Coral Reefs (2001) 20: 245–251
DOI 10.1007/s003380100165

REPORT

S. Wilson

Multiscale habitat associations of detrivorous blennies (Blenniidae: Salariini)

Received: 17 November 2000 / Accepted: 17 May 2001 / Published online: 14 August 2001

Abstract The distribution and habitat associations of detrivorous blennies on a tropical coral reef were investigated at several spatial scales and compared with other fish that feed on the epilithic algal matrix to assess density and biomass contributions of small detrivorous fishes to these assemblages. At broad spatial scales total blenny abundance and biomass were highest on the tops of reefs exposed to prevailing winds. On the finer scale of microhabitat use, all species showed a preference for non-living corals, although the type of coral utilised differed between species. The high abundance of blennies on reef tops and non-living corals may be partially related to the quality and availability of detritus in these habitats. Comparisons of total blenny abundance and biomass with other territorial detrivores found that blennies accounted for approximately 60% of this functional group's density and 21% of their biomass on exposed reef tops. Overall, territorial detrivores were found to constitute approximately 37% of the density and 26% of the biomass of the detrivorous/herbivorous fish assemblage on exposed reef tops. Small detrivorous fish therefore represent a substantial proportion of fish assemblages that feed on epilithic algae and associated detritus on coral reefs.

Keywords Habitat associations · Detrivorous fish · Biomass · Blenniidae

Introduction

Fish that feed on epilithic algae and associated detritus provide an essential link between primary production and secondary consumers on coral reefs (see reviews by Horn 1989; Choat 1991). Because of their importance to coral reef ecology the distribution of fish that feed on primary resources has been widely studied. However, many of these studies have tended to concentrate on the large, conspicuous species and excluded the smaller, cryptic fish (e.g. Russ 1984a, 1984b; Meekan and Choat 1997). Small fish with total lengths of <100 mm are usually the most diverse and abundant size class of fish on coral reefs (Munday and Jones 1998) and constitute a significant portion of the fish biomass (Akerman and Bellwood 2000). Furthermore, as small fish have a higher mass specific metabolic rate than larger bodied fish (Clarke and Johnston 1999) and generally higher turnover rates, high abundance suggests they play an important role in the transfer of energy on coral reefs (Akerman and Bellwood 2000).

There are a number of different processes that are likely to influence the distribution patterns of coral reef fishes (Williams 1991). The availability of resources, in particular dietary resources, is one process that may have an important role in determining the distribution of herbivorous and detrivorous fishes. To satisfy high energy requirements, herbivorous and detrivorous fishes ingest large amounts of algae or detritus and selectively feed on protein-rich material (Bowen et al. 1995). Spatial variation in the availability and quality of dietary resources may therefore influence the abundance and distribution of the fish that feed on them. Previous studies have examined how algal availability may affect the abundance of herbivorous fishes (e.g. Russ 1984c; Hart et al. 1996); however, the influence of detrital quality and availability on the distribution of coral reef fishes is yet to be established. This is despite recent studies which have found that the quality of detritus can vary across reef zones (Purcell and Bellwood 2001).

Apart from broad-scale patterns of detritus quality, fine-scale distributions of food resources may be particularly important for small detrivores, as many of these fish are site attached (Nursall 1977; Horn 1989; Goncalves and Almada 1998) and rely on resources within

S. Wilson
Department of Marine Biology, James Cook University,
Townsville 4811, Queensland, Australia
E-mail: shaun.wilson@jcu.edu.au
Tel.: +61-7-47815761
Fax: +61-7-47251570

territories to satisfy dietary requirements. The type of microhabitat utilised by these fish must, therefore, be capable of accumulating enough detritus to satisfy their relatively high energetic requirements, as well as provide adequate shelter.

Variation in the availability of suitable habitat resources at both broad and fine scales may have an effect on the distribution of fish. Furthermore, the influence of a habitat resource is likely to vary with spatial scale (Syms 1995) and therefore it is important to examine fish distributions and their relationships with habitat resources at a range of spatial scales.

Blenniid fish from the tribe Salariini are small (5–17 cm total length) cryptic fish (Randall et al. 1990), which feed on the epilithic algal matrix, primarily ingesting detrital aggregates (Wilson 2000). On high-latitude reefs, blennies are an abundant component of fish assemblages (Townsend and Tibbetts 2000), which, in conjunction with other small fish, are responsible for removing large amounts of material from the epilithic algal community (Hatcher 1981). In this environment, salariin blennies represent an abundant and ecologically significant group of small detrivores; however, their significance on tropical coral reefs remains to be determined.

