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Spatial patterns in the distribution of damselfishes on a fringing coral reef

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Abstract. Damselfishes are an important element of the fauna of coral reefs. This study describes spatial patterns in the distribution of 15 species of damselfishes at Lizard Island, northern Great Barrier Reef (GBR). The aim of the work was to identify the spatial scales at which major changes in the composition and abundance of the fauna occurred. These patterns were then compared with previous studies in an attempt to determine if distributions followed general patterns at a range of localities. The assemblage found at Lizard Island was similar to that of reefs in the central GBR. The most important changes in the composition of the fauna occurred among reef zones. Shallow zones (the reef flat and crest) were dominated by herbivorous species while planktivorous and omnivorous species were most abundant in deeper zones (the reef slope). Densities of herbivorous damselfishes in shallow reef zones at Lizard Island averaged 45.5 individuals per 80 m^2, a value comparable to densities found in similar zones on reefs in the central and southern GBR and at one locality in the Caribbean. Comparisons of relative distributions suggested that abundant species tend to be widely distributed among zones and habitats, while rare species have restricted distributions at Lizard Island. However, computer simulation of the sampling program suggested that the ability of our study to describe the distribution patterns of rare species was limited, despite intensive sampling. Correlations between breadth of distribution and abundance may have occurred simply because rare species were less likely to be recorded within a transect. Our results suggest that it will be difficult to compare the distribution patterns of species among studies. Furthermore, the interpretation of relative patterns of distribution at a single locality in terms of ecological specialization or partitioning may first require an assessment of the ability of the sampling program to accurately record spatial patterns.

Introduction

Damselfishes (Pomacentridae) occur in shallow habitats throughout tropical seas (Allen 1975). The greatest diversity of species is found on coral reefs, where damselfishes are conspicuous and abundant members of the fish fauna. Many of the species inhabiting coral reefs are herbivorous, maintaining algal gardens within a territory. Such gardening behaviour may have a great range of effects on local communities by altering coral recruitment and bioerosion, microfaunal abundance, algal abundance and diversity and nitrogen fixation (reviewed by Hixon 1983; Horn 1989). Furthermore, the defense of feeding territories can affect the local distribution of larger, mobile fish such as scarids, acanthurids and siganids (e.g. Robertson et al. 1979) and invertebrates (e.g. Sammarco and Williams 1982).

Numerous studies have documented patterns in the distribution and abundance of this important element of the fauna. On the Great Barrier Reef (GBR) variability in the abundance of herbivorous damselfishes has been described at a variety of spatial scales: among reefs at differing positions on the continental shelf (Williams 1982; Williams and Hatcher 1983); among habitats differing in wave exposure and/or topography within a reef (Sale and Dybdahl 1978; Robertson and Lassig 1980; Birdsey 1989); and among sites within a reef habitat (Robertson and Lassig 1980; Sale et al. 1980; Williams 1982; Birdsey 1989).

In this study, we describe the distribution and abundance patterns of herbivorous and omnivorous damselfish on a fringing reef at Lizard Island, northern Great Barrier Reef (14°40′ S, 145°28′ E) with the aim of identifying the spatial scales at which major changes in composition and abundance occur. Following this description of pattern, we examine the extent to which our results at Lizard Island

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are typical of those recorded by previous studies both on the GBR and on coral reefs worldwide. These comparisons address the question: to what extent can we identify general patterns that might indicate the existence of some general rules governing the distribution of damselfishes on all reefs?

Materials and methods

Study areas

Abundance patterns of damselfishes were described during June 1987. The fringing reef surrounding Lizard Island was divided into windward habitats that were exposed to the prevailing southeast winds and swell; oblique habitats, oriented parallel to the southeasterly wind direction; granite habitats on the leeward side of the island where the fringing reef was absent and corals grew directly upon granite rock; and the lagoon, which was encircled by fringing reef (Fig. 1).

Sampling design

A pilot study was used to identify both the common species of damselfishes and any major topographical features present in the four habitats. At two sites within each habitat, two 50 m transect tapes were laid from the lower edge of the reef slope to the reef flat. Sites were separated by approximately 150 m, and transect tapes by 10 m within each site. Divers identified and counted herbivorous damselfishes within 2 m of either side of the tape. The depth and major substratum type were recorded at 2 m intervals along the tape so that reef profile could be constructed.

A total of 15 species of damselfishes were recorded by the pilot study, 11 of which were strictly herbivorous and territorial. These species were *Dischistodus perspicillatus*, *D. prosopotaenia*, *D. pseudochrysopoecilus*, *Plectroglyphidodon lacrymatus*, *Pomacentrus bankanensis*, *P. chrysurus*, *P. grammorhynchus*, *P. wardi*, *Stegastes apicalis*, *S. fasciolatus*, and *S. nigricans*. The four remaining species were omnivorous. Three of these fed on benthic algae and plankton (*P. amboinensis*, *P. nagasakiensis* and *Neoglyphidodon nigroris*) while one species, *N. melas*, fed on benthic invertebrates and algae (Allen 1975). All species were included in the analysis. Due to difficulties with accurate identification, counts did not distinguish between two morphologically similar species, *P. bankanensis* and *P. chrysurus*.

The reef profiles identified three major topographic features (zones) in the four habitats: the reef flat zone, an area of low-relief substrate in shallow water (1–3 m depth), extending from the low-water mark to the top of the reef crest; the reef crest zone (3–6 m depth), which started where the reef profile began to drop away to deeper water and included the part of the reef where the steepest decline in the profile occurred; and the reef slope zone (6–12 m depth), which began at the lower edge of the reef crest and included the area of reef where the profile declined gradually to sand at the reef edge. These definitions of zones follow those of Choat and Bellwood (1985). The area of reef encompassed by zones was not equivalent in all habitats. The reef flat covered an extensive area in the windward

