DOMINANT MACROPHYTE STANDING STOCKS, PRODUCTIVITY AND COMMUNITY STRUCTURE ON A BELIZEAN BARRIER REEF

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INTRODUCTION

Tropical reefs often consist of massive structures derived mainly from the fossil remains of coelenterate corals and calcareous algae. The biological communities responsible for such formations are noted for their diversity, complex structure and high primary productivity. Macroalgae play essential roles in the geology as well as the biology of reef complexes (e.g., James et al. 1976). The aragonite skeletal materials derived from calcareous green algae (Chlorophyta) and hard corals (Cnidaria) provide much of the structural bulk (James and Ginsburg 1979), while the calcite crusts produced by coralline algae (Rhodophyta) consolidate this material and other debris to augment reef formation. Additionally, the non-articulated coralline algae may form an intertidal algal ridge at the reef crest that buffers wave forces and prevents erosion and destruction of the more delicate corals and softer organisms typical of back-reef habitats. A diverse group of calcified green algae (Chlorophyta), belonging to the orders Caulerpales and Dasycladales, are the source of much of the sediment found throughout modern reefs.

One of the world's most extensive reef systems is the Belize Barrier Reef, 10 to 32 km wide and about 250-km long (James et al. 1976), the largest continuous reef in the Atlantic and the second largest in the world (Smith 1948). However, little quantitative information concerning the standing stocks, productivity, community structure and ecology of macrophytes is available for this impressive reef system. The few studies of plants to date include taxonomic collections taken along the shore or by dredging (e.g., Taylor 1935, den Hartog 1970, Tsuda and Dawes 1974). Norris and Bucher (1982) recently provided a floristic account of macrophytes near Carrie Bow Cay and vicinity. Several unique secondary metabolites have been revealed for Belizean macroalgae (e.g., McConnell and Fenical 1978,

* Department of Botany, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560
** Biological Oceanography Program - OCE, National Science Foundation, 1800 G Street, N.W., Washington, D.C. 20550

Gerwick and Fenical 1981, Norris and Fenical 1982, Paul and Fenical 1983, Gerwick et al. 1985). The important role of herbivory in structuring macrophyte communities has been thoroughly investigated for the Carrie Bow Cay reef and surrounding environs (Hay 1981a, Littler et al. 1983a, 1983b, Lewis 1985, 1986, Lewis and Wainwright 1985, Littler et al. 1986, 1987, Lewis et al. 1987, Macintyre et al. 1987). Quantitative studies concerning macrophyte abundances are limited to those within unidentified algal turfs (Dahl 1973, 1976) and on mangrove root and bank communities (Littler et al. 1985, Taylor et al. 1986). While Rützler and Macintyre (1982) established a permanent transect near Carrie Bow Cay that has been examined qualitatively by many zoologists over the past decade, no quantitative baseline assessment by plant specialists existed. Therefore, as a necessary first approach to the design of ecologically relevant experiments, we initiated a detailed survey of macrophyte distributions, abundances and productivities in the reef system seaward of Carrie Bow Cay.

STUDY AREA

This research was performed at the Smithsonian Institution's field station located on Carrie Bow Cay, Belize, Central America (16° 48'N, 88° 05'W; Fig. 1) during 11 to 15 April 1980. Carrie Bow Cay is one of several small islands composed of calcareous debris that has accumulated on the outer margin of the Belizean barrier-reef system. The island and its surrounding habitats comprise a well-developed biotic reef system removed from major anthropogenic influences. The topography, geology and general biology are well known due to nearly two decades of study (see Rützler and Macintyre 1982).

On the basis of dominant biological and geological characteristics, the barrier reef seaward of Carrie Bow Cay can be divided into four major habitat units: back reef, reef crest, inner fore reef and outer fore reef. Each unit, except for the reef crest, can be further subdivided into distinct zones (see Rützler and Macintyre 1982). Water movement and depth have been suggested (Rützler and Macintyre 1982) to be the main factors controlling these biological/geological zonation patterns. The back reef (0.1-1.0 m deep) is subjected to strong currents and the lagoonward transport of sediments. The water over the intertidal reef crest is in an almost constant state of agitation. The inner fore reef (1-12 m deep) is strongly affected by waves related to both normal trade wind conditions and storms. Conversely, the outer fore reef (>12-m deep) is impacted only by long-period storm waves generated primarily by hurricanes.

METHODS AND MATERIALS

Standing Stocks

A single transect on compass heading 90° magnetic and 627-m in length was established seaward of the laboratory on Carrie Bow Cay (Figs. 1 and 2), beginning on the reef flat in 0.2 m of water and extending to a depth of 32.0 m. Depths shallower than 1.0 m were measured at the time of sampling with a meter stick, whereas deeper depths were read to an accuracy of 0.3 m using a Tekna expanded-scale depth gauge. Tidal amplitude is minimal relative to wave height at Carrie Bow Cay so average depths between wave peaks and troughs are given without reference to tidal stage. Quantitative samples were obtained on 11-15 April 1980 by photographing 1.0 m^2 quadrats at every third meter to meter 292, with the exception of meters 100-113 which were sampled at every meter due to rapid vegetational changes; every fifth meter was assessed from meters 292-627. Photographs were taken perpendicular to the substratum using a 35-mm Nikonos camera equipped with an electronic flash unit and Kodachrome-64 transparency film. Simultaneously, voucher specimens of all macrophytes and turf algae for taxonomic purposes were taken from each quadrat and placed in individually labelled bags. Vouchers were subsequently studied and deposited in the Algal Collection of the U.S. National Herbarium, National Museum of Natural History, Smithsonian Institution. The species and taxonomic authors are given in Table 1.

In the laboratory, the developed transparencies were projected onto a sheet (40 x 40 cm) of white paper containing a grid pattern of dots at 2.0-cm intervals on the side of the reflected light; this has been shown (Littler and Murray 1975) to be an appropriate density (i.e. 1.0 per cm^2) for consistently reproducible estimates of cover. The number of dots superimposed on each species was then scored twice (i.e. replicated after movement of the grid) with the percentage cover values expressed as the number of "hits" for each species divided by the total number of dots (~800) contained in the quadrats. Species present in vouchers but not abundant enough to be scored by the replicated grid of point intercepts were assigned a cover value of 0.1%. In cases of multi-layered communities, more than one photograph per quadrat was taken to quantify each stratum after upper strata had successively been moved aside.

The method as applied here does not allow for the quantification of microalgae (small epiphytic or endolithic forms) when they occur in low abundances. Our measurements were restricted to macrophytes that could be discerned in the field with the unaided eye. However, we did quantify small algae when they occurred in high abundances as components of algal turfs.

