

PATTERNS OF BENTHIC COMMUNITY STRUCTURE, 10-250M, THE BAHAMAS

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ABSTRACT

The benthic community off Lee Stocking Island exhibits a pronounced bathymetric zonation. Filamentous and macroalgae dominate from 10-50m and occupy 60-90% of the hard substrate. Corals cover 3-23% of the hard substrate above 50m. Below this depth corals decline and sponges increase in abundance and diversity. Coralline algae are abundant between 50-100m. The deepest zones are occupied by sponges, polychaetes and endolithic? algae. Although living cover is high (75-90% of total bottom) above 100m, it declines (4-60%) below this depth. Substrate microtopography exerts a strong control on the distribution of the deep reef benthos with organisms largely restricted to vertical and overhanging surfaces where they are protected from sediment accumulation. The clear, oligotrophic waters of Exuma Sound apparently enable light penetration to relatively great depths. This results in a 15m downward shift of the benthic zonation relative to certain Western Atlantic sites such as Jamaica.

INTRODUCTION

Although hundreds of studies have been conducted on shallow-water (<30m) communities from the tropical Western Atlantic region (Colin 1978; Liddell and Ohlhorst 1987), studies of deeper environments, particularly those below 60m, are much less common (Ginsburg and James 1973; Hartman 1973; Porter 1973; Lang 1974; Lang et al. 1975; James and Ginsburg 1979; Macintyre et al. 1991). Quantitative data on deep-reef communities are rarer still (but see Fricke and Meischner 1985; Littler et al. 1985; Reed 1985; Liddell and Ohlhorst 1988; Liddell et al. 1988; Ohlhorst and Liddell 1988). In addition to the above work from the Atlantic, Fricke and Schuhmacher (1983) and Hillis-Colinvaux (1986) have examined deep-reef communities at the Red Sea and Enewetak Atoll in the Pacific, respectively (see Liddell and Ohlhorst 1988 for summaries).

Several submersible studies have addressed a variety of geological (Mullins and Neumann 1979; Schlager and Chermak 1979) and biological questions (Porter 1973; Littler et al. 1985; Reed 1985; Freile et al. 1995) in the Bahamas. The availability of a submersible, since 1992, at the Caribbean Marine Research Center (CMRC) laboratory on Lee Stocking Island (LSI) in the Exuma Chain has opened up the possibility of a variety of long-term biological as well as geological studies (Avery and Liddell 1996; Ballantine and Aponte 1996; Dennis 1996; Kiene et al. 1996; Parsons et al. 1996).

In September 1993 a study was initiated to characterize patterns of disturbance and change occurring over time in the benthic community from 10-250m off LSI. Change was evaluated through repeated censusing of settling tiles and permanent photoquadrats. In addition to change at the level of the individual experiment/photoquadrat, large-scale community change was assessed through phototranssects conducted at the beginning and end of the study period. This community census data also enabled the determination of bathymetric trends in community composition and diversity and comparison to other sites and is reported herein.

MATERIALS AND METHODS

Field

The study was conducted from the CMRC laboratory on LSI, Exuma Cays, the Bahamas (23°46'N Lat., 76°06' W Long.). Census data were collected along two permanent transects ("AB" and "BA", Fig. 1) established by CMRC. These transects extended from 10-250m. The "AB" and "BA" transects have been proposed to differ in current intensity and sedimentation rates, with both being higher on the former (G. Dennis personal communication).

Sites at 10 and 20m were sampled via SCUBA in September 1993, while the 30m site was sampled in September 1994 (Fig. 2). A total of eleven 10m lines were deployed at each depth and arrayed in such a manner as to allow a 1m spacing between each line and also to prevent the lines from extending off the reef into sandy areas or to traverse bathymetric contours. These lines were photographed every meter with a Nikonos V underwater camera and strobe (total

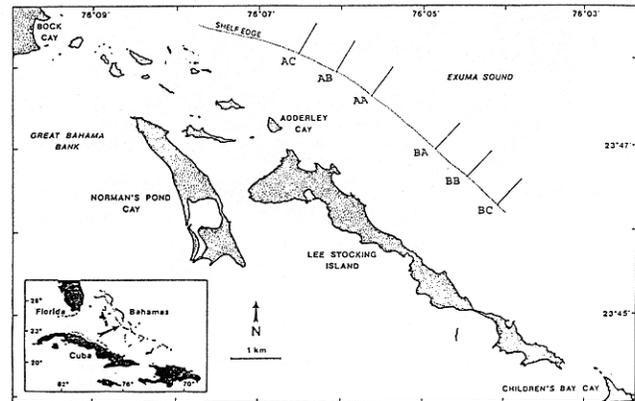


Fig. 1: Index map showing location of transects off Lee Stocking Island.

of eleven transparencies per line, one hundred and twenty-one per site). Resulting transparencies each encompassed 0.2 m² of bottom and enabled resolution of objects down to 1mm in diameter when analyzed in the laboratory.

