Coral Reefs

Patterns in the use of space by benthic communities on two coral reefs of the Great Barrier Reef

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Abstract. A rapid benthic line-transect survey method for use by non-specialist observers is described. At both Davies Reef (mid-continental shelf) and Myrmidon Reef (outer-continental shelf) in the central Great Barrier Reef a set of 6 sites of varying depths on the reef flat, crest and slope were sampled using this method. At least 10 contiguous 10 m transects were made at each site. Benthic organisms were recorded as life forms with categories based on both high level taxa and morphologies, and including scleractinian corals, alcyonarians, sponges, algae and others. Percentage cover data for 19 benthic categories are presented for all sites. Coral cover on both reefs is high on the crest and slope but low on the reef flat. At all sites the cover of soft corals and sponges is much less than cover of hard corals and algae. Abundances of soft corals and sponges increase with depth. Analysis of gaps between hard corals show that many colonies grow close to each other (<1 cm) even when total coral cover is low.

Introduction

The ability to occupy space is important for the growth of all epibenthos and particularly for photosynthetic organisms. Although the occupation of space on coral reefs has been studied for a wide variety of benthic organisms, few studies have analysed the use of space by all of the large sessile benthos in one area at one time. Barnes et al. (1971), Benayahu and Loya (1977, 1981), Drew (1977) and Bak and Luckhurst (1980) are some who have included most of the living cover in their studies of reefs in the Indian Ocean, the Red Sea and the Caribbean.

The hard corals, soft corals and algae often account for a high proportion of the living cover (Benayahu and Loya 1977, 1981). The interactions between these groups relative to their occupation of space have received considerable attention, particularly for the hard corals (Sheppard 1979; Lang 1973) and less so for the algae (Banner and Bailey 1970; Potts 1977; Sammarco 1983) and soft corals (Benayahu and Loya 1981).

The patchiness and diversity of benthos distribution on coral reefs are features that make coral reefs interesting yet difficult to study on a large scale either by experiment or by observation. Experimental work on reefs is often done without describing the surrounding benthic "milieu" and in some cases, coral recruitment studies for instance, the type of reef surrounding the experiment could be of critical importance. As another example, on a smaller scale Kohn (1983) and Reichelt (1982) found that microhabitat distribution played a significant role in determining the distribution of coral reef gastropods.

This paper describes a survey method that allows broad scale survey of coral reef benthos to be done rapidly yet does not require specialist taxonomic skills (Webb et al. 1976; Steneck and Watling 1982). Bradbury et al. (1986) have already shown the efficacy of the method in describing coral reef zonation patterns. The present paper is intended to describe the method in more detail and present the data, which were drawn on in the earlier paper, for 2 reefs in the central Great Barrier Reef region.

The focus is on the distribution of all types of substrata, living and non-living, rather than on any single group of organisms. The separate distributions of each of several major groups of organisms in this region of the Great Barrier Reef has been studied recently: hard corals (Done 1982); fish (Williams 1982); soft corals (Dinesen 1983); the calcareous alga, *Halimeda* (Drew 1983).

The reefs were sampled using line transects (Loya 1978), which permit the quantitative description of percentage cover and one dimensional spatial pattern of benthic organisms and non-living substrata at varying depths on the reef slope. Specific questions addressed in this paper are: What is the distribution of non-living substrata on the reef slope? What is the distribution of space between particular groups of organisms? What is the distribution of observable interactions between benthic organisms?

Life form categories were used, rather than data at species level, for several reasons. Coral community pat-

terns have been demonstrated previously in a quantitative study of taxonomic groupings above the species level (Bradbury and Loya 1978) and a strong relationship between morphological form and ecological function has been shown for algal assemblages (Littler et al. 1983).

Study sites and methods

Davies Reef (147°39′ E, 18°50′ S), a mid-continental shelf reef, and Myrmidon Reef (147°23′ E, 18°16′ S), an outer-continental shelf reef, are about 60 km apart in the central region of the Great Barrier Reef. On each reef 6 sites were sampled with 10 m line transects that each followed a depth contour. These sites were at the reef crest, 5 m, 10 m, 15 m and 20 m depths on the windward slope and one reef flat site running parallel to and about 50 m leeward of the reef edge. The depths are measured using the reef crest lip as datum. The locations of each of these sites are shown in Fig. 1.

