

SPATIAL VARIATION IN CORAL RECRUITMENT AROUND LIZARD ISLAND, AUSTRALIA.

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ABSTRACT

Spatial variation in recruitment is characteristic of marine organisms with planktonic larvae and is generally apparent at all spatial scales. In this study spatial variation in the abundance and taxonomic composition of coral recruits was examined, using settlement panels, at a number of scales between depth zones on the fringing reef surrounding Lizard Island. Within the reef crest, variations in abundance between sites were small compared to within site variation. In all taxa the scale of patchiness in recruitment was finer than the site. However, the pattern was strikingly different for recruits from the families Acroporidae and Pocilloporidae, which suggests that different processes operating at different scales are influencing recruitment in these taxa. The abundance of recruits varied significantly between depth zones, with a pronounced reduction in recruitment of all taxa on the reef slope (4m). The abundance of recruits on more exposed surfaces of the settlement panels did not increase with depth. Depth zonation of the recruit assemblage suggests that coral larvae have either the ability to regulate their position within the water column or recognise depth specific substratum characteristics. In contrast, the taxonomic composition of the recruits did not vary between sites within the reef crest despite marked differences in the adult assemblages. These patterns suggest that patterns established at the time of settlement contribute to the depth zonation of adult assemblages and that the importance of post-settlement processes varies between zones.

INTRODUCTION

Spatial and temporal variation in recruitment is characteristic of marine organisms with planktonic larvae and is important in determining the structure of marine benthic communities. Recruitment patterns are particularly important in determining the recovery of reefs following disturbance as recovery is largely dependent on the supply of new recruits.

Coral recruitment varies at all spatial scales: across broad longitudinal gradients (Sammarco 1991); between reefs within a given location (e.g. Fisk and Harriott 1990), between sites within reefs (e.g. Baggett & Bright 1985) and within sites (Babcock 1989). Another consistent pattern is for coral recruitment to decline with depth (e.g. Wallace 1985), sometimes with a peak at intermediate depths (e.g. Birkeland 1977; Rogers et al. 1984).

Spatial variation in coral recruitment has a number of causes including: patterns of water movement (e.g. Sammarco & Andrews 1987); larval response to other organisms (e.g. Morse et al. 1988); differences in the physical or chemical properties of the environment (e.g. Hunte and Wittenburg 1992) and patterns of post-settlement mortality (Rylarsdaam 1983).

The objective of this study was to examine spatial variation in coral recruitment at Lizard Island, both within and between habitats. In particular, we wished to identify differences in the abundance of coral recruits, in the taxonomic composition of the coral recruit assemblages, and the scale at which any differences were evident.

METHODS

Coral recruits were sampled using three pairs of unglazed unconditioned clay tiles (11 * 11 cm) bolted either side of wire racks which were secured to the substratum in early January 1994 and removed 8 weeks later. On removal tiles were bleached, rinsed and dried. The horizontal surfaces of all tiles were censused microscopically for coral recruits. At this stage of development only three families of Scleractinian recruits can be unambiguously identified, the Acroporidae, Pocilloporidae and Poritidae. The remaining coral recruits were classified as "others".

Within habitat patterns of coral recruitment were examined by placing four racks (separated by 4-6 m) on

the crest of the fringing reef which surrounds Lizard Island at each of 4 sites, 2 on the northern side of the island and 2 on the southern side. The sites were separated by between 0.5 and 8 km. Between habitat patterns were examined by placing five racks in each of 4 depth zones at North 1; the flat (2 m), crest (2 m), slope (4 m) and base (8 m). Differences in the abundance of coral recruits were tested with Nested 2-Factor ANOVAs (Within habitat: Factors site and rack both random. Between habitat: Factors depth and rack, depth fixed). All variables were $\log_{10}(x + 1)$ transformed to emphasise proportional differences. Differences in the structure of the recruit assemblages were tested using MANOVA. Only three variables were used in these analyses as the poritid recruits were rare and highly aggregated. MANOVA was followed by Canonical Discriminant Analysis (CDA) to determine which groups differed and the variables responsible for those difference.