Sites from 50-250m (Fig. 2) were censused using the submersible Nekton Gamma. All deep sites with the exception of AB 150m and AB 200m were sampled in September 1993. The latter two sites were sampled in September 1994. At each site transects were oriented parallel to bathymetric contours and extended laterally for approximately 100m. Photographs, utilizing an internal 35mm camera and external strobe, were taken approximately every meter along the transects. The area encompassed by each photograph was 0.2m² of bottom. A total of approximately one hundred photographs were taken per site.

In addition to photographic data, CTD (Conductivity, Temperature, Depth) profiles were frequently collected during submersible dives by CMRC. Temperature, salinity, dissolved oxygen and irradiance values were collected using a Seabird SBE19 (Dennis and Proft 1994).

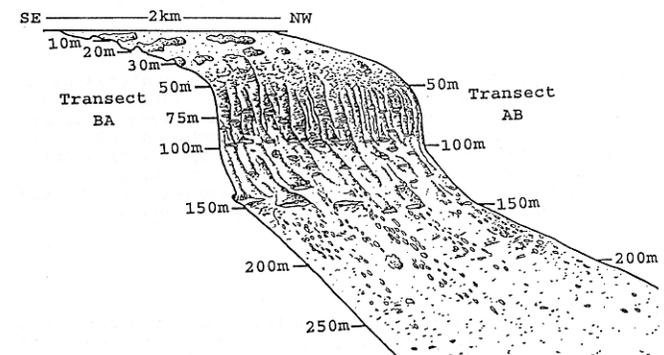


Fig. 2: Submarine profile off LSI showing location of study sites.

Laboratory

Photocensus data were processed in the laboratory by projecting each transparency at natural size onto a screen containing a random array of seven points. Objects occurring under each point were identified to the lowest possible taxonomic unit and entered into a spreadsheet. Means and standard deviations were calculated by treating each line (eleven transparencies) from the shallower sites as a subsample. Descriptive measures for deeper sites were

calculated by treating each successive group of eleven photographs along the 100m long transects as a subsample. Diversity indices (S, H' [natural log], J') were also determined from these data. Correlations were tested with the nonparametric Spearman Rank Correlation Coefficient (SRC).

A semi-quantitative "rugosity" scale (Table 1) of 0-5 was based on the estimation of the amount of relief shown in the transparencies. For example, 0 = very low relief, substrate entirely covered by sand; 1 = > 50% of substrate covered by sand; 2 = < 50% covered by sand; 3 = < 10% covered by sand; 4 = no sand cover, exposed substrate with moderately high relief (< 50% beyond depth of field of transparency); 5 = no sand cover, exposed substrate with very high relief (> 50% beyond depth of field).

Table 1: Bathymetric distribution of substrate types (means with 95% confidence intervals in parentheses). Hard substrate includes both bare hard substrate and hard substrate occupied by benthos.

Depth (m)	Transect	N	Rugosity	Cobble	Sand	Hard Substrate
10	BA	820	3.9 (0.1)	0.0	0.1 (0.2)	99.9 (0.2)
20	BA	821	3.7 (0.1)	1.3 (1.3)	1.0 (1.1)	97.7 (1.7)
30	BA	737	2.8 (0.2)	0.0	15.6 (7.4)	84.4 (7.4)
50	BA	497	2.5 (0.2)	3.7 (7.3)	14.7 (4.2)	84.9 (4.4)
75	BA	519	3.3 (0.2)	0.8 (1.1)	6.8 (3.7)	92.4 (4.2)
100	BA	546	2.9 (0.2)	0.2 (0.4)	12.6 (7.0)	87.2 (7.2)
150	BA	485	2.3 (0.3)	1.4 (1.6)	38.4 (6.3)	60.2 (7.2)
200	BA	480	1.0 (0.2)	0.0	68.6 (9.5)	31.4 (9.5)
250	BA	525	0.8 (0.2)	0.0	75.6 (5.7)	24.4 (5.7)
50	AB	644	2.2 (0.1)	0.1 (0.3)	23.0 (6.6)	76.8 (6.7)
100	AB	553	3.0 (0.1)	0.0	4.3 (1.8)	95.7 (1.8)
150	AB	734	2.7 (0.2)	1.9 (1.5)	20.5 (5.9)	77.5 (6.5)
200	AB	763	0.4 (0.1)	0.7 (0.7)	86.6 (9.0)	12.7 (8.8)