This study will provide baseline information on the distribution and abundance of salariin blennies which will enable future evaluation of the importance of these small detrivorous fishes to coral reef trophodynamics. Distribution patterns of blennies will be examined at broad and fine spatial scales, and used to assess the relationship between blenny abundance and dietary resource availability. Estimates of blenny abundance and biomass will also be compared with that of other herbivorous and detrivorous fishes, providing information on the relative contribution of blennies and small detrivores to assemblages of fish that feed on epilithic algae and associated detritus.

Methods

Visual censuses were conducted on the fringing reef around Lizard Island (14°42′S, 145°30′E) at three locations of differing wind and wave exposure (Fig. 1). The most exposed locations were subjected either directly or obliquely to the prevailing southeasterly winds, whilst sheltered locations were protected from these conditions. The third location was inside the lagoon, where censuses were conducted on contiguous reef. Within each location three sites were selected haphazardly and from each site three transects were conducted on the top and three on the side of the reef. The reef tops were at a depth of 1–2 m at mean high tide and the sides were surveyed at a depth of 2–5 m at mean high tide. Transects of 50×2 m were censused for approximately 20 min by swimming at a constant rate along an underwater tape measure. The transect width and census time were predetermined by a pilot study that compared precision of blenny density estimates at different swimming speeds and transect widths. Visual censuses were conducted at all locations, sites and zones during August 1998 (Austral winter). All censuses were performed between 10:00 and 17:00, as a pilot study had shown that time of day and tidal height had no significant influence on estimates of blenny densities during these hours.

Blennies within transects were identified to species level, their total length estimated and the microhabitat on which they were first observed recorded. The types of microhabitat available to blennies were assessed using point intercept transects. For all blenny-censused transects, available microhabitat was estimated by recording the type of substratum at every marked meter of the transect tape. This provided 50 microhabitat readings for each transect. Microhabitats were classified into: massive, branching, corymbose, encrusting, soft and other corals, as well as rock, rubble, sand and miscellaneous. The different coral categories were based on growth forms described in Veron (1993) and each coral category was further classified as either living or non-living. The miscellaneous category included macroalgae, clams and sponges.

To estimate the total biomass of blennies, total length estimates for each blenny seen on transects were converted to fish weight using length–weight relationships obtained from a representative sample of blenny species collected during the course of the study. The accuracy of fish length estimates was assessed throughout the study by estimating the length of fish in areas adjacent to sampling sites, then capturing the fish and measuring total length with callipers. For 190 fish, with measured total lengths of between 15 and 70 mm, estimated length was 98 ±1% of the actual fish length.

To investigate the relative importance of blennies on coral reefs, their density and biomass at exposed and sheltered locations were compared with those of other detrivorous/herbivorous fishes. Each fish species was assigned a functional group based on published gut content analyses (Sano et al. 1984 ; Wilson and Bellwood 1997 ; Wilson 2000) and their feeding behaviour. Those species with more than 50% detrital material in their guts were classified as detrivores and those with less than 50% detritus but greater than 50% algae were classified as grazers. Densities of territorial pomacentrids were estimated from Meekan et al. (1995), whilst density and size estimates of other species were provided by J.H. Choat (unpublished data). Sites used by Meekan et al. (1995) and J.H. Choat corresponded with those surveyed in this study, although these sites were surveyed at different times. Given the temporal differences between these studies and my own, abundance estimates should be considered as approximations, which were used to suggest the relative importance of blennies as a trophic group on coral reefs. Length–weight relationships from Kulbicki et al. (1993) and L. Bay (unpublished data) were used to convert estimated fish lengths into biomass.

Statistical analyses

The distribution of the six most abundant blenny species at Lizard Island was compared between zones (top and side) and locations

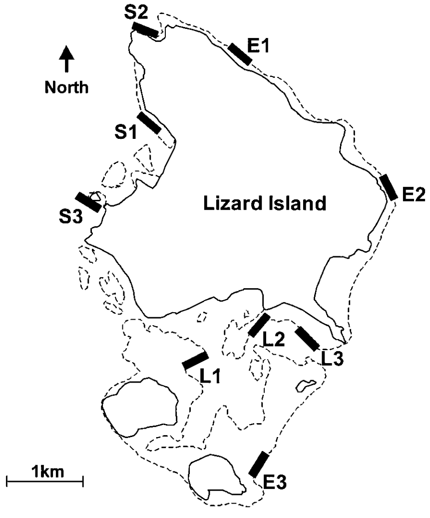

Fig. 1 Map of Lizard Island showing sites in exposed (*E1*, *E2*, *E3*), sheltered (*S1*, *S2*, *S3*) and lagoon (*L1*, *L2*, *L3*) locations