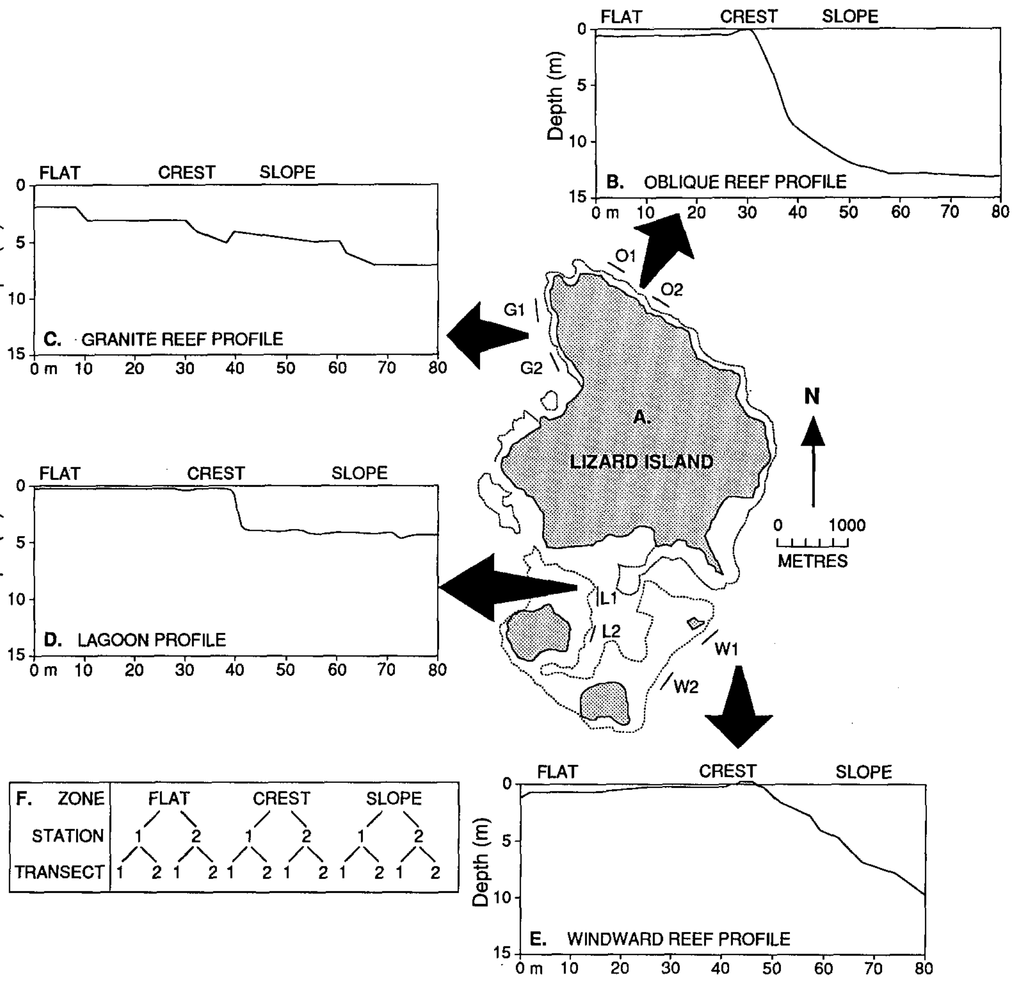


Fig. 1 A Map of Lizard Island showing sites in windward (*W1*, *W2*), oblique (*O1*, *O2*), granite (*G1*, *G2*) and lagoon (*L1*, *L2*) habitats; **B–E** profiles of the reef in each habitat; **F** sampling design within each site

habitat, but was much smaller elsewhere. The area of the reef slope zone in the lagoon habitat was relatively small, as the sand began almost immediately at the base of the reef crest. In the granite habitat, the distinction between reef zones was blurred as the reef profile did not have clear points of inflexion (Fig. 1).

The distribution and abundance patterns of 15 species of damselfishes were examined within three zones in each of the four habitats at Lizard Island. Two stations separated by 50 m were established in each of the sites used previously in the pilot study. Within each station, two 20 m transect tapes were laid parallel to the reef margin in each of the three zones, giving a total of 12 transects per site and 24 transects per habitat (Fig. 1). Damselfishes were counted for 2 m on either side of the transect tape.

Data analysis

Multivariate techniques of classification and ordination were used to analyze patterns of abundance and faunal composition. The classification analysis calculated Bray-Curtis similarity coefficients among replicate transects ($n = 96$) and then among abundances of individual species. A cumulative, "unweighted group mean" sorting strategy (Abel et al. 1985) was used to classify each similarity matrix. Cramer values identified the relative contribution that each species made to groupings identified from the analysis of transect counts.

Hybrid, multidimensional scaling (MDS), an ordination analysis, was used to examine abundance and species composition among sites ($n = 24$). This technique constructs a similarity map based on rank order of species where the distance between sites on the map reflects dissimilarity. Data were transformed to $\log_{10}(x + 1)$ values and between-sample similarities quantified using the Bray-Curtis coefficient. Principal axis correlation was then used to determine the association between the ordination vectors calculated by the MDS and the abundance of each species. The results of this analysis were also plotted on the similarity map. The groupings from the classification analysis of transect counts were then superimposed on both ordination plots to assess the consistency of results using the two types of multivariate analysis.

A four-factor, mixed-model analysis of variance (ANOVA) was used to analyze the abundance patterns of individual species. Habitat and zone were fixed orthogonal factors. Site and station were nested hierarchically within habitat and zone. Examination of residuals suggested a $\log_{10}(x + 1)$ transformation of raw data was required to satisfy the assumptions of normality and homoscedascity made by the ANOVA. When significant differences in abundance were indicated by the ANOVA, comparisons among means were made using Tukey tests (Zar, 1984).

Results

Multivariate analysis of damselfish abundance

The classification analysis distinguished five groups of transect counts (Fig. 2A). In the first split of the dendrogram, transects in reef flat and crest zones in windward and oblique habitats were separated from all reef slope, granite reef, and some lagoon transects. The flats and crests grouping was then split into one group consisting only of crest transects in windward and oblique habitats (group I) and a second group consisting of all transects in reef flat zones in the windward and oblique habitats, and some transects from flat zones in the lagoon (group II). The other group made by the initial division of the dendrogram that included all reef slope, granite, and some lagoon transects was further divided into a group of reef slope transects from windward, oblique, and granite habitats (group III) and a group of granite flat and crest transects and lagoon crest and slope transects. This latter group was divided into lagoon crest and some slope transects (group IV) and a group consisting of reef flat and crest transects from the granite habitat and slope transects from the lagoon (group V).