Community zonation was determined by cluster analysis using MVSP (Multivariate Statistical Package) Plus Ver. 2.0 (Kovach 1990). Taxonomic data in Table 2 were modified with the logratio transformation (Aitchison 1986) to counter the effects of closure in proportional data. Euclidean Distance was employed as a dissimilarity coefficient and clustering was performed using the unweighted pair group (average linkage) procedure.

RESULTS

Topography

From the shoreline out to approximately 35m depth the slope is gentle and reefs are largely restricted to areas of elevated relict Pleistocene topography. From 35-50m the slope extends seaward at 30-45°. At approximately 50m the slope becomes vertical and continues as such to 100-125m (the deep fore reef of Goreau and Land 1974). This area includes vertical to overhanging surfaces and shelves which are frequently cut by sand channels. Below 100-125m the slope becomes more gentle and sand and silt accumulate on most surfaces. Consequently, the amount of hard substrate available for colonization by epi- and endobenthos declines below this depth (Table 1, Fig. 2).

The amount of sand present is positively correlated with increasing depth, while the amount of available hard substrate is negatively correlated with depth (Table 1; SRC $p < 0.002$ for both trends). Although our methodology enhanced the amount of hard substrate sampled in shallow (≤ 30 m) water (transects were restricted to reef areas), the trend of decreasing hard substrate with increasing depth still holds when the submersible transects (no attempt to restrict transects to areas of hard substrate) alone are considered (SRC $p < 0.05$).

Rugosity values were variable, but, in general, declined with increasing depth (Table 1; SRC $p < 0.005$). In particular, rugosity declined greatly below 150m. Rugosity was strongly correlated with % living cover (SRC $p < 0.001$ for living as percent of total bottom) and also with diversity (S: SRC $p < 0.001$; H': SRC $p < 0.05$).

CTD data collected by CMRC (Dennis and Proft 1994) commonly show a thermocline located at approximately 100m and corresponding to the base of the deep fore reef (Oct. - Dec. intervals, Fig. 3). Other physical factors (e.g. dissolved oxygen and salinity) show similar patterns. Preliminary analysis of light data collected by CMRC suggests that the 1% of surface irradiance value occurs at approximately 90m depth during the Oct. - Dec. interval, with the 1% level occurring at shallower depths (e.g. 70m) during May.

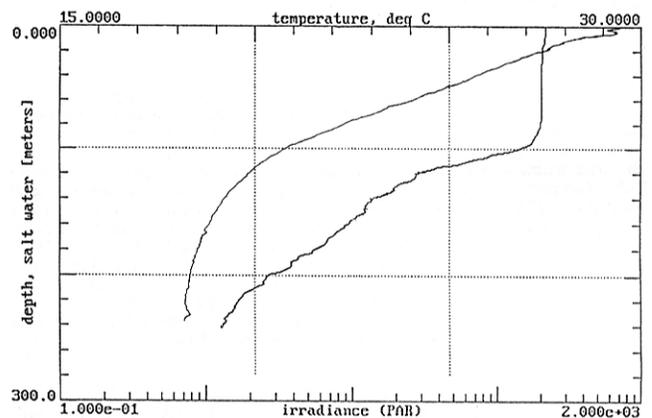


Fig. 3: Composite temperature and irradiance profiles for LSI, Dec. 5, 7, 1993, respectively (modified from Dennis and Proft 1994).

Community zonation

The benthic community off LSI exhibits a pronounced bathymetric zonation (Table 2, Figs. 4-6). Table 2 presents data as percentages of hard substrate, rather than total bottom, in order to more clearly delineate community patterns. Data in Table 1 allow Table 2 data to be converted to percent of total bottom if so desired.

Although living cover is high (74-89% of the total bottom) above 100m, it declines below this depth (4-63% of bottom; Table 2). Substrate microtopography exerts a strong control on the distribution of the benthos with organisms largely restricted to vertical and overhanging surfaces where they are protected from sediment accumulation. Living cover is inversely correlated with increasing depth (Table 2, Fig. 4; SRC $p < 0.005$ for living cover as percent of hard substrate; SRC $p < 0.001$ for living cover as percent of total bottom). This corresponds to the increase in sand cover with increasing depth, particularly below 100m (Table 1; SRC $p < 0.001$ for sand versus living cover as percent of total bottom).

