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THE EFFECT OF SUBSTRATA MICROTOPOGRAPHY ON REEF COMMUNITY STRUCTURE, 60-120 M

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ABSTRACT

Along the north-central coast of Jamaica, communities existing below 55m inhabit a vertical to overhanging wall of reef limestone, the deep fore reef (DFR), which extends to approximately 130m. On the DFR turbulence and predation/grazing are greatly reduced relative to shallower sites. Light intensity and sedimentation, however, exert important controls on community zonation. Superimposed on the overall vertical profile of the DFR are numerous overhangs and small ledges, creating a spatial mosaic at any one depth. These microtopographies interact with light and sedimentation to influence community structure, thus promoting increased community heterogeneity at any one depth as well as local shifts in depth-related community zonation. Low-angle sites display reduced living cover and diversities relative to vertical sites due to the accumulation of sediment on the former. Low-angle sites receive more illumination than vertical exposed and vertical sheltered sites, thus causing upward shifts in the bathymetric distribution of certain taxa.

INTRODUCTION

Although hundreds of studies of tropical shallow-water (<30m) reef communities from the Western Atlantic exist (see Glynn 1973, Milliman 1973, Colin 1978, Liddell & Ohlhorst in press a), studies of deeper environments, particularly those below 60m, are much rarer (but see Ginsburg and James 1973, Hartman 1973, Lang 1974, Lang et al. 1975, James & Ginsburg 1979, Fricke & Meischner 1985, Littler et al. 1985, and Liddell & Ohlhorst 1988 and in press b) due to physiologic constraints on SCUBA diving and the expense of submersible time. The present study examines the influence of site microtopography on deep-water communities and builds upon that of Liddell & Ohlhorst (1988), which presented quantitative bathymetric trends in community composition and diversity over the range of 1-120m at Jamaica. Particular attention is directed towards the effect of spatial heterogeneity in influencing community structure at any one depth.

STUDY LOCALITY

Discovery Bay lies on the north-central coast of Jamaica at Lat. 18°30'N and Long. 77°20'W. The well developed fringing reefs occurring along this coast display a striking, depth-related macrobiotic zonation which has been described in several papers (Goreau 1959, Goreau & Goreau 1973, Kinzie 1973, Lang 1974, Liddell & Ohlhorst 1987, 1988, Liddell et al. 1984a,b). The deep reef studied occurs off the West Fore Reef and seaward of the Zingorro fringing reef (A-A', Figs. 1-2).

A slope break occurring between 45 and 65m, typically at 55m, marks the boundary between the fore reef slope and the wall of the deep fore reef. The steep (60-90°) escarpment ends at approximately 120-130m where the more gently sloping (20-45°) and sediment covered island slope begins.

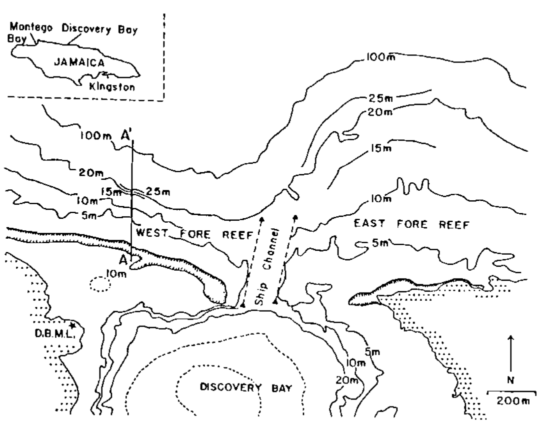

Figure 1. Index map of Discovery Bay Jamaica showing location of traverses sampled by Liddell & Ohlhorst (1988) (modified from Liddell et al. 1984a).

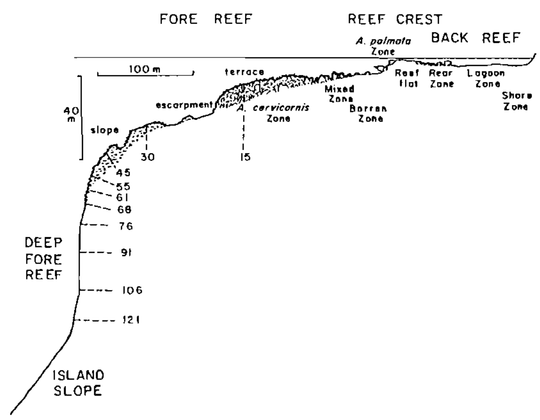

Figure 2. Profile along A-A' (Fig. 1) showing location of stations sampled by Liddell & Ohlhorst (1988) (modified from Liddell et al. 1984a).

