

The Barrier Reef sediment apron: Tobacco Reef, Belize

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Abstract. Sedimentological and biological surveys of the back-reef sediment apron of Tobacco Reef, a continuous segment of the Belizean Barrier Reef, reveal five distinct biogeological zones: (1) coralline-coral-*Dictyota* pavement, (2) *Turbinaria-Sargassum* rubble, (3) *Laurencia-Acanthophora* sand and gravel, (4) bare sand and (5) *Thalassia* sand. These zones parallel the entire 9-km reef. The distribution of these zones is related to the spatial patterns of fish herbivory, the size of bottom sediments, and the stability of the substrate. Sedimentological and hydrodynamic studies indicate that most of the sediments in this area are transported from the reef crest and fore reef during periods of storm or hurricane activity and that their size distribution is largely the result of differential transport by high bottom-water velocities during those periods.

Introduction

This study focuses on the back-reef apron of a segment of the barrier-reef complex that extends approximately 250 km along the coast of Belize, Central America, and is the largest continuous reef system in the Atlantic (Smith 1948). It measures 10 to 32 km wide (Purdy et al. 1975; James et al. 1976) and has three distinct provinces: northern, central and southern (Burke 1982). The central province (120 km long) is distinguished by its long and wide uninterrupted shallow reefs. One of the best examples of these features is Tobacco Reef, which has an exposed crest extending almost 9 km from the pass south of Tobacco Cay to South Water Cay (Fig. 1).

Sediment aprons, particularly those associated with barrier reefs, are impressive physiographic features that document the leeward accretion of these reefs. Yet they have received surprisingly little attention in the literature. Their zonal patterns, which are particularly striking from the air (Fig. 1), are characterized by sharp boundaries that rival those found in temperate, rocky intertidal communities. This study investigates the biological, geo-

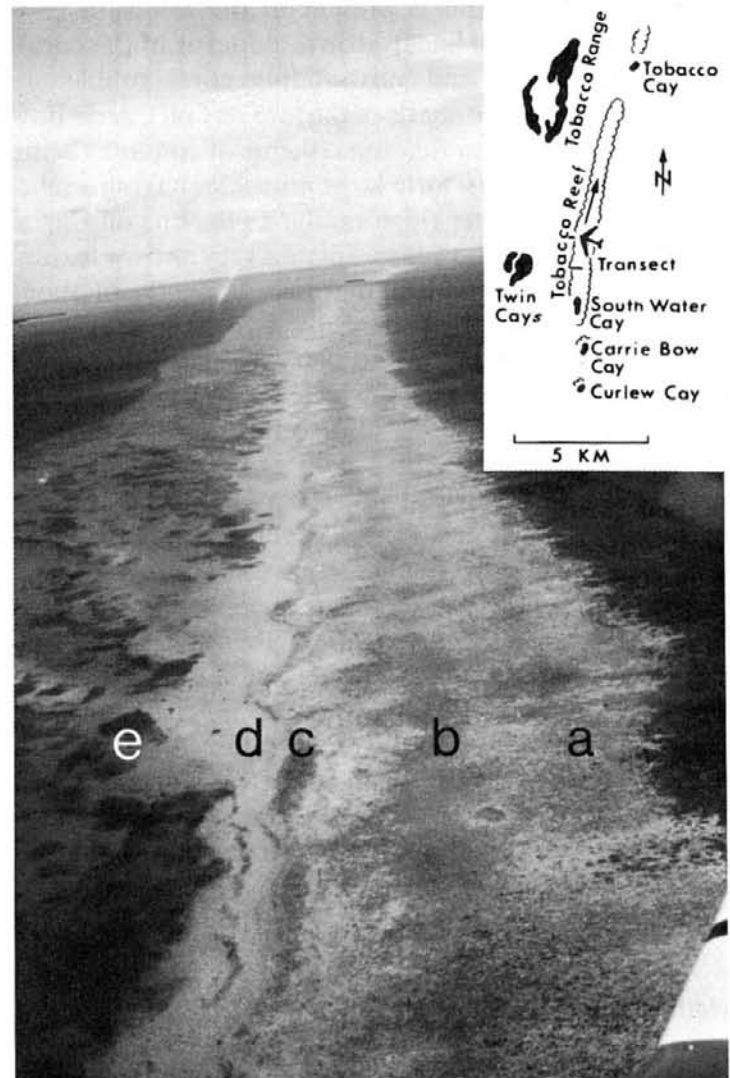


Fig. 1. Aerial view of Tobacco Reef showing zones of sediment apron that occur leeward of and parallel to the emergent reef crest (zones identified by letters in Fig. 11). Open fore-reef on right. Insert shows location of study transect and orientation of photograph

logical, and physical oceanographic characteristics of the Tobacco Reef sediment apron with a view to explaining the hydrodynamic and biological parameters that control the zonal patterns of this back-reef environment.

Study area

A site representative of the entire reef (Fig. 1) was identified on the sediment apron of Tobacco Reef approximately 1 km north of South Water Cay in an area remote from the direct influence of the island. The sediment apron was studied in detail along a 240-m transect lagoonward of the reef crest. At this site the crest is 28 m wide and consists of coral rubble, which is bound in mats of *Halimeda* and *Caulerpa* and is encrusted by *Porolithon pachydermum*. Most of this rubble field is partly exposed during low tide. The outer edge of the reef crest is flanked by shallow fore-reef colonies of *Acropora palmata* and massive growths of *Millepora* that form the intermittently emergent cappings of pronounced buttresses having a relief in excess of 6 m.

Seaward of these buttresses, the outer reef is similar to the reef off Carrie Bow Cay (Rützler and Macintyre 1982), except that little sand is present in the low spur-and-groove zone and the linear growth patterns of the coral-head communities and surrounding coral rubble are indistinct. Unlike the corals of the fore reef off Carrie Bow Cay, many of those in this zone (the most common being *Montastrea annularis*) form large pinnacles having a relief of up to 5 m. An outer ridge similar to the one off Carrie Bow Cay is present, however. This is a very narrow feature (about 5 m wide at the top) that rises to depths of about 18 m, where it is dominated by a mixed coral-head community that gives way to platy *M. annularis* on the almost vertical inner slope, which drops to a sediment-filled trough at 30 m. The fore reef at our study site is about half as wide (about 250 m) as its counterpart off Carrie Bow Cay and resembles the fore reef off South Water Cay, which has been described by James and Ginsburg (1978).

Directly shoreward of the reef crest, the sediment apron slopes gently from a depth of about 0.5 m to 2.5 m, where the sea floor begins to level out at the edge of the lagoon. This point, which marks the inner limit of the study transect, is about 200 m from the reef crest. The bottom characteristics along this transect exhibit a lagoonward transition, from pavement to rubble, to gravel and sand (with associated changes in the coral-algal assemblages), and finally to a *Thalassia*-covered sand floor.

Methods

Sedimentological studies

In June 1983 we documented bottom characteristics in detail along the study transect and collected surface sediment samples at 20 m intervals. In addition, we measured the largest dimension of rubble fragments located within 1 m² of the sample site and made a series of probings with a 1-cm diameter steel rod to determine maximum penetration depths.