Filamentous and macroalgae dominate from 10-50m and occupy 60-90% of the hard substrate (Fig. 5). Corals cover 3-23% of the hard substrate above 50m. Below this depth, corals decline and sponges increase in abundance and diversity. Below 50m coralline algae and possible endolithic algae (appear as green stains on rocks) are the dominant plants. The deepest zones exhibit very low living cover and are occupied by demosponges, endolithic? algae and polychaetes.

Shallow-water (≤ 30 m) coral assemblages are dominated by the typical western Atlantic suite of corals (*Agaricia agaricites*, *Montastrea annularis*, *M. cavernosa*, *Porites astreoides*, *P. porites* and others). The deeper assemblages are dominated by *M. cavernosa* and various *Agaricia* spp.

Dictyota, *Sargassum* and *Microdictyon* comprise over 80% of the shallow-water (≤ 30 m) macroalgal community. *Halimeda*

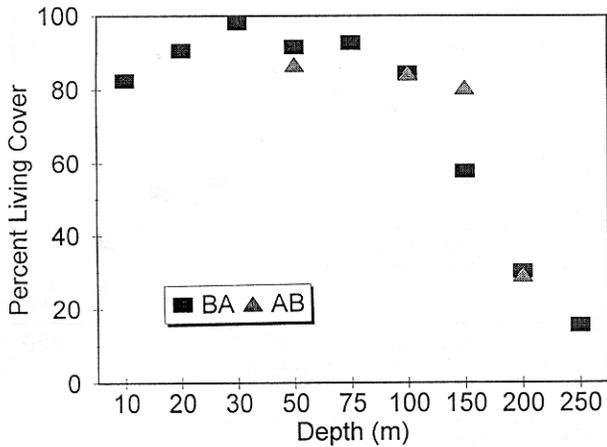


Fig. 4: Bathymetric trends in living cover (% of hard substrate) along the AB and BA transects.

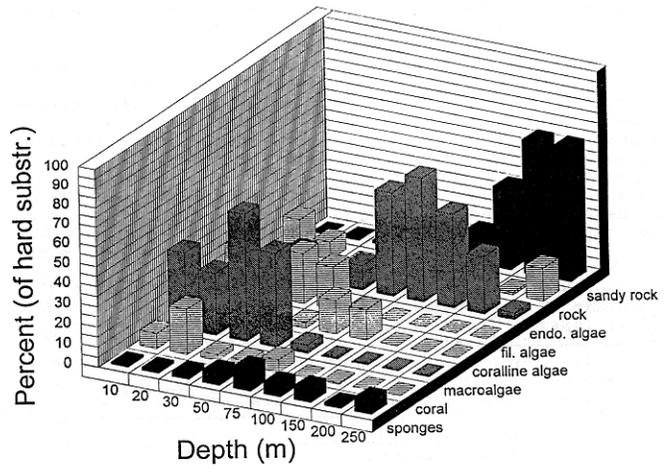


Fig. 5: Bathymetric distribution of benthos along the BA transect (endo. algae = possible endolithic algae, observable as green stain on rock surfaces, fil. algae = filamentous algae).

Table 2: Mean percent cover of hard substrate and organism categories (95% confidence intervals in parentheses). Corals occurring at 150m are ahermatypes. Other Cnid. = Noncoral Cnidarians, Cor. Alg. = Coralline Algae, Fil. Alg. = Filamentous Algae, Endo. Alg. = Possible Endolithic Algae (appears as a green stain on rock surfaces), Mac. Alg. = Macroalgae, S = Species Number, H' = Diversity (natural log), J' = Evenness (natural log).