Table 1. Mean cover (±standard error) of the dominant macrophyte taxa in each zone indicated by cluster analysis.

Dominant Taxa

	1	2	3	4	5	6	7	
Zones	1	2	3	4	5	6	7	
Distance from shore (m)	0-72	73-112	113-131	132-327	328-470	471-557	558-630	Means
Depth range (m)	0.2-0.4	0.1-0.8	0.1-0.9	2.5-8.8	7.9-15.2	23.2-29.0	16.5-31.1	
Mean depth (m)	0.3	0.3	0.6	5.8	10.3	25.1	24.6	
N =	24	22	7	61	28	18	14	
Amphiroa rigida var. antillana Boerg.	5.65 ±1.74							0.94
Amphiroa tribulus (Ell. et Sol.) Lamouroux				0.02 ±0.01	0.04 ±0.03			0.01
Amphiroa sp.				0.02 ±0.01	0.04 ±0.03	0.19 ±0.09	0.22 ±0.17	0.06
Anotrichium tenue (C. Ag.) Naegeli		0.64 ±0.26						0.11
Caulerpa racemosa (Forssk.) J. Ag.		0.66 ±0.32	0.06 ±0.05					0.12
Centroceras clavulatum (C. Ag.) Mount.		16.52 ±2.04		0.02 ±0.01				2.76
Ceramium nitens (C. Ag.) J. Ag.				0.04 ±0.01				0.01
Ceramium sp.		0.08 ±0.02						0.01
Champia parvula (C. Ag.) Harvey		0.04 ±0.01						0.01
Crustose coralline (unidentified)		16.77 ±2.83		0.01 ±0.01				2.80
Filamentous diatom		0.16 ±0.10						0.02
Dictyota bartayresii Lamouroux				0.32 ±0.01	1.84 ±0.30	1.38 ±1.21	1.65 ±0.61	0.64
Dictyota divaricata Lamouroux	0.13 ±0.09							0.02
Dictyota sp.		0.14 ±0.01						0.02
Galaxaura lapidenscens Lamouroux				0.17 ±0.04	0.01 ±0.03			0.02
Halimeda copiosa Goreau et Graham				0.16 ±0.04	0.20 ±0.08	0.17 ±0.16	2.36 ±1.24	0.45
Halimeda discoidea Decaisne				0.08 ±0.03	0.23 ±0.07	0.01 ±0.01	0.55 ±0.27	0.11
Halimeda goreauii Taylor					0.06 ±0.03	0.51 ±0.23	1.06 ±0.55	0.27
Halimeda opuntia (L.) Lamouroux	0.43 ±0.23	2.31 ±0.92	1.08 ±0.89	0.18 ±0.05	0.24 ±0.24			0.97
Hydrolithon boergesenii (Foslie) Foslie	0.19 ±0.08							0.03
Hypnea cervicornis J. Agardh			0.06 ±0.03					0.01
Jania adhaerens Lamouroux	0.15 ±0.08	2.64 ±1.07						0.46
Jania capillacea Harvey	0.11 ±0.11	1.94 ±0.74	1.38 ±0.89	<0.01 ±0.01				0.92
Jania rubens (Linneaus) Lamouroux		6.09 ±2.45						1.01

Species								%
Laurencia obtusa (Huds.) Lamouroux		1.15 +0.47						0.19
Laurencia papillosa (Forssk.) Grev.		0.72 +0.72						0.12
Laurencia spp.		0.85 +0.25	0.01 +0.01	<0.01 +0.01				0.14
Liagora spp.				0.47 +0.28	0.32 +0.22			0.07
Lobophora variegata (Lamour.) Womersley	0.05 +0.05		0.59 +0.38	0.01 +0.01	0.25 +0.07	0.74 +0.57	3.84 +1.43	0.88
Neogoniolithon strictum (Fosl.) Setch. et Mason	0.20 +0.12							0.03
Neomeris annulata Dickie	0.02 +0.01	0.03 +0.01	0.01 +0.01					0.02
Padina jamaicensis (Collins) Papenfuss		0.31 +0.17						0.05
Penicillus dumetosus (Lamouroux) Blainville				0.05 +0.02		<0.01 +0.01		0.01
Peyssonnelia sp.	0.01 +0.01	0.05 +0.05	4.97 +1.83					0.84
Polysiphonia howei Hollenberg		2.35 +0.48						0.39
Porolithon pachydermum (Foslie) Foslie	1.20 +0.50	1.55 +2.80	26.91 +8.97					4.94
Porolithon sp.	0.31 +0.31	0.07 +0.03	0.02 +0.01					0.06
Rhipocephalus phoenix (Ell. et Sol.) Kuetz.				0.02 +0.01	0.04 +0.01	<0.01 +0.01		0.01
Sargassum hystrix J. Ag.				0.07 +0.02	0.11 +0.05	0.02 +0.02	0.42 +0.15	0.09
Sphacelaria tribuloides Meneghini		0.85 +0.33						0.14
Stypopodium zonale (Lamour.) Papenfuss				0.44 +0.07	0.29 +0.10	0.22 +0.13	0.86 +0.36	0.24
Taenioma nanum (Kuetz.) Papenfuss		0.34 +0.07						0.06
Thalassia testudinum Banks ex Koenig	60.08 +5.51							10.01
Trichogloeopsis cf. pedicellata (Howe) Abbott et Doty				0.28 +0.07				0.05
Udotea cyathiformis Dec.				0.01 +0.01	0.04 +0.03	0.03 +0.01	0.03 +0.01	0.01
Wrangelia argus Montagne		0.44 +0.40	4.30 +2.79					0.79
Others (21)		0.27	0.01	0.32	0.16	0.14	0.01	
Total	68.53	56.97	39.40	2.71	3.87	3.43	11.00	30.91

Productivity

To compare the dominant macrophytes in terms of their functional-form groups (Littler 1980), and their net apparent photosynthetic performances, specimens were taken from the most abundant in situ populations along the transect line and allowed to acclimate in a running seawater system for one day. Four replicate incubations per species were conducted in a shallow current channel at ambient water temperatures (27°C) on 12 April 1980 between 0900 and 1430 hrs, under a photon flux of 900 to 2100 micro Einsteins $\cdot$ m^{-2} $\cdot$ sec^{-1} of photosynthetically active radiation. This was within the range of light saturation values documented for other macroalgal species (King and Schramm 1976; Arnold and Murray 1980; Lapointe et al. 1984). Net productivity was measured to 0.1 parts per million of dissolved oxygen by means of a YSI Model 57 oxygen analyzer and calculated as milligrams carbon fixed per unit of thallus weight per hour assuming a photosynthetic quotient of 1.00. The methods concerning the selection of material, handling, incubation and oxygen analysis were within the limits recommended by Littler and Arnold (1985).