The analysis of the size distribution of sand and finer sediments (<2 mm) was based on standard sieve and settling techniques (see Folk 1961). Volume percentages of the main constituents were estimated in thin sections of sand fractions greater than 0.125 mm by a point-count technique (see Ginsburg 1956). The six dominant carbonate components – *Halimeda*, coral, molluscs, foraminifera, coralline algae and echino-

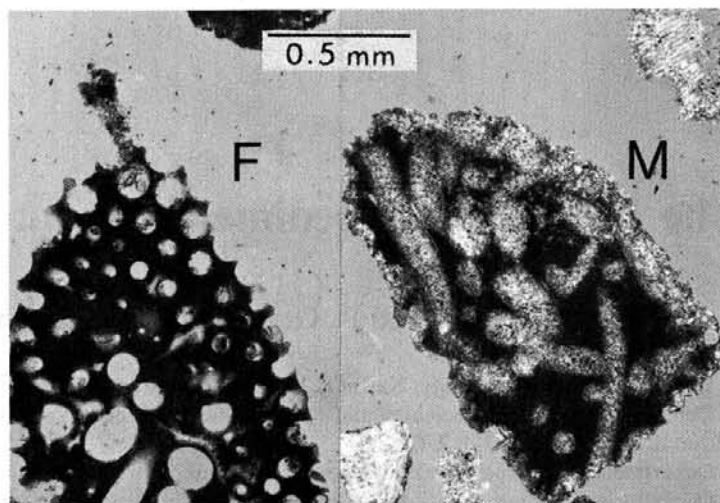


Fig. 2. Photomicrographs showing fresh (F) and mature (M) *Halimeda* grains. Note the secondary aragonite infill of medullary tubes in the mature grains

derms – were tabulated separately and all other miscellaneous, lithic and unknown material were identified as “others”. Material in this last category never exceeded 10% in any of the thin-section counts. The *Halimeda* category was further subdivided into fresh and mature grains (Fig. 2), the latter being assigned to grains having a secondary aragonite cement infill of filament or medullary tubes (Glover and Pray 1971).

Bottom-community studies

Our biological measurements were based on the biotic cover, which we took to be an important ecological parameter inasmuch as space and light are considered to be limiting resources in shallow marine communities (Connell 1972) and sessile organisms utilize their cover to compete for space and light. Fifty-six color photo-samples of 30 × 50-cm (0.15 m²) quadrats were taken along the study transect at fixed 2.0-m intervals for the first 20 m (narrow zones) and then at 5.0-m intervals (broad zones). This work was done in April 1984, one year after the initial sedimentological survey was completed. In areas where multilayered canopies were present, additional photographs were taken to measure stratification after the upper layers had been moved aside. Detailed field notes and taxonomic vouchers for the various quadrats aided in the interpretation while the photo-samples were being scored. Species composition and cover in each quadrat were determined in the laboratory by a point-intercept method (Littler 1980) and used to plot distribution and abundance patterns.

Data obtained by photogrammetric sampling made it possible to quantify the distributions and abundances of standing stocks in relation to transect distance and depth. All quadrat data were summed and averaged to yield mean cover values and used to interpret changes in macrophyte populations and communities in relation to environmental gradients.

To ensure that natural species assemblages and distributional patterns would be characterized in an unbiased manner, we subjected the cover data for each quadrat to hierarchical cluster analysis (flexible sorting; Smith 1976) using the Bray and Curtis (1957) coefficient of similarity. Owing to the patchy nature of the environment, quadrat groupings by this technique reveal tendencies or trends and not statistically clear-cut assemblages. The resultant dendrogram of quadrat groupings was interpreted according to the dominant biota and environmental affinities.

Diversity measurements have been widely employed for assessing the effects of environmental factors on biotic communities. Species diversity is often measured by indices that include components of both richness and equitability (see Poole 1974 for references and definitions). The problem with any single index is that both components of diversity are confounded. Moreover, the underlying assumption of many diversity indices is that the ecological importance of a given species is proportional to its abundance.

We attempted to avoid these problems by using the standardly applied Shannon and Weaver (1949) H' index (incorporating both richness and evenness). We also used separate indices to partition richness (Margalef's (1968) D') and evenness [equitability (E')] components independently. These were calculated for the cover data using natural logarithms and provided supplementary information for between-habitat comparisons of community structure.

Hydrodynamic studies

An analysis of wave hydrodynamics was undertaken to account for the distribution of bottom substrates along the Tobacco Reef transect. First, deepwater wave heights and periods were derived for three sets of wave conditions – maximum tradewind, average storm, and Hurricane Greta (1978) – using standard wave forecasting techniques. Then, with the help of a computer model called COREEF (Graus et al. 1984), these waves were routed across a simulated profile and zonation pattern of the reef, from the outer ridge back to and including our study transect. COREEF was used to determine changes in wave height and maximum horizontal bottom velocities at 20 m horizontal intervals along the profile. These changes developed in response to shoaling, bottom friction, wave reflection, refraction, and breaking. The predicted velocities were then compared with those required for the breakup of the *Acropora palmata* Zone (Hernandez-Avila et al. 1977) in the fore reef and for the transport of coral rubble as well as sand across the reef crest into the back reef.

In deriving deep-water wave characteristics, we found that tradewind-generated waves tended to be obstructed by nearby offshore atolls and would therefore be fetch-limited. The effective fetch was calculated over a 90° sector about the mean wave direction of 74.5° (Burke 1982) following the procedure given in the Shore Protection Manual (SPM) (US Army Corps of Engineers 1977). The maximum tradewind speed was obtained by plotting the cumulative frequency of all oceanic wind speeds at Belize (US Naval Weather Service Command 1974) and locating the sharp change in slope at the 95% level that marks the boundary between the tradewind and storm signatures. Deep-water wave height and period were then read directly from forecasting curves of Bretschneider (1966).

Deep-water wave characteristics for average storm conditions were derived with the help of a computerized storm surge model called GINT (Graus et al. 1984; Herchenroder, in preparation). Storm parameters used for this derivation are given in Table 1.

The distance from the study site to the average storm was determined by averaging the distances of closest approach of 83 storms that had passed within a radius of 400 km from Tobacco Reef since 1886 (Neumann et al. 1981). The radius of maximum wind speed was set at the approximate boundary value between tropical storms and hurricanes in

view of the fact that 60% of the 83 storms had been tropical storms and 40% had been hurricanes.

Deep-water wave characteristics for Hurricane Greta were taken from Kjerfve and Dinnel (1983). Although these values apply to Carrie Bow Cay, they are probably also valid for Tobacco Reef, which lies 3 km to the north.

Stillwater flood levels for the average storm and for Hurricane Greta were predicted by GINT.

Fish herbivory studies

In May 1984 we transplanted eight samples of reef macrophytes to determine fish grazing activity along the study transect as a function of distance from the reef crest. The resulting information was related to the observed patterns of macrophyte zonation.

The macrophytes used in the grazing assay were *Turbinaria turbinata*, *Sargassum polyceratum*, *Thalassia testudinum*, *Padina jamaicensis*, *Acanthophora spicifera*, *Laurencia papillosa*, *Laurencia intricata* and *Dictyota divaricata*. The *T. testudinum* consisted of segments of upper blades that were free of epiphytes. The patterns of herbivory were assessed by clamping spin-dried, weighed samples of each macrophyte in wooden clothespins that were cable-tied to metal rods placed flat on the sea floor. Four samples were tied to each rod approximately 25 cm apart, and two rods were used in each complete assay. The clothespin method has proved to be successful in previous experiments (Hay 1981a, 1984; Lewis 1985, 1986).

A mixed assay allowed us to determine grazing intensity with respect to the variety of herbivore groups observed to be active in this area. For example, the *T. turbinata*, *S. polyceratum*, *T. testudinum* and *P. jamaicensis* are consumed primarily, if not entirely, by parrotfish (*Sparisoma* and *Scarus* spp.). In contrast, the red algal species *A. spicifera*, *L. papillosa* and *L. intricata* are eaten, for the most part, by acanthurid species. The grazing activity on *D. divaricata* could not be determined.