Site	BA	BA	BA	BA	BA	BA	BA	BA	BA	BA	AB	AB	AB	AB
Depth	10	20	30	50	75	100	150	200	250	50	100	150	200	
Points	819	802	622	424	479	477	291	152	168	493	531	574	98	
Coral	7.3 (3.8)	22.2 (5.5)	2.8 (1.3)	2.6 (1.5)	6.1 (3.3)	0.0	0.5 (0.9)	0.0	0.0	2.6 (2.1)	0.0	0.2 (0.3)	0.0	
Other Cnid.	0.2 (0.3)	1.1 (1.5)	0.1 (0.3)	0.2 (0.4)	0.0	0.0	0.7 (1.4)	0.0	1.0 (2.0)	0.0	0.0	0.0	0.0	
Sponge	1.2 (0.8)	1.5 (1.5)	2.7 (1.5)	6.3 (3.1)	11.1 (3.0)	6.3 (2.6)	7.2 (3.8)	1.6 (3.1)	7.3 (5.9)	7.8 (2.6)	8.9 (4.8)	6.5 (3.5)	0.0	
Sclero-sponge	0.0	0.0	0.0	0.0	0.0	0.8 (0.6)	0.5 (0.9)	0.0	0.0	0.0	0.0	0.0	0.0	
Cor. Alg.	5.4 (1.8)	3.5 (1.7)	1.9 (1.2)	2.8 (1.9)	16.6 (3.3)	15.0 (3.5)	0.0	0.0	0.0	8.6 (2.7)	25.5 (5.5)	5.2 (3.1)	0.0	
Fil. Alg.	22.3 (3.2)	17.5 (3.9)	24.7 (4.2)	20.9 (6.4)	0.0	0.0	0.0	0.0	0.0	1.2 (1.1)	0.0	0.0	0.0	
Endo. Alg.	7.1 (1.6)	13.5 (3.0)	2.2 (1.5)	12.1 (3.9)	52.5 (10.2)	63.0 (5.7)	47.2 (5.3)	28.3 (8.3)	3.4 (3.2)	24.0 (5.4)	49.0 (4.3)	67.8 (4.8)	27.3 (14.9)	
Mac. Alg.	37.9 (4.5)	30.7 (3.1)	63.7 (6.5)	46.5 (14.9)	3.9 (1.7)	0.0	0.0	0.0	0.0	42.8 (10.3)	0.0	0.0	0.0	
Poly-chaete	0.0	0.0	0.0	0.0	0.0	0.0	1.0 (0.9)	0.4 (0.7)	2.3 (1.8)	0.0	0.0	0.7 (0.5)	2.3 (4.0)	
Bryo-zoa	0.0	0.0	0.0	0.0	1.0 (0.8)	0.4 (0.8)	1.2 (1.9)	0.0	1.4 (1.4)	0.0	0.4 (0.5)	0.2 (0.3)	0.0	
Tuni-cates	0.0	0.0	0.0	0.0	0.8 (0.9)	0.0	0.0	0.0	0.0	0.0	0.3 (0.4)	0.2 (0.4)	0.0	
S	55	44	36	38	39	19	11	5	8.0	33	25	18	3	
H'	2.67	2.74	1.96	2.03	2.19	1.47	1.38	1.04	1.84	2.19	1.59	0.99	0.74	
J'	0.67	0.72	0.55	0.56	0.60	0.50	0.58	0.65	0.88	0.63	0.49	0.34	0.67	
Living	82.4 (6.7)	90.7 (3.4)	98.5 (1.8)	91.7 (8.5)	91.8 (5.4)	84.6 (8.3)	57.8 (6.3)	30.3 (11.5)	17.4 (9.5)	86.9 (5.6)	84.5 (6.4)	80.6 (7.0)	29.6 (10.7)	
Hard Bare	17.3 (4.0)	8.7 (1.8)	0.4 (0.7)	0.0	0.2 (0.4)	0.0	0.8 (1.0)	1.2 (1.7)	16.1 (4.7)	0.6 (0.6)	2.8 (2.6)	0.8 (0.9)	14.4 (19.6)	
Hard w/ Sand	0.3 (0.3)	0.6 (0.6)	1.5 (1.2)	8.3 (6.8)	7.0 (4.3)	15.4 (6.6)	41.5 (5.2)	68.5 (10.5)	68.4 (4.7)	12.5 (3.8)	12.7 (5.8)	18.6 (4.6)	56.3 (31.8)	

species comprise only 3-8% of the shallow macroalgal community, but comprise 50-95% of the macroalgae at 50 and 75m. Although abundant elsewhere in the western Atlantic, *Lobophora variegata* accounts for only 0-12% of the macroalgae occurring over the range of 10-75m.

Cluster analysis divides the community into three depth-related zones (Fig. 6). Sites from 10-50m group together, as do sites from 75-150m and 150-250m. These breaks closely correspond to changes in topography (Fig. 2), suggesting a strong interrelationship between geomorphology and community structure.