(exposed, lagoon and sheltered) using MANOVA. Before comparisons were made, data within each site were pooled and the mean number of each species on the top of each site and side of each site treated as a replicate. These data were then $\log_{10}(x+1)$ transformed to meet the assumptions of MANOVA. Significant differences in MANOVA were further investigated using a two-way ANOVA for each species, with location and zone as fixed factors. Significance levels were corrected using sequential Bonferroni adjustments (Rice 1989), which reduced the probability of type 1 error which is associated with multiple tests. The mean abundance of each species at different zones and locations was also examined graphically to help interpret ANOVA results. To compare the total density and biomass of salariin blennies, a two-way ANOVA, with reef location and zone as fixed factors, was used. Total biomass data were square root transformed to meet the assumptions of ANOVA and any significant differences were scrutinised using Tukey HSD tests. Fine-scale distribution patterns of blennies were examined using selectivity indices to compare the relative availability and usage of different types of microhabitat. Indices and 95% confidence intervals were calculated using the methods described by Manly et al. (1993) (sampling design II, protocol A). For each blenny species, indices were only calculated for microhabitats where three or more individual fish were seen to use that microhabitat. The remaining microhabitats were pooled into the "other" category. Blennies were considered to use a microhabitat that was at a significantly greater level than was proportionally available if the lower bound of the 95% confidence interval exceeded 1. Conversely, if the upper bound of the confidence interval was less than 1, fish were considered to be using significantly less of the microhabitat than was proportionally available. When the confidence interval intersected with 1, fish use did not exhibit significant selectivity.

Results

Broad-scale habitat associations

Fifteen species of salariin blenny from eight genera were identified during visual surveys of the reefs around Lizard Island (Table 1). The relative abundance of the six most common blenny species varied amongst reef locations and zones. Four of the species were predominantly found at either the lagoon or exposed reefs, whilst the other two species were distributed more evenly between the lagoon, exposed and sheltered locations (Fig. 2). All six species of blenny were found on the tops of reefs and four of the species used this zone almost exclusively (Fig. 2). In contrast, only two species were found in relatively high numbers on the side of reefs and both of these species were also regularly seen on reef tops. MANOVA, conducted on the relative abundance of the six blenny species, confirmed that there were differences in distribution patterns, with a significant interaction between zone and location (Pillai's trace $P<0.001$).

Salarias patzneri was the most abundant blenny species and was mostly found on the top of lagoon reefs (Fig. 2). *Salarias fasciatus* had a similar distribution pattern to *S. patzneri*, with the highest levels of abundance also occurring on the top of lagoon reefs. The relative density of *S. patzneri* is, however, an order of magnitude greater than *S. fasciatus*. The other highly abundant species at Lizard Island is *Cirripectes stigmaticus*, which was observed predominantly on the top of exposed reefs (Fig. 2). Two-way ANOVAs comparing the relative density of individual species found significant interactions between locations and zones for each of the aforementioned species (Table 2). Significant interactions can be attributed to higher densities on the top of lagoon reefs for *S. patzneri* and *S. fasciatus*, and exposed reef tops for *C. stigmaticus* (Fig. 2). No interactions were detected for the other three blenny species, although there were significantly more *Glyptoparus delicatulus* on the top of reefs and significantly more *Atrosalarias fuscus* in the lagoon (Table 2). Of the six species investigated, *E. stictus* was the only species where there was no significant difference detected in broad-scale distributions.

When densities for all blenny species were combined (Fig. 3) the total abundance was significantly higher on the tops of reefs ($F=39.3$, $df=1, 12$, $P<0.001$) and at the lagoon and exposed locations ($F=11.1$, $df=1, 12$, $P=0.002$). There was no significant interaction between zone and location. The weight of individual blennies, calculated from length estimates and the relationships in Table 3, was used to estimate the biomass of blennies at different zones and locations. There was a significant interaction when the biomass of blennies at different zones and locations were compared ($F=14.7$, $df=2, 12$, $P=0.001$). Tukey's HSD test confirmed graphical comparisons (Fig. 3) that the interaction was due to a sig-

Table 1 Salariin blennies observed whilst conducting visual surveys at Lizard Island. Mean total lengths (T. L.) are calculated from visual estimates of fish seen during surveys