Herbivore pressure as a function of distance from the reef crest was measured by placing complete sets of the assay in the back reef at distances of 0, 40, 90 and 150 m behind the reef crest. All trials were run for 8 h, from 0830 to 1630 h. The samples were then spin-dried and reweighed. Each trial was repeated four times at each locality. The amount of macrophyte used in each trial was consistent with the size of the macrophytes observed in the study area. In all trials a small piece of the macrophytes remained in the clothespin, where it was inaccessible to herbivores. Grazing scars and field observations indicated that these macrophytes had not been removed by wave action.

Fish counts were made along a series of four replicated visual transect censuses (50 m × 2 m) between 0800 and 1600 h at each experimental grazing site. The methodology applied here is similar to that used by Lewis and Wainwright (1985) to determine the distribution and relative abundances of herbivorous fishes. All parrotfishes and surgeonfishes were counted to determine distributional patterns and densities. *Diadema antillarum*, another herbivore that was prominent throughout the Caribbean before its massive die-off (Lessios et al. 1983), was not considered in this study because even long before the reported die-off it was not common on this back-reef sediment apron of Tobacco Reef. Moreover, fish are considered to be the grazers of primary importance on most tropical reefs (Hay 1984; Lewis 1985, 1986). No other organisms were found grazing on any of the assays.

Results

Sedimentological studies

The transition in the sedimentological characteristics of the sea floor along the study transect are shown in Fig. 3. A well-cemented and interlocking coral pavement extends lagoonward for a distance of about 70 m and then gives way to a 40-m wide band of loose rubble (> 6.4 cm) resting in a matrix of gravel (6.4 cm to 2 mm) and sand. This rubble bottom grades into a narrow (20-m wide) sand and gravel belt, which grades into a sandy bottom that forms the last 110 m of sea floor along the study transect.

Table 1. Parameters required for the calculation of deep-water wave characteristics for average storm conditions and still-water flood levels off the Tobacco Reef study transect

Storm parameter	Value	Source
Speed of average storm	19.4 km/h	Hope and Neumann (1969)
Mean direction of storm motion	287°	Hope and Neumann (1969)
Maximum sustained wind speed	97 km/h	Jarvinen and Neumann (1979)
Radius of max. wind speed	74 km	Estimated (this paper)
Distance to storm center	155 km	Calculated (this paper)
Central storm pressure	993 mb	Gradient wind formula US Army Corps of Engineers (1977)
Peripheral storm pressure	1013 mb	Assumed
Wind speed at Tobacco Reef	15.6 m/s	Calculated as per Graus et al. (1984)
Wind direction at Tobacco Reef	131°	Calculated as per Graus et al. (1984)
Mean Tidal Range	0.15 m	Kjerfve et al. (1982)

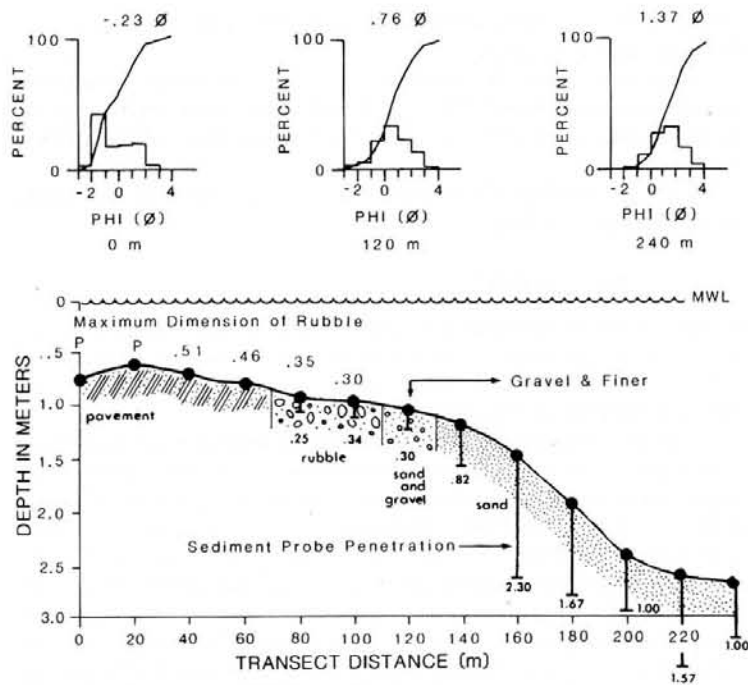


Fig. 3. Study transect of Tobacco Reef sediment apron showing substrate characteristics, size distribution of rubble (P indicates pavement with no loose rubble), and maximum penetration depths of sediment probe. Three representative plots of histograms and cumulative curves (with graphic mean) in phi scale, graphically illustrate the variation in size distribution of the sand-size and finer fraction

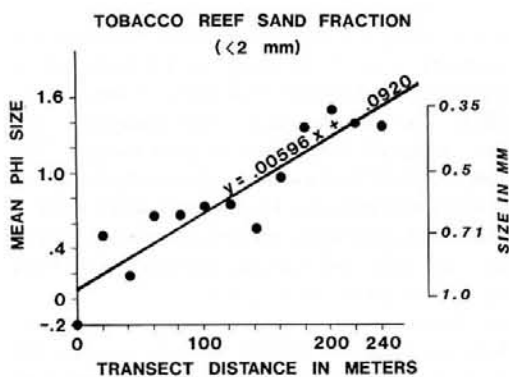


Fig. 4. Plot of graphic mean of sand-size and finer fraction (phi scale - negative logarithm to the base 2 of particle diameter in mm) with respect to distance from reef crest along study transect. Correlation coefficient, $r = 0.91$, with $P < 0.001$

As can be seen in Fig. 3, the rubble dimensions range from 0.51 m at 40 m along the transect to 0.3 m at the 100-m sample site, which is near the inner limit of rubble distribution. Beyond this point, only gravel and finer sediment occur.

The penetration achieved with our sediment probe ranged from no significant penetration in the pavement areas to penetration of about 0.3 m in the dominantly rubble and gravel bottom and penetration of 1 m or more (maximum of 2.3 m) in the sandy floor of the inner limits of the sediment apron (Fig. 3). In addition, these probings indicate that, for the time represented by the deposition of the probed section (at least 1 m of sediment), very little coarse debris has been transported more than 150 m from the reef crest.

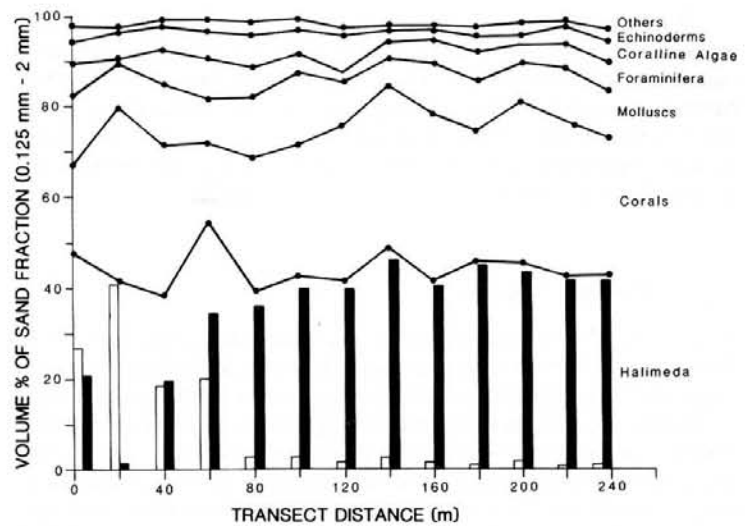


Fig. 5. Volume percentages of sand-size sediment components across study transect. Histograms show percentages of fresh (open) and altered or mature (black) *Halimeda* grains

In size analyses of the sand and finer fraction (<2 mm), no samples contained more than 2% clay-size material (<4 μm). The silt-size fraction (4–63 μm) was 5% or less for most of the transect, but increased to almost 10% at the lagoonward limit. The mean grain size also shows a lagoonward trend: very coarse sand (1–2 mm) lies directly behind the reef crest and from there the mean grain size continues as coarse sand (0.5–1 mm) to the 160 m mark, where it decreases to medium sand (0.25–0.5 mm) at the inner limit of the transect (Figs. 3 and 4).

