The Habitat Distribution and Community Structure of the Barrier Reef Complex at Carrie Bow Cay, Belize

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ABSTRACT

The reef complex near Carrie Bow Cay, which is representative of the entire Belizean barrier reef, is separated from the mainland by a deep and wide lagoon, which grades into shallow seagrass bottoms, patch reefs, and mangrove cays on the outer barrier platform. A study transect west (lagoon) to east (open ocean) shows a distinct zonation of substrates and organisms that reflects primarily water depth and the prevailing wave and current regime. The shallow back reef shows massive coral growth, extensive pavement areas, and large rubble accumulations caused by hurricane surge; it is separated from the inner fore reef by a narrow intertidal reef crest pounded by waves. The inner fore reef (to 14 m depth) shows a characteristic spur and groove structure, with high buttresses in the shallow depth zone (to 10 m) and low-relief formations on the deeper terrace. The outer fore reef includes a steep inner-reef slope, a sand trough and an outer coral ridge. The steep fore-reef slope drops off at the top of the outer ridge. Many topographic features are comparable to those present on north Jamaican reefs. Corals of the genus *Acropora* suffer heavy damage but also gain wide distribution from storm swells. *Halimeda* plates dominate the coarse fraction of the sand substrates across the entire transect even far below the occurrence of the alga. Submarine pavement lithification is most pronounced in areas of low sediment accumulation. The outer ridge, although now dominated by *Acropora cervicornis* on the study transect, appears to be built up by more solid framework. The reef at Carrie Bow Cay has a community composition representative of the central barrier reef province to which it belongs, but structurally it is a composite, including features characteristic of the discontinuous northern and southern province reefs.

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Introduction

The barrier reef complex—10–32 km wide (James et al., 1976) and approximately 250 km long—off Belize, Central America, is said to be the largest continuous reef in the Caribbean Sea (Smith, 1948; Adey, 1977). Beginning as a fringing reef off the Pleistocene peninsula of Ambergris Cay, it extends southward into the Gulf of Honduras. This reef complex consists of an almost unbroken barrier reef and numerous patch reefs and mangrove cays in its shoreward lagoon. The shelf lagoon is 20–25 km wide in the northern section of the complex, but where the lower third of the reef bends eastward towards Gladden Spit, the lagoon becomes more than 40 km wide before it opens into the Gulf of Honduras. The point at which the reef complex bends eastward is marked by two islets, one of which—Carrie Bow Cay—is the subject of this volume (Figure 1; Plate 1).

Carrie Bow Cay (16°48′N, 88°05′W), known as Ellen Cay up to 1944, is situated on top of the barrier reef proper, 22 km southeast of Dangriga (Stann Creek) (Figure 2) and 18 km east of Sittee

FIGURE 1.—Tobacco Reef looking south toward South Water and Carrie Bow cays; note cuts isolating Carrie Bow Cay from barrier reef trend.

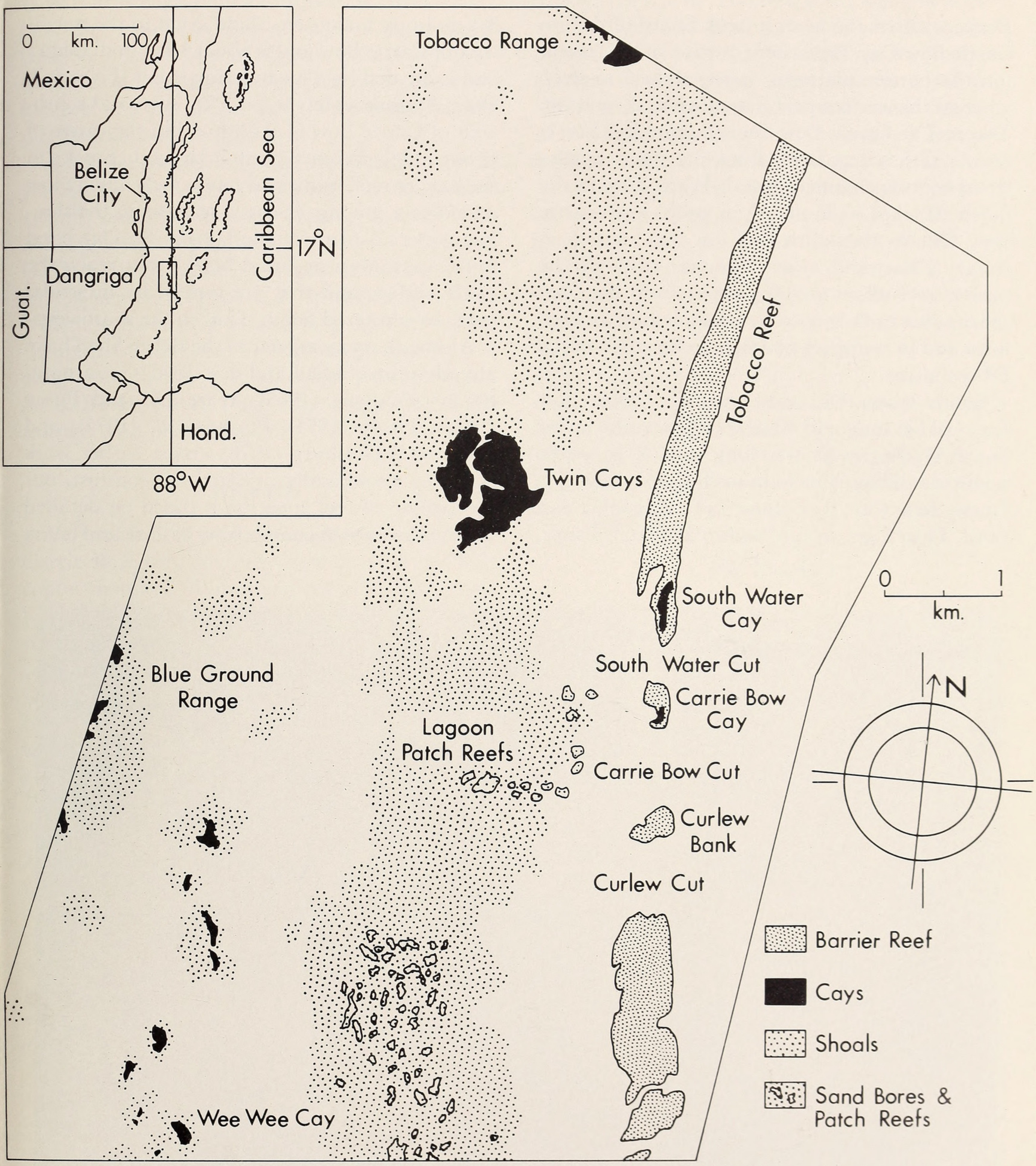


FIGURE 2.—Index map of barrier reef complex in the vicinity of Carrie Bow Cay; area of larger map located on inset by rectangle.

Point, which is the nearest land. Shoreward from Carrie Bow Cay, the eastern portion of the lagoon (on the barrier platform) is less than 5 m deep whereas the western part is as much as 20 m deep. The reef at Carrie Bow Cay (Figure 3; Plate 1: *center right*) is separated from the main barrier trend by two channels, South Water Cut to the north (0.4 km wide and 4 m deep) and Carrie Bow Cut to the south (0.7 km wide and 5 m deep). These and other channels through the barrier reef allow oceanic waters from the Caribbean Sea to flow onto the shallow barrier platform and to transport platform sediments to deep off-reef areas.

South Water Cut also separates Carrie Bow Cay (120 m long and 40 m wide) from the larger South Water Cay (440 m long and 100 m wide), a low island less than 1 km to the north that, like Carrie Bow Cay, is composed of reef rubble and sand. Twin Cays, locally known as Water Range, is a swampy mangrove island 2 km to the northwest of Carrie Bow and is about 1 km in diameter and is divided by a meandering canal (Figures 3, 28*a*). Approximately 0.5–1.5 km west and southwest of Carrie Bow Cay and within the range of strong tidal currents passing through breaks in the barrier reef, numerous patch reefs having low relief occur among *Thalassia* seagrass in the shallow water (3–6 m) of the lagoon. Similar coral build-ups known as "sand bores" that reach the water surface and that are topped by intertidal sand are clustered about 3 km to the southwest.

Although many aspects of the Belize Shelf have already been studied and described—most notably by Stoddart (1963), Wantland and Pusey (1971), Purdy (1974), Purdy et al. (1975), and James and Ginsburg (1978)—most earlier work has been geologically oriented. In contrast, our description of reef zonation is based on detailed information about composition of flora and fauna

FIGURE 3.—Aerial view of Carrie Bow Cay looking northwest. South Water Cay (right) is a reef island on the barrier trend; Twin Cays (left) is a mangrove island in the shallow lagoon.

as well as topographic and substrate characteristics. Our study focuses on a 650 m research transect (just north of Carrie Bow Cay) that extends west to east from the lagoon to the deep fore reef and is representative of the entire barrier reef (Burke, herein: 509).