Cramer values suggested that the relative abundances of *Pomacentrus amboinensis* and *Stegastes nigricans* were the most important determinants of these groupings (Fig. 2). *Pomacentrus amboinensis* occurred in large numbers in groups III, IV, and V, while *S. nigricans* was abundant in group IV and present in low numbers in group V. *Pomacentrus bankanensis/chrysurus* also had a high Cramer score and was the most common species in groups I, II and IV, the second most abundant species in group V, and occurred in relatively low numbers in group III.

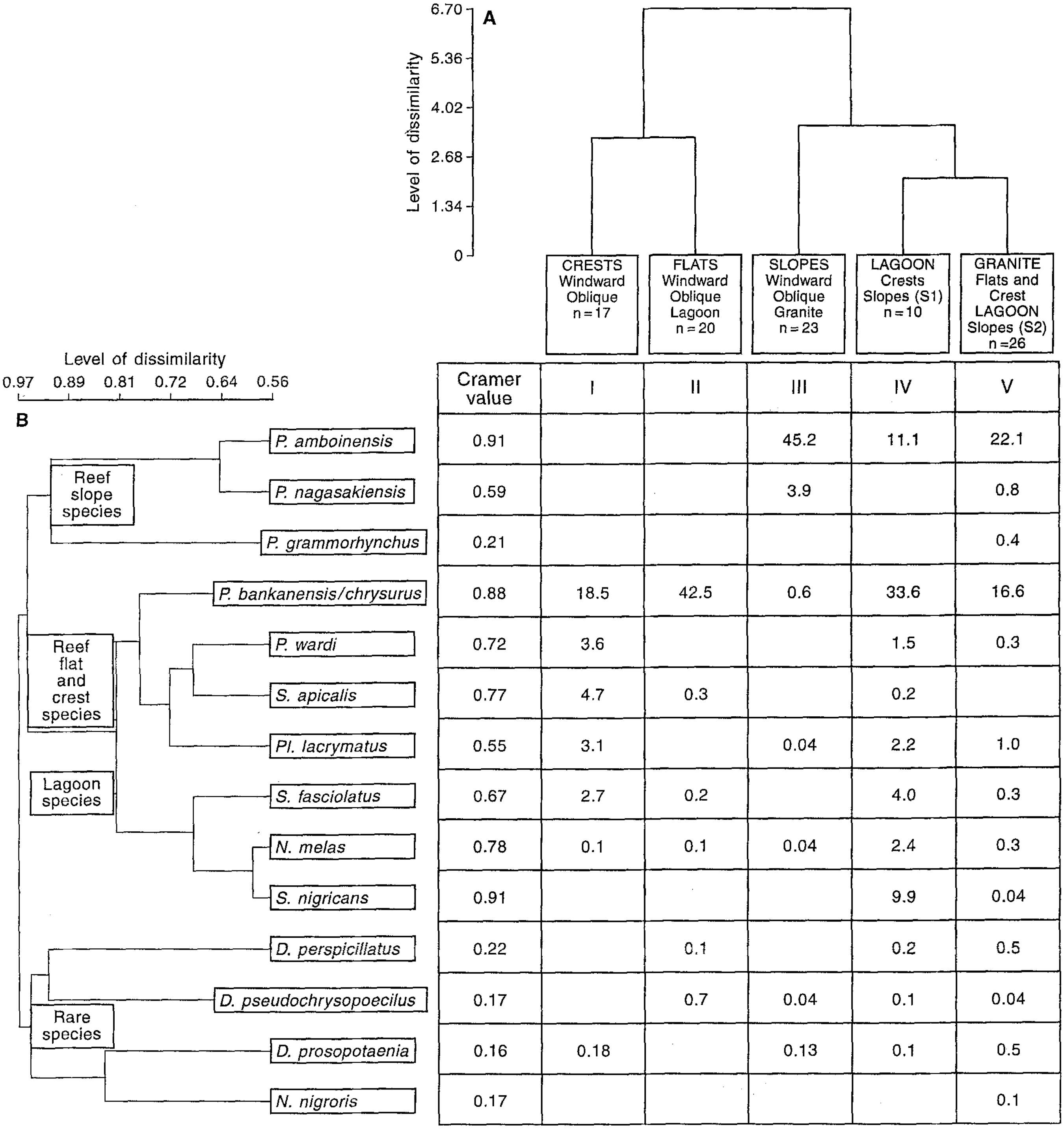
Classification analysis of the species abundance matrix identified four groups (Fig. 2B). A group of rare species was distinguished in the first split of the dendrogram. Two more divisions were recognized within the remaining group. The first separated a group of species common on the reef slope (*Pomacentrus amboinensis*, *P. nagasakiensis*, and *P. grammorhynchus*) from the remainder, which was subdivided further into a group of shallow water (*P. bankanensis/chrysurus*, *P. wardi*, *Stegastes apicalis*, and *Plectroglyphidodon lacrymatus*) and lagoon species (*Neoglyphidodon melas*, *S. nigricans* and *S. fasciolatus*).

Multidimensional scaling analysis confirmed the patterns identified in the classification analysis of transect counts. Sites in the reef flat of windward, oblique, and lagoon habitats grouped together and were most similar to reef crest sites in windward and oblique habitats. Reef slope sites in windward, oblique, and granite habitats were the most dissimilar from these two groups. Sites on the reef flat and crests in the granite reef habitat grouped together, adjacent to the grouping of reef slope sites. Crest and slope sites in the lagoon formed the last group, equidistant between the group of granite crest and flat sites and the group of windward and oblique crest sites. A single reef slope site in the lagoon grouped with the granite crest and slope sites.

The position of species plotted in the ordination space also suggested similar patterns to those discerned by the classification analysis of species abundances. The species characteristic of the reef slope, *Pomacentrus amboinensis* and *P. nagasakiensis*, grouped together close to *P. grammorhynchus*. Species common on the reef crest, *Plectroglyphidodon lacrymatus*, *P. wardi*, and *Stegastes apicalis*, grouped together with the lagoon species *Neoglyphidodon melas*, *S. nigricans*, and *S. fasciolatus*. The rare species, *Dischistodus pseudochrysopoecilus*, *D. perspicillatus*, and *N. nigroris* formed a separate group. *Pomacentrus bankanensis/chrysurus*, which was common in nearly all habitats and zones other than the reef slope, was plotted separately from most other species.