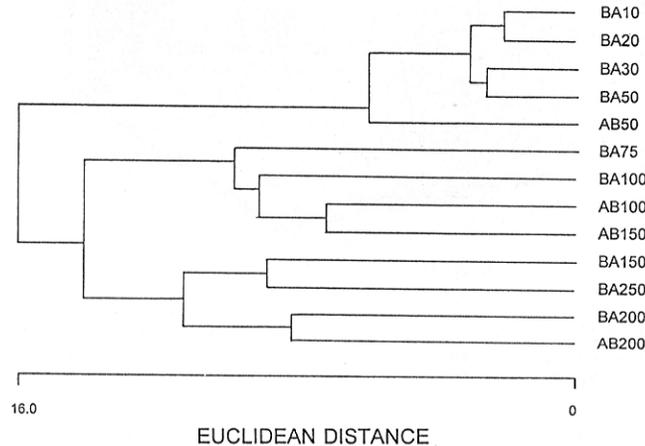


Fig. 6: Cluster dendrogram of AB and BA transect sites.

Diversity

Diversity (H') and species number (S) show parallel trends. Diversity values for the 10 and 20m sites are similar, decrease at 30m and are then relatively constant until 75m or so until, finally, declining once again below this depth (Table 2, Figs. 7-8; SRC $p < 0.001$ for both S and H' versus depth). Diversity (H') is positively correlated with percent living cover (SRC $p < 0.05$ for living as percent of hard substrate; SRC $p < 0.005$ for living as percent of total bottom). Finally, evenness (J') shows no strong bathymetric pattern.

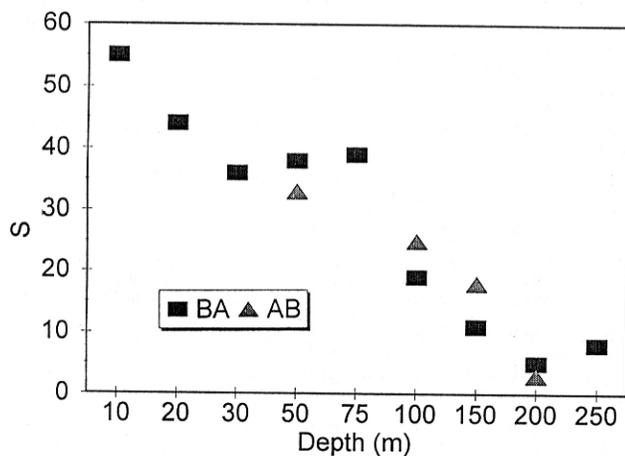


Fig. 7: Bathymetric trends in species number (S) along the AB and BA transects.

Intermediate-scale lateral variation

Although anecdotal evidence suggests that the "AB" and "BA" transects differ in current and sedimentation regimes (G. Dennis, personal communication), overall bathymetric trends in percent living cover and diversity are very similar, suggesting that these factors have relatively little effect (Table 2, Figs. 5, 7-8). The cluster analysis also suggests that the AB sites are very similar to the BA sites (Fig. 6). Slight differences do exist in community composition along the two transects, but it is difficult to ascribe a causal factor to any of the differences.

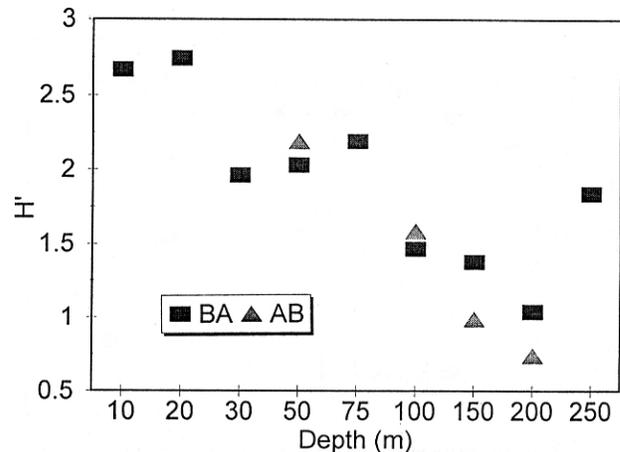


Fig. 8: Bathymetric trends in diversity (H' natural log) along the AB and BA transects.

DISCUSSION

Deep reef topography

The profile of the deep reef off LSI closely resembles that described for the Tongue of the Ocean area of the Bahamas (Schlager and Chermak 1979), Belize (James and Ginsburg 1979) and Jamaica (Lang 1974; Goreau and Land 1974; Ohlhorst and Liddell 1988). These profiles, presumably, reflect Pleistocene sea-level oscillations (Goreau and Land 1974; Schlager and Chermak 1979). As discussed below, deep reef topography may influence the benthos through mediation of light levels and sedimentation.