Species	Number observed	Mean T. L. ± SE (cm)	Favoured location/zone
Atrosalarias fuscus	37	7.2 ± 0.3	Lagoon/top and side
Blenniella periopthalmus	1	8.0	Exposed/top
Cirripectes chelomatus	13	6.7 ± 0.4	Lagoon/top
Cirripectes filamentous	5	5.4 ± 0.2	Lagoon/top
Cirripectes polyzona	8	5.3 ± 0.2	Exposed/top
Cirripectes stigmaticus	153	8.6 ± 0.2	Exposed/top
Crossosalarias macrospilus	2	5.0 ± 0.5	Exposed and lagoon/side
Ecsenius aequalis	1	4.0	Lagoon/side
Ecsenius bicolor	15	5.2 ± 0.2	Exposed/side
Ecsenius mandibularis	6	4.4 ± 0.2	Lagoon/side
Ecsenius stictus	126	4.1 ± 0.1	Exposed/side
Exallias brevis	3	11.0 ± 0.6	Exposed/top
Glyptoparus delicatulus	29	3.2 ± 0.1	Exposed/top
Salarias fasciatus	22	8.1 ± 0.5	Lagoon/top
Salarias patzneri	188	4.1 ± 0.1	Lagoon/top

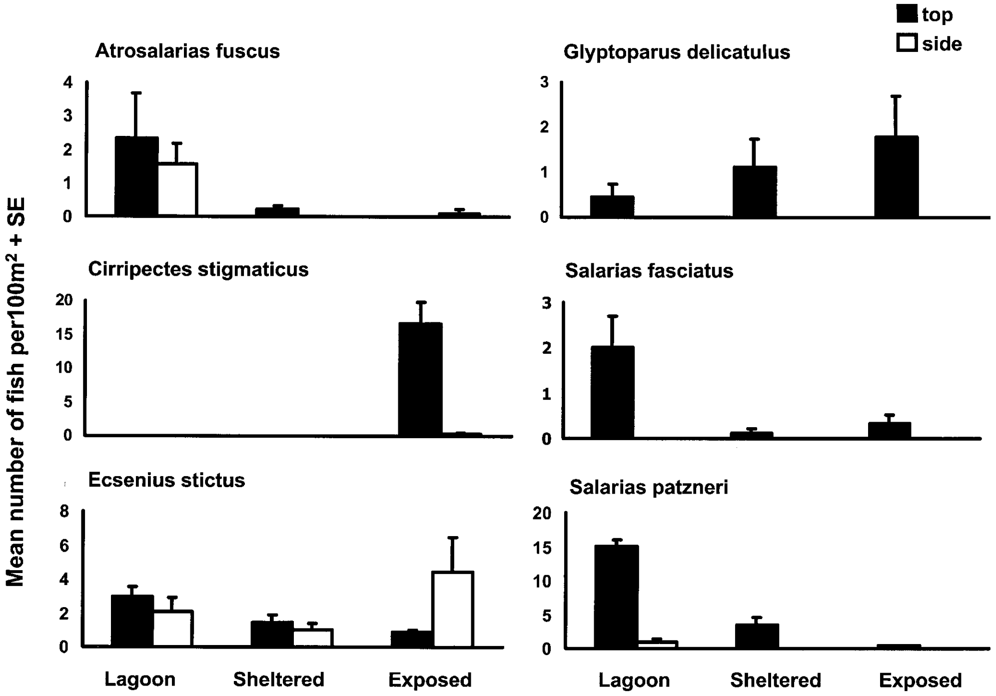

Fig. 2 Broad-scale distribution patterns of the six most abundant species of salariin blenny at Lizard Island. A total of three sites each with three transects were surveyed for each combination of zone and location

Table 2 Summary of significant differences in the broad-scale distribution of six species of salariin blennies. Results are from two-way ANOVAs comparing the relative abundance of each species at different reef locations and zones. ANOVAs were used as a post-hoc investigation of a significant MANOVA interaction between zone and location (Pillai's trace $P < 0.001$)

Species	Significant factor	df	F	P
Atrosalarias fuscus	Location	1, 12	6.2	0.01
Cirripectes stigmaticus	Zone × location	2, 12	25.8	0.001
Ecsenius stictus	None			
Glyptoparus delicatulus	Zone	1, 12	8.6	0.01
Salarias fasciatus	Zone × location	2, 12	6.0	0.01
Salarias patzneri	Zone × location	2, 12	64.3	< 0.001

nificantly greater biomass of blennies on the top of exposed reefs.

Fine-scale habitat associations

Each of the six blenny species investigated in this study was found in one or two microhabitats at a disproportionate level to the microhabitat availability (Fig. 4). Preferences for microhabitats varied between species; however, all species used at least one non-living coral growth form at significantly higher levels than the availability of that microhabitat. *Salarias patzneri*, *Glyptoparus delicatulus* and *Ecsenius stictus* all showed a positive selection for non-living massive corals, whilst *Atrosalarias fuscus* and *Salarias fasciatus* selected non-living branching corals. In addition, *E. stictus* displayed a preference for living massive and *A. fuscus* for living branching corals; however, their use of these microhabitats was less frequent than that of the corresponding non-living growth forms (Fig. 4). *Cirripectes stigmaticus* showed preferences for corymbose corals, living and non-living, as well as encrusting corals.