Species richness and abundance

The greatest species richness of damselfishes was recorded in the granite and lagoon habitats (11 species), although



	Cramer value	I	II	III	IV	V
P. amboinensis	0.91			45.2	11.1	22.1
P. nagasakiensis	0.59			3.9		0.8
P. grammorhynchus	0.21					0.4
P. bankanensis/chrysurus	0.88	18.5	42.5	0.6	33.6	16.6
P. wardi	0.72	3.6			1.5	0.3
S. apicalis	0.77	4.7	0.3		0.2	
Pl. lacrymatus	0.55	3.1		0.04	2.2	1.0
S. fasciolatus	0.67	2.7	0.2		4.0	0.3
N. melas	0.78	0.1	0.1	0.04	2.4	0.3
S. nigricans	0.91				9.9	0.04
D. perspicillatus	0.22		0.1		0.2	0.5
D. pseudochrysopoecilus	0.17		0.7	0.04	0.1	0.04
D. prosopotaenia	0.16	0.18		0.13	0.1	0.5
N. nigroris	0.17					0.1

Fig. 2. Summary of classification analyses. Dendrograms generated from the classification analysis of transect counts (**A**) and analysis of abundances of 14 species of damselfishes (**B**) are shown. Cramer values indicate the relative contribution of each species to the discrimination between groups in the analysis of transect counts. Values in the table represent the mean number per 80 m^2 of a species in counts from each of the classification groups

total richness in other habitats was only marginally lower (8–10 species, Table 1). Species richness did not vary among zones when counts in all habitats were combined. There was, however, considerable variation in richness among zones within habitats (Table 1). Richness varied from three species in the reef flat to 11 in crest zones in the lagoon, while eight species occurred in crest zones and two in reef slope zones in the windward habitat. Less variation in richness occurred among zones in other habitats.

The total abundance of damselfishes in counts averaged 45.5 individuals per 80 m^2. Densities varied significantly among habitats, ranging between 60.3 individuals in the

Table 1. Mean total abundance ($\pm$standard error, SE) per 80 m^2 of damselfishes in each of 4 habitats and 3 zones at Lizard Island. Richness is the total number of species counted in each habitat or zone

Habitat		Topographic zone Flat	Crest	Slope	Total
Windward	Abundance $\pm$ SE	37.3 $\pm$ 6.4	31.1 $\pm$ 3.1	57.0 $\pm$ 11.8	41.8 $\pm$ 5.0
	richness	5	8	2	8
Oblique	Abundance $\pm$ SE	42.2 $\pm$ 7.4	31.3 $\pm$ 4.6	33.5 $\pm$ 3.5	35.7 $\pm$ 3.2
	richness	5	5	8	10
Granite	Abundance $\pm$ SE	30.8 $\pm$ 6.0	34.4 $\pm$ 5.6	67.5 $\pm$ 13.0	44.2 $\pm$ 6.0
	richness	9	6	6	11
Lagoon	Abundance $\pm$ SE	56.5 $\pm$ 3.9	66.6 $\pm$ 5.1	57.8 $\pm$ 8.4	60.3 $\pm$ 3.5
	richness	3	11	9	11
Total	Abundance $\pm$ SE	41.7 $\pm$ 3.3	40.8 $\pm$ 3.5	53.9 $\pm$ 5.2	45.5 $\pm$ 2.4
	richness	12	12	12	14

Table 2. Summary of 4 factor mixed-model ANOVAs examining the abundance patterns of damselfishes at Lizard Island

Species	Sources of variation					
	Habitat	Zone	Habitat* zone	Site	Station	Residual
df	3	2	6	12	24	48
Total damselfish[a]	* 13%	ns 3%	ns 9%	* 14%	ns 0%	61%
Pomacentrus amboinensis	*** 16%	*** 58%	** 13%	** 4%	ns 1%	8%
Pomacentrus nagasakiensis	*** 15%	*** 14%	** 7%	ns 0%	ns 6%	58%
Pomacentrus bankanensis/chrysurus	** 14%	*** 68%	ns 2%	*** 9%	ns 1%	6%
Pomacentrus grammorhynchus	ns 3%	ns 0%	ns 0%	ns 0%	ns 0%	97%
Pomacentrus wardi	ns 2%	*** 26%	ns 7%	ns 0%	** 24%	41%
Neoglyphidodon melas	* 31%	ns 3%	ns 0%	*** 15%	ns 0%	51%
Neoglyphidodon nigroris	ns 0%	ns 0%	ns 0%	ns 0%	ns 0%	100%
Plectroglyphidodon lacrymatus	ns 0%	** 23%	ns 21%	ns 1%	* 11%	44%
Stegastes apicalis	ns 11%	ns 11%	ns 5%	*** 38%	ns 0%	35%
Stegastes fasciolatus	ns 10%	* 14%	ns 15%	* 19%	* 13%	29%
Stegastes nigricans	** 35%	ns 6%	ns 6%	ns 6%	** 18%	29%
Dischistodus perspicillatus	ns 6%	ns 0%	ns 0%	*** 36%	ns 0%	58%
Dischistodus prosopotaenia	ns 0%	ns 1%	ns 0%	*** 28%	ns 0%	71%
Dischistodus pseudochrysopoecilus	ns 0%	ns 0%	ns 0%	ns 0%	ns 0%	100%

$*P < 0.05$; $**P < 0.01$; $***P < 0.001$; ns $P > 0.05$

The percentage of total variance accounted for by each factor is also given

[a] Shows the analysis of mean total number of damselfishes per 80 m^2

lagoon to 35.7 individuals in oblique habitats (Table 1, Table 2), but did not vary among zones within habitats. The species *Pomacentrus amboinensis* and *P. bankanensis/chrysurus* accounted for 84% of the total numbers of fish sampled. These occurred in overall densities of 18.2 ($\pm$ 2.7 SE) and 20.1 ($\pm$ 2.1 SE) per 80 m^2 respectively. The remaining species all occurred in mean densities of less than 1.3 individuals per 80 m^2.