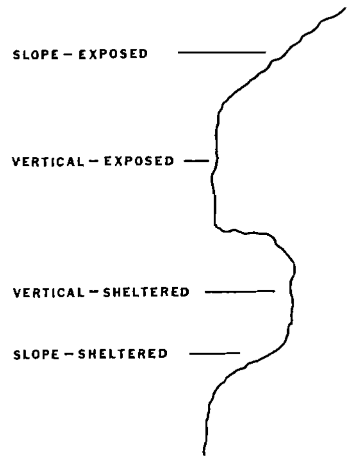

Figure 3. Microtopographies sampled along the deep fore reef.

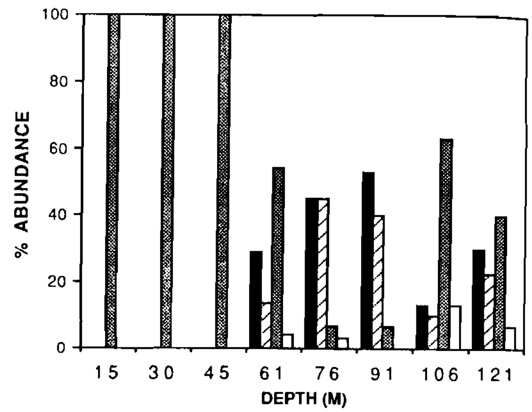

Figure 4. Bathymetric distribution of microtopographies. Substrates from left to right are vertical exposed, vertical sheltered, slope exposed, and slope sheltered. Data plotted for 15-45m is from line transects from Liddell & Ohlhorst (1987).

METHODS

A Perry submersible (PC-8), owned and operated by Research Submersibles Ltd., Grand Cayman, was utilized in data collection over the range of 53-120m on the vertical to overhanging escarpment of the deep fore reef. The submersible's external camera and strobelight were used to conduct photo transects in which color transparencies of 0.14m^2 areas were taken at 1m spacings at each depth. At the time each photo was taken, data on microtopography and substratum type (sheltered or exposed, vertical or gently inclined, sediment cover or hard substratum; Fig. 3) were recorded on audio tape.

Photo census data were processed by projecting transparencies at natural size onto a screen with a fixed array of points (27 points each with an approximate 10cm spacing) and the identity of the organism occurring at each point recorded (planar point intercept method). Community composition (larger taxa) and diversity were determined for each substratum type at each depth. Species number (S = number of taxa per transparency), dominance diversity (H', nat. log; Shannon & Weaver 1948), evenness (J', nat. log; Pielou 1966), and richness (R, nat. log; Margalef 1958) were employed as diversity indices. Diversity values so obtained must be viewed as approximations. The filamentous algae category represents multispecies aggregations which could not be identified from the slides. Also, sponge species separations are tentative as spicule preparations have not yet been made; thus, some species may have been incorrectly subdivided while others were incorrectly combined. Differences in diversity (expressed per slide) between substrata were tested with the Mann Whitney U (MWU) statistic. Differences in taxonomic compositions were tested with the chi-square (X^2) statistic.

Reef sites at Jamaica are characterized by low water turbidity (light attenuation coefficient 0.06/m; Brakel 1979). This coefficient was used to extrapolate irradiance values to a depth of 120m in the water column, yielding a 1.0% of surface illumination value at approximately 65m and a 0.05% value at 110m. Irradiance values generated by this procedure are, of course, no substitute for in situ quantum irradiance measurements and must be regarded with caution.

RESULTS

Although the faunal composition of the upper part of the deep fore reef wall (55-60m) is similar to that of the lower fore reef slope, corals are less abundant while demosponges increase dramatically in abundance. By 70-75m corals become extremely rare (observed by researchers, but not detected by photocensuses); crustose coralline algae and macroalgae (largely various *Halimeda* species, Liddell & Ohlhorst in press b) remain important community components. Sclerosponges are common in more sheltered areas. Community diversity is similar to that of shallower sites.

The slope of the wall decreases by 105m and sediment accumulation on exposed surfaces becomes a major problem for the epibenthos. Endolithic algae and encrusting demosponges are the most important community components, while macroalgae and sclerosponges decrease greatly in abundance.

Finally, by 120-130m, the wall of the deep fore reef ends and the steeply-dipping (45+$^{\circ}$) sediment-covered island slope begins. Encrusting organisms are restricted to isolated blocks of talus derived from above. Refer to Liddell & Ohlhorst (1988) for more details.