At each site there were 12 line transects at Davies Reef and 10 at Myrmidon Reef. On each transect a plastic fibre tape marked in centimetres was laid along the depth contour and the intercepts of each substrate category were recorded as a series to the nearest centimetre. Instances of one benthic type visibly influencing its near neighbours on the transect were recorded where dead patches were visible along the boundaries of one or both the neighbours. Here we make the assumption that the dead patches are evidence of interaction between neighbours (see Sheppard 1979, 1981 for justification).

The reef substrata were categorized as in Table 1 using morphological descriptors, some of which are taxonomically based (Bradbury et al. 1986; Devantier et al. 1985); for example "branching *Acropora*". The *Acropora* categories were included as special cases in this study because of the very high diversity and abundance of this genus, not only in the central Great Barrier Reef region (Done 1982) but in the Indo-Pacific as a whole (Veron and Wallace 1984). These descriptive categories are directly comparable to the physiognomic-structural categories used in plant geography (Webb et al. 1970, 1976).
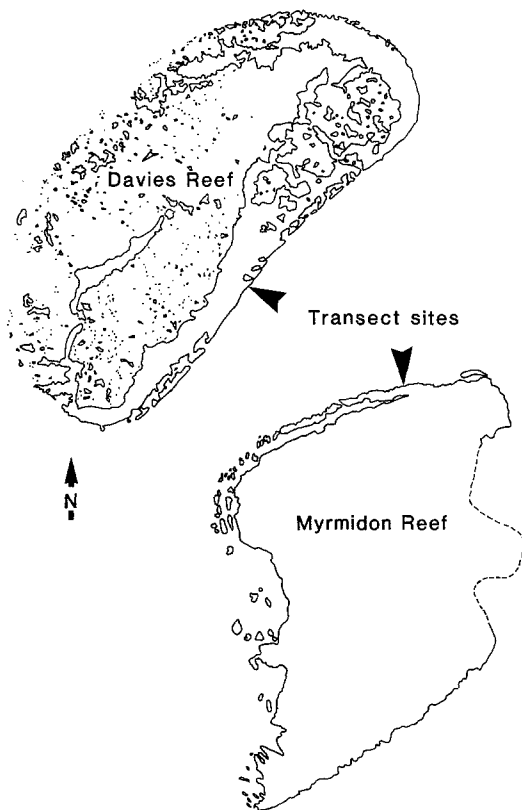

Fig. 1. Site locations on Davies and Myrmidon Reefs; length of Davies Reef = 6.25 km and Myrmidon Reef = 3.25 km

Table 1. Categories of reef substrata

	Description	Code
Hard corals – *Acropora*		
	Acropora branching	ACB
	Acropora table	ACT
	Acropora encrusting	ACE
	Acropora submassive	ACS
Hard corals – non-*Acropora*		
	Coral branching	CB
	Coral massive	CM
	Coral encrusting	CE
	Coral submassive	CS
Other fauna		
	Soft coral	SC
	Gorgonian	GO
	Sponge	SP
	Other benthos	OT
Algal		
	Macro-algae	MA
	Turf algae	TA
	Coralline algae	CA
	Halimeda	HA
Non-living		
	Sand/rubble	SR
	Recently killed coral	DC
	Water	WA
	(cracks deeper than 50 cm)	

Results

Although the speed of the method varies considerably depending on diving conditions and the nature of the substratum, an estimate of the speed is about 40 transect metres per diver per hour. This was slowed by about half when hard corals were recorded to genus level.

The percentage cover of each category averaged over all the replicate transects at each site is shown in Table 2. In order to illustrate the gross distribution of benthos on the two reef slopes, Fig. 2 shows histograms of percent cover for the lumped categories: hard corals, algae, soft corals (i.e. alcyonarians), sponges, non-living substrata.

The cases of visible interactions between corals are summarized in Table 3. The analysis of gaps between colonies was restricted to Davies Reef because of the greater number of coral-coral interactions observed at that reef compared with Myrmidon. There were only three instances where the members of the interacting pair were not both hard corals. At the slope site at 20 m on Davies Reef a branching *Acropora* appeared to have killed part of a soft coral colony, and a massive coral killed part of a sponge. At 15 m a soft coral appeared to have killed part of a massive coral colony.