ACKNOWLEDGMENTS.—We are indebted to I. Jewett for patiently preparing the maps and graphs, some of which are based on low-altitude helicopter aerial photographs taken by Captain G. Thomas. H. Adolfi, A. Antonius, G. Bretschko, M. Carpenter, R. Larson, B. Spracklin, and P. E. Videtich assisted in establishing and surveying the main transect and in field mapping other reef and lagoon habitats. A. Antonius, W. T. Boykins, R. B. Burke, M. R. Carpenter, and K. Sandved assisted with photography.

Methods

Vertical overlapping aerial photographs of the Carrie Bow Cay environs were made by a helicopter-mounted 70 mm camera with timed motorized film advance. Black and white or color prints (12 × 12 cm) were used to make photo composites (for instance, Frontispiece) from which topographic features could be traced on transparent overlays. The scales of the original maps, shown here in reduced figures, are 1:15,000 (Figure 2), 1:1500 (Figure 4), and 1:800 (Figure 5). Low-altitude aerial photographs (like Figure 8) were taken by balloon-suspended camera (Rützler, 1978a). The bottom topography in depths greater than eight meters is not discernible on aerial photographs and therefore had to be ascertained from underwater wide-angle photographs, as well as compass, depth-gauge, and tape measurements. Sediment thickness in each zone was determined with the aid of a steel probe (1 cm diameter) that could be extended in 3 m sections.

The study transect is approximately 200 m north of Carrie Bow Cay, midway across and perpendicular to the crescent-shaped reef crest that half encloses the island (Figure 4). Metal stakes driven into the coral and submerged and surface buoys anchored permanently mark the transect along its projected length (not bottom contour) of 650 m. The zero point was established arbitrarily in a seagrass community in the shallow lagoon. Zones were determined on the basis of bottom configuration, substrates, and relative abundance of predominant organisms. Surveys were carried out along both the transect line and a 50 m strip on either side of it. Relative abundance of organisms within zones was measured by pointcounting organisms inside a 0.25 m^2 frame randomly positioned (Rützler, 1978b:310, fig. 3). Objects overlayed by a 16-intersection grid (line stretched across every 10 cm) were recorded. Vertical projections of the points were used where the three-dimensional configuration of the substrate did not permit direct contact. In areas of high bottom relief, this method was more reliable and efficient than surface coverage estimates employed by Rützler (1975:206) for it avoids distortions due to nonhorizontal substrate surfaces (Dahl, 1973).

The Transect

On the basis of dominant biological and geological characteristics, the barrier reef along the transect off Carrie Bow Cay can be divided into five major units: lagoon, back reef, reef crest, inner fore reef, and outer fore reef (Figure 5; Table 1). Each unit except for the reef crest can be subdivided into distinct zones. The movement and depth of water apparently are the main factors controlling the biological and geological zonations of this area. The lagoon unit (1.5–2.0 m depth) is marked by weak currents and a significant accumulation of fine sand and silt; the back reef (0.1–1.0 m) is subjected to strong currents and the lagoonward transportation 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) similarly is strongly affected by both storm waves and waves related to normal trade wind conditions; the outer fore reef (at least 12 m deep), on the other hand, is affected only by long-period storm waves. Following is a detailed description of each unit.

LAGOON.—This environment consists of a sand and seagrass (*Thalassia*) zone (Figure 6) and a

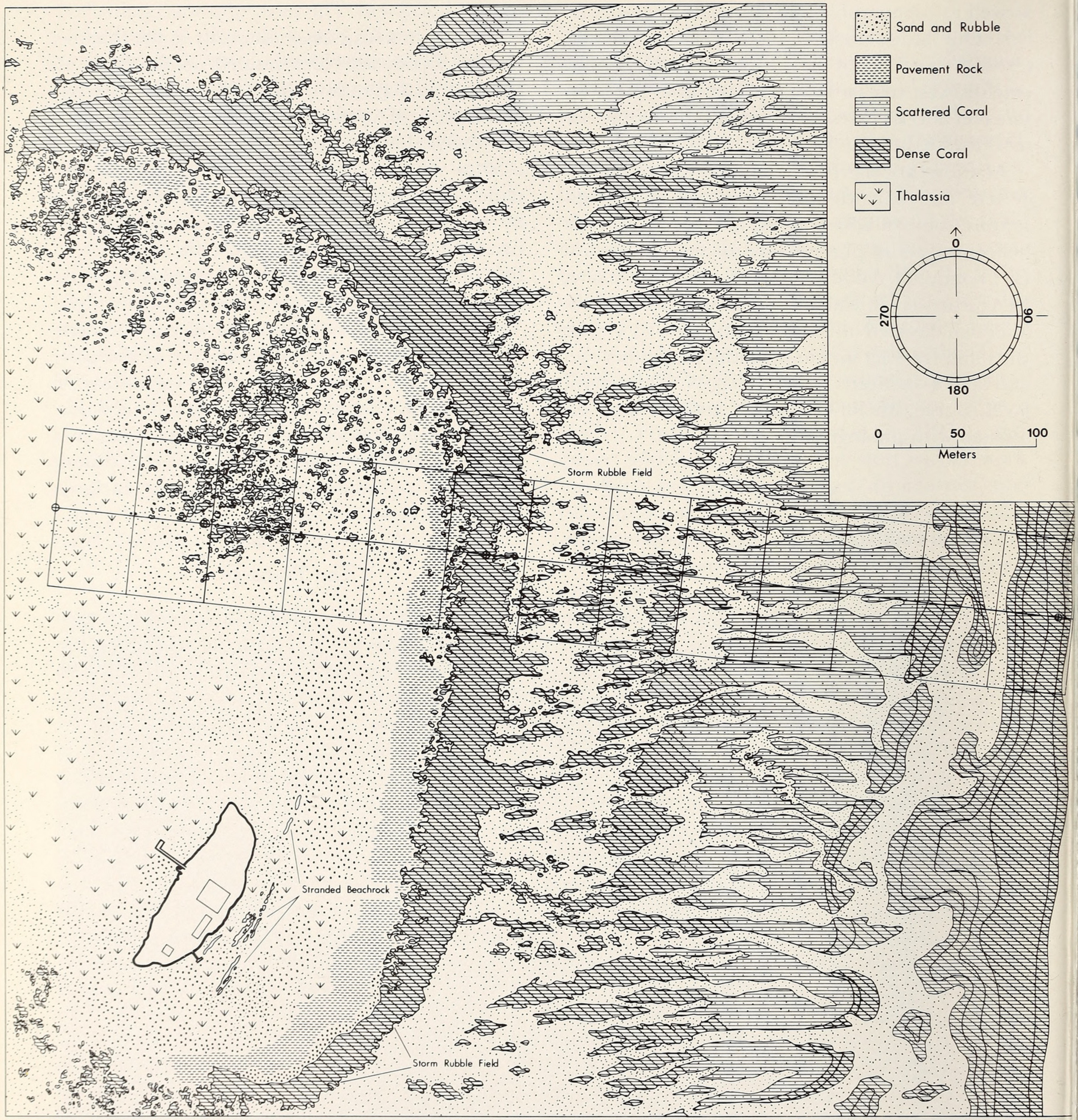


FIGURE 4.—Map of sea-floor characteristics of Carrie Bow reef with location of permanent study transect.

sand and rubble zone (Figure 7) that together extend only 50 m along the transect line. The first section, which extends for about 20 m from the zero point northwest of Carrie Bow Cay, covers a patch of seagrass (*Thalassia testudinum* Banks ex König, along with a few *Syringodium filiforme* Kützing) on a silty sand bottom (Figure 6*a*; Plate 2: *top left*). This sand is fair sorted, dominantly very fine to medium, and 1.0–1.2 m thick. It consists mainly of coral, mollusks, benthic Foraminifera (including *Homotrema*), and *Halimeda* plates. During one of our surveys (May 1975) the lower 10–15 cm of the plants were buried in sediments, presumably as a result of hurricane Fifi in 1974. The alga *Dictyota* sp., which was sparse in 1975, was very common during May and June of 1976, 1977, and 1978. Other algae regularly interspersed with *Thalassia* belong to the genera *Halimeda*, *Udotea*, and *Penicillus*. Empty conch shells and other rubble are covered by algal felts and patches of crustose coralline algae. Uncommon but conspicuous invertebrates include the anemone *Bartholomea annulata* (Lesueur) inside conch shells, the corals *Acropora cervicornis* (Lamarck) and *Siderastrea radians* (Pallas), the gastropods *Strombus gigas* Linnaeus and *Turbinella angulata* Lightfoot, the echinoid *Tripneustes ventricosus* (Lamarck), and the holothuroid *Holothuria mexicana* Ludwig. Benthic macroinvertebrates associated with this *Thalassia* community were studied by Young and Young (herein: 115).