The distribution patterns of species varied among habitats (Table 2). *Pomacentrus bankanensis/chrysurus*, *Neoglyphidodon melas*, and *Stegastes nigricans* were most abundant in the lagoon, while *P. amboinensis* and *P. nagasakiensis* occurred in greatest numbers in the granite reef habitat. *Pomacentrus nagasakiensis* was not recorded in the lagoon (Fig. 3). Distributions of six species varied significantly among topographic zones. Abundance of *P. bankanensis/chrysurus* were greatest on the reef flat and crest, while numbers of *P. wardi* and *Plectroglyphidodon lacrymatus* were highest on the reef crest. *Pomacentrus amboinensis* and *P. nagasakiensis* were abundant on the reef slope and virtually absent from other reef zones (Fig. 3). However, these patterns were not consistent in all

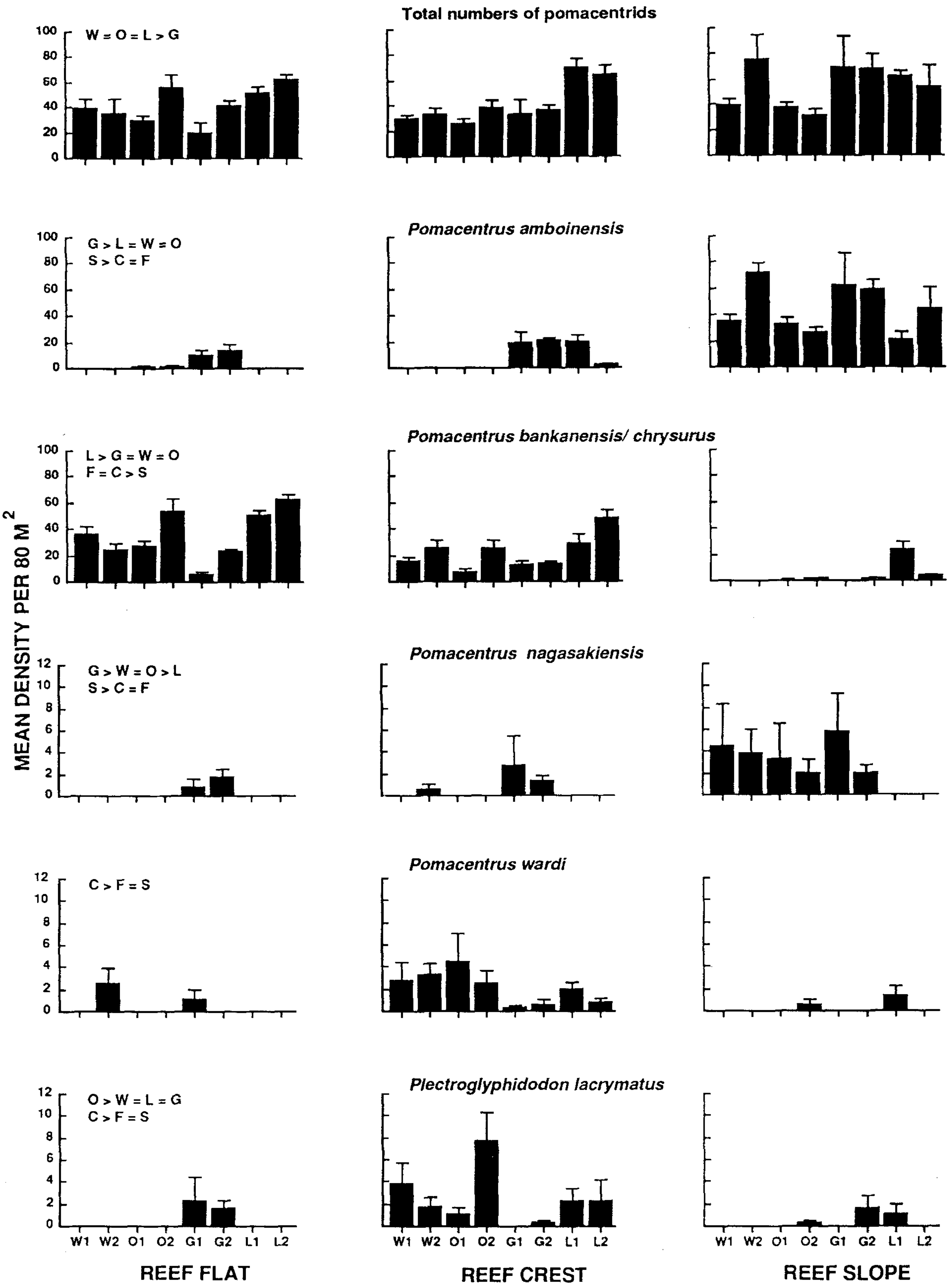


Fig. 3. Mean density per 80 m^2 ($\pm$SE) of the total number of damselfishes and 12 species by zone at each site. Distribution patterns of *P. grammorhynchus*, *N. nigroris*, *D. pseudochrysopoecilus* are not shown; these occurred in very low mean numbers ($<$0.19 individuals per 80 m^2). The latter two species were only recorded in flat and slope zones at one site in the granite habitat. Sites in each habitat are shown as in Fig. 1. Where the factors habitat or zone were significant in the ANOVA analysis, the results of a Tukey test (significance level $P < 0.05$) for the multiple comparison of means are shown *W* windward habitat, *O* oblique habitat, *G* granite habitat, *L* lagoon habitat, *F* reef flat zone, *C* reef crest, *S* reef slope