Analyses of Data

Data obtained by photogrammetric sampling (Littler and Littler 1985) enable quantification of the distributions and abundances of standing stocks in relation to transect distances and depths. To characterize natural species assemblages over the entire length of the transect in an unbiased manner, the cover data of every species for all quadrats (except those with only bare sand) were subjected to hierarchical cluster analyses (flexible sorting, unweighted pair-group method; Smith 1976) using the Bray and Curtis (1957) coefficient of similarity. Due to the patchy nature of the biota, quadrat groupings by this technique reveal only trends and not statistically clear-cut assemblages. The resultant dendrogram of quadrat groupings was interpreted according to the dominant biota and environmental affinities and used to map the prevalent zonational patterns. All quadrat data within the clustered zones were summed and averaged to yield mean cover values that enabled us to interpret differences in macrophyte populations and communities between habitats.

Diversity measurements have been widely employed by those responsible for assessing the effects of disturbances on biotic communities. Species diversity is often measured by indices (see Poole 1974 or Pielou 1975 for references and definitions) that include components of both species richness and equitability (the evenness with which the individuals are apportioned

among species). The problem with any single index is that both the richness and equitability components of diversity are obscured. Many diversity indices also contain the underlying assumption that the ecological importance of a given species is proportional to its abundance. We have attempted to avoid these problems by using the commonly-applied Shannon and Weaver (1949) H' index (incorporating both richness and evenness) along with separate indices for richness (counts of taxa) and equitability (E'; Buzas and Gibson, 1969). These were calculated for the mean cover data by zone using natural logarithms and provided supplementary between-habitat comparisons of community structure.

RESULTS

Standing Stocks

The cluster analysis revealed seven general zones in the reef system off Carrie Bow Cay (Fig. 3) grouped as a function of both distance and depth. Because of the patchy distribution and low abundances of some organisms and sand, several quadrats are clustered with samples outside their habitat groups. A total of 70 macrophyte taxa occurred in the photographic samples (Table 1) with the majority present in zones 2 and 6 and the least number in zone 3 (Table 2). Zone 1, between 0 and 72 meters from the shoreline and extending over a depth range from 0.2 to 0.5 m (mean = 0.3 m) on the shallow reef flat (a portion of the back-reef region, Fig. 3), included a discrete grouping of quadrats with a high level of similarity. Total plant cover averaged 68.5% and the seagrass Thalassia testudinum was dominant (average cover of 60% with maxima to >100%, Figs. 4 and 5). Other major species of zone 1 were the articulated coralline Amphiroa rigida var. antillana, which occurred predominantly on the shoreward half of the zone (mean cover of 5.6%), and the crustose coralline Porolithon pachydermum (1.2% mean cover) growing mainly on the exposed skeletons of dead and living Porites porites (Pallas) primarily toward the seaward portion of the zone.

Zone 2, between meters 73-111 (depth range 0.1-0.8 m, mean = 0.3 m), included the rubble-pavement current channel of the back reef and inner slope of the reef crest (see Rützler and Macintyre 1982) and was dominated by crustose corallines overgrown by microfilamentous algae (Figs. 4 and 6). Total plant cover averaged 66.8% with the primary taxa being an unidentified crustose coralline (16.8%) and the filamentous red alga Centroceras clavulatum (16.5%), which together with other filamentous species such as Polysiphonia howei (2.4%) formed a turf-like mat. Also abundant in zone 2 (Fig. 4) were Porolithon pachydermum (11.6%), the turf-forming articulated corallines Jania rubens (6.1%), J. adhaerens (2.6%) and J. capillacea (1.9%). The articulated, calcareous green alga Halimeda opuntia (2.3%) and the coarsely branched red alga Laurencia obtusa (1.2%) also were conspicuous in patches on the shallow inner slope of the reef crest area.

Table 2. Measures of diversity within the six cluster zones.

| | Zones | | | | | | | |
Distance from shore (m)	1 0-72	2 73-112	3 113-130	4 131-327	5 328-470	6 471-555	7 556-630	Entire Transect
Shannon-Weaver Diversity (H')	1.64	2.52	1.89	2.35	2.38	1.63	0.29	3.32
Equitability (E')	0.37	1.43	0.55	0.47	0.57	0.01	0.06	0.41
Number of Species in Photo-samples	11	18	13	33	27	15	12	64

Zone 3 comprised a narrow biological habitat (meters 112-130, depth range 0.1-0.9 m, mean = 0.5 m) on the uppermost portion of the intertidal reef crest (Fig. 2) and had a total plant cover of 49.4%. This portion of the reef was dominated by a pink pavement of Porolithon pachydermum (34.6% mean cover, maxima to 80%, Figs. 4 and 7) containing excavations made by the chiton Acanthochitona lata Pillsbury (J. Houbrick personal communication; Fig. 8). Other prevalent species (Table 1) on the seaward crest were the encrusting red alga Peyssonnelia sp. (6.4%), turf-forming Wrangelia argus (5.5%) and Jania capillacea (1.8%). Beneath ledges and deep in crevices beyond the range of our photo-samples, the encrusting form of the green alga Codium intertextum predominated on the outer margin of the zone 3 reef crest.

Contrasting with zones 1-3, the remaining 4 zones occurred over regions with indistinct physical environmental boundaries and were biotically much less discrete (Fig. 3). For example, zone 4 was a broad region extending from meters 131-170 (depth range 1.5-4.6 m, mean = 3.6 m) that contained quadrats with relatively low algal abundances which showed low levels of floristic similarity (Fig. 3). This region corresponded to the upper fore-reef slope habitat (i.e., the high spur and groove system of Rützler and Macintyre 1982). Total plant coverage in zone 4 averaged only 4.5% (Table 1), dominated by Porolithon sp. (2.6%) and Halimeda opuntia (1.2%) along with sparsely scattered thalli of various coarsely branched algal forms (Figs. 4 and 9).

Zone 5 (meters 171-322, depth range 4.9-8.8 m, mean = 7.3 m) included most of the lower spur and groove habitat on the lower fore reef described by Rützler and Macintyre (1982), which had extremely low macrophyte cover (mean of 2.5%) composed of epilithic forms on reef rock and scattered rubble. The dominant species were the sheet-like Stypopodium zonale (0.6% cover) and Dictyota bartayresii (0.4%, Figs. 4 and 10).