Community zonation

General

The benthic community off LSI displays strong depth-related zonation (Figs. 4-8). The present study is most easily compared to Liddell and Ohlhorst's (1988) study at Jamaica, as methodologies are similar. Along the north coast of Jamaica, the deep reef communities occurred on a vertical to overhanging wall of limestone (the deep fore reef, dfr) which extended from 55-130m. At 60m the community resembled that of shallower water, although scleractinians were less abundant and encrusting and erect demosponges were much more so. Coralline algae and macroalgae were also important space occupants at 60m, where living cover approached 65% of the total bottom. Encrusting sponges and coralline, filamentous and macroalgae were abundant in the middle region of the dfr (75m). A low-diversity assemblage occupying 40% of the substrate and dominated by small encrusting and endolithic demosponges and endolithic algae occurred from 100-130m, the lower limit of the dfr. Percent living cover was similar at the Jamaican and LSI deep-reef sites.

The major community break, determined by cluster analysis, in the Jamaican deep reef community was between 45 and 55m, as compared to between 50 and 75m at LSI. Similarly, the deepest corals recorded in transects at Jamaica were at 60m, as compared to 75m at LSI. However, other major categories (e.g. macroalgae) showed similar bathymetric patterns at the two localities.

Corals

The deepest hermatypic corals (*Agaricia*) encountered in transects at LSI occurred at 75m (Table 2), although *Agaricia* was observed at 90m. This depth is comparable to that of other reports from the western Atlantic region and elsewhere. The deep coral association at LSI consisted of *Agaricia* spp. and *Montastrea cavernosa*. These occurred in very low numbers, occupying only 2-6% of the bottom from 30-75m. The number of coral species at LSI declined sharply from eleven species detected in transects at 20m to only four species at 30m and two to four species between 50-75m.

Reed (1985) found the corals *Agaricia grahamae*, A. sp., *Leptoseris cucullata*, *Madracis* sp. and *Montastrea cavernosa* occurring at maximum depths of 108-119m off San Salvadore Island, the Bahamas. Liddell and Ohlhorst (1988) found hermatypic corals, principally *Agaricia*, occurring to 60m depth in transects and Lang (1974) noted the presence of *Agaricia* at 90m at Jamaica.

Fricke and Meischner (1985) found the deep-water (>60m) hermatypic association at Bermuda to consist of *Agaricia fragilis*, *Montastrea cavernosa* and *Scolymia cubensis*, with *M. cavernosa* occupying the greatest amount of space and being the only coral to extend below 70m (to 78m). Coral diversity was relatively constant ($H': 1.5-1.75$) over the range of 0-39m. Diversity then decreased to 1.2 by 49m and finally to 0.0 by 79m due to lack of suitable hard substrate.

Algae

At LSI macroalgae, principally *Halimeda*, extended to 75m, however, macroalgal abundance declined sharply below 50m. Although *Halimeda* occupied 20-26% of the bottom at 50m, it accounted for only 4% of the bottom cover at 75m. In shallow water (10-30m) other species, such as *Dictyota*, *Lobophora*, *Microdictyon* and *Sargassum*, were much more abundant than *Halimeda*.

Freile et al. (1995) examined sediment production by *Halimeda* from the bank top to lower slope (10-300m) along the western edge of the Great Bahama Bank. *Halimeda*, principally *H. copiosa* and *H. goreauii*, extended to at least 80m and occupied up to 30% of available substrate on the upper portions of a cemented rocky escarpment which extended from 60-150m. These findings correspond closely with those of the present study.

Little et al. (1985) studied the algae occurring on the steep face of a seamount off San Salvador Island. From 81m (the top of the seamount) to 268m, algal diversity decreased with increasing depth. The macroalga *Lobophora variegata* dominated (59.4% of the substratum) the algal community from 80-88m. *Halimeda copiosa* dominated (20% coverage) from 117-130m. These depth ranges and abundances are much greater than encountered at LSI.

Liddell and Ohlhorst (1988) found that macroalgae extended to 75m at Jamaica, occupying 11% of the bottom at this depth. Coralline and filamentous algae dominated below this depth. *Halimeda* was the dominant deep macroalga.

Community diversity

At LSI community diversity (S, H') declined with increasing depth, particularly below 75m. This is presumably in response to declining amounts of living cover as diversity and living cover were positively correlated.