Between 20 and 50 m along the transect, sand appears along with rubble (sand and rubble zone) largely covered by algal felts (13%) and by *Dictyota* spp. (6%) (Figure 7). The poorly sorted sediment in this zone ranges in size from silt to gravel and its composition is similar to that of sediments in the *Thalassia* zone. The metal probe recorded sediment thickness of 1.0–1.4 m over a hard bottom. *Acropora cervicornis* was absent from the sand and rubble zone in 1972, appeared in only two percent of samples by 1975 (but was very common in patches nearby, particularly just north of the transect), and by 1977 had taken over extensive areas on both sides of the transect (Figure 7*a*). A subsequent survey in spring 1979 after hurricane Greta (September 1978) showed that thickets of *A. cervicornis* had been broken up and carried deep into the lagoon by storm surge. New growth, however, was evident on some coral branches that had not been completely buried in sediment. During this survey, thick growths of the red alga *Champia parvula* (C. Agardh) Harvey (Norris and Bucher, herein: 201) appeared in patches throughout both the *Thalassia* and the sand and rubble zones (Figures 6*b*, 7*b*).

Back Reef.—This unit, in which the bottom rises steadily from an average of 1 m to the intertidal reef crest, consists of a patch-reef zone (Figures 8, 9) and a rubble and pavement zone (Figure 11) that together extend from the 50 m mark to the 245 m mark along the transect. The substrate in the patch-reef zone (50–150 m marks) consists of gravel scattered in a poorly sorted silt to very coarse sand. The coarse fraction is composed mainly of *Halimeda*, coral, *Homotrema* and other benthic foraminiferans, mollusks, crustose coralline algae, and echinoids. Maximum sediment thickness recorded with the metal probe was 0.3 m. This zone is characterized by local build-ups of dead coral framework forming isolated patch reefs that consist primarily of *Montastrea annularis* (Ellis and Solander) and some *Diploria labyrinthiformis* (Linnaeus) and *Agaricia agaricites* (Linnaeus) (Figure 9). Approximately 50 percent of the surface area of the coral is dead and overgrown by crustose coralline algae and algal turfs (Figure 8). Characteristically, the vertical sides of many coral heads and boulders are alive but the top surfaces are dead, evidently because exposure at low tide has limited the upward growth of the corals. At the same time, considerable damage to this coral population is being caused directly or indirectly by the blue-green alga *Oscillatoria submembranacea* Ardissone and Strafforello (Antonius, 1973, 1977). Overhangs and crevices are commonly populated by the sea urchin *Diadema antillarum* Philippi, which, along with several species of parrot fishes, is responsible for extensive bioerosion of dead coral surfaces typical of this zone. Clusters of the corals *Acropora*

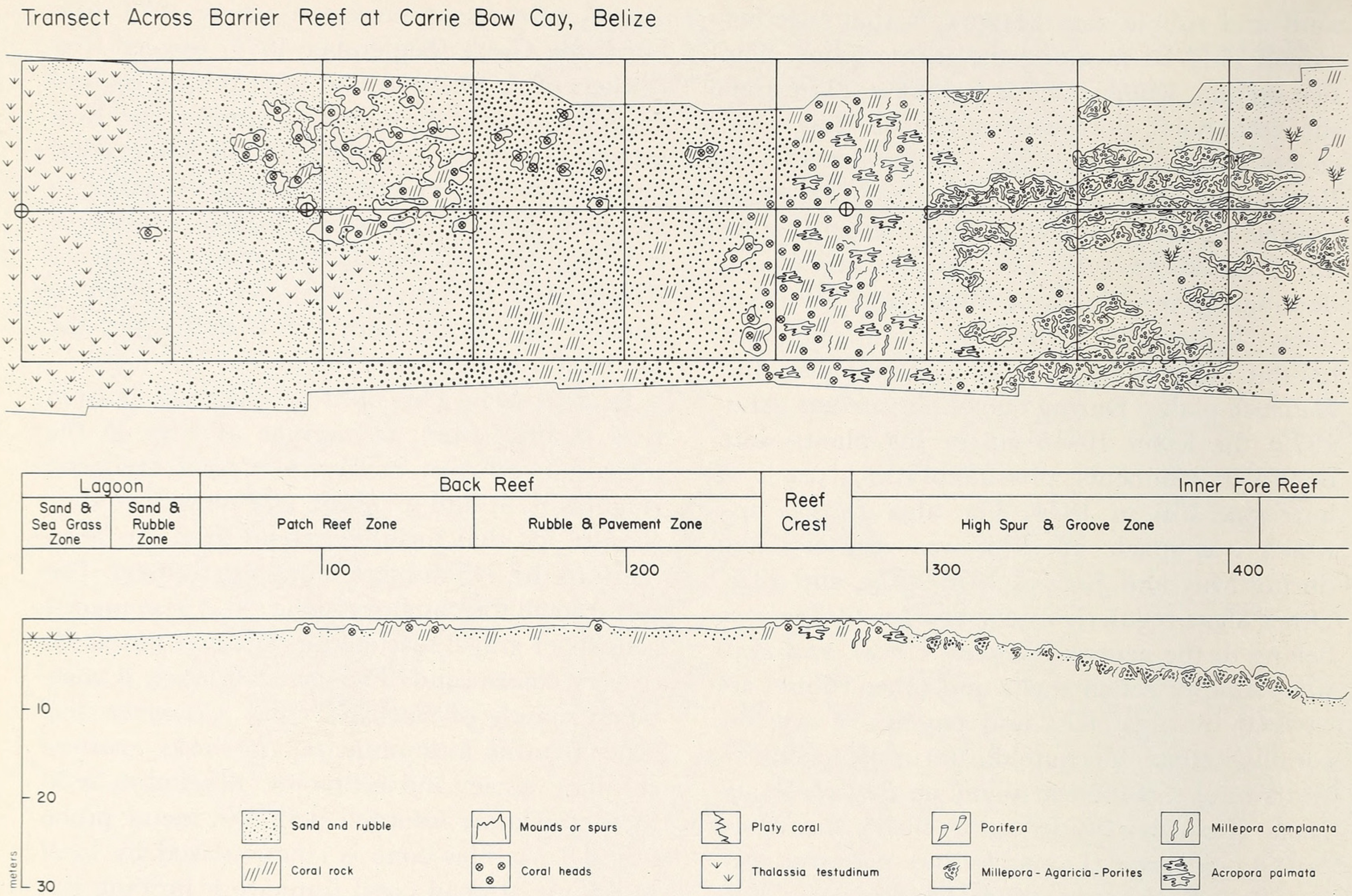
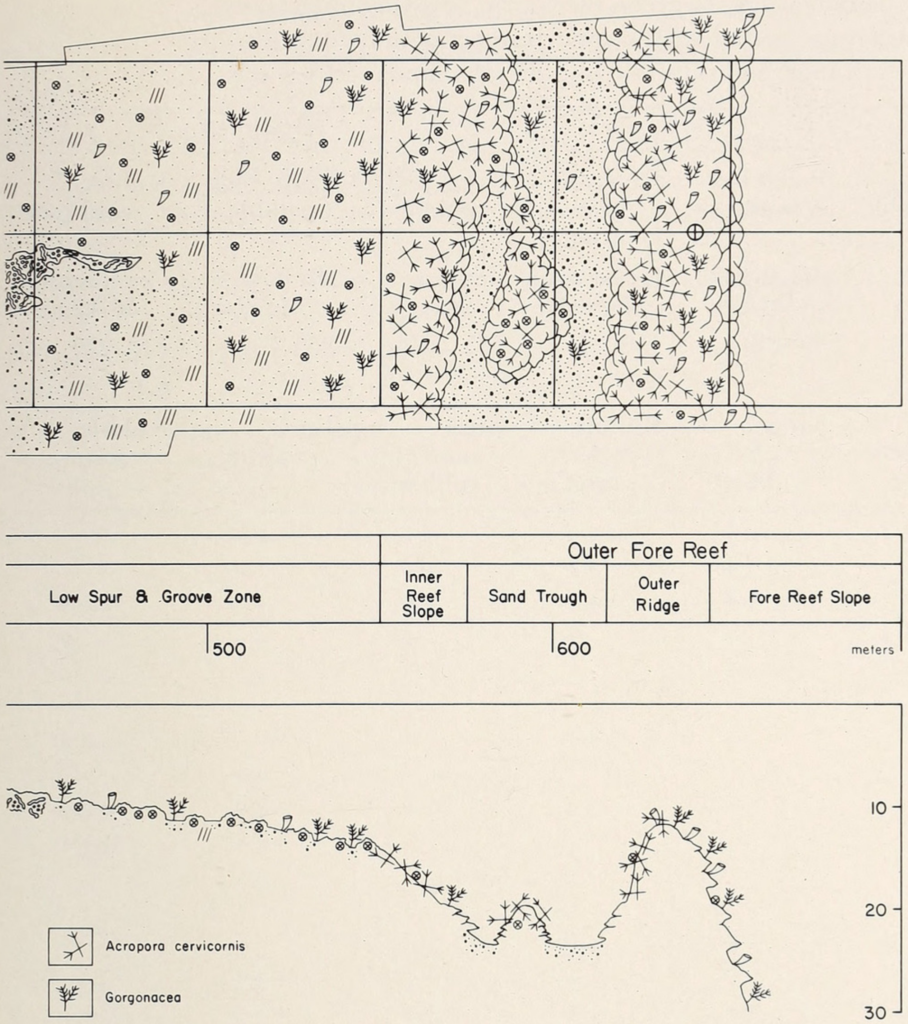


FIGURE 5.—Map and bottom profile of the permanent study transect with zonation terminology (⊕ = permanent markers).

cervicornis and *Porites astreoides* Lamarck, and the octocoral *Plexaura* spp. are dispersed throughout the sandy flats (Figure 8), with a variety of biota including *Dictyota* sp., *Cliona caribbaea* Carter, *Thalassia testudinum*, *Strombus gigas*, *Udotea flabellum* (Ellis and Solander) Lamouroux, *Amphiroa* sp., and *Penicillus capitatus* Lamarck—in order of abundance—growing in between. In the spring of 1979, as a result of hurricane Greta, most of the *A. cervicornis* showed extensive damage, and drifts of *A. cervicornis* debris were piled up against the patch reefs (Figure 10; Plate 2: *center left*). The corals *Acropora palmata* (Lamarck), *Porites porites* (Pallas), *Diploria strigosa* (Dana), *Siderastrea siderea* (Ellis and Solander), and *Agaricia fragilis* Dana were observed close to this zone but were not included in the counts.