Apart from the relative abundance of the benthic types, the line transect data also provides a description of the distribution of non-living substrata. In order to show how space is distributed between hard corals, soft corals and sponges, we treated a gap between two colonies as the sum of the non-living categories and the algal categories in the intervening space. Thus a gap in this case

Table 2. Percentage covers of benthic categories -12×10 m transects/site at Davies; 10×10 m transects/site at Myrmidon. RF = reef flat; RC = reef crest; RS5 = 5 m reef slope; RS10 = 10 m reef slope; RS15 = 15 m reef slope; RS20 = 20 m reef slope

Davies reef sites

	RF	RC	RS5	RS10	RS15	RS20
ACB	1.3	8.0	8.4	5.8	5.1	9.6
ACT	0.9	8.8	6.3	3.7	7.5	3.7
ACE	6.6	5.9	0.2	0.0	0.0	0.0
ACS	4.1	15.4	1.8	0.3	0.1	0.0
CB	0.4	0.7	1.8	0.3	0.1	0.0
CM	1.7	2.0	7.8	5.2	6.8	4.0
CE	6.3	5.4	28.1	20.0	14.0	10.1
CS	0.3	2.9	4.1	4.0	2.3	3.7
SC	1.9	0.2	5.2	12.7	11.5	12.4
GO	0.0	0.0	0.0	4.4	8.7	4.3
SP	0.0	0.0	0.7	0.7	2.3	6.8
OT	0.0	0.3	2.9	3.2	4.8	2.5
MA	1.0	1.4	1.3	3.5	0.7	0.7
TA	65.4	39.3	0.1	0.0	0.0	0.0
CA	6.4	9.2	25.5	9.3	10.9	14.6
HA	0.1	0.0	2.1	0.9	0.1	0.1
SR	3.3	0.0	0.1	11.1	10.6	15.8
DC	0.5	0.8	1.7	3.1	2.7	2.7
WA	0.0	0.3	1.9	2.6	1.5	1.8

Myrmidon reef sites

	RF	RC	RS5	RS10	RS15	RS20
ACB	2.2	2.8	6.9	3.9	1.5	3.1
ACT	1.5	0.6	8.4	3.7	4.0	0.8
ACE	0.3	4.1	0.6	0.2	0.4	0.1
ACS	5.5	26.9	3.5	0.2	0.8	0.7
CB	0.0	0.0	0.0	1.2	0.0	0.2
CM	2.6	0.4	15.9	9.4	2.5	3.7
CE	1.8	7.3	9.7	16.0	20.2	3.6
CS	3.0	1.8	6.8	4.5	3.8	4.6
SC	0.4	0.5	13.8	27.7	34.3	17.6
GO	0.0	0.0	1.0	1.0	1.7	0.3
SP	0.0	0.0	0.4	1.4	1.1	1.1
OT	0.8	1.8	1.9	2.2	0.5	0.2
MA	0.2	0.2	0.6	2.1	1.7	0.1
TA	13.7	23.0	2.8	3.0	4.6	2.1
CA	8.0	27.7	11.9	9.5	12.3	1.9
HA	0.0	0.0	0.7	4.0	0.9	0.3
SR	51.7	2.8	0.0	2.2	5.1	59.2
DC	8.3	0.3	1.2	0.5	0.4	0.1
WA	0.0	0.0	14.2	7.3	4.3	0.3

Table 3. Number of cases where interactions between neighbouring coral colonies were visible as dead patches on the colonies

Reef	Sites					
	RF	RC	RS5	RS10	RS15	RS20
Davies	1	6	11	14	13	9
Myrmidon	1	1	3	1	0	0

Table 4. Relative frequency of gaps between hard corals at Davies Reef. The 0 cm category contains cases where gap was < 1 cm

No. of gaps	Site	Gap length (cm)						
		0<1	1–2	3–4	5–6	7–8	9–10	>10
120	RF	76	5	1	4	2	3	11
209	RC	77	4	1	3	2	3	10
383	RS5	69	8	7	5	3	3	5
161	RS10	84	7	1	2	1	1	4
107	RS15	74	4	3	3	5	3	9
56	RS20	89	2	5	0	0	4	0