The lower, fore-reef, sand-channel habitat characterized zone 6 (Fig. 3), which extended from meters 323-547 over a broad depth range of 7.9-29.0 m (mean = 13.5 m). Cover was sparse (3.4%), consisting mainly of epilithic forms on scattered rubble or psammophytic, rhizoidal, green-algal species embedded in sand. Dictyota bartayresii (1.6% cover) was most abundant (Fig. 4) followed by Lobophora variegata (0.2%), Stypopodium zonale (0.2%) and Halimeda goreauii (0.2%).

As in the cases of zones 4, 5 and 6, zone 7 also was characterized by a diffuse assemblage of relatively loosely clustered quadrats (Fig. 3). The zone included the outer reef ridge from meters 548-630 (depth range from 16.5-32.0 m, mean = 24.5 m) extending well beyond our maximum depth of 35 m. Algal cover averaged 10.3% (Figs. 4 and 11), composed mostly of the shelf-like form of the brown alga Lobophora variegata (3.7%), Halimeda copiosa (2.0%), Dictyota bartayresii (1.4%), H. goreauii (1.2%) and Stypopodium zonale (0.8%).

Table 3. Productivity (as mg C fixed per unit of thallus weight per hour at 1500 μE $m^{-2} \cdot s^{-1}$) of the dominant taxa found on the Carrie Bow Cay transect. (± 1 Standard Deviation)

Species	Productivity		
	Dry weight (g)	Organic weight (g)	% Organic
Sheet group			
Dictyota divaricata	4.52 ±0.31	9.64 ±0.71	47.04 ±3.97
Dictyota bartayresii (turf-form)	1.20 ±0.21	2.91 ±0.58	41.84 ±6.66
Mean	2.86	6.28	44.44
Filamentous group			
Centroceras clavulatum (turf-form)	0.54 ±0.05	1.48 ±0.24	23.13 ±2.63
Caulerpa verticillata (turf-form)	0.66 ±0.17	1.86 ±0.40	21.13 ±0.78
Mean	0.60	1.67	22.13
Coarsely branched group			
Trichogloeopsis cf. pedicellata	2.39 ±0.39	10.14 ±0.35	25.65 ±3.86
Liagora farinosa	1.59 ±0.67	10.01 ±2.58	15.40 ±3.34
Liagora sp. #2	0.76 ±0.13	8.04 ±1.24	9.37 ±0.29
Laurencia obtusa	3.41 ±0.51	7.99 ±0.96	42.61 ±1.87
Liagora sp. #3	0.73 ±0.06	7.15 ±0.79	10.27 ±0.72
Gelidium sp.	3.21 ±1.33	5.92 ±2.26	54.31 ±5.08
Liagora pinnata	0.99 ±0.18	4.59 ±0.75	21.54 ±0.73
Rhipocephalus phoenix	0.79 ±0.34	4.59 ±1.19	17.15 ±4.30
Laurencia papillosa	1.39 ±0.13	3.71 ±0.42	37.45 ±2.54
Udotea cyathiformis	0.55 ±0.31	3.15 ±0.88	16.83 ±5.04
Neomeris annulata	0.39 ±0.07	2.37 ±0.37	16.29 ±0.60
Penicillus pyriformis	0.37 ±0.07	2.70 ±0.92	14.21 ±3.18
Caulerpa racemosa	0.45 ±0.18	0.88 ±0.36	51.07 ±0.78
Mean	1.31	5.48	25.54
Thick leathery/rubbery group			
Sargassum hystrix	2.14 ±0.06	3.63 ±0.17	59.06 ±2.98
Stypopodium zonale	1.55 ±0.33	2.97 ±0.59	52.30 ±7.29
Lobophora variegata	1.52 ±0.41	2.53 ±0.46	59.70 ±9.71
Thalassia testudinum	0.85 ±0.05	1.41 ±0.13	60.10 ±4.44
Padina jamaicensis	0.66 ±0.06	1.21 ±0.12	55.37 ±7.01
Mean	1.35	2.35	57.34
Jointed calcareous group			
Jania adhaerens	0.25 ±0.02	2.06 ±0.21	12.34 ±0.67
Halimeda opuntia	0.21 ±0.12	1.94 ±0.98	10.06 ±1.92
Amphiroa rigida var. antillana	0.11 ±0.01	0.98 ±0.11	11.36 ±0.13
Halimeda discoidea	0.21 ±0.07	0.96 ±0.33	21.97 ±0.41
Halimeda goreauii	0.04 ±0.01	0.77 ±0.19	5.27 ±0.25
Halimeda copiosa	0.05 ±0.02	0.95 ±0.52	12.43 ±0.86
Mean	0.14	1.27	12.24
Crustose group			
Neogoniolithon strictum	0.06 ±0.004	0.32 ±0.06	17.39 ±2.56
Peyssonnelia sp.	0.01 ±0.001	0.12 ±0.01	6.21 ±0.22
Hydrolithon boergesenii	0.01 ±0.001	0.11 ±0.01	6.21 ±0.99
Porolithon pachydermum	0.01 ±0.003	0.09 ±0.02	10.75 ±1.24
Mean	0.03	0.16	10.14

Community Diversity

Overall Shannon-Weaver (H') diversity was 3.35 and equitability (E') was 0.40. Zone 2, the narrow inner reef crest and pavement region, was by far the habitat of greatest diversity (Table 2); although comprising only 6% of the total area studied, it contained 42% of the total species encountered, a Shannon-Weaver (H') diversity of 2.59 and E' of 0.44. Zones 1 and 3 were dominated by extensive cover of relatively few species (Tables 1 and 2), and, along with zone 7, contained the fewest species numbers. Equitability values were especially low for the fore-reef zones 4, 5 and 6 (Table 2).

Productivity

Members of the sheet group had the greatest mean net photosynthetic rate in terms of thallus organic content (Table 3), with 6.28 mg C fixed · g organic dry wt^{-1} · h^{-1}, and the crustose group the lowest with 0.16. The mean for the coarsely branched group was surprisingly high (5.48 mg C fixed · g organic dry wt^{-1} · h^{-1}), whereas the turf-forming filamentous forms showed relatively low rates (mean of 1.67). The sheet-like Dictyota divaricata (4.52 mg C fixed · g total dry wt^{-1} · h^{-1}) showed the highest rate on a total dry weight basis, followed by the coarsely branched Laurencia obtusa (3.41) and Gelidium sp. (3.21) along with the thick leathery species Sargassum hystrix (2.14). The crustose and calcified species were by far the lowest producers (Table 3). The turf forms, such as D. bartayresii, Centroceras clavulatum and Caulerpa verticillata contained tightly bound inorganic and organic sediments in their mats and were incubated in this natural condition.