The rubble and pavement zone appearing between 150 and 245 m along the transect consists of gravel in a silt to very coarse sand matrix that grades into a relatively smooth and undulating rock pavement adjacent to the reef crest (Figure 11). As can be seen on the map (Figure 4) the pavement is generally 40 m wide and forms the shoreward border of the entire reef crest trend. This pavement (described in detail by James et al., 1976) consists of a conglomerate of coral (*Millepora*), mollusk, and crustose coralline algal fragments lithified by a magnesium calcite submarine cement. We noted a maximum pavement thickness of only 4 cm although James et al. (1976) reported lithification down to 0.5–1.0 m in other areas of the barrier reef off Belize. Rock surfaces in this zone are overgrown by isolated



coral heads (*Siderastrea siderea* and *Porites astreoides*), scattered *Dictyota* spp., coralline crusts, and the boring sponge *Cliona caribbaea.* Less abundant organisms are algae of the genera *Halimeda*, *Caulerpa*, and *Penicillus* and the corals *Agaricia agaricites*, *Diploria clivosa* (Ellis and Solander), and *Acropora palmata.* The depth of water in this zone averages 0.6 m. *Acropora cervicornis* was abundant in this zone in spring 1978 (Figure 11*a*) but had nearly disappeared by the 1979 survey (Figure 11*b*), apparently owing to storm surges associated with hurricane Greta, which transported almost all living *A. cervicornis* lagoonward. Due south from the 150–200 m marks, between the transect and the island, the same zone changes into a *Thalassia*-dominated rubble flat, with *Porites porites*, *Siderastrea radians*, crustose corallines (on rubble), and *Diadema* (Plates 1: *bottom right*, 2: *top right*).

Reef Crest.—A transition zone (0.2 m deep) occurs between the back reef and fore reef at the 245–265 m marks along the transect. This zone is distinguished by a framework of dead (60%) and living *Acropora palmata* along with *Agaricia agaricites* and *Porites astreoides* (Figure 12; Plate 2: *bottom left*, *bottom right*). The bottom consists mainly of rubble and rock pavement covered by crustose coralline algae along with patches of fine to medium, well-sorted sand, the coarser fraction of which is mainly *Halimeda*, coral, *Homotrema*, and crustose coralline algae. This sand supports scattered growths of *Dictyota* sp. whereas the dead coral rock is commonly covered by algal turfs and dense stands of *Caulerpa racemosa* (Forsskål) J. Agardh. The section of the reef crest unit between 265 and 270 m along the transect (depth of 0.1 m) is dominated by the coral *Acropora palmata*, the hydrocoral *Millepora complanata* Lamarck, and the

TABLE 1.—Relative abundance of dominant organisms on the Carrie Bow Cay main transect (column heads designate region, structural and biological zone, transect position in meters from 0, depth in meters as average or range, and substrate in order of abundance; +++ =

Biota	Lagoon		Back reef		Reef crest		
	Sand-mud	Sand-rubble	Patch reef-sand	Rubble-pavement	Coral rock-sand	Coral rock-rubble	Rubble-coral rock
	Thalassia	Algal felts	*Montastrea-Diploria*	*Siderastrea-Porites*	*Acropora-Agaricia*	*Acropora-Millepora*	Corallines-*Millepora*
	0–20	20–50	50–150	150–245	245–265	265–270	270–275
	2	1.8	1	0.6	0.2	0.1	0.1
	Muddy sand	Sand rubble	Sand rock rubble	Rubble rock sand	Rock sand rubble	Rock rubble	Rubble rock
Fleshy macro-algae	++	++	+	+++	++		
Calcareous macro-algae	++		+	++	++	+	
Crustose Corallinacea			++	++	++	++	+++
Algal felts and turfs		+++	+	+	+	++	+
Thalassia testudinum	+++		+				
Massive Demospongea							
Cliona spp.			+	++			
Millepora alcicornis							
M. complanata					+	+++	+++
Palythoa caribaeorum						+++	+++
Stephanocoenia michelinii							
Madracis mirabilis							
Acropora cervicornis	P	+	++	P			
A. palmata			P	+	+++	+++	
Agaricia agaricites			++	++	+++	+++	++
A. fragilis			P				
A. lamarcki							
A. tenuifolia							
Leptoseris cucullata							
Siderastrea siderea			P	+++	+		
Porites astreoides			++	+++	++	++	
P. porites furcata			P	+			++
Diploria clivosa				+	+		
D. labyrinthiformis			+++				
D. strigosa			P	P			
Colpophyllia natans							
Montastrea annularis			+++	P			
M. cavernosa							
Meandrina meandrites							
Dichocoenia stokesi							
Dendrogyra cylindrus							
Mycetophyllia danaana							
Eusmilia fastigiata							
Erythropodium caribaeorum							+
Erect Gorgonacea spp.			++	+			+
Strombus gigas			+				
Diadema antillarum			++	+			
Didemnidae							

very common (>10% presence); ++ = common (5%–10% presence); + = less common (1%–5% presence); P = present and obvious but not encountered in the statistical samples)

Inner fore reef			Outer fore reef				
	Spur and groove				Outer ridge		
Coral pinnacles	High relief	Low relief	Inner reef slope	Sand trough	Inner slope	Top	Fore reef slope
Millepora-Acropora	*Agaricia-Acropora*	Gorgonacea-*Montastrea*	*Acropora-Montrastrea*	Gorgonacea-*Montastrea*	*Acropora-Diploria*	*Acropora*-Gorgonacea	*Montastrea*-Gorgonacea
275–330	330–410	410–550	550–575	575–615	615–625	625–645	645–655
1.8	5	10	15–22	23	12–22	14	15–30
Rock sand rubble	Sand rock rubble	Sand rubble rock	Rubble	Sand rubble	Rubble	Rubble sand	Rock rubble sand
	++		+		+	++	+
		++			++		
++			+				+
	+						
		+++	++	+	++	++	+++
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	++	+++	+++	P	+++	+++	
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P		+					
P		++			++		++
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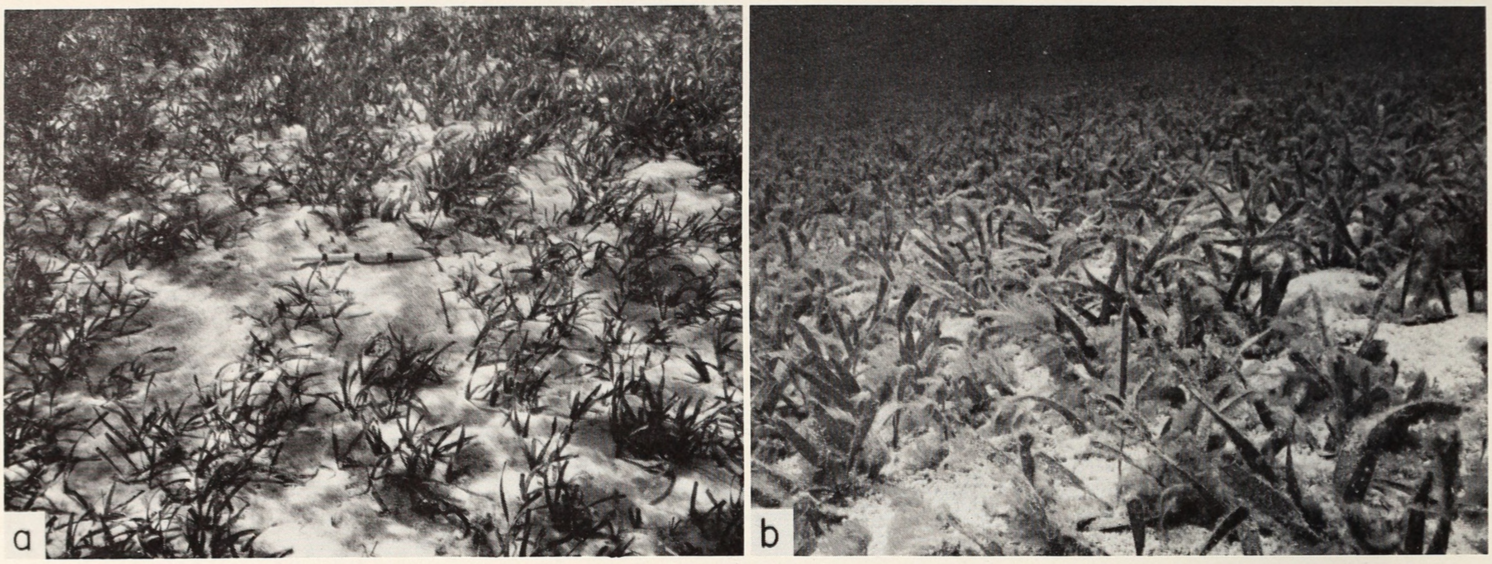


FIGURE 6.—Sand and seagrass zone before and after hurricane Greta: *a*, March 1978; *b*, April 1979. (Note extensive development of epiphytic red alga *Champia parvula* on *Thalassia testudinum* blades; scale = 40 cm.)