Volume percentages of the main sand constituents do not vary significantly across the entire transect (Fig. 5). However, the percentage of fresh unaltered *Halimeda* material decreases markedly beyond the 60-m station.

Bottom-community studies

Five macrophyte species account for 79% of the biotic cover (Table 2) along the entire 245-m transect. Of these, *Thalassia testudinum* constitutes 45% of the total cover, *Turbinaria turbinata* 12%, crustose coralline algae (mostly *Hydrolithon reinboldii* and *Porolithon pachydermum*) 9%, *Dictyota divaricata* 8% and *Sargassum polyceratum* 5%. Sessile animals (mostly corals) contribute only 4.5% of the total biotic cover.

The cluster plot (Fig. 6) revealed four biological assemblages. Because of the patchy distribution of some organisms and sand, several quadrats (m 10 = mostly sand, m 105 = crustose corallines, m 110 = *Dictyota*) are clustered with samples outside their areas.

Area 1 (with 19.3% mean biotic cover consisting of 23.8% sessile invertebrates and 76.2% macroalgae), which extends from meter 0 to meter 50 (Fig. 6), is dominated by crustose coralline algae (7.3% cover), *Dictyota divaricata* (4.7%) and the coral *Porites astreoides* (2.8%). These three components along with the *Jania* turf (intertangled thalli), make up 84% of the biotic cover in this area. The two subgroups that clustered in this area

Table 2. Mean percentage cover of dominant sessile organisms by biotic area identified in cluster analysis

Species	Area				Total mean
	1	2	3	4	
Macrophytes					
<i>Thalassia testudinum</i>				98.50	19.02
<i>Turbinaria turbinata</i>		27.70			5.03
Crustose corallines	7.29	5.63	3.27		3.81
<i>Dictyota divaricata</i>	4.69	10.93	2.46	<0.01	3.31
<i>Sargassum polyceratum</i>	0.05	11.51	0.09		2.00
<i>Laurencia intricata</i>		3.92	3.31		1.19
<i>Laurencia papillosa</i>		0.24	5.88		1.00
<i>Gelidium acerosa</i>		4.41	0.09		0.81
<i>Acanthophora</i> sp.			3.95	0.26	0.74
<i>Halimeda incrassata</i>		2.57	0.72		0.54
<i>Jania turf</i>	1.73	0.01			0.52
<i>Champia parvula</i>				1.25	0.43
<i>Halimeda monile</i>				1.23	0.44
<i>Halimeda opuntia</i>	0.90	0.47			0.36
<i>Spyridia filamentosa</i>			1.37		0.23
<i>Penicillus capitatus</i>			0.19	0.27	0.17
<i>Hypnea</i> sp.			0.77		0.13
<i>Dictyosphaeria cavernosa</i>				0.31	0.11
<i>Galaxaura</i> sp.		0.45		<0.01	0.09
<i>Jania adhaerens</i>			0.99	0.17	0.08
<i>Udotea flabellata</i>		0.41		<0.01	0.07
<i>Amphiroa fragilissima</i>		0.24	0.07		0.06
Total macrophyte cover	14.66	68.49	23.16	102.02	40.14
Macroinvertebrates					
<i>Porites astreoides</i>	2.77				1.13
<i>Diploria</i> sp.	0.99				0.30
<i>Porites porites</i>		0.45	0.33	0.20	0.20
<i>Favia fragum</i>	0.58				0.18
Zooanthids	0.34				0.10
Total macroinvertebrate cover	4.68	0.45	0.33	0.20	1.91
Total cover	19.34	68.94	23.49	102.22	42.05

(Fig. 6) are based on only minor differences in the quantity of *D. divaricata* present.

Area 2 (with 64.4% biotic cover consisting of 0.6% macroinvertebrates and 99.4% macroalgae) falls between meter 50 and meter 100 of the transect and is characterized by the large brown rockweeds *Turbinaria turbinata* (27.7% cover) and *Sargassum polyceratum* (11.5%), along with *Dictyota divaricata* (10.9%). These three species account for 72% of the total biotic cover in area 2. *Porites astreoides* was absent from samples within area 2, but the conspicuous branching coral *P. porites* appeared here and there (mean cover 0.5%; Table 2) and extended into areas 3 and 4.

Area 3 (with 23.5% biotic cover, 1.4% sessile animals and 98.6% macroalgae), which extends from about meter 100 to meter 145, contains a sparse community (Table 2) dominated by the fleshy red algae *Laurencia papillosa* (5.9% cover), *Acanthophora spicifera* (4.0%) and *Laurencia intricata* (3.3%), which together make up more than 50% of the living cover. A narrow area consisting predominantly of sand cover is present in the interval

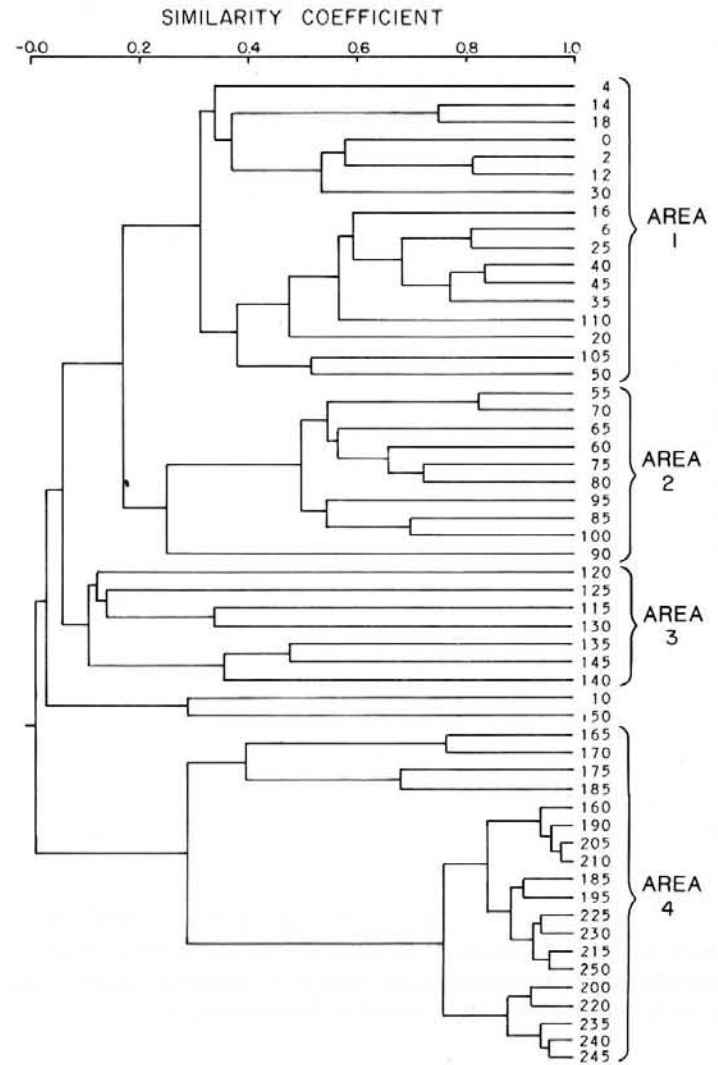


Fig. 6. Cluster analysis of biotic cover along Tobacco Reef study transect. Bray Curtis similarity coefficient with a clustering of unweighted pair-groups for quadrats identified by location in meters from reef crest

between meters 130 and 160; one quadrat (m 150) here contains 100% sand.