Effect of Microtopography

Microtopographies are unequally distributed over the bathymetric range of our study (Fig. 4). Exposed low-angle surfaces predominate above 61m, while vertical exposed or sheltered (beneath overhangs) surfaces predominate on the upper portions of the deep fore reef. On the lower

Table 1. Influence of microtopography on community composition and diversity, 61-121m. V-E=vertical-exposed, V-S=vertical-sheltered, S-E=slope-exposed, S-S=slope-sheltered.

	61M				76M				91M			106M				121M			
	V-E	V-S	S-E	S-S	V-E	V-S	S-E	S-S	V-E	V-S	S-E	V-E	V-S	S-E	S-S	V-E	V-S	S-E	S-S
Corals	9.8	0.0	30.1	7.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cnidaria	1.0	0.0	4.9	0.0	0.9	3.0	0.0	0.0	1.0	0.3	0.0	3.8	0.9	1.4	2.3	0.0	0.0	0.0	0.0
Sponges	12.7	23.0	11.5	14.8	15.4	23.7	2.0	7.4	25.1	24.2	12.9	24.2	28.6	17.7	16.8	27.5	41.0	7.2	12.7
Sclerosp.	0.0	4.7	0.0	0.0	0.3	5.7	2.0	0.0	6.6	7.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Macroalgae	14.2	15.5	11.5	3.7	14.7	15.3	26.0	11.3	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Fil. algae	2.0	3.1	0.7	3.7	4.1	7.5	6.0	3.7	17.2	19.4	1.9	20.4	29.6	15.3	15.4	20.4	27.1	7.8	8.9
Cor. algae	11.3	26.4	6.4	0.0	22.7	17.1	14.0	11.1	20.4	15.6	5.6	0.0	6.5	0.0	1.5	0.4	1.6	0.3	0.0
Misc.[1]	0.5	0.8	2.5	0.0	0.9	3.3	0.0	0.0	3.4	3.2	0.0	3.0	1.9	3.1	3.1	5.5	11.2	0.0	1.3
% living	51.5	73.5	67.6	29.6	59.0	75.6	50.0	33.5	73.7	70.0	22.3	51.4	67.5	37.5	39.1	53.4	80.9	15.3	22.9
Bare-hard	23.5	10.9	14.5	48.1	8.1	12.3	12.0	33.3	17.2	14.3	1.9	10.6	3.7	3.7	3.8	8.5	10.1	4.7	1.3
Sediment	25.0	14.0	17.9	22.2	32.6	12.0	38.0	33.3	9.1	15.6	75.9	37.9	28.7	58.6	56.9	37.4	9.0	80.0	75.9
N (# slides)	8	5	15	1	13	13	2	1	16	12	2	4	3	19	4	9	7	11	3
S (# species)	24	15	36	4	29	42	7	6	40	32	6	16	13	38	13	18	18	10	4
H'	2.62	2.40	2.65	1.21	2.68	3.07	1.51	1.68	2.90	2.74	1.63	2.08	1.83	2.51	1.83	1.89	2.07	1.57	1.05
R	4.94	3.09	6.30	1.44	5.31	7.48	1.86	2.27	6.89	5.80	2.01	3.58	2.82	7.13	3.07	3.60	3.46	2.31	1.06
J'	0.82	0.89	0.74	0.87	0.80	0.82	0.78	0.94	0.79	0.79	0.91	0.75	0.71	0.69	0.71	0.65	0.72	0.68	0.76

[1]**Miscellaneous** includes such organisms as *Gypsina*, boring sponges, bryozoans and unidentified living.

portions of the deep fore reef, vertical to moderately inclined exposed surfaces predominate.

Microtopography influences the irradiance available to the benthos. Brakel (1979) demonstrated that a north-facing vertical surface would receive only 25% and a 60° slope only 50% of the illumination received by a horizontal surface. Thus, the estimated depth of the 1.0% of surface illumination value for the water column (65m) must be shifted upward to approximately 55m for a 60° surface on the upper deep fore reef or lower fore reef slope and to 45m for a vertical surface. Similarly, the depth of the 0.05% value must be shifted upward from 110m in the water column to approximately 90m for a vertical surface and 100m for a 60° surface.

On the deep fore reef living cover is typically lower than on the fore reef and fore reef slope (Fig 5). Vertical sites consistently exhibit the highest percent living cover (often 70%) while low-angle sites consistently exhibit the lowest percent living cover (almost always < 50%, Table 1, Fig. 5). This effect is most pronounced at the deeper (91-121m) sites (MWU, $p<0.05$), largely due to the accumulation of sediment on low-angle surfaces (Fig. 6). While vertical sheltered sites typically have higher living cover than vertical exposed sites (MWU, $p<0.05$ for all except 91m), no consistent differences exist between low-angle sheltered and exposed sites.

