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THE SIGNIFICANCE OF HALIMEDA AS A SPACE-OCCUPIER AND SEDIMENT-PRODUCER, 1-750M, NORTH JAMAICA

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ABSTRACT

Halimeda is an important space-occupier over the bathymetric range of 1-75m and a significant contributor to sediment to 300m along the north central coast of Jamaica. The alga's distribution is noncontinuous, however; it occurs abundantly in shallow lagoonal settings, is relatively uncommon on the shallow (1-45m) fore reef, and is, again, important between 55-75m, where it may occupy up to 19% of the substratum. Grazing is thought to limit the alga's abundance on the shallow fore reef, while the alga's lower depth limit appears to be mediated by light intensity, with the rapid decrease in the alga below 75m linked to irradiance values approaching 0.05% of surface illumination. The abundance of the alga in sediment parallels its living distribution with the exception of the addition of calcareous skeletal elements to the upper island slope (120-300m) by Halimeda occurring upon the vertical escarpment of the deep fore reef (50-120m). Below 300m (samples collected to 750m) the sediment is largely pelagic, with few or no Halimeda allochems.

INTRODUCTION

Although the significance of the alga Halimeda (f. Codiaceae) as a member of the benthos (Hillis-Colinvaux 1977, 1980, Drew & Abel 1985, Phipps et al. 1985) and a sediment producer (Emery et al. 1954, Goreau & Goreau 1973, Milliman 1974, Neuman & Land 1975, Scoffin & Tudhope 1985) in shallow (<60m) tropical marine settings is well established, our knowledge of algal distributions in deep water settings (>60m) is much more limited. Recently, submersibles have enabled research in this poorly-known area (Lang 1974, James & Ginsburg 1979, Agegian & Abbott 1985, Littler et al. 1985, Hillis-Colinvaux 1986, Liddell & Ohlhorst 1988). The present paper presents some of the first quantitative data on the abundance and bathymetry of living Halimeda over the range of 1-120m in fringing reef and platform margin environments. In addition, the contribution of the alga to reef and island slope sediments is documented over the range of 1-750m.

STUDY LOCALITY

This study was conducted at Discovery Bay on the north central coast of Jamaica at Lat. 18°30'N and Long. 77°20'W. The well developed fringing reefs occurring along the north central coast of Jamaica display a striking, depth-related macrobiotic zonation which has been described in several papers (Goreau & Goreau 1973, Lang 1974, Liddell & Ohlhorst 1987, 1988, and others). The fringing reefs studied occur on the West Fore Reef and are known as LTS (A-A'), Watertower and Zingorro (B-B'), and Mooring One (C-C', Figs. 1-2).

The following succession of structural/geomorphic zones is encountered along an onshore to offshore traverse across the West Fore Reef: back reef, reef crest, fore reef terrace, fore reef escarpment, fore reef slope, deep fore reef, and island slope. The back reef (or lagoon) is a shallow area of reduced coral growth due to both

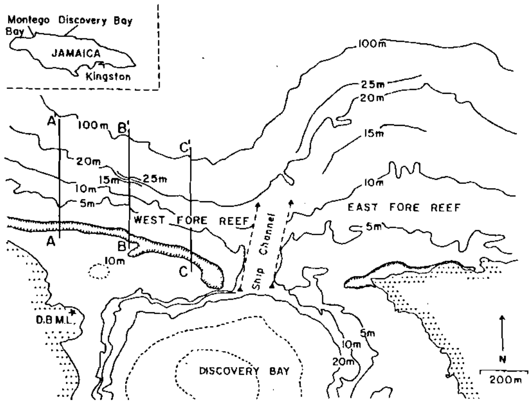

Figure 1. Index map of Discovery Bay, Jamaica area (modified from Liddell et al. 1984). A-A' LTS, B-B' Zingorro-Watertower, C-C' Mooring One.

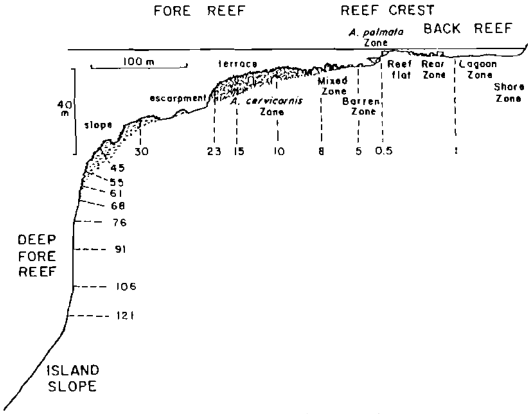

Figure 2. Profile along B-B'(Fig. 1) showing location of sampling stations (modified from Liddell et al. 1984).