Area 4 (with 102% biotic cover, due to layering, of which 0.2% consists of animals and the remainder macrophytes) extends from 160 m lagoonward and is covered primarily by *Thalassia testudinum* (98.5% cover) containing the epiphyte *Champia parvula* (1.2%). Quadrats 165, 170, 175 and 185 contain *Laurencia intricata* as well, and therefore constitute a sub-area in Area 4. In addition, some colonies of the rhizomatous alga *Halimeda monile* are interspersed in low cover (1.2%) with other organisms (Table 2).

Of the four major areas, area 1 is most diverse ($H' = 2.61$), followed by area 3 ($H' = 2.11$), area 2 (1.66) and area 4 (1.55); Fig. 7). This sequence was paralleled by D' richness, which was 4.86 for area 1, 3.75 for area 3, 2.47 for area 2 and 2.12 for area 4. The E' measure of equitability also followed the same trend, with area 1 = 0.59 E' , area 3 = 0.46, area 2 = 0.40 and area 4 = 0.39 (Fig. 7).

Hydrodynamic studies

The information from the analysis of the wave hydrodynamics along the study transect are shown in Fig. 8 in

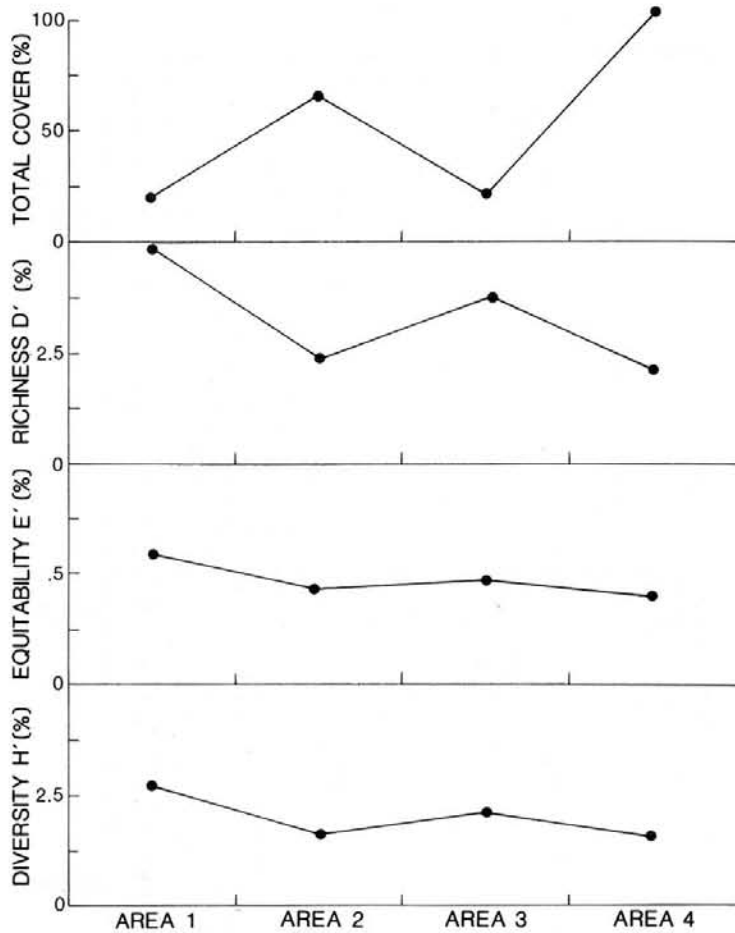


Fig. 7. Variations in diversity (Shannon and Weaver 1949), evenness or equitability and richness (Margalef 1968), and total percentage of cover of biotic communities for areas identified in cluster analysis

relation to regimes of sediment transport and stability. The boundary line for the initiation of sand movement was calculated by inserting mean PHI values (converted to cm) from the regression equation of Fig. 4 into the velocity equation given by Komar (1976)

$$U_t = \left[0.46 \pi g \left(\frac{\rho_s - \rho}{\rho} \right) D^{0.75} d_0^{0.25} \right]^{0.5},$$

where U_t is the initiation velocity in cm/s, g is the gravitational acceleration, ρ_s is the density of sand ($=2.366 \text{ g/cm}^3$, the mean density of back reef carbonate sand from Tobacco Reef), ρ is the water density ($=1.026 \text{ g/cm}^3$), D is the mean particle diameter (actually the geometric mean when converted from PHI), and d_0 is the orbital diameter of wave motion. The line for the planation of ripples is $3.0 U_t$ (Manohar 1955).

The threshold velocity line for the lift-off of broken *Acropora palmata* branches was calculated using an expression from Graus et al. (1984):

$$U_1 = \left[0.65 \pi g D \left(\frac{\rho_s - \rho}{\rho} \right) \right]^{0.5},$$

where U_1 is the lift-off velocity in cm/s, ρ_s is the skeletal density of *A. palmata* ($=2.330 \text{ g/cm}^3$, the mean density of branch fragments from 8 colonies), and D is the mean

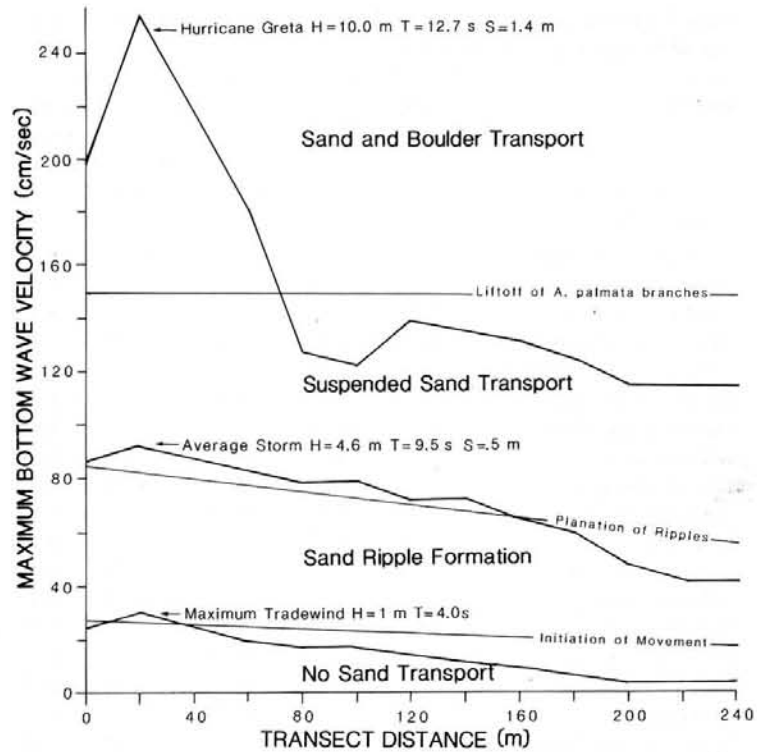


Fig. 8. Bottom velocities across study transect for different wave conditions at high tide. H = wave height; T = wave period; S = storm surge

diameter of the broken ends of the branch. For this calculation, the branch was assumed to be a truncated cone 50 cm long with $D = 8.75 \text{ cm}$.