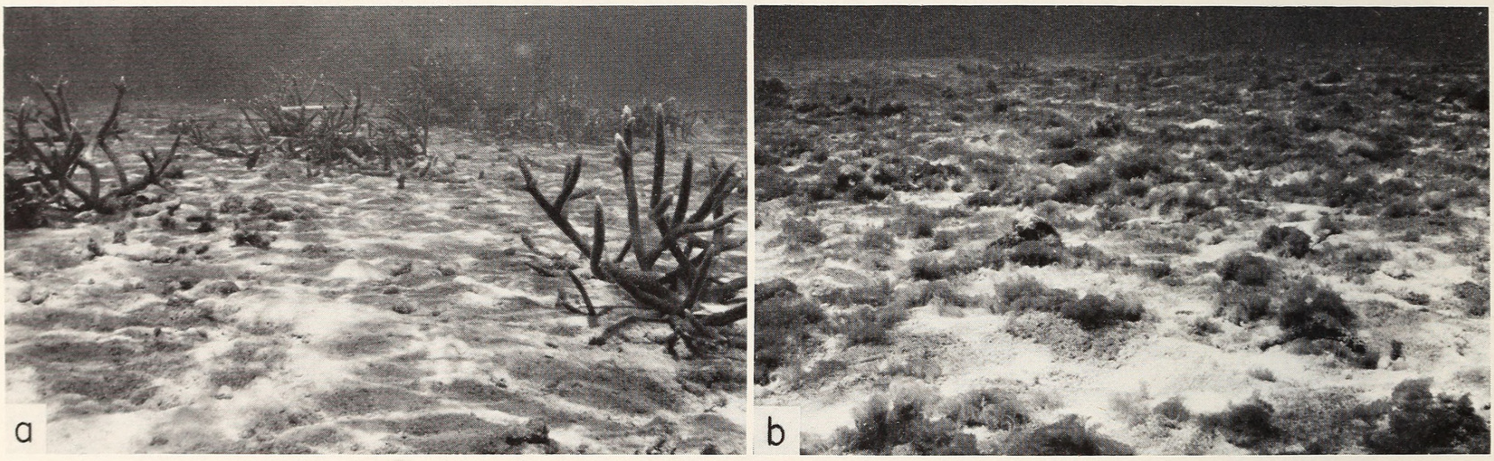


FIGURE 7.—Sand and rubble zone before and after hurricane Greta: *a*, March 1978, stands of *Acropora cervicornis* on plain substrate; *b*, April 1979, heavy red algal growth (*Champia parvula*) on substrate devoid of living *A. cervicornis*. (Scale = 40 cm.)

zoanthid *Palythoa caribaeorum* Duchassaing and Michelotti (Figure 13*a*,*b*; Plate 3: *top left*, *top right*). Coralline algal crusts, algal turfs, and *Porites astreoides* are attached to massive, extensively bored coral rock. The last windward section of the intertidal reef crest unit (270–275 m along the transect) is built up by rubble and coral rock (60%), covered by coralline crusts, *Palythoa caribaeorum*, *Millepora complanata*, some *Porites porites*, *Agaricia agaricites*, algal felts, and extensive crusts of the alcyonacean *Erythropodium caribaeorum* (Duchassaing and Michelotti). Just south of the transect line and at four or more other locations the reef crest is interrupted by perpendicular channels (Figure 13*c*), which facilitate the water exchange between lagoon and fore reef (Kjerfve, herein: 59).

At its southern limit, due southeast of Carrie Bow Cay, the reef crest zone grades into a coral-rubble storm ridge, which is actively accreting over the rubble and pavement zone (Figures 4, 14; Plates 2: *center right*, 5: *top left*). Our observations indicate that the shoreward transportation of this material occurs only during severe storms

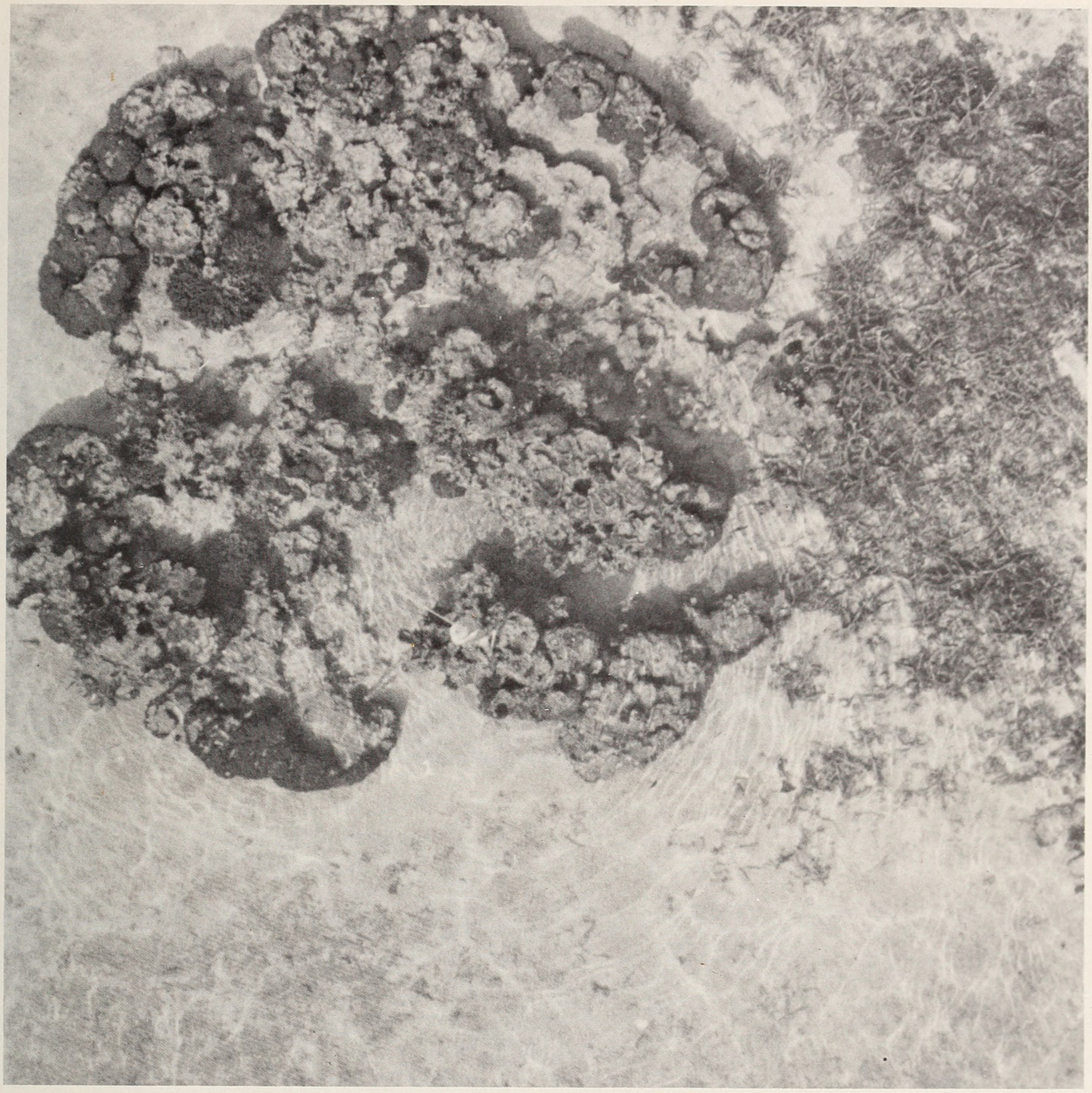


FIGURE 8.—Low-altitude aerial view of patch reef zone at the 100 m transect mark (lower center). Most of the patch reef is built up by *Montastrea annularis* (light areas are dead), accompanied by *Agaricia agaricites* and *Acropora cervicornis*; the latter also forms an extensive thicket on the right flank of the patch reef. (Picture area: 6 × 6 m.)

or hurricanes. During lesser storms this rubble is quite stable because much of it is platy (derived from *Acropora palmata*) and offers protection to a diverse interstitial invertebrate fauna (Plate 5: *top right*). Another comparable area on the reef crest is a small incipient rubble field located 50 m north of the transect line (Figure 4).