DISCUSSION

This paper presents the first quantitative description of the macrophyte zonational patterns and primary productivity of dominant plant-life for the seaward margin of the Belize Barrier Reef. The zonational patterns, with minor exceptions, correlate well with the physiographic regions determined by Rützler and Macintyre (1982) along a parallel transect to the north. The community composition and zonation of the Carrie Bow Cay portion of the Belizean barrier reef, despite some variation (Burke 1982), is thought to be representative of the entire reef platform. Distinct similarities exist between the Belizean barrier reef's biological/geological zonation and the barrier reefs of the north coast of Jamaica (Goreau 1959, Goreau and Land 1974). Also bearing close similarities to the system we studied are the high relief spurs and ridges on Haiti's north coast and off southeast Alarcran (Burke 1982). Some portions of the Belizean barrier reef contain large standing

stocks of <u>Turbinaria</u> spp. and <u>Sargassum</u> spp. leeward of the back-reef rubble and pavement zone [e.g., the leeward sediment apron of Tobacco Reef (Macintyre et al. 1987)], whereas other regions (Burke 1982) appear to be more similar to the system we measured.

<u>Halimeda</u> has been documented (James and Ginsburg 1979, Rützler and Macintyre 1982) as a major sediment producer on Belizean reefs, extending from the shallow lagoon to its living depth range of 100 m. Four species of <u>Halimeda</u> covered an average of 1.3% of the total area transected, which indicates the considerable abundance of this genus throughout the reef system. Articulated corallines averaged 2.7% cover and crustose corallines totaled 9.6% mean cover, further substantiating the dominance of calcifying algae at Carrie Bow Cay, a phenomenon also noted (e.g., Littler 1976, Connor and Adey 1977, Wanders 1977) for other reef systems exposed to high grazing pressures.

The upper and lower spur and groove system (zones 4 and 5 and sand channel zone 6) had very low equitability values (Table 2) due to the clumped distribution of algae near relatively unpalatable larger plants and animals. Littler et al. (1986, 1987) have explored this phenomenon in some detail for the Carrie Bow Cay fore-reef system and experimentally documented refuges from fish predation afforded a group of 11 marine algae by the purple sea fan, <u>Gorgonia</u> <u>ventalina</u> Linnaeus, the fire coral, <u>Millepora</u> <u>alcicornis</u> Lamarck and the herbivore-resistant brown alga, <u>Stypopodium</u> <u>zonale</u>.

Productivity values for the six habitats indicated by the cluster analysis could not be calculated because of the large environmental differences involved (e.g., depth, light quality and quantity, etc.) and the fact that all incubations were done under uniform conditions. However, because of considerably higher algal cover, greater light energy and a preponderance of the more productive macrophytes, the shallower zones 1, 2 and 3 would be expected to contribute considerably more per unit area to overall reef productivity than zones 4-7.

Previous studies (Littler 1980, Littler et al. 1983a) have shown a strong correlation between algal functional-form groups and net photosynthesis, with sheet-like and filamentous forms producing at the highest rates. In contrast, our data showed extremely low rates for <u>Dictyota</u> <u>bartayresii</u>, a sheet form with unusual natural products (Norris and Fenical 1982), and both of the filamentous species (<u>Centroceras</u> <u>clavulatum</u> and <u>Caulerpa</u> <u>verticillata</u>). All of these occurred predominantly as tightly clumped

mat-like turfs containing particulate matter, which lowered their weight-based productivity. Also, such a compact configuration results in intraspecific competition for light, nutrients and gas exchange, which greatly limits the photosynthetic capacity of potentially productive forms. Conversely, the lightly calcified nemalian algae Trichogloeopsis pedicellata, Liagora farinosa and Liagora sp.(#2) had very high rates based on their organic contents. These forms appear to be annuals that reach their maxima in the spring. As has been noted often (e.g., Marsh 1976, Littler 1980, Littler et al. 1983a, Littler and Littler 1984), the heavily calcified crustose algae, such as Hydrolithon boergesenii, Porolithon pachydermum and Neogoniolithon strictum, show dramatically lower production rates, whether calculated on the basis of total dry weight or organic weight.

Herbivory, due primarily to grazing fishes, appears to be one of the most important causal agents determining the zonational patterns we observed. Rützler and Macintyre (1982) and Burke (1982) suggest that the direction and force of water motion controls the zonation of the Belizean Barrier reef biota, particularly corals (Geister 1977). However, Carrie Bow Cay and its surrounding habitats have been sufficiently studied in regard to the role of fishes and sea urchins to enable strong correlations and predictions to be made concerning the relative dominance of fleshy vs. calcareous macrophytes and the intensity of fish grazing (Hay 1981a, Littler et al. 1983a, 1983b, 1986, 1987, Lewis 1985, 1986, Lewis and Wainwright 1985, Taylor et al. 1986, Lewis et al. 1987, Macintyre et al. 1987). Assays of grazing intensity (Hay 1981a, Lewis and Wainwright 1985) and fish abundances (Lewis and Wainwright 1985) showed the following ranking from areas of lowest to highest herbivore activity: the Thalassia-area (zone 1), the lower fore reef (zones 5 and 6), the outer ridge (zone 7), the upper fore reef (zone 4) and the rubble and pavement portion of the back reef (zone 2). Because large fishes can not gain access to the shallow reef flat (zone 1), Thalassia testudinum becomes dominant in this sedimentary environment. Even during exceptionally high tides, the lack of protective cover would make fish vulnerable to the predatory osprey, Pandion baliaetus (Linnaeus), which we have observed frequently (i.e., usually twice daily) foraging on the shallow reef flat, and often landing with fish prey in the palm trees of Carrie Bow Cay. Also, the intertidal reef crest (zone 3) is too shallow for foraging fishes, enabling desiccation-resistant turf formers (Dawes et al. 1978, Hay 1981b) to persist on the less turbulent landward margin. However, the seaward portion of the reef crest gets buffeted by the shearing forces of occasional storm waves (Macintyre et al. 1987) that may tend to periodically eliminate much of the relatively delicate filamentous turf algae. The seaward crest also contains an abundance of the physically resistant, crustose coralline Porolithon pachydermum that appears to be maintained free of competitively superior epiphytes (Littler and Doty 1975, Wanders 1977) by its association with an undescribed grazing chiton (Fig. 8).