Figure 3. Halimeda and other algae at 1m depth in back reef at Discovery Bay. Scale bar is 10cm.

Figure 4. Abundant Halimeda at 70m on the wall of the deep fore reef. Scale bar is 10 cm.

high sediment production by macroalgae and high sediment resuspension. Plant life, including the marine angiosperm Thallasia and numerous algae such as Halimeda, Penicillus, and others (Fig. 3), is abundant. The reef crest extends from the surface seaward to approximately 7m depth; coral rubble is heavily encrusted with crustose coralline algae.

The fore reef terrace extends from 7 to 15m and consists of large parallel lobes of coral oriented perpendicular to the reef crest and extending seaward at a moderate (15-20°) slope for approximately 200m where they terminate in a steep (45+°) escarpment extending from 15 to 25m. Macroalgae are rare over the range of 1-25m on the fore reef due to intense grazing activity, principally by the urchin Diadema (Sammarco et al. 1974, Carpenter 1981).

The landward portion of the fore reef slope, which begins at 25-30m depth, usually consists of a low angle (5-20°) sand 'moat' containing scattered coral heads. Coral cover increases by 30 to 35m, often forming parallel lobes and occasional pinnacles which may rise up to 10m above the sand. Whereas the dominant algae on the fore reef terrace are crustose corallines, the fore reef slope is characterized by abundant noncrustose macroalgae, chiefly the brown alga Lobofora and the calcareous green alga Halimeda. At approximately 35m the slope increases to between 45-60°.

A slope break occurring between 45 and 65m, typically at 55m, marks the beginning of the steep (60-90°) deep fore reef 'wall'. Although corals and macroalgae, including Halimeda (Fig. 4) are abundant on the upper portions of the wall, they are replaced by sclerosponges, demosponges, and crustose coralline algae below 75m. Filamentous and endolithic algae and encrusting demosponges dominate below 90m. The deep fore reef ends at approximately 120-130m where the more gentle (20-45°) and sediment covered island slope begins.

METHODS

Shallow-water census data were collected over the range of 1-55m in 1982. Divers using SCUBA employed a linear point intercept method in which a 10m line with points located every 20cm was draped over the reef and the identity of the organisms or substratum type occurring beneath each point recorded (Liddell & Ohlhorst 1987). Up to 10 parallel lines, spaced at 1m intervals and oriented perpendicular to the depth gradient, were censused at each site (Fig. 2).

A Perry submersible (PC-8), owned and operated by Research Submersibles Ltd., Grand Cayman, was utilized in data collection over the range of 60-120m on the escarpment of the deep fore reef in 1984. 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 (Liddell & Ohlhorst 1988).

SCUBA divers collected shallow cores of sediment over the range of 1-75m in 1982 (Boss & Liddell 1987). Research Submersibles Ltd's. Perry PC-8 submersible was used to collect shallow sediment cores from 130-240m in 1984 (Liddell et al. 1987) and Research Submersible's Pisces was used to collect sediment cores from 250-850m in 1987. Sediment samples were not collected between 75-120m on the deep fore reef due to the difficulty of maneuvering the submersible on the vertical escarpment.

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 or substratum category occurring at each point recorded (planar point intercept method; Liddell & Ohlhorst 1988). Bathymetric trends in the distribution of algal groups were tested with the Spearman Rank Correlation Coefficient (SRC).

Jamaican fore reef sites are characterized by low water turbidity (light attenuation coefficient 0.06/m for the upper 30m of the water column, Brakel 1979). Although the attenuation (a combination of absorption and scattering) of sunlight by seawater is nonlinear in the upper 5m of the water column, the attenuation coefficient approaches a constant at greater depths (Jerlov 1977). Therefore, Brakel's (1979) attenuation coefficient was used to extrapolate irradiance values to a depth of 120m in the water column. Correction for slope angle and orientation (Brakel 1979) yielded a 1.0% value at approximately 55m on the lower fore reef slope and a 0.05% value at 90m on the steeply-inclined, north-facing wall of the deep fore reef. Irradiance values generated by this procedure are, of course, no substitute for *in situ* quantum irradiance measurements and must be regarded with caution.

Sediment samples from 0-234m were epoxy-embedded and thin-sectioned. Abundances of grain types were determined by counting 300-600 points per section, depending upon allochem diversity. Thirteen samples from 300-750m were scanned under a binocular microscope and visual estimates of *Halimeda* abundance made.