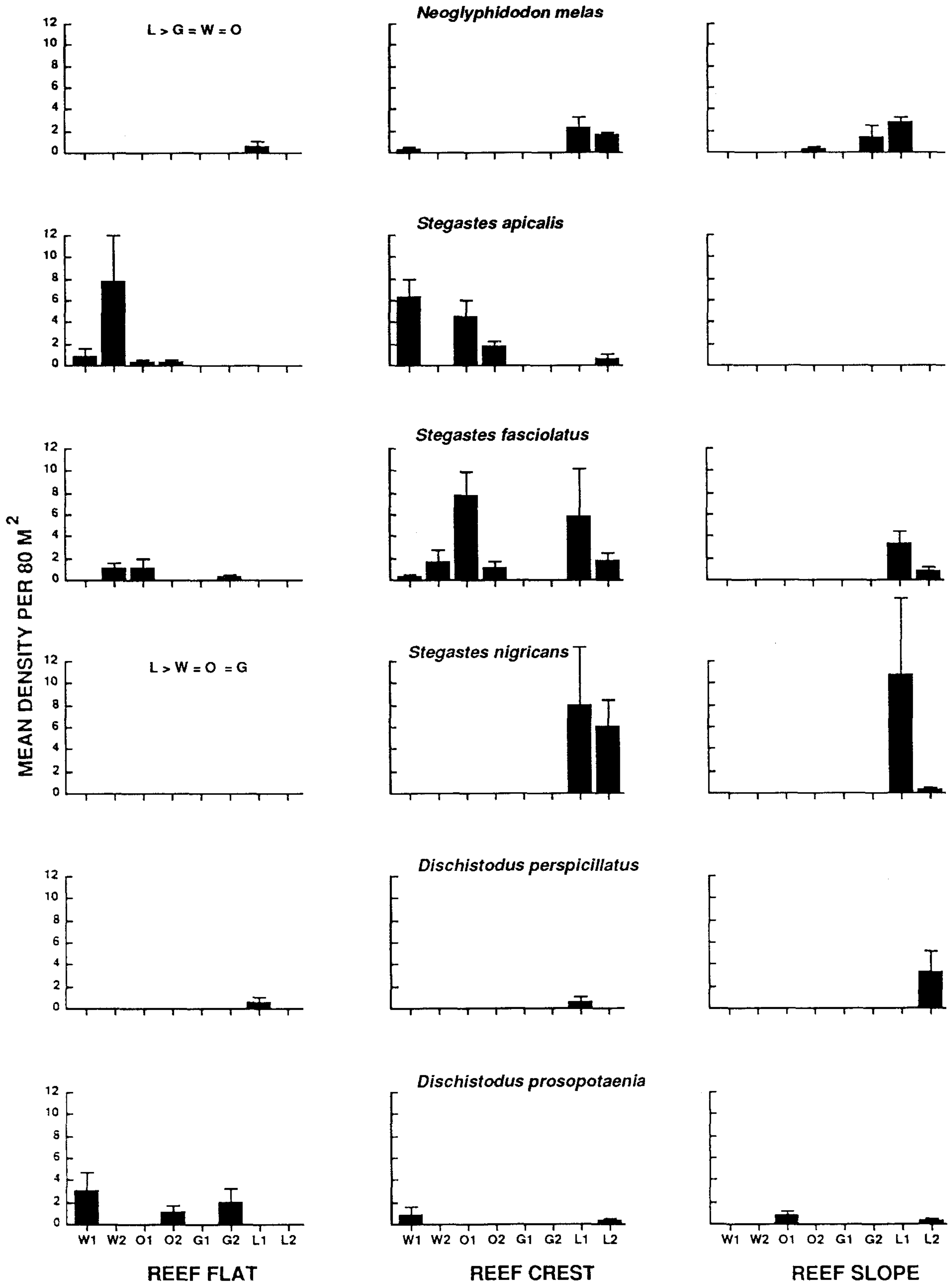


Fig. 3. (Continued)

habitats; low numbers of *P. amboinensis* occurred in the crest zone in the lagoon and both *P. amboinensis* and *P. nagasakiensis* were found in reef flat and crest zones in the granite habitat. Changes in abundance among zones explained the majority of variability in the distribution of the two most common species, *P. bankanensis/chrysurus* and *P. amboinensis.* This factor accounted for less variation in the abundance of *P. wardi* (26%), *Pl. lacrymatus* (23%) *P. nagasakiensis* (14%) and *S. fasciolatus* (14%).

The total numbers of damselfishes per count and the abundances of seven species varied significantly between sites within a habitat, although this factor explained relatively little of the variability in counts of the two most common species, *Pomacentrus amboinensis* and *P. bankanensis/chrysurus* (4% and 9% of total variance respectively) or variability in the total numbers of fish per count (14%). Between-site differences in abundance were more important for *Stegastes apicalis* (38% of total variance), *Dischistodus perspicillatus* (36%), *D. prosopotaenia* (28%) and *S. fasciolatus* (19%), most of which occurred in relatively low numbers. Counts of *Pomacentrus wardi, Plectroglyphidodon lacrymatus, Stegastes fasciolatus* and *S. nigricans* varied between stations approximately 50 m apart; however, this factor accounted for less than 25% of the total variation in abundance of these species.

The greatest proportion of the variation in abundance of *Pomacentrus nagasakiensis, P. wardi, Neoglyphidodon melas, Plectroglyphidodon lacrymatus, Stegastes fasciolatus, Dischistodus perspicillatus, D. prosopotaenia,* and total numbers of damselfishes occurred between replicate transects. Differences at this spatial scale accounted for over 50% of the total variability in abundance of *P. nagasakiensis, N. melas, D. perspicillatus,* and *D. prosopotaenia,* and over 60% of the variability in total numbers of damselfishes. In contrast, differences between transects explained only 8% of the variability in counts of *P. amboinensis,* and 6% of the variability of *P. bankanensis/chrysurus.* This result implies that many species occur in small (<20 m) patches within a station. The ANOVA failed to detect any significant differences in the abundance of *P. grammorhynchus, N. nigroris* and *D. pseudochrysopoecilus* at any spatial scale. These species all occurred in mean densities of less than 0.1 individuals per 80 m^2, thus the power of analyses to detect changes in abundance was probably too low.

Discussion

The fauna of herbivorous and omnivorous damselfishes occurring on the fringing reefs of Lizard Island was similar to that of reefs in the central section of the GBR. All of the species we recorded were found at John Brewer Reef on the central GBR by Birdsey (1989), with the exception of *Neoglyphidodon nigroris.* Two species, *Chrysiptera leucopoma* and *Pomacentrus tripunctatus,* both of which are territorial herbivores, were present at John Brewer Reef (Birdsey 1989; McCormick et al. unpubl. data), but were not recorded in our counts. Average densities of damselfishes were also similar at both localities (approximately 40 individuals per 80 m^2 at John Brewer Reef; 45.5 individuals per 80 m^2 at Lizard Island) as were patterns of relative abundance. Faunas at both reefs were dominated by *P. amboinensis* and *P. bankanensis* although, at Lizard Island, some individuals of *P. chrysurus* were included in the counts of *P. bankanensis.*

The great variety of methods used to sample distributions of damselfishes complicates any attempt to compare estimates of densities among localities. With the exception of Birdsey (1989), quantitative estimates are available from only two other studies, one at Puerto Rico in the Caribbean (Waldner and Robertson 1980) and the other at Heron Island on the southern GBR (Robertson and Lassig 1980). Both recorded densities of damselfish in shallow zones (0–9 m depth) that were remarkably similar to those found at Lizard Island. In Puerto Rico, abundances averaged 42 individuals per 80 m^2 (range 55.2 to 36.8 individuals) while at Heron Island, the average density in shallow zones (excluding the intertidal) was 39.8 individuals per 80 m^2. The variation in densities at Heron Island was large, ranging from 77.1 individuals on the reef flat to 5.5 individuals per 80 m^2 on the reef crest.