INNER FORE REEF.—Just east of the 275 m mark along the transect the bottom drops to a depth of 1.8 m and the inner fore reef begins in a transition zone (to 330 m along the transect) of tall but unorganized coral pinnacles on a sand and rubble bottom (Figure 15; Plate 3: *center left*). These pinnacles are the result of turbulent water movement related to oscillating wave energy that is partly reflected by the reef crest. This area is comparable to Chevalier's (1973) Type II Outer Reef at Mururos, in which he related "pillar structure" of corals to heavy wave swell. Approximately half of these massive pinnacles off Carrie

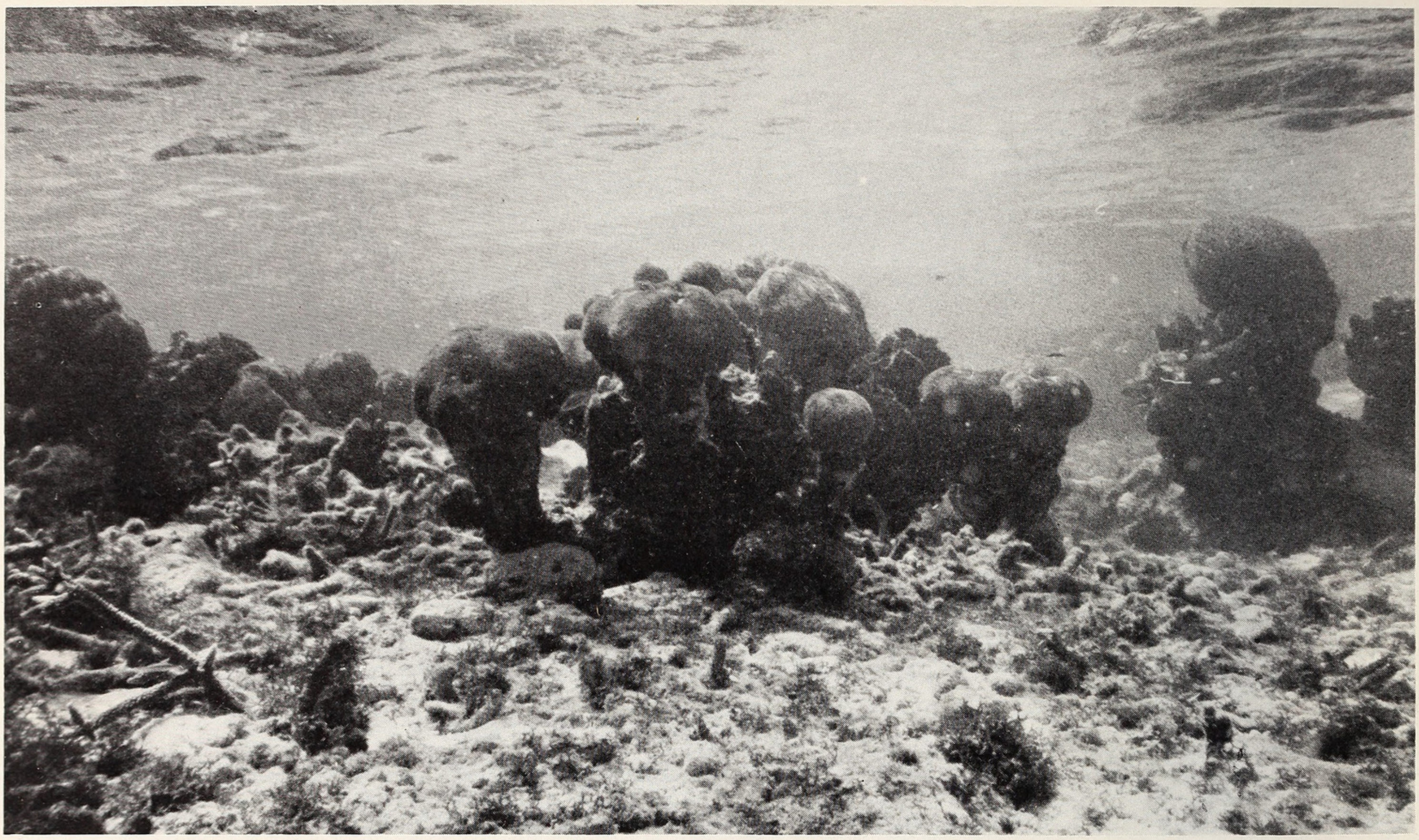
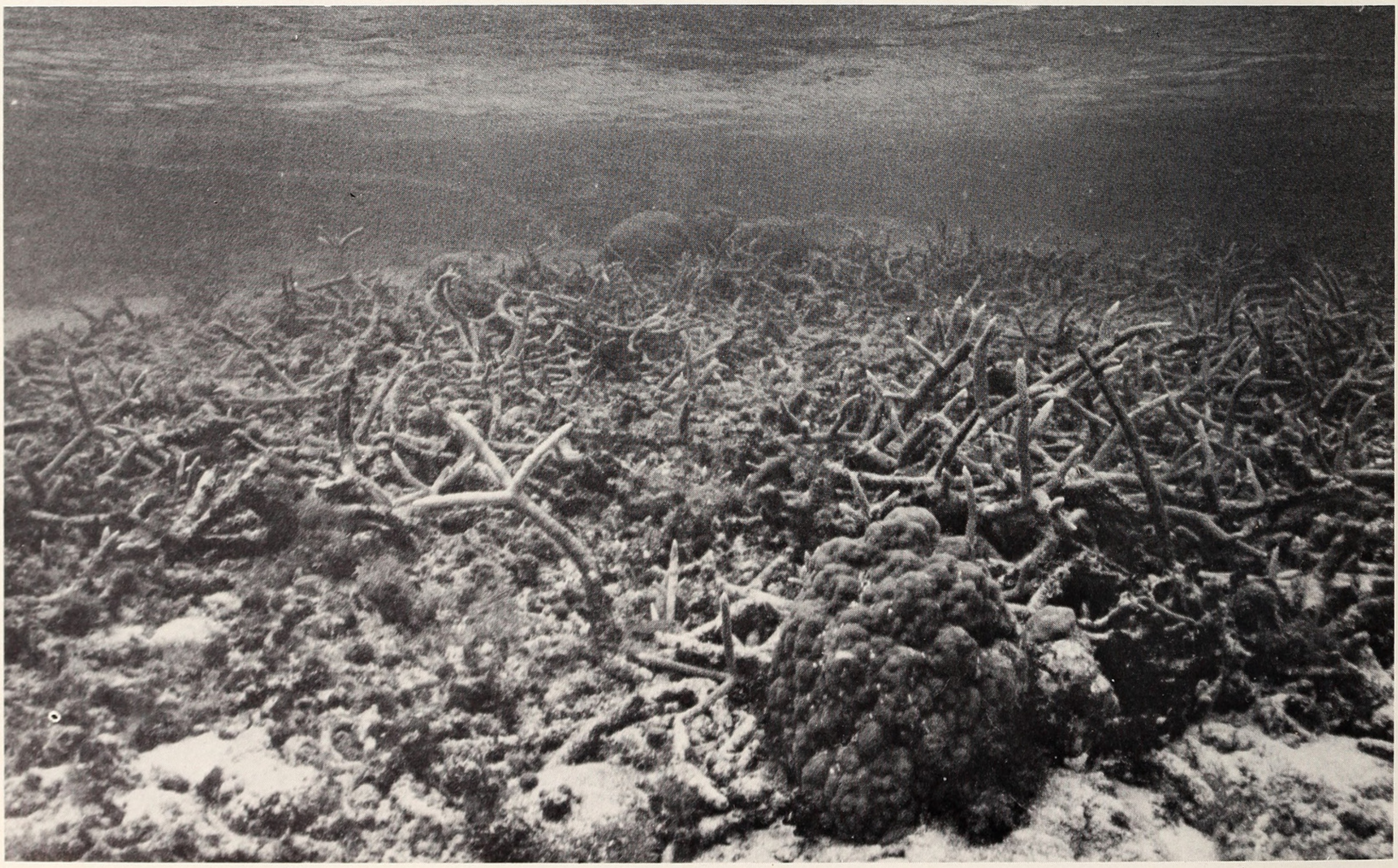


FIGURE 9 (above).—*Montastrea annularis* patch reef on rubble substrate. Massive corals in this zone tend to form pedestal-shaped bases.

FIGURE 10 (below).—*Acropora cervicornis* thicket in patch reef zone badly damaged by hurricane Greta, September 1978. (Photograph taken April 1979.)