Table 5. Relative frequency of gaps between hard corals and soft corals at Davies Reef

No. of gaps	Site	Gap length (cm)		
		0<1	1–5	6–20
6	RF	67	17	17
0	RC	0	0	0
58	RS5	67	14	19
104	RS10	95	1	4
82	RS15	87	4	10
26	RS20	85	12	4

Table 6. Relative frequency of gaps between hard corals and sponges at Davies Reef

No. of gaps	Site	Gap length (cm) between sponge – hard coral		
		0<1	1–5	6–20
0	RF	–	–	–
0	RC	–	–	–
20	R/S5	80	0	0
4	R/S10	100	0	0
20	R/S15	75	0	25
46	R/S20	87	7	7

is defined as any or all of the types MA, CA, TA, HA, WA, SR and DC (Table 1). These were chosen in order to exclude those potentially complicating cases such as two corals separated by a sponge.

The relative distribution of gaps between hard coral colonies at Davies Reef slope is shown in Table 4. A G-test on the raw frequency data, excluding the sparse 20 m slope site, shows that the frequency of gap lengths is not independent of depth ($P < 0.05$). Notable features of this gap distribution are firstly, the high frequencies of 0 cm gap length (i. e. < 1 cm gaps) at all depths, and secondly, the higher proportions of 1 cm to 5 cm gaps between hard corals at the 5 m slope site.

Again for Davies Reef, the distribution of gaps between hard coral colonies and soft corals and between hard corals and sponges are shown in Tables 5 and 6 respectively. These are unremarkable except that, as with the gaps between hard corals, the frequency of gaps less than 1 cm is relatively high. The distribution of gaps between the remaining combinations of soft corals and sponges are not shown but they were very similar to the distributions shown in Tables 5 and 6.
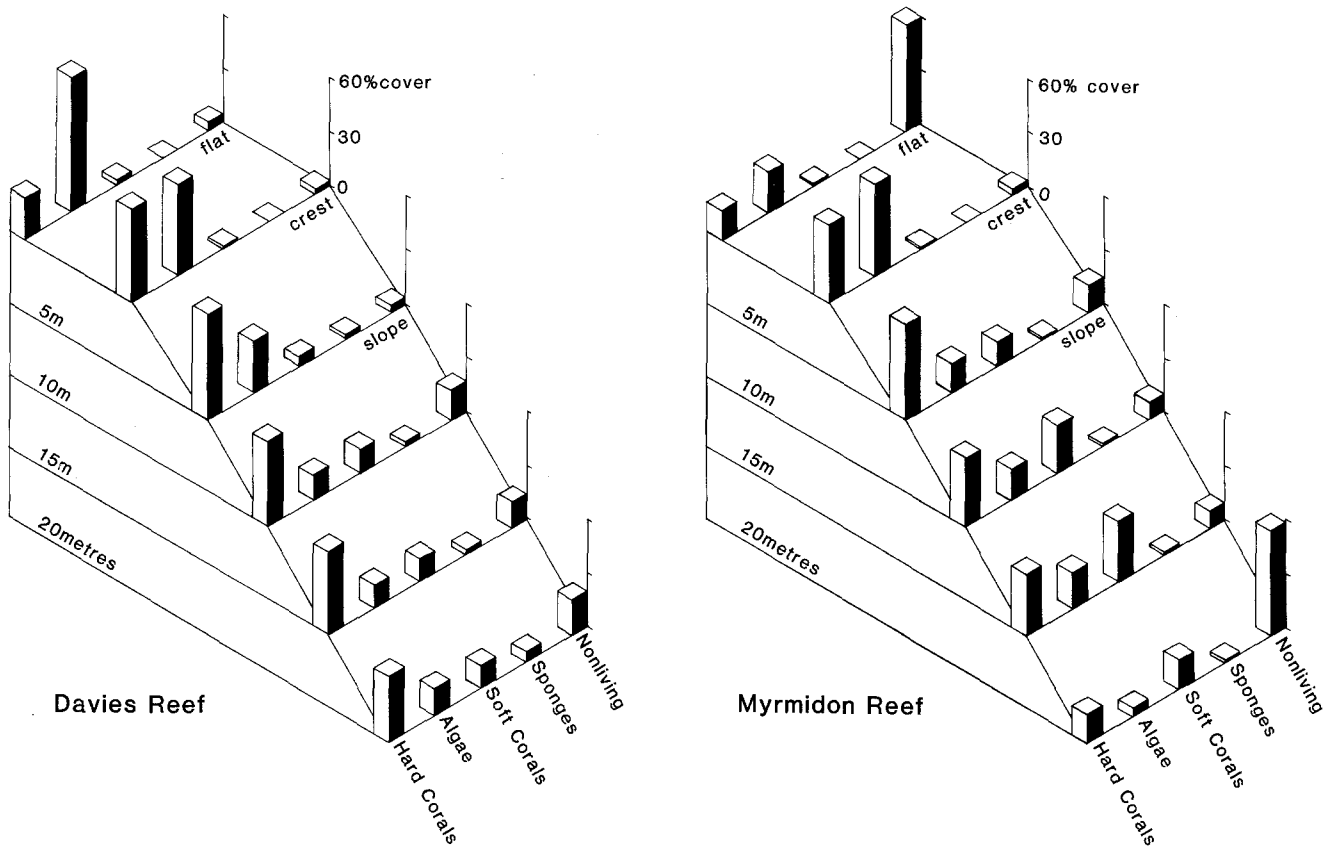
Fig. 2. Histograms of percentage cover of five main benthic categories on Davies and Myrmidon Reefs