Microtopographies strongly influence the community composition at any one depth resulting in significant (X^2, $p<0.05$) differences between almost all microtopography pairs for any given depth. At 61m corals are restricted to exposed (vertical or low-angle) sites, presumably due to increased light intensity relative to more sheltered sites. At 76m noncrustose algae (mainly macroalgae) reach their greatest abundance at low-angle, exposed sites, again, presumably due to increased light intensity (Table 1, Fig. 5). Conversely, at 76m sclerosponges reach their highest abundance at vertical, sheltered sites, those with lowest light intensities. When they occur on the shallower reefs, they are restricted to highly cryptic locations on the shallow reef (Hartman & Goreau 1970, Jackson et al. 1971). Crustose coralline algae exhibit an interesting trend with highest abundances occurring at vertical sheltered sites at 61m, highest abundances occurring at vertical exposed sites at 76m, and, finally, nearly equal abundances across vertical exposed and sheltered and slope exposed sites at 91m. At 120m noncrustose algae (here, mainly filamentous and endolithic forms) are most abundant at low-angle exposed sites, presumably due to increased light levels.

Microtopographies also influence diversity (Fig. 5) with vertical sites typically (and significantly for half of the pairs tested; MWU, $p<0.05$) having the highest number of taxa per sample (6-9 taxa per transparency vs. 3-6 for low-angle sites). This probably reflects reduced living cover due to high sediment cover (thus lack of hard substrata) at the nonvertical sites as well as reduced numbers of taxa capable of dealing with sedimentation. Whether sites are sheltered or exposed appears to have no consistent effect on diversity.

DISCUSSION

Studies of deep-water (>60m) tropical marine communities are rare. Even more so are quantitative studies of deep-water macrocommunities (but see Fricke & Schuhmacher 1983, Fricke & Meischner 1985, Littler et al. 1985, and Hillis-Colinvaux 1986, Liddell & Ohlhorst 1988 and in press b; a review of these articles is provided by Liddell & Ohlhorst 1988).