Blenny abundance and biomass relative to other detrivorous/herbivorous fishes

Density and biomass estimates of all functional fish groups were highest on the top of exposed reefs (Fig. 5). Salariin blennies, which were classified as territorial detrivores, were an important constituent of this functional group, accounting for approximately 60% of the density and 21% of biomass estimates on exposed reef tops. Overall, the territorial detrivores were found to be a substantial component of the total detrivorous/herbivorous fish community. On the top of exposed reefs they contributed 37% to the total density and 26% to the total biomass of detrivorous/herbivorous fishes.

Discussion

The major dietary items ingested by the six species of blenny investigated in this study are detrital aggregates (Wilson 2000). In order to satisfy dietary requirements it is expected that detrivorous fishes, like blennies, will selectively feed at locations rich in protein (Bowen et al.

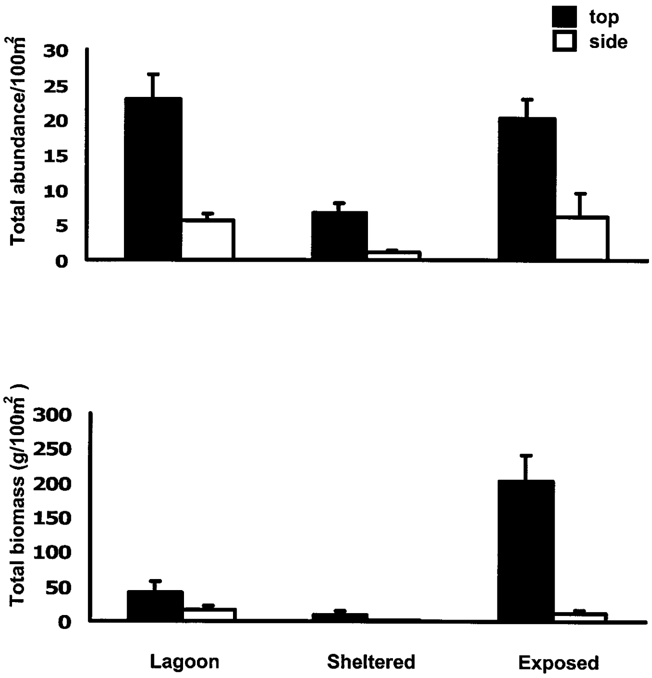

Fig. 3 Broad-scale patterns of total abundance and total biomass of salariin blennies. *Error bars* are standard errors calculated from three sites for each combination of zone and location

Table 3 Length–weight relationships for salariin blennies. W Weight (g); *TL* total length (cm). Equations are based on weight and length measurements of blennies collected from Lizard Island

Species		*n*	r^2
Atrosalarias fuscus	$W=0.013TL^{2.92}$	73	0.98
Cirripectes spp.	$W=0.023TL^{2.81}$	8	0.98
Ecsenius spp.	$W=0.015TL^{2.60}$	49	0.93
Glyptoparus delicatulus	$W=0.01TL^{2.88}$	10	0.91
Salarias fasciatus	$W=0.015TL^{2.87}$	13	0.97
Salarias patzneri	$W=0.007TL^{3.09}$	127	0.97

1995). Of the six blenny species investigated in this study, four were found at significantly higher densities on reef tops, and when blennies were considered as a single group, their density and biomass are highest on the top of reefs at all locations. On an exposed reef at Lizard Island, Purcell and Bellwood (2001) found that although the C:N ratio of detritus did not differ between reef zones, the percentage of organic detritus in sediments was greatest on the crest. Blennies feeding at this location therefore have access to sediments with a higher percentage of organic detritus and nitrogen.

The presence of sediments with a high percentage of organic detritus on exposed reef tops at Lizard Island coincides with high estimates of blenny abundance and biomass in this environment. High levels of blenny abundance on coral reefs have previously been documented by Odum and Odum (1955), who reported a prevalence of small blennies on the reef ridge at Eniwetok, and more recently by Townsend and Tibbetts (2000), who estimated high densities and biomass of blennies on the rim of reefs on the southern Great Barrier Reef. The association of high blenny abundance with exposed reef tops is therefore consistent over a large geographical range of coral reefs. Furthermore, the acanthurid, *Ctenochaetus striatus*, which has a similar diet and feeding technique to many salariin blennies (see Wilson 2000), is also found in high numbers on exposed reef crests (Russ 1984b; Choat and Bellwood 1985). It