RESULTS

The Jamaican reefs suffered a major disturbance event, the mass mortality of the urchin grazer, *Diadema antillarum*, in August, 1983. The reduction in urchin densities from $14/m^2$ at some sites to nearly $0.0/m^2$ resulted in a rapid and dramatic increase in filamentous and erect macroalgal biomass, which occurred at the expense of other benthos, such as corals, boring sponges, and crustose coralline algae (Liddell & Ohlhorst 1986). In as much as the urchin did not occur in great numbers at depths in excess of 20m, the effects of the urchin mass mortality were restricted to the shallower reefs. As of July, 1987, the shallow reefs have still not recovered from this perturbation (personal observation). The data we are presenting herein for shallow (<30m) reef sites were collected prior to this disturbance event. For consistency, the present tense will be used in describing both shallow, now greatly altered, and deeper reef sites.

Halimeda as a Space-Occupier

At this stage of the present study, the various *Halimeda* species have not been distinguished from the census data. *H. incrassata* is abundant in back reef settings, while *H. goreaui* and *H. opuntia* occur at relatively shallow fore reef sites. *H. copiosa* appears to dominate on the deep fore reef, where lesser amounts of *H. discoidea* also occur.

In the rear zone of the back reef, immediately behind the reef crest, living *Halimeda* occupies up to 6.5% of the mixed sand and coral rubble substrata (Table 1, Fig. 5). *Halimeda* may also be abundant in sandy areas of the back reef, which were not censused. The alga is not abundant in shallow water on the fore reef (0.5-45m), presumably due to intense herbivory over this range. *Halimeda* reaches its greatest abundance over the range of approximately 55-75m, where it occupies up to 18.6% of the hard substratum. *Halimeda* rapidly declines in abundance below this depth, occupying only 0.0-0.3% of the substratum at 90m. *Halimeda* abundance is significantly correlated with depth over the range of 0.5-75m on the fore reef (SRC, $p<0.01$).

Table 1. Abundance of *Halimeda* and total macroalgae at Discovery Bay, Jamaica (means with ± 95% confidence intervals in parentheses).

Depth m[1]	Zingorro		Mooring One	
	Halimeda	Total	*Halimeda*	Total
BR 1.0	6.5(3.1)	17.2(2.2)		
0.5	0.0	0.1		
5.0	0.0	3.8(1.9)		
8.0	1.1(0.9)	5.5(2.1)		
10.0	0.9(0.9)	6.9(2.1)		
15.0	2.7(1.5)	10.9(4.0)		
23.0	1.3(0.8)	2.7(1.3)		
30.0	1.2(2.3)	8.2(7.8)		
45.0	0.7(1.1)	26.5(5.5)		
55.0	18.6(16.6)	27.5(16.0)	12.1(5.2)	12.6(5.1)
61.0	11.3(5.3)	12.4(5.2)	17.0(7.0)	17.0(7.0)
68.0			16.4(7.0)	16.6(6.9)
76.0	14.6(5.5)	14.6(5.5)	11.3(6.0)	11.3(6.0)
91.0	0.0	0.0	0.3(0.5)	0.3(0.5)
106.0			0.0	0.0
121.0	0.0	0.0		

[1] Fore reef 0.5 m site censused by Huston (1985) in 1976, Zingorro back reef 1.0m and fore reef 5.0-55.0m sites censused by Boss & Liddell (1987) in 1982, Mooring One 55m and all deep fore reef 61.0-121.0m sites censused by Liddell & Ohlhorst (1988) in 1984. Number of transect points for 0.5m site is 4782; for 30m, 45m, and 55m, approximately 250; for all other sites, approximately 500.

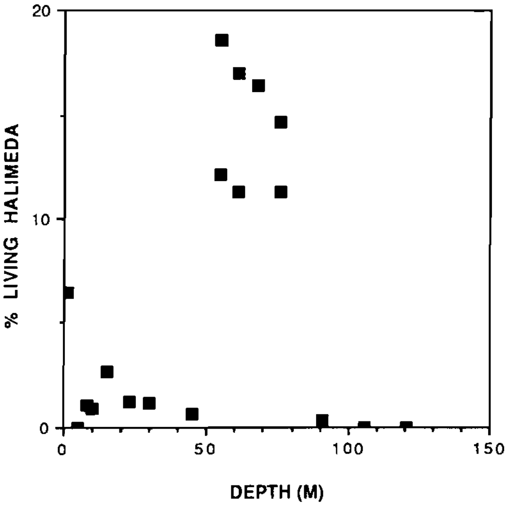

Figure 5. Bathymetric distribution and abundance of living *Halimeda* along traverse B-B'(Fig. 1). *Halimeda* increases significantly (SRC, $p < 0.01$) with increasing depth on the fore reef to a depth of 75m.