Although the bottom-velocity curves in Fig. 8 differ in magnitude, they all show bottom velocity decreasing with increasing distance lagoonward from the reef crest. The magnitude differences can be explained by variations in water depth at the reef crest caused by tides and storm surge. Because breaking wave height increases with water depth, conditions leading to greater water depth at the reef crest cause larger waves to propagate into the back reef and thereby generate higher bottom velocities. The lagoonward decrease in bottom velocity is due to a combination of bottom friction, which progressively reduces wave height, and an increase in water depth with distance.

Although trade wind conditions account for about 95% of the waves at Tobacco Reef, all the back-reef velocities, except at the 20-m station, fall below the velocity required for the initiation of sand movement (Fig. 8). Therefore, sand remains stationary most of the time. During high spring tides, velocities would increase slightly and thus ripples would form at most stations.

Most of the sand transport in the back reef takes place during brief intervals ($<1\%$ frequency) of storm activity. Average storm conditions are sufficient to cause suspension and lagoonal movement of sand over much the study transect. Bottom velocity calculations indicate that material is continually supplied, even during calm periods, by sand transported from the reef crest. During storms, sand can be mobilized throughout the entire shallow fore reef and transported across the crest into the back reef.

Evidently boulders (>25.6 cm) can be transported into the back reef only during hurricane conditions. The point at which the bottom-velocity curve of Hurricane Greta intersects with the lift-off velocity line for fragmented *Acropora palmata* branches (Fig. 8) represents the outermost limit of lagoonward transport for boulders 0.5 m long. Lower threshold velocities for smaller boulders of the same shape (e.g., 142 cm/s for L=0.46 m, 124 cm/s for L=0.35 m and 115 cm/s for L=0.30 m) explain the fact that boulders tend to decrease in size with increasing distance from the reef crest.

In order for *Acropora palmata* boulders to be transported to the back reef, the maximum bottom velocity in the fore reef *A. palmata* zone must exceed the level of 4.0 m/s required for the fragmentation of this coral (Hernandez-Avila et al. 1977). In general, tropical storms do not reach this threshold velocity, whereas hurricanes – which can generate bottom velocities of 6.0 m/s – far surpass it.

Fish herbivory studies

A distinct fish-grazing pattern emerges from the data on macrophyte species with this study (Fig. 9). Except for *Dictyota divaricata*, grazing pressure is homogeneously heavy at 0 to 40 m from the reef crest. For two macrophyte species, *Padina jamaicensis* and *Thalassia testudinum*, the homogeneity of heavy grazing pressure extends to 90 m. Both these species are highly preferred by parrotfish in paired choice feeding trials (Lewis and Reinthal, in preparation). *Turbinaria turbinata* and *Sargassum polyceratum* appear to be subject to the same heavy grazing pressure at 0 and 40 m, but little or moderate pressure was found at 90 m.

The situation is similar for the macrophytes preferred by surgeonfish (Acanthuridae) (Lewis 1985; Lewis and Reinthal, in preparation). For *Acanthophora spicifera* and *Laurencia papillosa*, grazing pressure was heavy at 0 and 40 m, moderate at 90 m, and weak at 150 m. The results for *L. intricata* show moderate to heavy grazing pressure at 0 and 40 m but homogeneously weak pressure at 90 and 150 m.

Grazing pressure appeared to be homogeneously light for *Dictyota divaricata*. The weight loss in this case is thought to be due primarily to experimental error caused

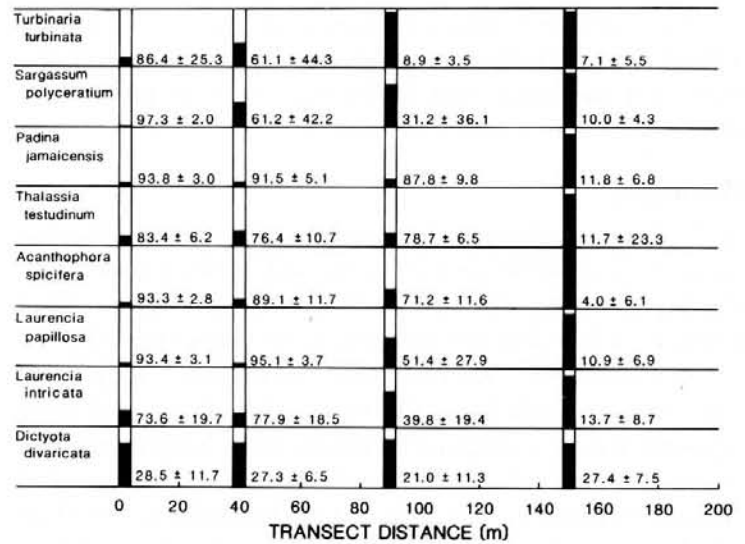


Fig. 9. Percentage weight loss (with standard deviation) of test samples of macrophytes transplanted to four locations along study transect. Dark areas indicate weight percent of sample remaining after an 8 h test period

by the removal of small fragments through wave action. This was the only macrophyte that proved difficult to retain as one piece in the clothespin. Surgeonfish were occasionally seen taking a small bite of *D. divaricata*, but were never seen grazing with the same intensity shown for *Laurencia papillosa* or *Acanthophora spicifera*. *Dictyota spp.* in general, probably because they contain noxious chemical compounds (Gerwick 1981; Norris and Fenical 1982) are notably avoided by herbivorous fishes (Montgomery 1980; Hay 1981a; Littler et al. 1983b).

For all macrophytes, except *Dictyota divaricata*, average percentage weight loss generally decreased with distance from the reef crest (Fig. 9). Data from the four trials did not differ significantly and so were pooled. Weight losses for *D. divaricata* did not vary greatly across the transect (ANOVA $P=0.68$). All other macrophytes showed highly significant weight-loss differences with respect to distance from the reef crest (ANOVA $P<0.005$ in all cases) (Reinthal, in preparation).

The distributional patterns identified for the herbivorous fish match the grazing patterns observed (Table 3). The densities of herbivorous fish were highest at 0 and 40 m, the areas with the greatest grazing pressure, and moderate at 90 m. However, only one *Sparisoma croicensis* was seen at 150 m. Even though most of the fish at 90 m

Table 3. Fish counts (densities per m²) along line transects (50 × 2 m) at the four herbivory test sites

Distance from reef crest (m)	Acanthuridae						Scaridae					Total
	<i>Acanthurus bahianus</i>		<i>Acanthurus coeruleus</i>		<i>Acanthurus chirugus</i>		<i>Sparisoma croicensis</i>	<i>Sparisoma chrysopterum</i>	<i>Sparisoma ruppinne</i>	<i>Sparisoma viride</i>	<i>Sparisoma radiens</i>	
	Juv	Adult	Juv	Adult	Juv	Adult						
150	0	0	0	0	0	0	0.25	0	0	0	0	0.25
90	16	0	0	0	0	0	0.50	0	0	0	2.75	19.25
40	23	4.50	0	2.50	1.25	1.25	5.00	0.50	0	0	0.25	38.25
0	14	1.50	0.50	2.50	0	0.75	10.50	1.25	1.00	3.50	0	35.50

were juvenile *Acanthurus bahianus*, the sighting of a large school of adult herbivorous fishes at this distance from the reef crest indicates that herbivores may increase their foraging territory when in schools.

Discussion

According to sedimentological data, qualitative observations of coral-algal distributions and quantitative community analyses, the sediment apron of Tobacco Reef consists of five distinct biogeological zones (Fig. 10):

1. *Coralline-Coral-Dictyota* pavement (Fig. 11a). This zone extends from the inner edge of the reef crest lagoonward for a distance of about 70 m. Scattered coral colonies – for the most part *Porites astreoides* and *Acropora palmata* – are attached to the crustose coralline algal encrusted pavement, which also supports an extensive cover of *Dictyota* with lesser amounts of *Jania*, *Halimeda* and *Neomeris*.