Liddell and Ohlhorst (1988) found that community diversity remained relatively constant to a depth of 90-100m at Jamaica (no significant correlation with depth). Diversity (S, H') was very similar at Jamaica and LSI with the exception of the 90-100m sites, which were much more diverse at Jamaica ($S = 29-43; H' = 2.30-2.98$). Diversity was not correlated with living cover at Jamaica. These differences between LSI and Jamaica suggest that the deep communities off LSI may be more controlled by physical factors (likely sedimentation, see below) than are those at Jamaica.

Controls on deep-reef community structure

Community structure and zonation on the shallow reefs is controlled by a number of biotic and abiotic factors, most notably predation/grazing, light intensity and turbulence (Sheppard 1982). Each of these factors will be examined below.

Predation/grazing

Glynn (1990) summarized a considerable body of work on grazing in the coral reef system. Most studies were in agreement that a steady decline in herbivory by invertebrates and fishes occurred with increasing depth on reefs. At LSI, Dennis (1996) noted a significant drop in fish abundance and diversity below 150m. The lack of herbivores may result in high standing crops of algae in deep reef settings, despite greatly reduced light intensities.

Sedimentation

That sedimentation plays an important role in structuring the deep reef community off LSI is suggested by the significant negative relationship existing between sediment abundance and percent living cover ($SRC p < 0.001$) and between sediment cover and diversity ($S: SRC p < 0.001; H': SRC p < 0.02$). In particular, the great drop in percent living cover (to 4-10% of total bottom) occurring below 200m corresponds to the increase in sand to 69-87% of the total bottom. Liddell and Ohlhorst (1988) similarly found the amount of sand to be negatively correlated with living cover, although sand amounts were not correlated with diversity at Jamaica. Fricke and Meischner (1985) attributed the rapid decline in coral abundance below 50m at Bermuda, in part, to lack of suitable hard substrate.

Light

The photic zone limit (i.e. the compensation point where photosynthesis equals respiration) is normally regarded as

1% of surface illumination (Ryther 1956). Porter (1973) found the 1% level to occur at 90m in the Tongue of the Ocean, Bahamas while Littler et al. (1985) found the 1% level to occur between 71m and 83m off San Salvador Island. The waters of Exuma Sound are extremely clear and preliminary analysis of CMRC data (Dennis and Proft 1994) suggests a comparable lower limit for the sites off LSI.

Reed (1985) found several genera of hermatypic corals growing between 108-119m off San Salvador Island. Light levels at these depths were only 0.15% of surface irradiance, resulting in greatly reduced growth rates. Littler et al. (1985) found the alga, *Halimeda*, occurring at 130m (0.08% surface irradiance) at this site. As noted, corals extended to somewhat greater depths at LSI than at Jamaica, perhaps due to greater light penetration at the former site.

Microtopography

Although the role of microtopography in determining irradiance levels (Jaubert and 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 great detail. A vertical surface will only receive some 25% of the irradiance of a horizontal surface at the same depth (Palkowski et al. 1990); such differences become significant as total irradiance declines with increasing depth.

Birkeland et al. (1981) found that, with increasing depth (6-37m), coral recruits shifted settlement patterns from vertical to horizontal surfaces and from lower (shaded) to upper surfaces. This trend was in response to differences in light intensity and reduced spatial competition with algae with increasing depth. Fricke and Schuhmacher (1983) found that the deepest occurring corals (100-109m) at their Red Sea site 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, Ohlhorst and Liddell (1988) found that the deepest-occurring corals in their transects at Jamaica (61m) were more abundant on exposed slopes (30% cover by corals) than on exposed vertical surfaces (10% cover).

Ohlhorst and Liddell (1988) documented the effect of small-scale variation in topography upon the Jamaican community zonation. Superimposed upon the overall vertical profile of the dfr were numerous overhangs and small ledges, contributing to patchiness at any one depth. These microtopographies interact with light and sedimentation, thus promoting increased community diversity at any one depth as well as local shifts in depth-related community zonation. Low-angle sites displayed reduced living cover and diversities relative to vertical sites due to the accumulation of sediment on the former. Low-angle sites, however, received more illumination than vertical exposed and sheltered sites, thus causing downward shifts in the bathymetric distributions of certain taxa.

At LSI the strong effects of microtopography on the distribution of benthos have also been observed. At the deepest sites (200m and 250m) living cover is restricted to the limited areas of vertical to overhanging surfaces (typically small, 20cm-high ledges). Despite greater illumination, exposed level or slightly-inclined surfaces are not occupied by benthos due to a heavy sediment cover. Thus the sites display a spatial mosaic, consisting of small islands of suitable habitat surrounded by a desert of barren sand.

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