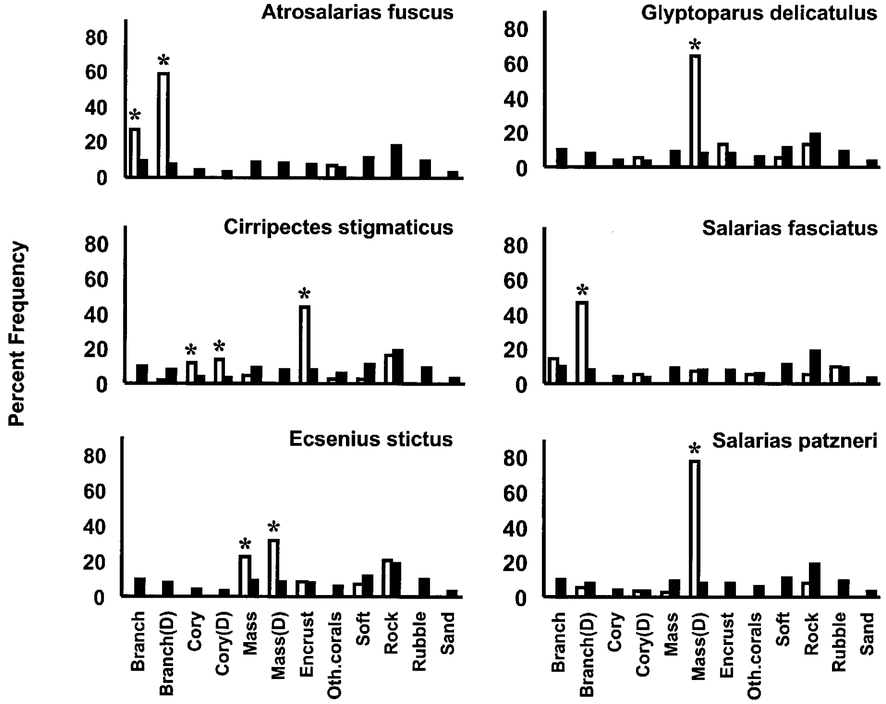

Fig. 4 Microhabitat associations of the six most abundant salariin blennies at Lizard Island. *Percentage values* for microhabitat availability and fish presence were calculated from 54 transects. *Black bars* represent percentage of microhabitat available and *white bars* percentage of fish found in that microhabitat. Asterisks indicate that based on selectivity indices with 95% confidence intervals, fish utilised microhabitat significantly more than expected. *Branch* Branching coral; *Cory* corymbose coral; *Mass* massive coral; *Encrust* encrusting coral; *Oth. corals* other corals; *(D)* coral is non-living