In the eastern Caribbean reefs of lower islands, where the force of water movement across intertidal ridges prevents intense grazing by fishes and echinoids, higher levels of algal standing stocks and productivity develop; on the eastern higher islands, where wave action is great, dense standing stocks of larger fleshy algae can extend to depths of at least 10 m (Connor and Adey 1977). Abiotic factors are also important in affecting the abundances and seasonality of algae on plant-dominated, fringing reefs, such as in Caribbean Panama (Kilar et al. in press). In agreement, the standing stocks of the intertidal reef crest at Carrie Bow Cay appear to be largely influenced by wave force and aerial exposure. Conversely, the macrophyte communities of the shallow subtidal zones are largely governed by fish herbivory. Thus, the relative importances of abiotic and biotic factors on algal standing stocks and productivity vary considerably throughout the different zones of this Belizean reef system.

ACKNOWLEDGEMENTS

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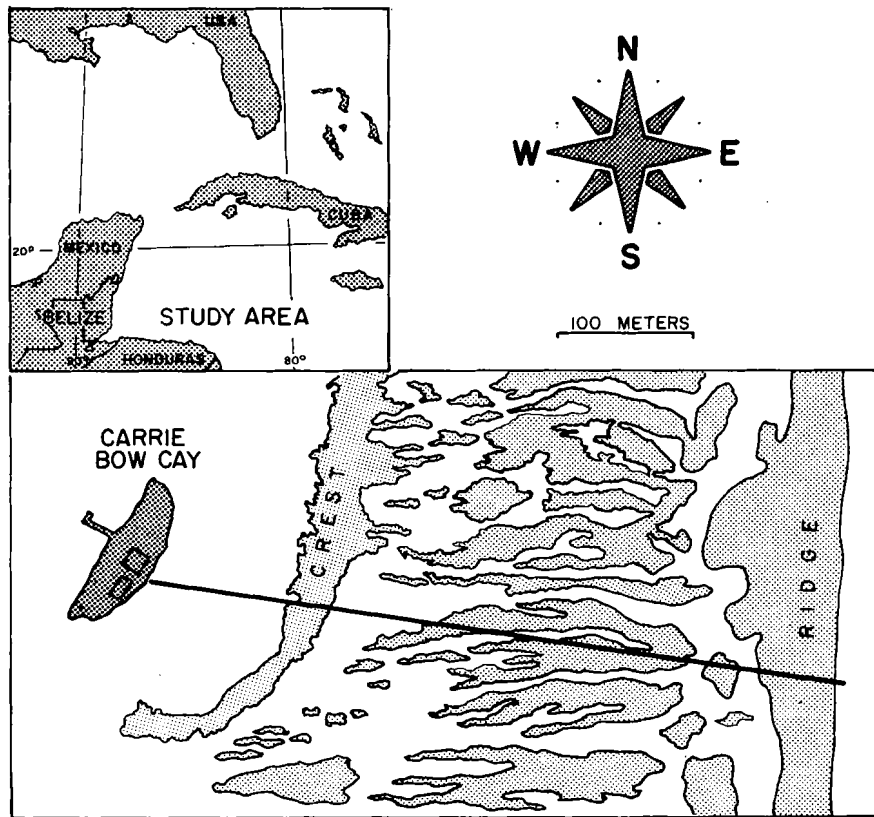
Figure 1.   Location of study area and transect (90° magnetic) in relation to the major topographic features of Carrie Bow Cay.
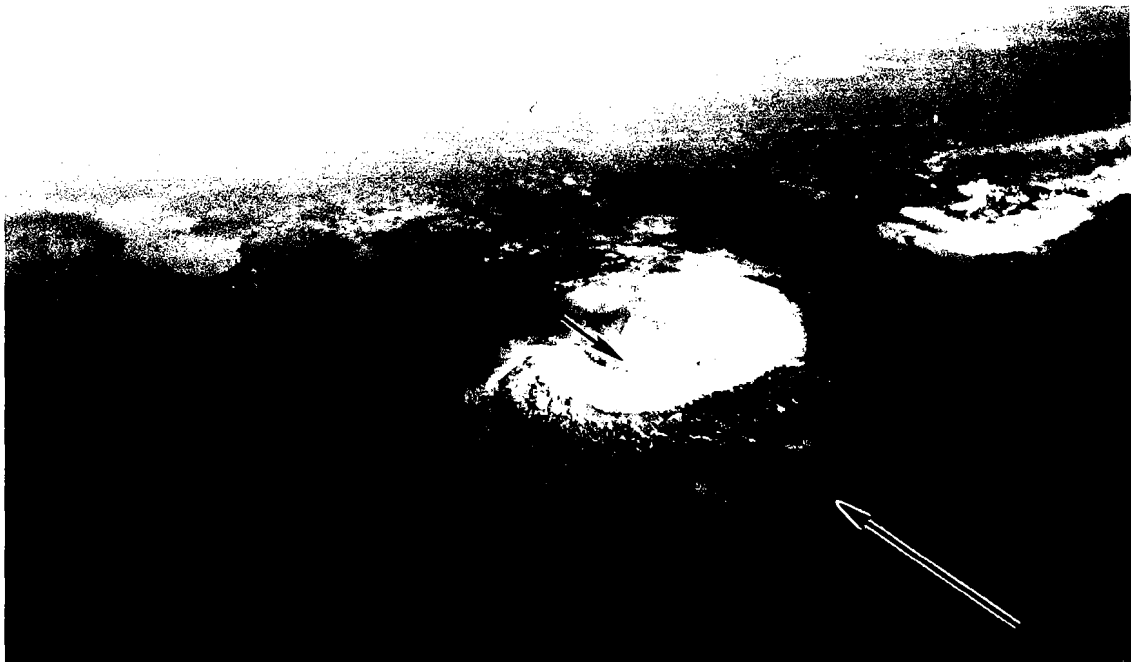

Figure 2.   Oblique aerial view of Carrie Bow Cay and surrounding reef systems showing the area transected (between the two arrows).