2. *Turbinaria-Sargassum* rubble (Fig. 11b). This zone is about 40 m wide and the rubble and sand substrate supports a rich cover of fleshy algae, particularly the large brown algae *Turbinaria turbinata* and *Sargassum polyceratum*. Among the other common algal genera here are *Dictyota*, crustose corallines, *Gelidium*, *Laurencia*, *Halimeda*, *Penicillus*, *Neomeris*, *Gracilaria*, *Galaxaura*, *Rhipocephalus*, *Udotea*, *Dictyosphaeria*, *Liagora* and *Caulerpa*. Small colonies of the coral *Porites porites* f. *furcata* are also characteristic of this zone and all areas lagoonward on the study transect, except for the bare sand zone.

3. *Laurencia-Acanthophora* sand and gravel (Fig. 11c). The loose substrate of this narrow (20 m wide) zone supports a variety of fleshy algae – most notably the red algae *Laurencia* and *Acanthophora*. Other common algae include crustose corallines, *Dictyota*, *Spyridia*, *Jania*, *Hypnea*, *Dictyosphaeria*, *Sargassum*, *Amphiroa*, *Neomeris*, *Halimeda*, *Turbinaria*, *Dictyota*, *Udotea*, *Liagora*, *Caulerpa* and *Penicillus*.

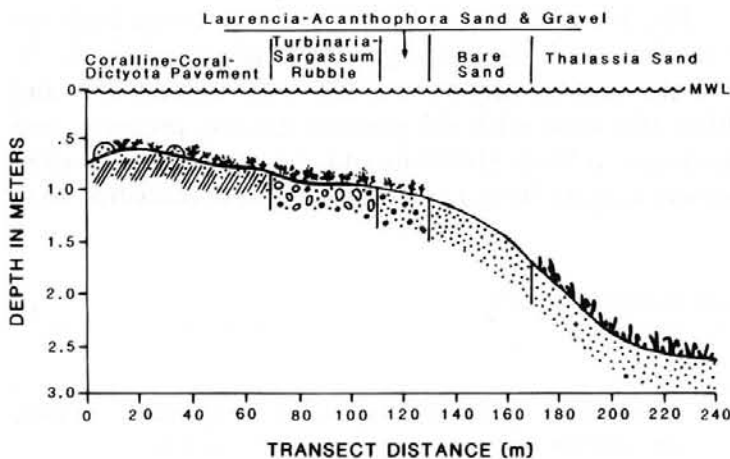
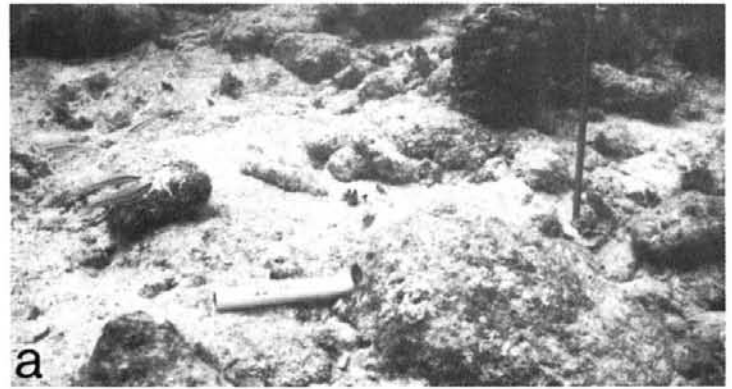


Fig. 10. Study transect of Tobacco Reef sediment apron showing biogeological zones

Fig. 11. Underwater views of the biogeological zone of Tobacco Reef sediment apron: a *Coralline-Coral-Dictyota* pavement, b *Turbinaria-Sargassum* rubble, c *Laurencia-Acanthophora* sand and gravel, d bare sand, e *Thalassia* sand. Sediment probe and 15 cm scale visible in a and d



4. Bare sand (Fig. 11d). About 130 m leeward of the reef crest, the bottom consists of relatively open sand with scattered gravel. From the air, this zone appears as a distinct white band about 40 m wide (Fig. 1). Plant cover is sparse, but here and there fleshy algae are present – primarily *Padina*, *Laurencia*, *Dictyota*, *Turbinaria*, *Hypnea*, *Halimeda*, *Udotea*, *Caulerpa*, *Rhypocephalus*, *Penicillus* and *Ceramium*.

5. *Thalassia* sand (Fig. 11e). At the shoreward limit of our study transect, the sand bottom with occasional scattered gravel-sized fragments supports a rich cover of the seagrass *Thalassia testudinum*. Some fleshy algae are also present, primarily *Champia*, *Penicillus*, *Acanthophora*, *Dictyota*, *Udotea*, *Rhypocephalus*, *Avrainvillea*, *Caulerpa*, *Dictyosphaeria*, *Laurencia* and *Halimeda*.

Although these zones were identified mainly on the more persistent substrate characteristics, they do closely parallel the areas categorized according to biological assemblage in the bottom-community analysis. Area 1, for example, which is dominated by crustose coralline algae, *Dictyota divaricata* and *Porites astreoides* coincides with the coralline-coral-*Dictyota* pavement zone and area 2 coincides with the *Turbinaria-Sargassum* rubble zone, except for a slight overlapping where significant numbers of *Turbinaria turbinata* and *Sargassum polyceratium* of area 2 are present on the pavement substrate. Similarly, the mixed algal area 3 matches up with the *Laurencia-Acanthophora* sand and gravel zone, but also overlaps, to some extent with both the *Turbinaria-Sargassum* rubble and the bare sand zones. Finally, the seagrass of area 4 correlates directly with the *Thalassia* sand zone.

The lagoonward decrease in rubble size and in mean grain size of sand samples indicates that reef debris is transported shoreward from the fore reef and reef crest. Some of the variations in the sand size analyses are undoubtedly related to in situ sources of carbonates, particularly *Halimeda* plates – this alga occurs along the entire study transect. The local introduction of carbonate material, however, is minor and does little to mask the pattern of leeward transport of material from the reef crest and beyond.

The relatively uniform volume percentage of main sand components across the transect confirms the sedimentation pattern of continued long-term lagoonward transport of material derived mainly from the fore reef and reef crest. Other evidence for this pattern is the sharp decrease in fresh *Halimeda* grains shoreward of the 60 m station; most of this material apparently derives from the thick *Halimeda* mats that bind the reef-crest rubble. In fact, the percentage of altered grains (microborings and secondary cement fillings) of all carbonate components increase with increasing distance from the reef crest. The dominance of *Halimeda* in these reef sediments is a common characteristic of western Atlantic reefs (e.g., Ginsburg 1956; James and Ginsburg 1978).

These surface characteristics of the sediment apron are by and large determined by hydrodynamic conditions associated with brief turbulent intervals (< 1% frequency)



Fig. 12. Large southern stingray (*Dasyatis americana*) reworking sediment floor in the *Laurencia-Acanthophora* sand-and-gravel zone. Note fine sediment plume

of storm and hurricane activity. Very little sand-size material appears to be transported under normal trade wind conditions except during high spring tides, when water flow over the reef crest is less restricted. However, winnowing of finer-than-sand material continues throughout the year, generally in association with bioturbation (Fig. 12). Bottom velocities at the reef crest ensure a constant supply of sand-size and finer sediment to the back reef, with the addition of sand- and boulder-size material from the fore reef during storms and hurricanes. Local hydrodynamic conditions also appear to affect the degree of transportation and the size distribution of back-reef sediments of several reef flats in the Great Barrier Reef (Marshall and Orr 1931; Flood and Scoffin 1978).