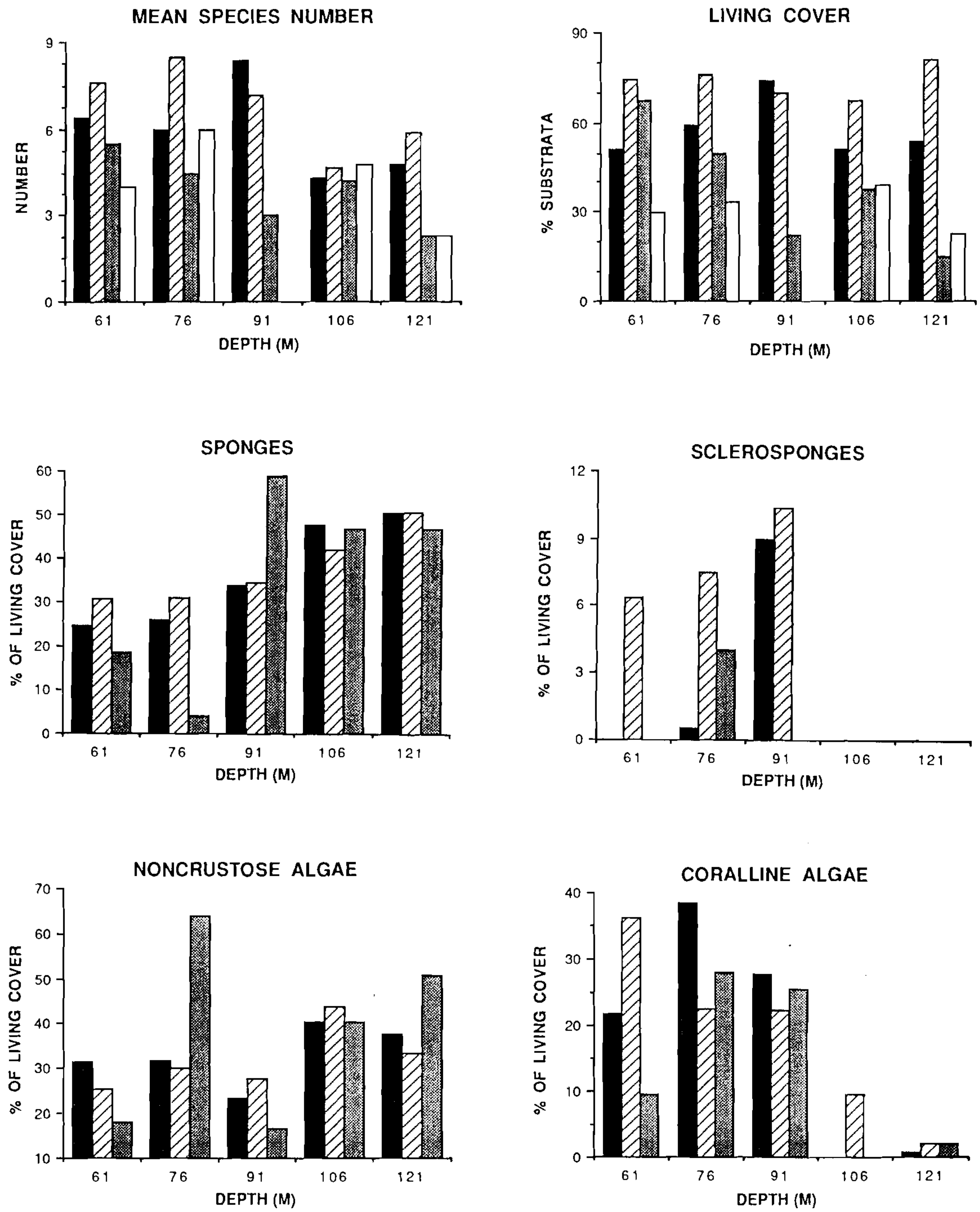

Figure 5. Effect of microtopography on percent living cover, diversity, and community composition. Substrata types from left to right are vertical exposed, vertical sheltered, slope exposed, and slope sheltered.

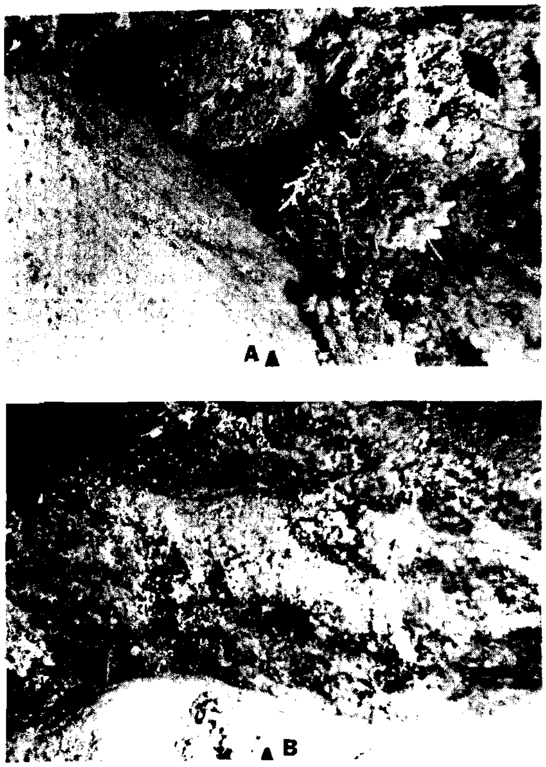

Figure 6. High living cover on vertical surfaces, heavy sediment accumulation on more gently inclined surfaces. "A" is from 76m, "B" is from 105m. Distance from the center reference point to edge of photograph is 22cm.

Although the role of microtopography in determining quantum irradiance levels (Jaubert & Vasseur 1974, Brakel 1979) and the distribution of shallow-water benthos (Birkeland et al. 1981) has been demonstrated, similar effects in deep-water communities have not been examined in any detail previously. Fricke & Schumacher (1983) indicated that, at their Red Sea study site, the deepest occurring corals (100-109m) were on slightly inclined sandy bottoms which allowed reflection of light. In contrast, on vertical walls, the deepest corals occurred at only 70-80m. Similarly, Birkeland et al. (1981) found that with increasing depth coral recruits shifted settlement patterns from vertical to horizontal surfaces, presumably in response to differences in light intensity. These findings are in accord with the present study.

Many Western Atlantic reef sites exhibit vertical, or nearly-so, escarpments beginning at approximately 50-60m and extending to 100m or more. These escarpments represent drowned seacliffs formed during the Wisconsin low stillstand (Goreau & Land 1974, Liddell & Ohlhorst 1981). Numerous overhangs and ledges are superimposed upon these escarpments and exert strong localized influences upon community composition and diversity. These effects are largely mediated through irradiance intensity and sediment accumulation. The overall result is one of increased diversity at any one depth and a potential blurring of community zonation if the effects of microtopography are ignored.

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