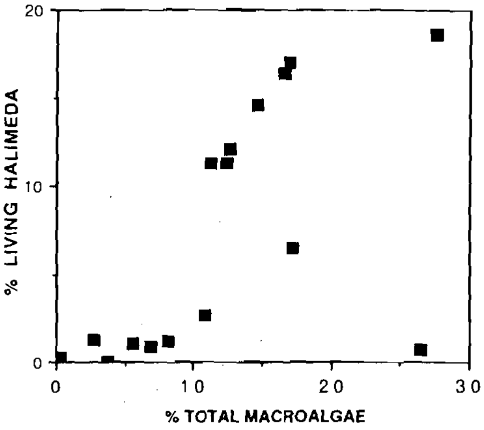

Figure 6. Plot of *Halimeda* abundance versus abundance of total macroalgae. The two are significantly (SRC, p <0.01) correlated.

When compared with total macroalgae (Table 1, Fig. 6), *Halimeda* is shown to closely parallel the trends shown by total macroalgae (SRC, p<0.01) with the exception of the 45m site where *Halimeda* is disproportionately uncommon. It should be noted that *Halimeda* comprises a significant amount of the total macroalgae at most 55-75m sites.

Table 2. Abundance of *Halimeda* in sediment at Discovery Bay, Jamaica (mean percent of identifiable sand-sized grains with ± 95% confidence interval in parentheses).

Depth m	No. Samples/ No. Points Ea.	*Halimeda* Abundance
BR 1-5	18/600	25.8 (8.7)
5	6/600	0.4 (0.3)
8	12/600	3.7 (2.0)
10	14/600	6.3 (3.6)
15	11/600	8.6 (4.4)
23	14/600	21.3 (8.5)
30	11/600	15.7 (3.8)
45	12/600	16.8 (3.1)
55	13/600	22.1 (7.4)
70	11/600	32.6 (9.2)
137	4/300	22.5 (8.4)
188	4/300	19.8 (2.5)
234	4/300	17.4 (4.4)

[1] Back reef and fore reef data from 1-70m from Boss & Liddell (1987), collected in 1982; island slope data from 137-234m from Liddell et al. (1987), collected in 1984. Data from 1-70m represents average of three traverses, A-A', B-B', and C-C'; data from 137-234m represents average of two traverses, B-B' and C-C' (Fig. 1).

Halimeda as a Sediment-Producer

Halimeda is most important as a sedimentary allochem at back reef sites and fore reef sites between 23-234m (Table 2, Fig. 7). *Halimeda* abundance in sediment is significantly correlated with increasing depth at fore reef sites to 70m (the location of the deepest sediment samples collected on the deep fore reef; SRC p<0.01). There is also a significant correlation between *Halimeda* abundance in back reef and fore reef sediment and live abundance at back reef and fore reef sites to 70m (SRC, p<0.05; Fig.8). Considerable quantities of *Halimeda* skeletal elements are contributed to the upper island slope by algae living on the steep escarpment of the deep fore reef. *Halimeda* plates may comprise up to 22.5% of the sand-sized and larger fraction of island slope sediment at 137m, gradually decline in volume to 234m or below (Fig. 8), and abruptly disappear from the sediment below approximately 300m. One sediment sample from 300m contained abundant *Halimeda*, two others from this depth lacked *Halimeda* allochems, as did all deeper samples (to 750m).

DISCUSSION

Controls on the Distribution of *Halimeda*

Substrata, turbulence, light, and grazing have been shown to be important controls on the distribution of *Halimeda* species (Taylor 1960, Goreau & Graham 1967, Hillis-Collinvaux 1977, 1980). Although certain species (e.g. *H. incrassata*) are capable of establishing themselves on sandy substrata, many others require hard substrata for attachment. While certain species (e.g. *H. goreaui* and *H. opuntia*) possess the biomechanical attributes to withstand strong currents or turbulence, others (e.g. *H. copiosa*) do not and are apparently restricted to deeper, quieter waters. The rapid decline in *Halimeda*

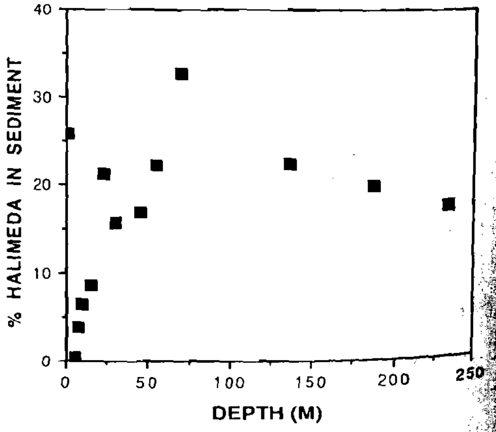

Figure 7. Bathymetric distribution of *Halimeda* grains in sediment. *Halimeda* increases in abundance in sediment with increasing depth (SRC, <0.01) to 70m.