Discussion

The broad scale distribution of macro-benthos on Davies and Myrmidon Reefs in the central Great Barrier Reef is similar to that found in the Red Sea (Benayahu and Loya 1981), in that hard corals and algae dominate the shallow water benthos, with soft corals becoming relatively more abundant below 5 m depth.

Comparison of gross distributions of macro benthos between Myrmidon and Davies Reef shows a number of trends. The cover of hard corals on both reefs is high on the reef crests and slopes and less on the reef flats. The cover of both soft corals and sponges is less than that of the hard corals at most sites with abundance of both increasing with depth. The abundance of algae at Davies was generally higher than at Myrmidon and at both reefs the shallow sites showed highest algal cover. A greater area of non-living substrata was recorded at Myrmidon, particularly on the reef flat and 20 m slope sites, than Davies Reef. We now deal with the major categories in turn.

Hard corals

The shallow sites at both Davies and Myrmidon are dominated by *Acropora* species and on both reef crests, *Acropora* covers three times more area than the non-*Acropora* corals. The types of *Acropora*, however, are quite different on the two reefs. The reef crest site at

Davies had less submassive *Acropora* and increased cover of branching, encrusting and tabulate *Acropora*. The distribution of the hard corals categories at the study sites is consistent with Done's (1982) description of reef slope communities on outer- and mid-continental shelf reefs. The difference in the distribution of the different morphological types is likely to be a reflection of the increased wave energy at Myrmidon Reef crest (Done 1982). The physical regime at Myrmidon favors more robust colony morphology for *Acropora*.

The percentage cover results presented here are quantitative measures and provide a different perspective on the coral communities from that of Done (1982). The present results should be treated as complementary to Done's relative abundance data.

Table 3 shows that Davies Reef had many more cases of visible interaction between coral colonies than Myrmidon. This difference between the 2 reefs cannot be explained solely by a difference in coral cover since the total hard coral cover at Davies was not vastly greater than that at Myrmidon. While the impact of such interactions on community structure is not clear (Bradbury and Young 1983; Reichelt and Bradbury 1984; Sheppard 1982; Bak et al. 1982), the results in Table 3 could be explained best by a study of the species involved. Although Sheppard (1981) worked mainly at Davies Reef, the degree of patchiness of the aggressive interaction phenomenon is unknown. Clearly, further studies on the within-

reef patchiness should be made before a conclusion can be drawn from the present data.