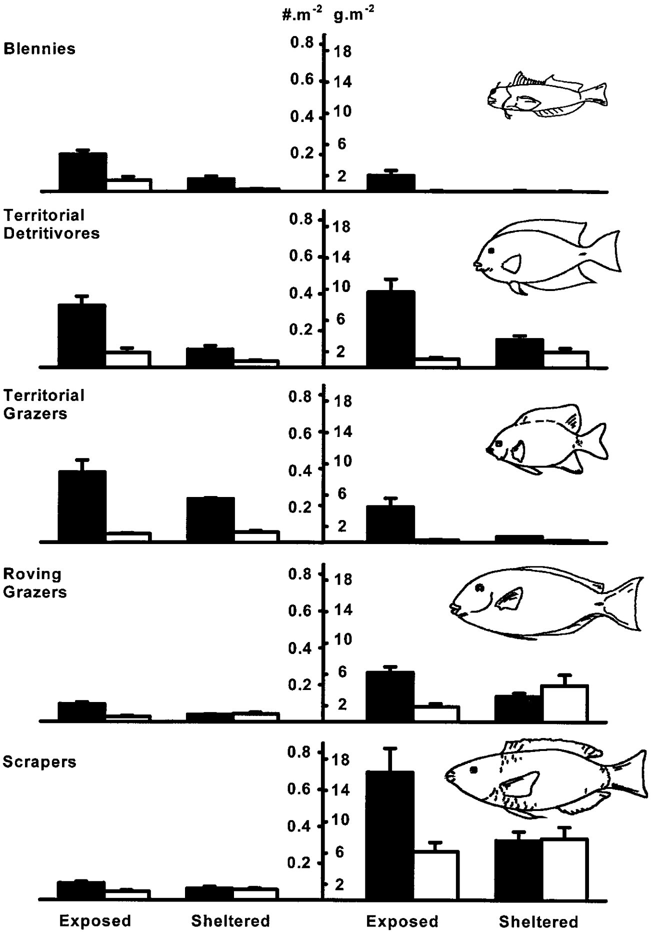

Fig. 5 Relative abundance and biomass of functional groups feeding on detritus and/or algae. Functional group composition: territorial detrivores (salariin blennies, *Stegastes nigricans*, *S. fasciolatus*, *Dischistodus* spp. and *Ctenochaetus* spp.); territorial grazers (*Pomacentrus* spp., *Plectroglyphidodon lacrymatus*, *Stegastes apicalis*, *Acanthurus lineatus*); roving grazers (all acanthurids with the exception of *Ctenochaetus* spp. and *Acanthurus lineatus*); scrapers (all Scarids). *Error bars* are calculated from the sum of standard errors for taxa in each group

therefore seems that the exposed reef crests are the favoured habitat for a range of detrivorous fishes. This may be partially related to the higher organic content of sediments at this location, as organic content can be used as an indicator of the nutritional value of detritus (Bowen 1987). However, other factors such as competition, recruitment and predation are also likely to influence the broad-scale distribution of detrivores. Competition and predation pressures, as well as recruitment levels, are known to vary spatially (Williams 1991) and the effect of these processes on blenny distributions may be substantial.

On a finer spatial scale, each of the blenny species investigated in this study displayed a preference for non-living coral microhabitats. It is possible that the association of blennies with non-living corals is related to the suitability of these microhabitats for accumulating food, as coral skeletons are generally overgrown with filamentous algae that incorporate a matrix of material, including detrital aggregates. Although all species showed a preference for non-living coral microhabitats, the type of coral microhabitat utilised by blennies varied between species. This may reflect the suitability of different microhabitats as a refuge from predators, as many small fish rely on very specific shelter sites (Munday and Jones 1998). Predation can play an important role in the distribution of fish on coral reefs (Stewart and Jones 2001), and the use of microhabitats that act as suitable predator refuges can affect survival and persistence of small fish (Beukers and Jones 1998). Consequently, on a fine scale, it appears that the distribution of blennies may be influenced by the availability of non-living coral microhabitats that act as sites of detrital accumulation as well as provide suitable refuge sites. However, as with broad-scale fish distributions, factors other than resource availability and predation are likely to influence the fine-scale distribution of blennies, and although not addressed in this study, these processes may have a significant affect on the abundance of blennies in different microhabitats.

Comparisons of salariin blenny numbers and biomass with other detrivorous/herbivorous fishes were used to suggest the relative importance of blennies as a trophic group. Blennies represented a substantial part of the functional group, territorial detrivores. On the top of exposed reefs, where the abundance and biomass of all functional groups were highest, blennies accounted for more than half of the density and approximately a fifth of the biomass estimates of territorial detrivores. Overall, territorial detrivores also accounted for approximately a third of the density and a quarter of the biomass estimates of the detrivore/herbivore fish assemblages on exposed reef tops. Temporal differences between blenny censusing and that of other detrivorous/herbivorous fish studies dictate that density and biomass estimates of trophic groups are approximations and that comparisons should be interpreted conservatively. The contribution by blennies and other detrivorous fishes is, however, substantial and suggests that detrital-feeding fish are an important component of coral reef food webs. The contribution of blennies to detrivorous/herbivorous fish assemblages may be even greater on higher latitudinal reefs of the Great Barrier Reef, where blenny biomass relative to other detrivorous/herbivorous fishes (see Townsend and Tibbetts 2000) was even higher than on the reefs surrounding Lizard Island. This suggests that the relative importance of blennies may vary with geographic location.

In summary, most salariin blennies displayed distinct distribution patterns at both broad and fine scales. On a broad scale, blenny numbers and biomass are greatest on the exposed reef top where the relative amount of detritus in sediments is high. On a finer scale they are associated with non-living corals which may act as places of detrital accumulation or shelter sites. This is not to say that detritus availability is the primary factor driving blenny distribution patterns, as other processes, such as competition and predation, are also likely to play an important role in blenny distribution. However, this study did show that at both spatial scales blennies could be associated with the availability of their primary dietary resource, detritus. On the top of exposed reefs, where the density and biomass of all functional groups were highest, blennies were found to be a major component of the functional group territorial detrivores. This functional group represented approximately a third of the density and a quarter of the biomass estimates for the detrivorous/herbivorous fish community. The substantial contribution of small territorial detrivores, like blennies, to the detrivorous/herbivorous fish community suggests these fish are an important component of fish assemblages which are responsible for secondary production on coral reefs.

Acknowledgements This manuscript was improved by discussions with D. Bellwood, R. Fisher, M. Marnane and P. Munday. I gratefully acknowledge the support of staff at the Lizard Island station along with R. Thomas and M. Marnane for help in the field. Special thanks to J.H. Choat and L. Bay for supplying unpublished data on the distribution and size of fish other than blennies.