RESULTS

Within habitat variation in coral recruitment

Despite up to 4 fold differences in the abundance of recruits between sites ANOVA indicated there was no significant difference in abundance between sites for any taxa (Table 1). Acroporid recruitment varied 4 fold between sites ranging from a mean of 2.3 (standard error 0.9) recruits per rack (rpr) at North 2 to 8.0 (1.63) rpr at North 1 (Fig. 1). Pocilloporid recruitment varied 2 fold between sites ranging from 18.0 (6.38) rpr at North 1 to 36.8 (12.20) rpr at North 2 (Fig. 1). Other recruits varied 3 fold in abundance between sites ranging from 2 (0.4) rpr at North 2 to 6.5 (2.3) rpr at North 1 (Fig. 1). Poritid recruits were highly aggregated with 11 of the 25 recruits found on just one rack at North 2. However, the between site differences are small when compared to variation within sites where the abundance of recruits varied up to 10 fold between racks. In other words recruitment was patchy at a finer scale than that of the site. When the number of recruits from all taxa are combined to give total recruit abundance the variation between sites is reduced substantially with less than 30 % difference between the site of maximum recruitment at North 2 (mean 44.5 se 14.38) and the site of minimum recruitment at South 1 (mean 32.5 se 3.42).

Table 1. ANOVA of densities of recruits between sites within the reef crest. All variables $\log_{10}(x + 1)$ transformed.

Effect: rack within site. F tests with 12,32 df				
variable	hyp. MS	err. MS	F	p>F
Acroporidae	0.067	0.052	1.296	0.268
Pocilloporidae	0.110	0.028	3.917	0.001
other	0.118	0.036	3.311	0.003
total	0.100	0.020	5.141	0.000
Effect: site. F tests with 12,32 df				
variable	hyp. MS	err. MS	F	p>F
Acroporidae	0.226	0.067	3.369	0.055
Pocilloporidae	0.117	0.110	1.064	0.401
other	0.135	0.118	1.143	0.371
total	0.013	0.100	0.140	0.936

To further examine the question of the scale of patchiness we partitioned the variation between the three scale of observation; site, rack and tile pair. In all taxa the variation attributable to site differences was negligible when compared to the variation at a finer scale (Fig 2). However, the patterns of variation are strikingly different between the taxa. In the Acroporidae 75% of the variation was between tiles and the variation between racks was negligible. In contrast, 50% of the variation was apparent at the scale of the rack in the Pocilloporidae (Fig 2).

The taxonomic composition of the recruit assemblage did not vary significantly between sites although once again there was there was significant variation at a finer scale with the recruit assemblages differing significantly between the racks (Table 2).

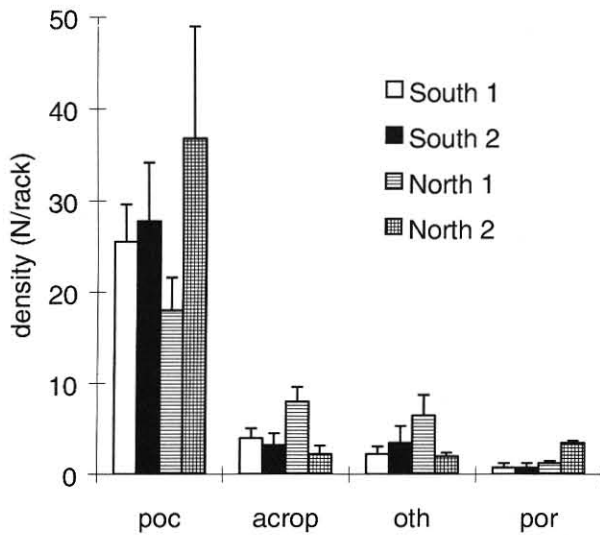


Fig.1: Mean and standard error of the density of coral recruits to four reef crest sites around Lizard Island (n = 4).

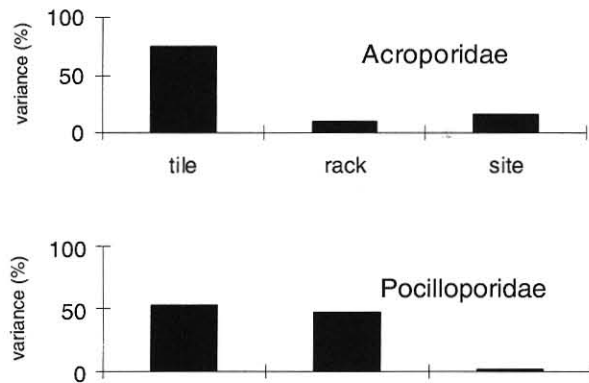


Fig.2: Proportion of the total variation in the density of coral recruits attributable to each scale of observation within the reef crest. Variables were log 10 (x + 1) transformed.