The distribution of the biological assemblages appears to be controlled mainly by the grazing pressure of herbivorous fish, which is a function of the distance from the reef crest, and by physical factors such as substrate type and stability. In turn, both of these physical factors depend on hydrodynamic conditions and therefore also vary with the distance from the reef crest. Similar algal zonation across reef flats in the northern Great Barrier Reef have been attributed to variations in sediment thickness (Flood and Scoffin 1978). In this study area, however, the processes responsible for biological zonation in the back reef are far more complex. The dominant biota of the coralline-coral-*Dictyota* pavement – the zone in which we measured the highest levels of herbivory (Fig. 9) – all have well-documented coexistence strategies for herbivore defense. The crustose coralline algae are well adapted to herbivory owing to their reduced calorific levels (Paine and Vadas 1969; Littler et al. 1983a; Littler and Littler 1984); tight adherence and flat shapes, which lower their accessibility and yield per bite; and structural materials (i.e., CaCO_3), which decrease palatability and nutritional value (Littler 1976). Another dominant alga is the unpalatable genus *Dictyota* (Fig. 9 also see Littler et al. 1983b), which contains high quantities of unique second-

ary compounds (Gerwick 1981) that have been found to be toxic to fish in laboratory experiments.

Note, too, that the high bottom velocities in the coralline-coral-*Dictyota* pavement zone, particularly during storms, will tend to eliminate plants and animals with high drag coefficients. Crustose coralline algae and massive corals can easily withstand such turbulent conditions. In addition, the closely adherent low-turf form of *Dictyota divaricata* that prevails in this zone is probably resistant to wave shear, and its productivity is high enough (Littler et al. 1983a) to enable it to repopulate rapidly by perennation from remnant holdfasts.

Grazing fishes and wave shear in this pavement zone create a continual intermediate level of disturbance (see Connell 1978) that enables a mosaic of resistant forms and opportunistic colonizers to undergo various stages of succession. As a result, the D' richness increases, E' equitability declines (so that one or several competitively superior species become dominant), and the overall H' diversity increases (Fig. 7).

Although herbivorous fishes do invade the *Turbinaria-Sargassum* rubble zone, they tend to consume only the more palatable macrophytes there and thus this region is exposed to considerably less grazing than the coralline-coral-*Dictyota* pavement (Fig. 9). As a result, the large brown fucal algae *Turbinaria turbinata* and *Sargassum polyceratum*, which are tough perennial forms reasonably resistant to wave shear and grazing (Littler et al. 1983a), dominate this zone. Because these species can grow relatively large, we suggest that they are able to compete effectively for space and light. Frondose macroalgal populations, when released from nutrient limitation and grazing constraints, can even overgrow and kill both coralline algae (Littler and Doty 1975; Wanders 1977; Adey et al. 1977) and corals (Banner 1974; Potts 1977; Birkeland 1977; Antonius 1982). As a result, the two fucal algal species may sequester available resources to the detriment of community diversity (Fig. 7).

Without a stable substrate, coral development in this rubble zone is limited to loose branching colonies of *Porites porites* and other scattered massive colonies, some of which have survived translocation from the shallow fore reef during high-energy events – as indicated by the common occurrence of inverted colonies. In addition, because *P. porites* is readily transported by bottom currents and is highly susceptible to parrotfish predation (Littler, Littler and Taylor, in preparation), it cannot survive in the seaward coralline-coral-*Dictyota* pavement zone.

Wherever tropical reefs have little relief (i.e., spatial heterogeneity), herbivore activity tends to be low (Brock 1979; Hay et al. 1983), usually because predatory fishes are present (Sphyraenidae, Lutjanidae, Carangidae) and large standing stocks of macrophytes are able to develop (Doty 1971; Wanders 1976; Connor and Adey 1977). Although we have no experimental evidence to explain why herbivorous fish do not graze farther from the reef crest, they may be constrained by predatory piscivorous fishes

(Ogden et al. 1973). Large barracuda (Sphyraenidae) and snapper (Lutjanidae) were often seen swimming in the study area. This might also be the reason why only schools of herbivorous fish were seen at the 90 m site and not solitary adults. Heterospecific schooling is widely believed to provide predator avoidance advantages to participants (see Morse 1977 for review). The characteristic plants of the zones shoreward of the *Turbinaria-Sargassum* rubble zone, which are most remote from suitable fish shelter, employ primarily noncoexistence escapes (Lubchenco and Gaines 1981) to minimize herbivory. Similar sandplain macrophyte refuges from herbivores have been documented by Dahl (1973), Earle (1972) and Hay (1981b).

Turbinaria turbinata and *Sargassum polyceratum* are restricted in their lagoonward development because the substrate is not massive enough to hold these large forms, which also have extensive supporting flotation structures. Thus many dead or dying thalli of these algae were observed attached to rubble that had been transported into deeper and calmer back-reef areas.

The shoreward limit of these large brown algae marks the beginning of the *Laurencia-Acanthophora* sand-and-gravel zone. At this distance from the reef crest, the fleshy red algae *Laurencia papillosa*, *Acanthophora spicifera*, and *Laurencia intricata* become primary. Grazing appears to be drastically reduced in this zone. The relatively high palatability values we obtained for the first two of these delicate frondose forms agree with those reported by Hay (1981a) and Littler et al. (1983b). Because of the significant accumulation of sand here and the resulting lack of stability (caused both by bioturbation and bottom currents), the frequently overturned substrate favors a variety of rapidly growing macrophytes – including *Laurencia* and *Acanthophora* (Littler et al. 1983a) – over the slower-growing, long-lived, and late-successional forms such as *Turbinaria*, *Sargassum* and *Thalassia* with the result that all diversity measures increase (Fig. 7).

The bare sand zone that lies lagoonward is much the same, except for a marked decrease in the amount of gravel substrate and wider areas of bare sand. The bottom-community studies indicated that the biotic association is similar to that found in the *Laurencia-Acanthophora* sand-and-gravel zone.

As the water becomes deeper, the sandy substrate becomes more stable and rhizomatous plants are able to establish themselves. The *Thalassia* sand zone is characterized by these specialized plants, which extract nutrients from both the water column and soft sedimentary substrate by means of root-rhizome systems that also serve to anchor them. Beyond 150 m from the reef crest and the high levels of herbivory, the bottom is dominated by this highly edible plant. Of the Belizean marine flora (Norris and Bucher 1982), only four members of the Angiospermae and several macroalgae (primarily members of a single algal order Caulerpales) have root-like or rhizomatous systems capable of attachment in soft sandy substrate. In the absence of other possible biotic components,

the potential diversity in soft sedimentary environments is greatly limited.

Conclusions

1. The bottom characteristics and dominant organisms indicate that the sediment apron leeward of Tobacco Reef consists of five well-defined biogeological zones: (1) coralline-coral-*Dictyota* pavement, (2) *Turbinaria-Sargassum* rubble (3) *Laurencia-Acanthophora* sand and gravel, (4) bare sand and (5) *Thalassia* sand.

2. The sediments – the rubble and sand, as well as the finer fractions – continuously decrease in size shoreward of the reef crest.

3. The size distribution is largely controlled by hydrodynamic conditions associated with storm and hurricane activity.

4. The size distribution and composition of the back-reef sediments indicate that, for the most part, these sediments derive from the fore reef and reef crest.

5. Differential patterns of fish grazing intensity are a function of distance from the protective habitat of the reef crest.

6. The distribution patterns of fish herbivory in combination with substrate suitability (which is related to both sediment size and stability) are the dominant factors controlling the distribution of biological assemblages on this sediment apron.

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