Algae

With the exception of *Halimeda* (Drew 1983), the broad distribution of algae on offshore reefs of the central Great Barrier Reef has not been described. In this region Morrisey (1980) described the algal assemblages at Magnetic Island, a nearshore fringing reef and Sammarco (1983) described algal assemblages on settling plates at on site on Britomart Reef, a midshelf reef. Benthic algal assemblages on coral reefs are important as they have been shown to be highly productive, even with low standing crops (Hatcher 1981). Their distribution can be influenced significantly by grazers (Lawrence 1975; Ogden 1976; Sammarco 1983; Hatcher 1983) and numerous physical factors (e.g. Lieberman et al. 1984).

The total cover by epilithic algae at the shallow sites, reef flat and reef crest, on both Davies and Myrmidon was greater than the area covered by the hard corals (Table 2). In particular the cover of turf algae on Davies' reef flat was 65% compared with 22% cover by the hard corals. On both reef crests the proportion of cover by corals and algae is similar and together these two benthic groups account for over 95% of the reef substrate at these shallow sites. This cover drops to 15%–20% at 20 m depth.

Dealing with the 4 algal categories separately (Table 2), the level of macro-algae and *Halimeda* are low everywhere. *Halimeda* was most abundant, with cover between 1% and 4%, at the 5 and 10 m depth sites on the slopes of both reefs. Turf algal cover was highest at the two shallow sites, reef crest and flat. Compared with turf algae, coralline algae were distributed more evenly among the sites at both Davies and Myrmidon Reefs.

The high cover of algae in the shallow sites compared with the deeper slope sites is consistent with the pattern described for One Tree Reef (Hatcher 1981). The high proportion of turf algae in the shallow sites may be due to the reduced time that grazers can be present given the tidal range and wave energy at these sites compared with the deeper slope sites. Alternatively, the algal distributions may be more directly influenced by the physical stress of high wave energy, as is the case with hard corals (Done 1982).

Coral reef systems have relatively high rates of grazing by fishes (Stephenson and Searles 1960; Randall 1961; Borowitzka 1981; Littler et al 1983) and, in the Caribbean at least, by sea urchins (Sammarco et al. 1974; Odgen 1976). Littler et al. (1983) argued that a specific relationship exists between morphology and resistance to herbivory, and also between morphology and primary productivity (Littler and Arnold 1982). In future studies the life-form categories adopted here should be modified to incorporate the functional-form groupings of Littler et al. (1983) in order to reflect the relationship between algal populations on a reef and the physical and biological factors that influence them.

Soft corals

At Davies Reef soft corals were relatively rare (2%–5% cover) at shallow sites (less than 5 m) and more abundant (about 12% cover) at the 10, 15 and 20 m sites. At Myrmidon soft corals were more abundant in the deep sites (10 m, 15 m, 20 m) and their abundance at the 5 m site was 13.8% compared with only 5.2% at the 5 m on Davies Reef.

These results are consistent with other soft coral survey data from this region (Dinesen 1983) identifying a trend of increasing soft coral abundance with depth. A point of contrast, however, is the relatively high abundance of soft corals at the 5 m site on Myrmidon compared with Davies Reef. This pattern runs contrary to the hypothesis that wave action inhibits soft coral abundance (Fishelson 1970; Dinesen 1983) because wave energy conditions are greater at Myrmidon Reef than at Davies (Done 1982). The variation in soft coral colony morphology at these sites is unknown and future studies will include three or four structural categories of soft corals to test their relationship with physical factors such as wave stress.

Sponges

Epilithic sponges are not relatively abundant at the two reefs (Table 2). Many coral reef sponge species, however, contain photosynthetic cyanobacteria and space in the light is likely to be an important resource for these sponges (Wilkinson 1981, 1983). There is a general trend for the space occupied by sponges to increase with depth on both Davies and Myrmidon Reefs. Maximum cover by sponges was recorded at the 20 m site on Davies reef slope (7%). Wilkinson and Trott (1983) reported that at 20 m depth on Davies' reef slope the sponge assemblage consisted of 56% phototrophs, 25% mixed photo- and hetero-trophs and 19% heterotrophs. The relative proportions of the sponges falling into these trophic groups showed much greater variation between samples from 10 m and 20 m depths on mid-shelf reefs than outershelf reefs (Wilkinson and Trott 1983). In the present study there was also a large change in sponge abundance between 10 and 20 m on Davies compared with 10 and 20 m at Myrmidon (Table 2). This change may be related to variation in the physical stress due to changes in water quality and wave energy, as suggested for hard corals (Done 1982, 1983), or there may be a more complex relationship involving variation in water quality and the relative success of different trophic types at the different sites.