Table 2: MANOVA of the structure of the recruit assemblage between sites within the reef crest. The analysis includes the variables Acroporidae, Pocilloporidae and others. All variables were log 10 (x+1) transformed.

Source	Pillais	F	df	p>F
rack (site)	1.436	2.451	36, 96	0.000
site	0.626	1.054	9, 36	0.418

Between habitat variation in coral recruitment

In contrast to the uniformity of recruitment within the reef crest the abundance of recruits from all taxa varied significantly with depth (Table 3). The difference between the depth zones is primarily a result of a pronounced reduction in the abundance of recruits from all taxa on the reef slope (Fig. 3). For example, Pocilloporid numbers varied 6 fold between zones ranging from 5.8 (2.18) rpr on the reef slope to 29.2 (3.85) rpr on the slope (Fig. 3). Acroporid recruitment varied 6 fold ranging from 1.4 (0.93) rpr on the slope to 7.6 (0.75) rpr on the crest (Fig. 3). Poritid recruits were

rare and highly aggregated with 5 of the 7 recruits occurring on the crest and none on the slope.

Table 3: ANOVA of densities of recruits between depths at North site 1. All variables log 10 (x + 1) transformed.

Effect: rack within depth. F tests with 12,32 df				
variable	hyp. MS	err. MS	F	p>F
Acroporidae	0.081	0.042	1.912	0.049
Pocilloporidae	0.061	0.073	0.840	0.636
other	0.059	0.325	1.812	0.064
Effect: depth. F tests with 12, 32 df				
variable	hyp. MS	err. MS	F	p>F
Acroporidae	0.480	0.081	5.593	0.006
Pocilloporidae	1.427	0.061	23.42	0.000
other	0.266	0.059	4.514	0.018

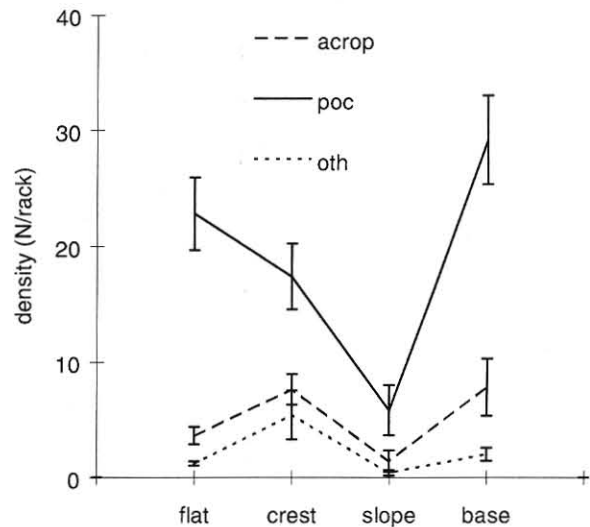


Fig.3: Mean and standard error of the density of coral recruits as a function of depth at North 1 (n = 5).

The structure of the recruit assemblage varied significantly between depth zones (Table 4). The most distinct assemblage occurred on the slope, which was characterised by low numbers of recruits from all taxa (Fig. 4). The crest assemblage is distinguished from the base and flat by higher numbers of other recruits (Fig. 4). The flat and base are similar, as indicated by the overlap of the confidence ellipses in Fig. 4, and characterised by high numbers of pocilloporid recruits.

Table 4: MANOVA of the structure of the recruit assemblage with depth at North site 1. The analysis includes the variables Acroporidae, Pocilloporidae and others. All variables were log 10 (x+1) transformed.

Source	Pillais	F	df	p>F
rack (depth)	1.096	1.440	48,120	0.058
depth	1.270	3.914	9,48	0.001

In no taxa was there a trend for an increase in the proportion of recruits on more exposed surfaces at depth. In fact, the proportion of recruits on the lower, less exposed, surface of the tiles increased with depth. Acroporids recruited in higher numbers to the lower surface at all depths (Fig. 5). Pocilloporids recruited in higher numbers to the lower surface in all zones except on the slope where they were more abundant on the bottom of the top tile (Fig. 5).