The most striking changes in composition of damselfish faunas at Lizard Island occurred among zones within a habitat. Reef flat and crest zones were characterized by herbivorous species, notably *P. bankanensis/chrysurus.* These species were absent or rare in most slope zones where the omnivorous/planktivorous species *P. amboinensis* and *P. nagasakiensis* dominated counts. This pattern appeared to be correlated with depth. In the lagoon, where there was a small reef crest and the reef slope began in shallow water, *P. bankanensis/chrysurus* was found on the reef slope, while both *P. amboinensis* and *P. nagasakiensis* were found on the reef flat and crest zones in the granite habitat. In the latter habitat, the reef profile sloped gradually to the sand and the reef flat and crest zones occurred in relatively deep water.

Depth-related zonation patterns of damselfishes are a common phenomenon and generally follow the pattern found at Lizard Island of peak abundances of herbivorous species in shallow reef zones, while planktivorous damselfishes are found in deeper zones (Allen 1975; Williams 1991). Examples of this distribution pattern have been described from inshore reefs in the northern and central GBR (Birdsey 1989), and midshelf reefs in the central (Hamner et al. 1988; Birdsey 1989) and southern GBR (Robertson and Lassig 1980). However, at the locality examined by the latter study (Heron Island), zonal distributions were not consistent among sites: on the southern side of the reef the abundance of herbivorous damselfishes declined from 77 individuals per 80 m^2 on the reef flat (subtransect 3 in Robertson and Lassig 1980) to 39 individuals per 80 m^2 on the reef slope (subtransects 7 and 8), while on the northern side of Heron Island, 52 damselfishes per 80 m^2 were recorded on the reef flat, 25.5 per 80 m^2 on the reef crest (subtransects 4, 5 and 6), and 36 per 80 m^2 on the reef slope. At Puerto Rico, Waldner and Robertson (1980) found that the density of herbivorous damselfishes (excluding an abundant omnivore, *Stegastes partitus*) declined from 42 individuals per 80 m^2 in depths of 0–9 m to only 6 individuals per 80 m^2 in depths of 9–18 m. In contrast, Clarke (1977) found no consistent trends in the distribution of damselfishes with depth on reefs at Bimini in the Bahamas. *Abudefduf saxatillis*, the most abundant planktivore at this locality, occurred in three zones in water less than 2.5 m deep. A similar pattern was recorded for another planktivorous species, *A. taurus*, although the remaining three planktivorous damselfishes sampled by his study (all of which were *Chromis* spp) were rare or absent in shallow zones and increased in abundance with depth. Counts of herbivorous and omnivorous damselfishes displayed few obvious patterns in abundance among zones, although these comparisons must be interpreted with caution as sampling effort was not equally partitioned among depths.

Distinctive patterns of zonal distribution are a feature of many families of reef fishes including the chaetodontids, acanthurids, scarids, siganids, scorpaenids, and serranids (reviewed by Williams 1991). Russ (1984) described the zonation patterns of the scarids, acanthurids, and siganids on mid- and outer shelf reefs in the Townsville region of the GBR. He found that shallow zones within a reef contained a fauna of herbivores that was distinct from that of deeper slope zones and that these differences in composition were accompanied by changes in the trophic structure of assemblages. Similarly, chaetodontid fishes also display strong patterns of zonal distribution within reefs at locations on the GBR, in Polynesia, and in the Red Sea (Fowler 1990; Bouchon-Navaro 1980; 1981; Williams 1991).

Williams (1991) noted that within nearly all families of reef fish, some members are widely distributed among zones and habitats, while others display restricted distributions. He suggested that this pattern is usually correlated with density, such that common species tend to be more widely distributed than rare species. Populations of damselfishes at Lizard Island conformed to this pattern (Table 3). Relatively uncommon species (e.g. *Neoglyphidodon melas*, *Stegastes nigricans* and *Dischistodus perspicillatus*) were found in a limited number of zones almost exclusively in the lagoon, while the abundant species *Pomacentrus amboinensis* and *P. bankanensis/ chrysurus* were recorded in most zone and habitat combinations. Other examples of a correlation between relative abundance and breadth of distribution have been recorded at John Brewer Reef, (Birdsey 1989), Heron Island (Robertson and Lassig 1980), the Bahamas (Clarke 1977), Jamaica (Itzkowitz 1977), Panama, and Puerto Rico (Waldner and Robertson 1980). At Heron Island, Robertson and Lassig (1980) found that the damselfish fauna was dominated by *Pomacentrus wardi* (78% of total numbers, average density 27.5 fish per 80 m^2) and this species was recorded in almost all of the zones sampled by their study. At Lizard Island where *P. wardi* was relatively rare (average density 1.08 individuals per 80 m^2), this species was found almost exclusively on the reef crest.

Such relationships between density and distribution have been interpreted in terms of differences in ecological specialization among species (Williams 1991; Hanski et al. 1993). Generalist species, as a consequence of their ability to exploit a wide range of resources, become both widespread and abundant, or alternatively, the resources used by some species are more abundant and widespread than those of other species, resulting in a correlation between abundance and distribution (McNaughton and Wolf 1970; Brown 1984; Gaston and Lawton 1990). However, the positive relationship between distribution and abundance may also be a sampling artifact, as rare species are more difficult to detect than abundant species and are thus are less likely to be sampled in all habitats (McArdle 1990; Hanski et al. 1993).