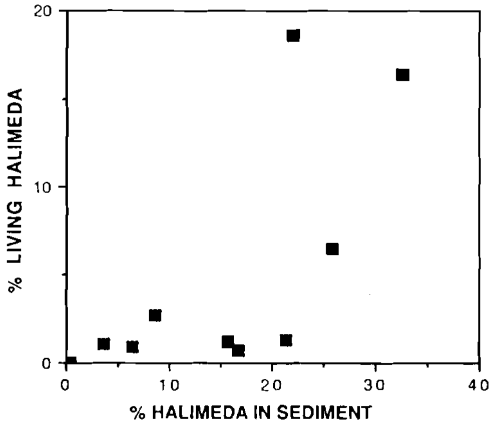

Figure 8. Plot of abundance of living *Halimeda* versus abundance of *Halimeda* grains in sediment. The two are significantly (SRC $p < 0.05$) correlated over the range of 0.5-70m at back reef and fore reef sites.

abundance below 75m at Jamaica is likely attributable to insufficient irradiance levels. The 1.0% of surface irradiance level, which is considered to represent the approximate lower threshold for photosynthesis (Ryther 1956) is reached at 55m and the 0.5% level at 90m at our study site. Intense herbivory is believed to nearly exclude *Halimeda* from shallow fore reef sites (Liddell & Ohlhorst 1986, 1987), although the alga apparently possesses chemical defenses against certain grazers (Paul & Fenical 1983).

Comparison with Other Studies

There are relatively few studies on algal distributions across depth ranges comparable to those of the present study (the papers by Agegian & Abbott 1985, Littler et al. 1985, and Hillis-Colinvaux 1986 are exceptions).

Agegian & Abbott (1985) studied the algae occurring from 0-250m on the deep escarpments off Johnston Atoll and the Penguin Bank in the Pacific. *Halimeda gracilis* reached a maximum abundance between 50-125m with a maximum depth of 136m at the former location while *H. copiosa* and *H. fragilis* reached maximum abundances between 55-75m with a maximum depth of 106m at the latter. The maximum recorded depth for macroalgae was 250m.

Littler et al. (1985) examined the algae (erect and crustose) occurring over the range of 81-280m on the steep face of a seamount off of San Salvador Island, the Bahamas. From 81m (the top of the seamount) to 268m, the algal community complexity and spatial heterogeneity decreased with increasing depth. *Halimeda copiosa* and *H. discoidea* were present at shallower (80-88m) depths and occupied 4-6% of the substratum. Between 117-130m *H. copiosa* was dominant and occupied up to 20% of the substratum. Other green algae were important between 130-157m.

Hillis-Colinvaux (1986) documented the distribution of algae, chiefly *Halimeda*, over the range of 30-367m on the steep fore reef at Eniwetok Atoll. From 30-65m the biota was composed of hermatypic scleractinians, *Halimeda*, and crustose coralline algae. From 65-110m *Halimeda* dominated the assemblage, although corals were also present. *Halimeda* achieved up to an estimated 50% cover above 90m and 10-25% cover between 90-110m, finally decreasing to 0% below 140m. The deepest recorded *Halimeda* specimens (approximately 140m) were living at light intensities perhaps as low as 0.05%. A total of 6 *Halimeda* species occurred below 60m. In contrast to the Bahamas (Littler et al. 1985), other macroalgae were rare over the depth range studied.

At Jamaica, the lower depth limit of *Halimeda* is considerably shallower than that determined by the above authors. Illumination levels appear to control the lower depth limit of *Halimeda* at Jamaica, as hard substrata extend to 120m, considerably below the alga's range. Along the north coast of Jamaica, algae occurring below 55m occupy a vertical or nearly so, north-facing escarpment (the deep fore reef); the slope angle and orientation greatly reduces irradiance levels relative to positions within the open water column.

Algae occurring to 75m on the deep fore reef contribute large quantities of skeletal elements to sediment on the upper portion of the Jamaican island slope (up to 22.5% of the sand-sized and larger fraction). We are not aware of quantitative data from other deep localities with which to make comparisons, although the abundant presence of *Halimeda* grains in deeper-water settings adjacent to carbonate platforms has been frequently noted. Our study has found *Halimeda* plates to be rare in sediment below 300m; this depth appears to mark the approximate boundary between shelf-influenced and more pelagic sedimentation for this bypass-type (McIlreath & James 1979) shelf margin.

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