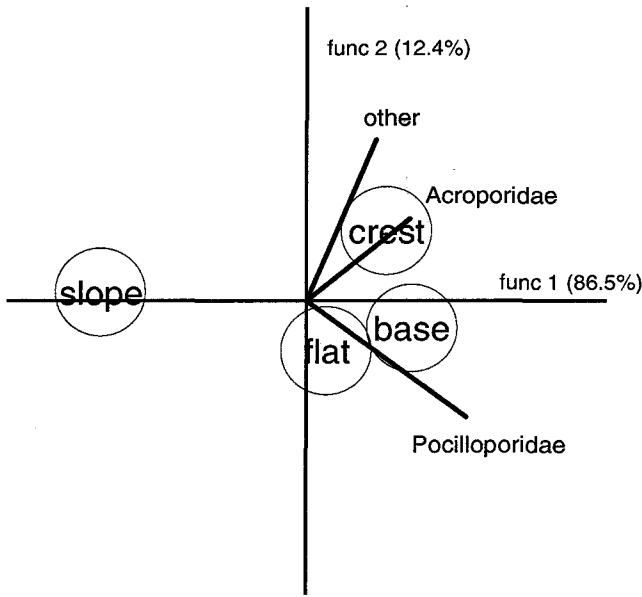


Fig. 4: Structure of the coral recruit assemblages as a function of depth zone at North Reef. Circles represent 95% confidence ellipses around the group means on the first two canonical variates, which describe 98.9% of the variation. Bold lines are vectors representing the three variables used in the analysis and indicate which taxa are responsible for defining differences in the structure of the assemblages.

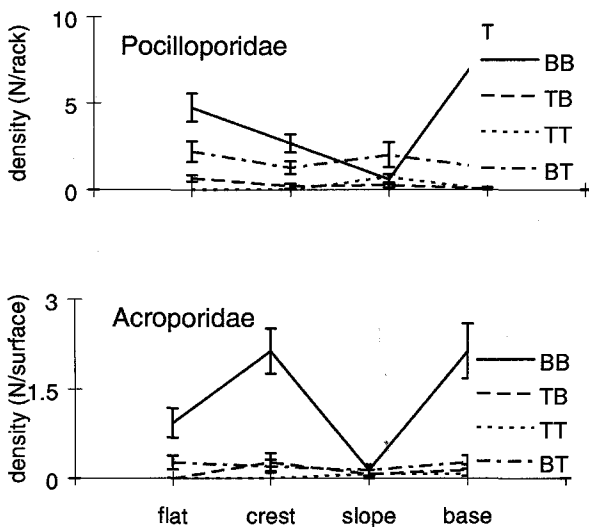


Fig. 5: Mean and SE of the density of coral recruits on each tile surface as a function of depth zone at North Reef (n = 5). BB: bottom of the bottom tile TB: top of the bottom tile TT: top of the top tile BT: bottom of the top tile.

DISCUSSION

Within habitat variation in coral recruitment

The lack of variation in the abundance of coral recruits between sites separated by between 0.5 and 8 km is unusual. All other investigations of coral recruitment at this scale have detected significant variation (e.g. Rylarsdaam 1983, Babcock 1989). The variation in total recruitment between sites was less than 30%. Given that annual rates of mortality in juvenile corals approach 95% (Rylarsdam 1983; Babcock 1985), this difference is unlikely to influence the dynamics of the adult assemblage. Site differences are usually attributed to

localised hydrological features such as water residence times. For example, Sammarco & Andrews (1987) recorded high recruitment in sites around Helix Reef where modelling predicted eddies would form and persist. Similarly, Fisk & Harriott (1990) recorded high recruitment to sites along a fringing reef where eddies had been observed. The lack of site difference recorded in this study suggests there is little difference in local hydrological conditions within the reef crest over a broad spatial scale. However, the more important and interesting result is that between site variation is small when compared to variation within sites and demonstrates that coral recruitment is often patchy at a finer scale than that of the site.