Table 3. Dispersion (*W*) mean abundance and standard deviation (SD) per 80 m^2 of damselfishes pooled among habitats, sites, and zones at Lizard Island. *W* was calculated using Clarke's (1977) modification of the Shannon-Weiner formula for niche breadth

Species	*W*	Mean abundance	SD
Pomacentrus bankanensis/chrysurus	0.827	20.29	18.73
Pomacentrus amboinensis	0.596	18.38	20.88
Pomacentrus nagasakiensis	0.402	1.18	1.62
Plectroglyphidodon lacrymatus	0.426	1.10	1.79
Stegastes fasciolatus	0.401	1.06	1.96
Stegastes nigricans	0.150	1.04	2.82
Stegastes apicalis	0.352	0.93	2.16
Pomacentrus wardi	0.415	0.91	1.33
Neoglyphidodon melas	0.332	0.37	0.84
Dischistodus prosopotaenia	0.279	0.26	0.73
Dischistodus pseudochrysopoecilus	0.190	0.18	0.70
Dischistodus perspicillatus	0.140	0.15	0.70
Pomacentrus grammorhynchus	0.094	0.10	0.32
Neoglyphidodon nigroris	0.051	0.01	0.05

In order to quantify and compare among-zone patterns, distributions of reef fish are usually converted to a common measure of dispersion for analysis. A weighted measure of dispersion across zones (*W*, Clarke 1977), a modification of the Shannon-Weiner formula for niche breadth, is commonly used for this purpose (Williams 1991). To examine the extent to which our estimates of dispersion (*W*) were influenced by abundance and by the intensity of sampling, our sampling hierarchy of habitats (windward, lagoon, leeward, and oblique), sites within habitats (2), stations within sites (2), and zones (flat, crest and slope) was simulated by computer. Equal numbers of individuals were randomly distributed in each station of the sampling space, so that $W = 1$. Increasing numbers of replicate transects (2, 3, 6, 9 and 12) were then sampled in all combinations of station and zone. *W* was calculated for each of the levels of replication and the process then repeated 100 times. Initially, density of the target species were set at 1 individual per 80 m^2, then the simulation was repeated using densities of 10, 50, and 100 individuals. Results are summarized in Table 4. The simulation suggests that the ability of the sampling program to accurately estimate the dispersion of fish was poor. At densities of 1 individual per 80 m^2, the values of *W* calculated during the simulation suggested that distributions were highly restricted, even when replication levels were relatively large. At the level of replication used by the study, (2 transects), accurate estimates of dispersion were not obtained until densities were greater than 50 individuals. As damselfishes are more likely to be clumped rather than randomly distributed at very small spatial scales (see

Table 4. Summary of results of simulation study of the sampling design. Our sampling hierarchy of habitats, sites, stations, and zones was simulated by computer. Densities of 1 individual per 80 m^2 were randomly distributed in each station of the sampling space, so that $W = 1$ (Clarke 1977, see Table 3). An increasing number of replicate transects (2, 3, 6, 9 and 12) were sampled in each combination of station and zone. For each level of replication, sampling was repeated 100 times and a mean and standard deviation (SD) calculated for *W*. The simulation was then repeated using increasing densities of individuals (10, 50, 100)

Density		Replicates 2	3	6	9	12
1	Mean dispersion	0.049	0.073	0.128	0.17	0.213
	SD	0.041	0.041	0.053	0.051	0.065
10	Mean dispersion	0.274	0.353	0.515	0.632	0.735
	SD	0.049	0.069	0.065	0.071	0.067
50	Mean dispersion	0.623	0.783	0.954	0.993	0.999
	SD	0.077	0.068	0.047	0.225	0.008
100	Mean dispersion	0.841	0.961	0.999	1	1
	SD	0.062	0.044	0.009	0	0

above), the results obtained by the simulation probably over-estimate the ability of the sampling program to describe dispersion patterns of rare species.

Our simulation implies that the positive correlations between breadth of distribution and abundance of damselfishes observed by our study may have been a consequence of the sampling method. Despite this problem, general patterns displayed by the assemblage such as the decline in the abundance of herbivorous species with depth were likely to be robust, since these were based on total densities. The variation in zonal distributions shown by *Pomacentrus amboinensis* and *P. bankanensis/chrysurus* among habitats were also likely to have reflected real changes in distribution, as these were abundant species that displayed relatively little variation in density at large spatial scales. However, the identification of a distinctive fauna within the lagoon by the multivariate analyses must be treated with caution, as this result was largely based on the distributions of the rare species *Stegastes nigricans*, *S. fasciolatus*, and *Neoglyphidodon melas*.

These problems in interpretation of the results occurred despite the fact that our study is the most comprehensive description to date of distributions of damselfishes at the scale of a single reef. Difficulties in discerning real changes in distribution patterns from artifacts of the sampling method are likely to be even more acute in studies where units of sampling are very small and/or few replicates are sampled, or where the sampling unit varies in size among habitats or zones, as is the case in nearly all previous descriptions of assemblages (e.g. Emery 1973; Sale 1974; Clarke 1977; Itzkowitz 1977; Sale and Dybdahl 1978; Robertson and Lassig 1980; Waldner and Robertson 1980). Thus, our search for general and consistent patterns in the distribution of damselfishes among localities was limited to the level of trophic groups and abundant species. The problems identified by our study may not only apply to comparisons among species, but also to comparisons of distribution among families of reef fishes, particularly where families differ in abundance or likelihood of being recorded. The latter problem might account for the perception (e.g. Clarke 1977) that families such as butterflyfishes, which are often brightly coloured and swim above the reef, are more widely distributed among reef zones than damselfishes, which are frequently drab and closely associated with their territories.

Damselfishes are typical of many of the common families of reef fishes in being rich in species, while having distributions that are in most sites numerically dominated by one or two highly abundant members (Goldman and Talbot 1976; Russ 1984; Williams 1982; Fowler 1990; Williams 1991). Thus the majority of species of coral reef fish tend to be rare. Our study suggests that it may require an intense logistical effort to obtain accurate estimates of distributions of rare species. It would be unwise to interpret relative patterns of distribution in terms of ecological specialization, or as evidence of resource partitioning, unless it can be clearly demonstrated that the sampling program is capable of accurately describing distributions of all members of the assemblage at the spatial scales of interest.

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