among-zone variation on coral reefs, but only in locations with high water movement. Microhabitat plays a consistent but secondary role. Regardless of the mechanism, whether direct through water movement impacts on swimming or indirect through habitat or food availability, water movement appears to be a significant factor shaping small cryptic coral reef fish communities.

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