The tendency for recruitment to be patchy at a finer scale than the site was apparent in all taxa. However, the scale of patchiness was strikingly different between the Acroporidae, where there was little difference between racks, and the Pocilloporidae, which were aggregated at this scale. A similar difference in the scale of patchiness between these taxa was interpreted by Babcock (1989) as resulting from differences in the patterns of dispersal of the taxa. This interpretation is based on the assumption that acroporid larvae, with an obligate planktonic life of 4-6 days, will become diffuse through advection, resulting in a more even pattern of recruitment when compared to pocilloporid larvae, which are brooded by the adults and are competent to settle within hours of release, resulting in aggregated recruitment. However, under certain conditions aggregations of coral larvae form and are maintained through time despite the patches traversing considerable distances (Oliver and Willis 1987). Data demonstrating clumped distribution of recruits are not sufficient to establish limited dispersal as the cause of patchiness as many other factors may act to aggregate recruits. For example, local differences in the abundance of organisms such as soft corals may reduce the abundance of recruits nearby (Maida et al. 1995). Alternatively, the abundance of coral recruits is increased within damselfish territories (Sammarco and Carleton 1982). The important point is that spatial pattern in recruitment cannot reveal the extent of dispersal. What these patterns suggest is that different processes operating at different scales control patterns of recruitment in these taxa. Processes that might operate to cause Pocilloporidae to aggregate at the scale of the rack have been discussed above. Processes that might cause the Acroporidae to cluster on tiles include aggregative settlement in response to confamilials or the induction of settlement by other organisms, such as crustose coralline algae, which are also patchy at this scale.

The taxonomic composition of the recruit assemblages did not differ between sites despite considerable differences in the established coral assemblages. For example, adult faviids and mussids are twice as abundant in terms of area cover at North 1 (unpublished data), yet there was no significant difference in the abundance of Other recruits between sites. Again, adult Pocilloporidae are twice as abundant at the southern sites, yet the abundance of pocilloporid recruits did not vary between sites. While it is difficult to generalise from this study with only 2 months data these patterns suggest that post-settlement processes are important in determining adult distributions within the reef crest.

Between habitat variation in coral recruitment

In contrast to other studies of recruitment on the GBR recruit densities did not decrease with depth. Wallace (1985) in a four year study at Broadhurst Reef found that recruitment rates were higher and more variable at tidal datum below which rates declined with increasing depth. When results for the years were averaged there was a threefold reduction in recruitment between the reef flat and 6m (Wallace 1985). Harriott (1985) reported a 50% reduction in recruitment between 2m and 8m on a patch reef in the lagoon at Lizard Island. Elsewhere in the Pacific and in the Caribbean (Birkeland 1977; Rogers et al. 1984), an increase in the abundance of coral recruits at intermediate depths has been attributed to a corresponding reduction of algae and other encrusting invertebrates. In the present study there was a positive correlation between the area cover of algae and coral recruit abundance. Coral recruitment was high on the flat, crest and base where filamentous algae were the most abundant organisms on the plates (unpublished data). In contrast, recruitment was low on the slope where bryozoans and serpulids dominated the tiles (unpublished data) which suggests that these encrusting organisms are the more important coral competitors at this site.

The difference in the taxonomic composition of the recruit assemblages is evidence of depth zonation of coral recruits. The differences would probably be more pronounced and correspond more closely to adult zonation patterns, if the recruits could be identified more closely. For example, while the reef flat and reef base assemblages are similar at the family level it is unlikely this similarity would remain if the recruits could be identified to the genus level. Within the adult assemblage there is a profound zonation within the family Pocilloporidae, with a shift from *Pocillopora edouxyi* which dominates the flat, to *Stylophora pistillata*, which dominates the base and it would be interesting to see whether this pattern is reflected in the recruits. Nonetheless, the data suggest that larvae have the ability to either control their position within the water column or identify depth specific differences in the substratum.

In contrast to other studies there was no trend for the number of recruits on exposed surfaces to increase with depth (e.g. Birkeland 1977, Rogers et al. 1984; Wallace 1985), a pattern that is generally attributed to a reduction in both light intensity and competitor abundance with increasing depth. The absence of recruits on the upper, more exposed surface, on the reef base is probably the result of high sediment accumulation at the base of filamentous algae, which were abundant on the upper surface of the plates in this zone (personal observation). Sediment accumulation is known to inhibit coral settlement (Babcock and Davies 1991). Alternatively, the pattern may indicate that larvae from coral species adapted to deeper waters also settle cryptically. Again this question could be resolved with greater taxonomic resolution of the recruits.

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