Figure 3.   Dendrogram display based on differential clustering analysis of the percentage cover data of macroalgal species for all quadrats (labelled by depth and distance from shore in meters).   The seven major zonal areas   are indicated.   Samples with no algae have been eliminated.
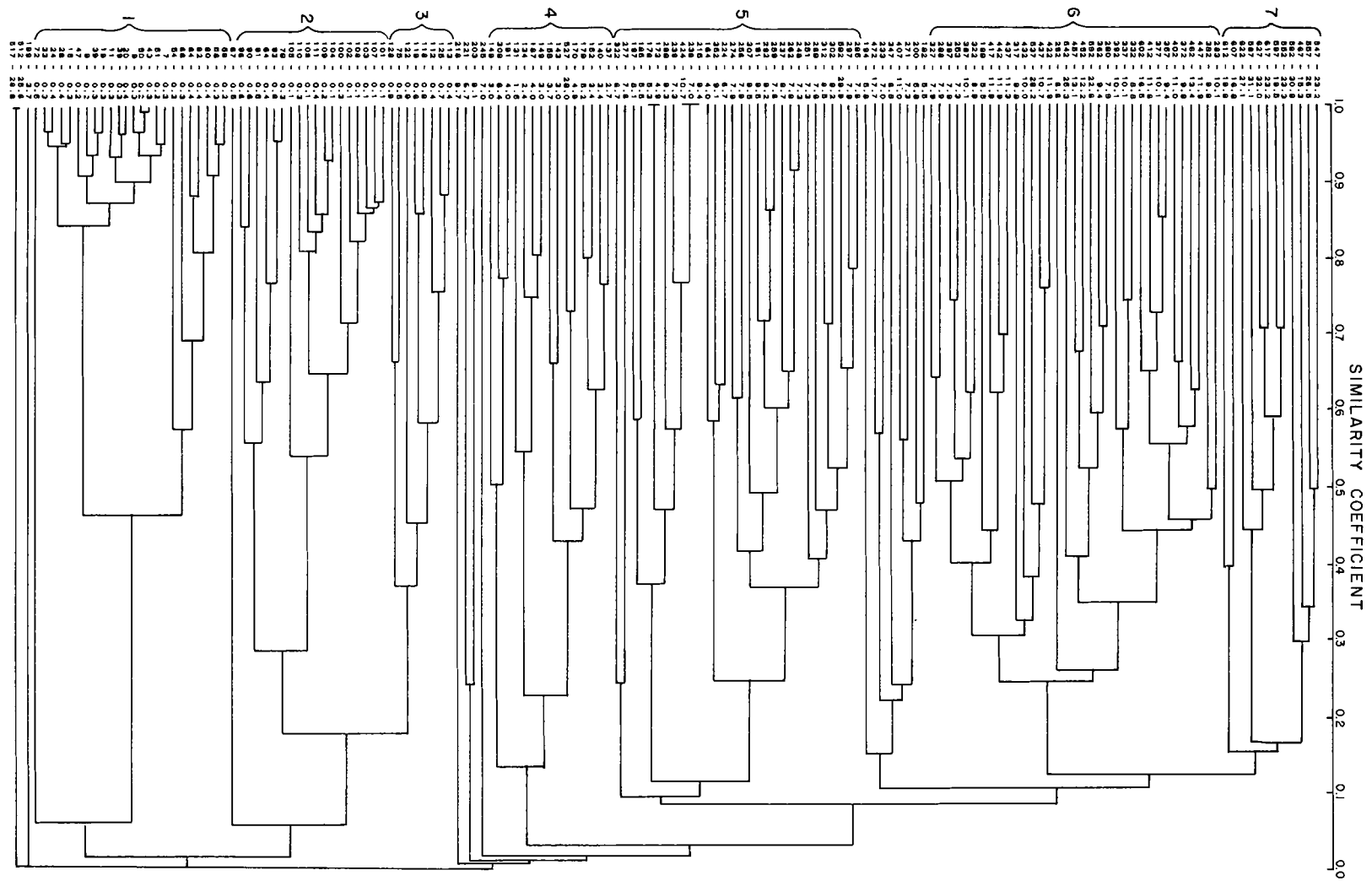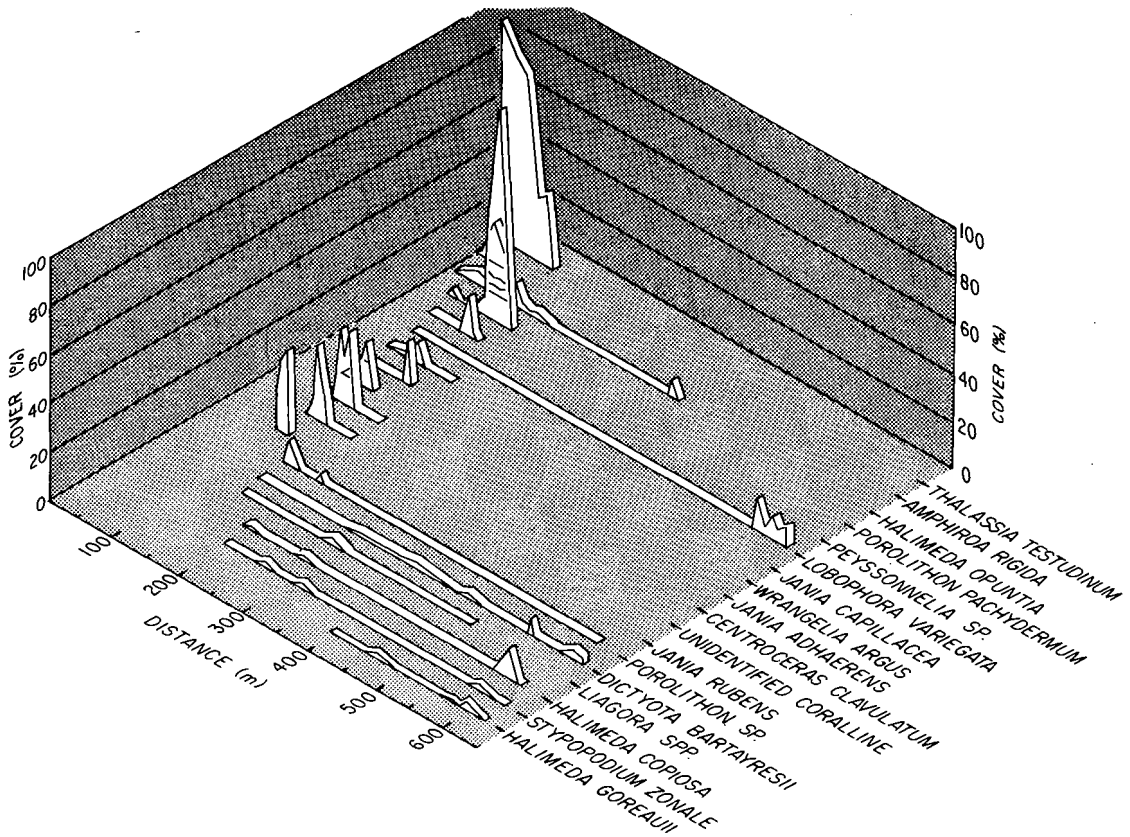
Figure 4. Distribution and abundance patterns of the major
plant cover.