Space between hard corals, soft corals and sponges

Space is often considered to be a limited resource for benthos on coral reefs and many organisms specialize in particular microhabitats. For light-dependent groups such as corals, algae and some sponges space in the light is essential. In this section we enquire about the distribution

of space that is *not* covered by the major space occupiers, namely, hard corals and soft corals. For this purpose we treated algae as part of the gaps between hard and soft corals, the same as dead corals, sand, rubble and water, even though in some circumstances algae can cover or overtop corals (Banner and Bailey 1970; Potts 1977) or exclude coral recruits by exploitative competition (Vine 1974).

The fact that at Davies Reef the majority of gaps between hard corals were less than 1 cm (Table 4) is consistent with observations at shallow sites on Heron Reef, southern Great Barrier Reef, where coral cover reached 80–90% and "standoffs were the most common type of coral-coral interaction apparent" (Bothwell 1983).

Bothwell (1983) notes a "coral free zone" ranging from about 1 to 5 cm around massive corals. At Davies Reef an increase in the frequency of gaps of this size was noted at the 5 m site where massive corals were marginally more abundant (8% cover). Since the "interactive" reach of many corals is in the 1 to 5 cm range (Sheppard 1981) the change in relative frequency of gaps within that range at the 5 m site could be due to competition between hard corals for a limited amount of space. Support for this view comes from the fact at the 5 m site hard coral cover was highest (58%) and the amount of non-living substrate was relatively low (4%).

The number of gaps less than 1 cm is highly correlated with the percent cover of hard corals (Spearman's $r = 0.94$, $P < 0.05$). In this study many adjacent colonies had little space between them. It could be that much of the substratum that is presently unoccupied is not actually available to the hard corals. The problem of assessing whether a particular unconsumed resource is really available to a consumer has been discussed previously (e.g. Menge 1972). This problem is difficult because the patchiness of settlement in the field introduces a high level of inexplicable variation in even the most carefully designed field experiment. The data show that many corals at Davies occur close to each other (Table 4) even when total coral cover is low (e.g. reef flat site, Table 2). Other studies have shown aggregation in corals (e.g. Lewis 1970; Babcock 1984) yet no clear explanation of this spatial pattern is available.

Such gap distribution patterns may indicate that hard corals saturate available space resources independently of the organisms (mainly algae) occupying the space between coral colonies. Other hypotheses include: (a) the coral populations are recruitment limited and the spatial pattern is a function of larval settlement behaviour; (b) the algae prevent most coral recruitment to the gaps between existing coral colonies.

Conclusions

The methods described here were designed to allow rapid survey of benthic coral reef communities. Previous workers have used life form categories to describe benthos, but the abundances were estimated either by divers towed behind boats (Done et al. 1981) or by using quadrat methods (Morton 1974; Dahl 1981). In this paper we have presented results from a study combining both line transects and life forms to describe benthos on two reefs. This approach allows a rapid, quantitative snapshot of reef communities. It does have significant limitations in certain applications, particularly as it does not provide data at species-level. In spite of this, with slightly modified procedures the method may prove useful for more detailed studies. Certain taxonomic groups in the transect could be identified to species level, thus allowing description of the benthic communities co-occurring with these species. In addition, the choice of life form categories can be made to reflect particular biological relationships such as that which exists between colony morphology and the physical regime of hard coral microhabitats (Veron and Pichon 1976) and the relationship between algal morphology, primary productivity (Littler and Arnold 1982) and grazing pressure (Littler et al. 1983).

The life form method is rapid and does not require specialist collectors. It would find application in countries with extensive coral reef areas but few specialists in reef biology and also in crisis situations such as large oil spills where the survey in front of a moving spill must be rapid. Another application, relating solely to the life forms, is the method's potential to allow comparison of reef communities and their physical environment in regions that may have few species in common. This type of analysis has been done for tropical rain forests (Webb et al. 1976, in press).

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