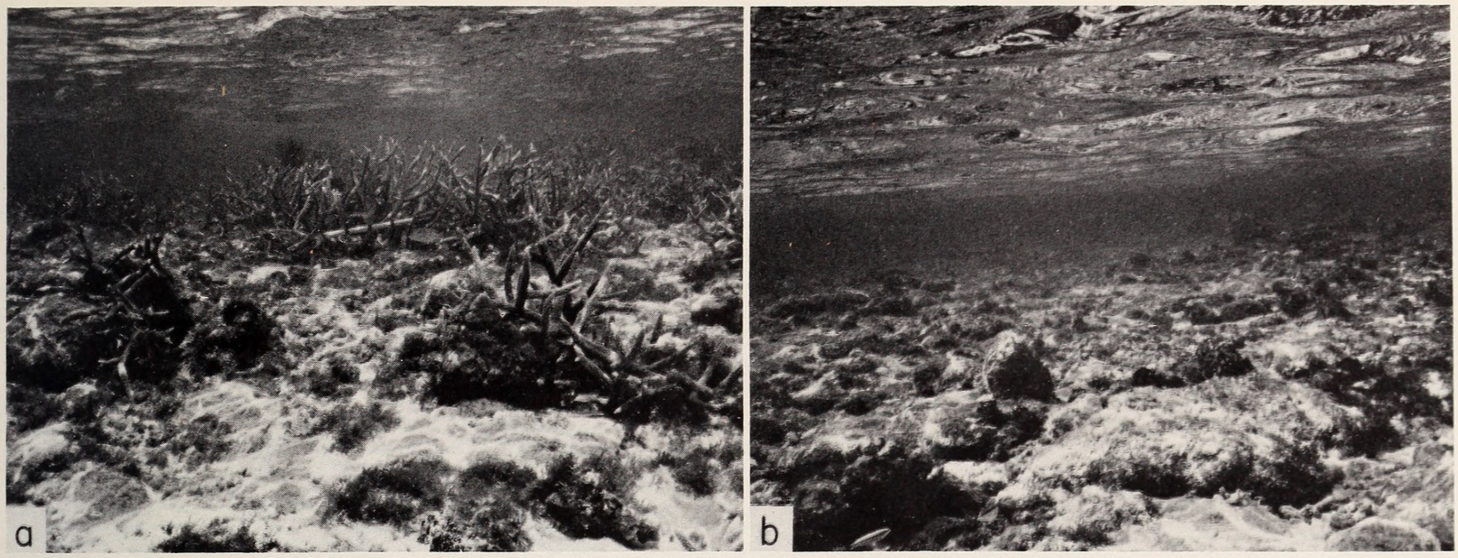


FIGURE 11.—Rubble and pavement zone before and after hurricane Greta: *a*, March 1978, extensive *Acropora cervicornis* and *Dictyota* sp. on sand and rubble bottom; *b*, April 1979, most of the dominant organisms and large quantities of sand have been transported lagoonwards. (Scale = 40 cm.)

FIGURE 12.—Inner margin of reef crest; algal turf covered coral rock surfaces show evidence of rasping action by parrot fish; *Caulerpa racemosa*, *Millepora complanata*, and *Porites astreoides* in foreground.

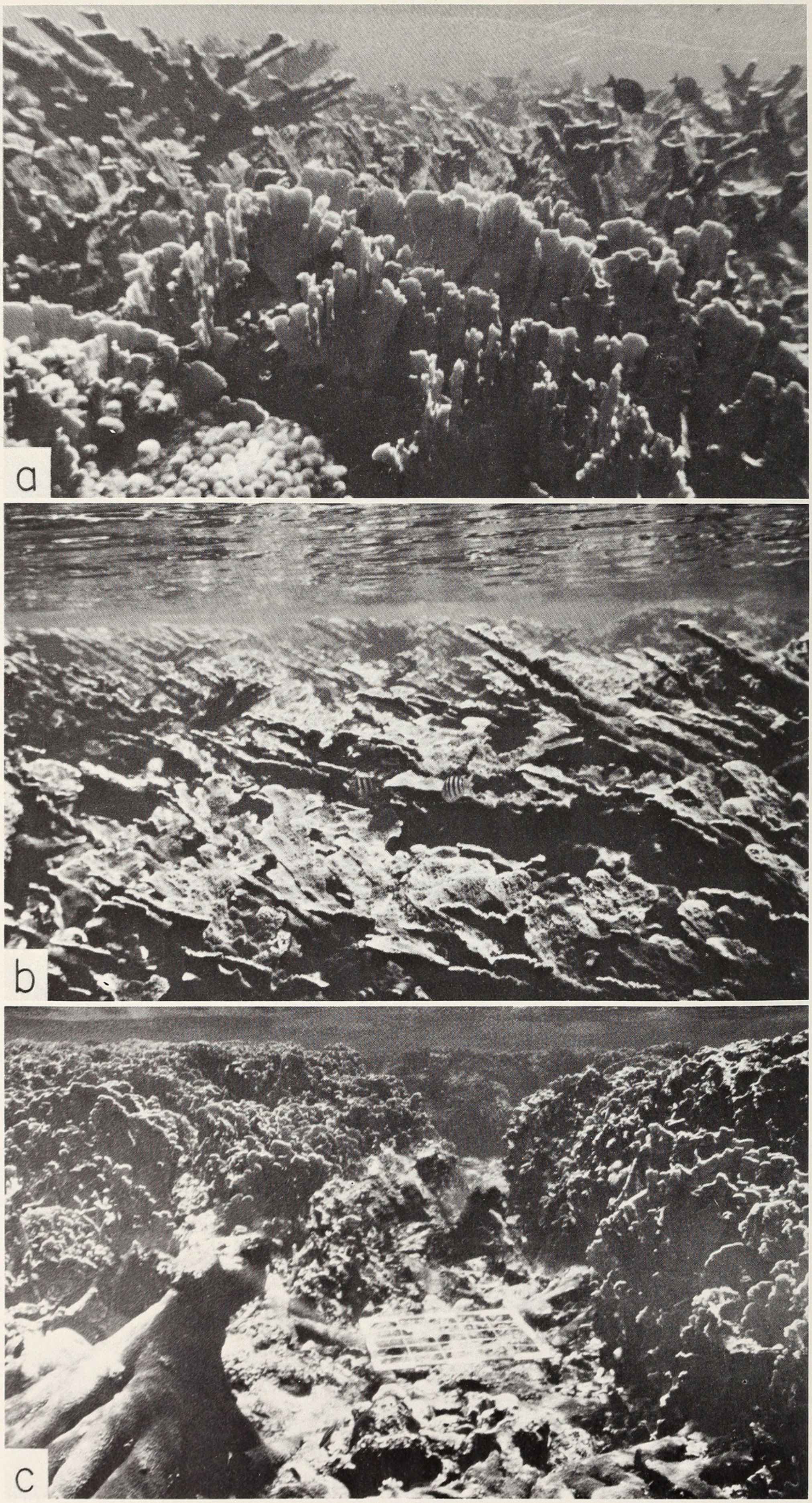

a
b
c

FIGURE 14.—Coral rubble storm ridge, south of the transect, photographed after hurricane Fifi (1974); rubble prograding over back-reef pavement, partly burying *Montastrea annularis* colony.

Bow Cay are formed by build-ups of dead *Acropora palmata*, the rest by live *Millepora complanata*, *A. palmata*, and *Agaricia tenuifolia* Dana. The dead framework is extensively covered by encrusting *Cliona caribbaea*, coralline algae, and some *Palythoa caribaeorum*. *Diploria strigosa*, *Porites astreoides*, *P. porites*, *Montastrea annularis*, and *M. cavernosa* (Linnaeus) are massive corals of secondary importance.

The spur and groove zone of high relief (330–410 m along the transect) has an average depth of 5 m, but depth ranges from 3 to 10 m between the highest coral spurs and deepest sand grooves (Figure 16; Plate 3: *center right*). This well-defined zone has been discussed by Wantland and Pusey (1971) and has been described in detail by James et al. (1976). The high-energy oscillating movement of water in this zone has promoted coral growth on the spurs (Shinn et al., herein: 63) and has caused erosion in the grooves. The buttresses are characterized by foliate *Agaricia tenuifolia* and *Millepora complanata* enclosing clusters of *Porites porites* (Figure 17; Plate 3: *bottom left*). The tops of many buttresses are dominated by stands of *Acropora palmata* and *A. cervicornis* (Figure 18) and their flanks and the sand grooves in between by *Agaricia agaricites*, *Diploria strigosa*, various species of gorgonians (Muzik, herein: 303) and fleshy

FIGURE 13.—Seaward margin of reef crest: *a*, *Millepora complanata*, with *Porites porites* (foreground) and *Acropora palmata* (background); *b*, *A. palmata* community; *c*, Reef channel through *Millepora* ridge looking toward shallow inner reef crest (note overturned live colony of *A. palmata* in foreground). (Scale frame = 50 × 50 cm.)

FIGURE 15.—Pinnacles of *Millepora complanata* and *Agaricia tenuifolia* in an area of transition between reef crest and high-relief spur and groove zone.

green algae (Figure 16; Plate 3: *center right*, *bottom right*). Of lesser importance are *Siderastrea siderea*, *Porites astreoides*, *Dichocoenia stokesi* Milne Edwards and Haime and *Stephanocoenia michelinii* Milne Edwards and Haime. A characteristic and abundant—but quantitatively unimportant—component of this fauna is the purple hydrozoan *Stylaster roseus* (Pallas) that occurs in niches and overhangs along the sides of the buttresses. Another hydrozoan, *Millepora alcicornis* Linnaeus, commonly grows over the dead skeletons of gorgonians, mainly of *Gorgonia ventalina* Linnaeus. The medium sand to gravel-sized sediment in the grooves has a maximum thickness of 0.3 m. It has fair sorting and is composed mainly of coral, *Halimeda*, *Homotrema*, and mollusk and echinoid debris.