References

Ackerman J, Bellwood DR (2000) Reef fish assemblages: a re-evaluation using rotenone stations. Mar Ecol Prog Ser 206: 227–237

Beukers JS, Jones GP (1998) Habitat complexity modifies the impact of piscivores on a coral reef fish population. Oecologia 114:50–59

Bowen SH (1987) Composition and nutritional value of detritus. In: Moriarty DSW, Pullin RSV (eds) Detritus and microbial ecology in aquaculture. In: Proc Conference on Detrital Systems for Aquaculture, ICLARM, Manila, pp 192–216

Bowen SH, Lutz EV, Ahlgren MO (1995) Dietary protein as determinants of food quality: trophic strategies compared. Ecology 76(3):899–907

Choat JH (1991) The biology of herbivorous fishes on coral reefs. In: Sale PF (ed) The ecology of fishes on coral reefs. Academic Press, San Diego, pp 120–155

Choat JH, Bellwood DR (1985) Interactions among herbivorous fishes on a coral reef: influence of spatial variation. Mar Biol 89:221–234

Clarke A, Johnston NM (1999) Scaling of metabolic rate with body mass and temperature in teleost fish. J Anim Ecol 68:893–905

Goncalves EJ, Almada VC (1998) A comparative study of territoriality in intertidal and subtidal blennoids (Teleostei, Blennioidei). Environ Biol Fish 51:257–264

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

Hatcher BG (1981) The interaction between grazing organisms and the epilithic algal community of a coral reef: a quantitative assessment. Proc 4th Int Coral Reef Symp 2:515–524

Horn MH (1989) Biology of marine herbivorous fishes. Oceanogr Mar Biol Annu Rev 27:167–272

Kulbicki M, Mou Tham G, Thollot P, Wantiez L (1993) Length–weight relationships of fish from the lagoon of New Caledonia. NAGA, Int Cent Aquat Resour Manage Q, April–July:26–30

Manly BF, McDonald LL, Thomas DL (1993) Resource selection by animals. Chapman and Hall, London

Meekan MG, Choat JH (1997) Latitudinal variation in abundance of herbivorous fishes: a comparison of temperate and tropical reefs. Mar Biol 128:373–383

Meekan MG, Steven ADL, Fortin MJ (1995) Spatial patterns in the distribution of damselfishes on a fringing coral reef. Coral Reefs 14:151–161

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

Nursall JR (1977) Territoriality in redlip blennies (*Ophioblennius atlanticus* – Pisces: Blenniidae). J Zool Lond 182:205–223

Odum HT, Odum EP (1955) Trophic structure and productivity of a windward coral reef community on Eniwetok Atoll. Ecol Monogr 25(3):291–320

Purcell SW, Bellwood DR (2001) Spatial patterns of epilithic algal and detrital resources on a windward coral reef. Coral Reefs in press

Randall JE, Allen GR, Steene RC (1990) Fishes of the Great Barrier Reef and Coral Sea. Crawford House Press, Bathurst

Rice WR (1989) Analyzing tables of statistical tests. Evolution 43:223–225

Russ G (1984a) Distribution and abundance of herbivorous grazing fishes in the central Great Barrier Reef. I. Levels of variability across the entire continental shelf. Mar Ecol Prog Ser 20:23–34

Russ G (1984b) Distribution and abundance of herbivorous grazing fishes in the central Great Barrier Reef. II. Patterns of zonation of mid-shelf and outershelf reefs. Mar Ecol Prog Ser 20:34–44

Russ G (1984c) Abundances of herbivorous fishes and measures of food availability across the continental shelf in the central Great Barrier Reef region. Productivity and processes in island marine ecosystems. UNESCO Rep Marine Sci 27:63–73

Sano M, Shimizu M, Nose Y (1984) Food habits of teleostean reef fishes in Okinawa Island, Japan. Publ 25. University Museum, University of Tokyo, pp 1–128

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

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

Townsend KA, Tibbetts IR (2000) Biomass and distribution of herbivorous blennies in the southern Great Barrier Reef. J Fish Biol 56:774–791

Veron JEN (1993) Corals of Australia and the Indo-Pacific. University of Hawaii Press, Honolulu

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

Wilson S (2000) Trophic status and feeding selectivity of blennies (Blenniidae: Salariini). Mar Biol 136:431–437

Wilson S, Bellwood DR (1997) Cryptic dietary components of territorial damselfishes (Pomacentridae, Labroidei). Mar Ecol Prog Ser 153:299–310