Figure 5. The outer portion of the shallow reef flat (zone 1)
showing extensive _Thalassia_ _testudinum_ cover. _Hydrolithon_
boergesenii predominates on the lower portions of the branched
coral _Porites_ _porites_ (Pallas).

Figure 6. The zone-2 pavement area covered by a mixed microalgal turf and the coral *Porites astreoides* Lamarck.
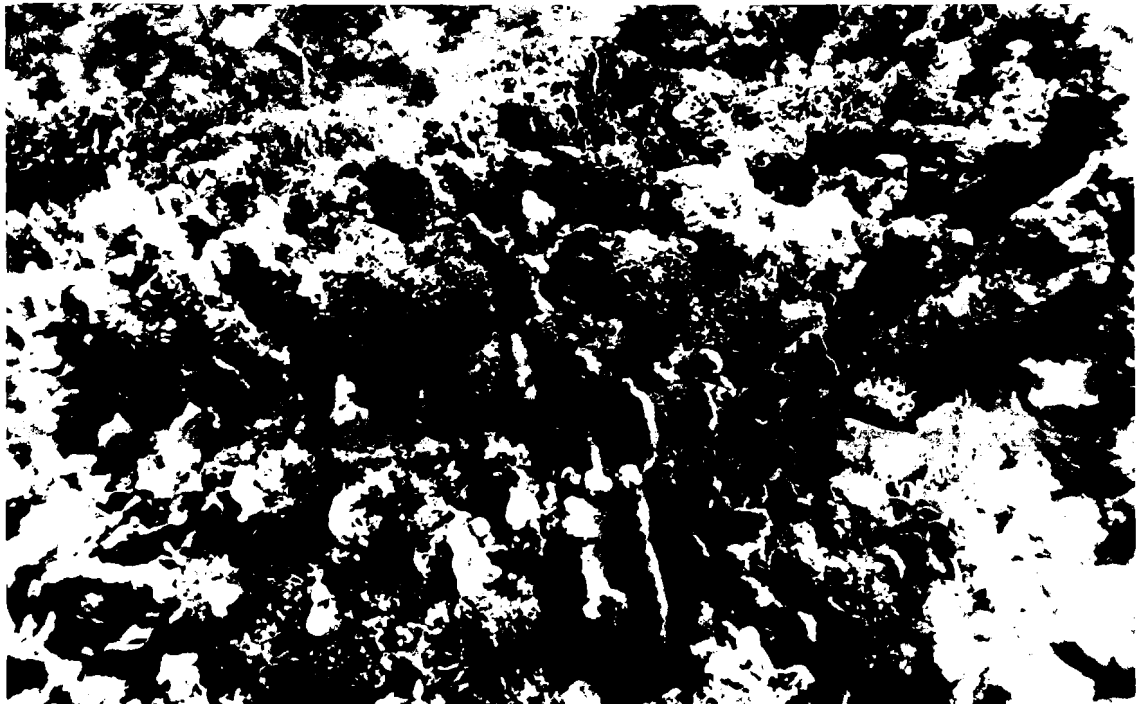

Figure 7. The shoreward portion of the reef crest (zone 3) showing coralline encrustations on the upper surfaces of the coral *Agaricia agaricites* (Linneaus) and clumps of *Halimeda opuntia* between the vertical plates.
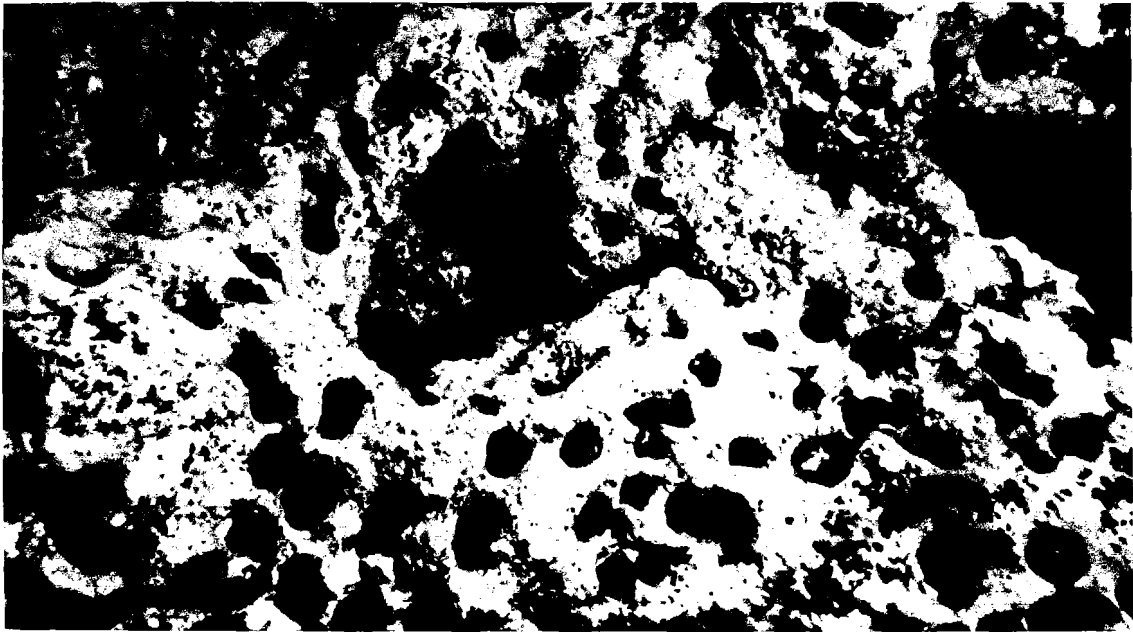
Figure 8. The _Porolithon_ _pachydermum_/_Acanthochitona_ _lata_ association characteristic of the zone-3 reef crest.

Figure 9. View of a shallow spur in zone 4. The dead _Acropora palmata_ (Lamarck) branches are encrusted with _Porolithon_ sp.

Figure 10. The gorgonian-dominated lower spur-and-groove section of the fore-reef (zone 5).

Figure 11. The zone-7 reef ridge characterized by the brown alga *Lobophora variegata* encrusting dead branches of the coral *Acropora cervicornis* (Lamarck).