The spur and groove system of low relief extends between 410 and 550 m along the transect (average depth, 10 m). A diverse population of gorgonians dominates the rock and rubble substrates of the sand flats as well as the low (about 1 m relief) coral spurs, which are formed of *Montastrea annularis*, *M. cavernosa*, *Acropora cervicornis*, and *Diploria strigosa* (Figure 19, 20; Plate 4: *top left*, *top right*). A few island-like coral pinnacles attain 3 m in height and diameter. Massive Demospongea become quantitatively important in this zone of reduced agitation of near-bottom water, for example, *Neofibularia nolitangere* (Duchassaing and Michelotti), *Callyspongia* spp., *Aplysina* spp., *Geodia neptuni* (Sollas), *Ircinia* spp., as well as the thickly encrusting *Anthosigmella varians* (Duchassaing and Michelotti). *Halimeda* spp. and *Dictyota* spp. are common algae. Conspicuous corals having patchy distribution are *Agaricia agaricites*, *A. tenuifolia*, *Diploria labyrinthiformis*, *Dendro-*

FIGURE 16.—High-relief spur and groove zone, having 5 m relief. (Water depth at sand bottom: 6 m.)

gyra cylindrus Ehrenberg, and *Eusmilia fastigiata* (Pallas). Probes of the sand-filled grooves indicated a maximum depth of 1.2 m at the shallow end of this zone. Seaward, these sand lenses thin out and eventually give way to sand pockets in a rock pavement. The sediment is similar to that found in the high-relief spur and groove zone. James et al. (1976:532) referred to this low-relief spur and groove zone as the "deep spur and groove," which was described as being separated from a "shallow spur and groove" system by a "rubble-covered terrace." There is no indication, however, that a terrace separates the high- and low-relief spur and groove zones off Carrie Bow Cay. In fact, the spurs having low relief are commonly a continuation of the shallower high-relief spurs, with one or more shallow grooves spilling into one of the deeper and wider grooves. Furthermore, the relief of the spurs is considerably less than that reported by James' group who described spurs having relief of 3–4 m that rise to within 2 m of the surface of the waters.

OUTER FORE REEF.—This region begins with a 25-degree slope—the inner reef slope—where the transect drops from 15 m depth at 550 m along the transect to 22 m at a position 575 m along the transect. Most of the bottom is covered by a thicket of living and dead *Acropora cervicornis* that offers substrate to some massive sponges—*Verongula gigantea* (Hyatt), *Callyspongia vaginalis* (Lamarck)—and various gorgonians. Columnar colonies of *Montastrea annularis* at the top of the slope give way to large platy colonies towards the base that are accompanied by *Porites astreoides*, *Siderastrea siderea*, and *Agaricia tenuifolia* (Figure 21; Plate 4: *center left*). Very poorly sorted sediment com-

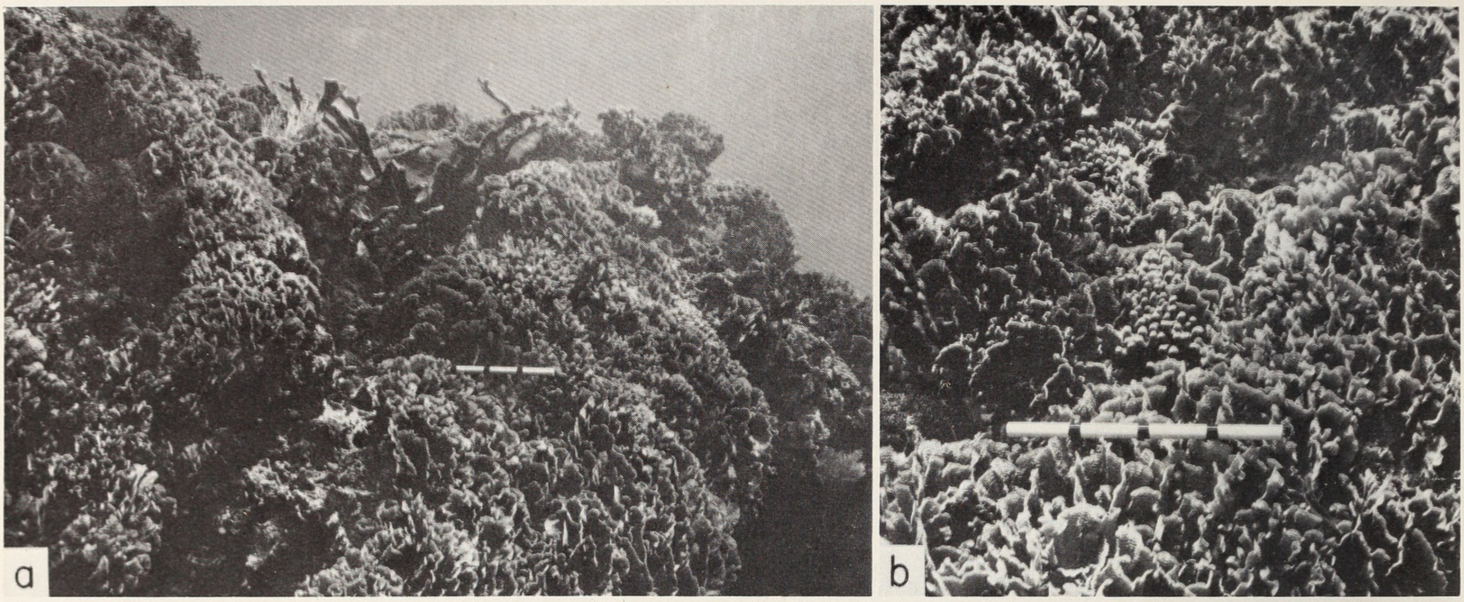


FIGURE 17.—Dominant framework builders of buttresses in high-relief spur and groove zone: *a*, *Agaricia tenuifolia* capped by *Acropora palmata*; *b*, close-up view of characteristic coral association consisting of *A. agaricites*, *Millepora complanata*, and *Porites porites*. (Scale = 40 cm.)

FIGURE 18.—*Acropora palmata* development on top of buttress in high-relief spur and groove zone. (Depth: 4 m.)

FIGURE 19.—Low-relief spur and groove zone with scattered coral heads (foreground: *Montastrea annularis*) among octo corals on the rock pavement of a low spur. (Depth: 10 m.)

FIGURE 20.—Sand-covered hard ground dominated by octocorals with islands of coral heads, near outer edge of low-relief spur and groove zone. (Depth: 13 m.)

posed of silt to medium-sized sand with scattered coarser debris, occurs in patches on this slope. *Halimeda* plates, mollusks, and echinoid spines make up most of the readily recognized coarse fraction. This inner reef slope is comparable to "the steep coral-veneered rock slope" that James and Ginsburg (1978:33–35) called the "reef step."

The next section along the transect is a sand trough 40 m wide (575–615 m marks) and an average of 23 m deep (Figure 22). The substrate is a poorly sorted, silt size to very coarse sand sediment plain. This sediment is mainly very fine to fine sand, but coarser material consisting of

FIGURE 21.—Platy coral development (*Montastrea annularis*) at base of inner reef slope; note brick with coral transplant (Graus and Macintyre, herein: 441). (Depth: 21 m; scale = 40 cm.)

Halimeda plates, mollusks, benthic foraminiferans, and echinoids is scattered throughout. Probings indicated that sediment varies in thickness from about 1 m at the toe of the inner reef slope to more than 12 m in the axis of the trough. Pieces of rubble support gorgonians and sponges, as well as some corals that form several small, isolated coral patches, predominantly of *Montastrea annularis* and *M. cavernosa* (Figure 22*a*). This sand trough zone on the transect also encompasses one tall coral pinnacle in the western part of the trough that has a coral-gorgonian composition similar to that of the inner slope with which it is connected by a low *Acropora cervicornis* ridge (Figure 4). This zone correlates with the seaward-dipping sediment terrace off Tobacco and Buttonwood cays, where the slope is not bordered by an outer ridge (James and Ginsburg, 1978).

At Carrie Bow Cay an outer ridge runs parallel to the intertidal reef crest and delineates the continental shelf (Figure 4). On the transect it is formed mainly by a thicket of *Acropora cervicornis* (Figures 22*b*, 23*a*), but south of the Carrie Bow transect *Montastrea annularis* becomes the principal framework builder (Figure 23*b*). The steep 45-degree landward slope of the outer ridge (Figure 22*b*) supports, among the branches of *A. cervicornis*, massive *Diploria labyrinthiformis*, *Porites astreoides*, and *Stephanocoenia michelinii*, gorgonians, large sponges—*Pseudoceratina crassa* (Hyatt), *Xestospongia* sp.—and conspicuous algae—*Halimeda* spp., *Stypopodium zonale* (Lamouroux), *Peyssonelia* sp. The top of the outer ridge lies between 625 and 645 m along the transect and its depth ranges from 12–14 m (Figure 23*a*). *Acropora cervicornis* and gorgonians are the dominant organisms, with

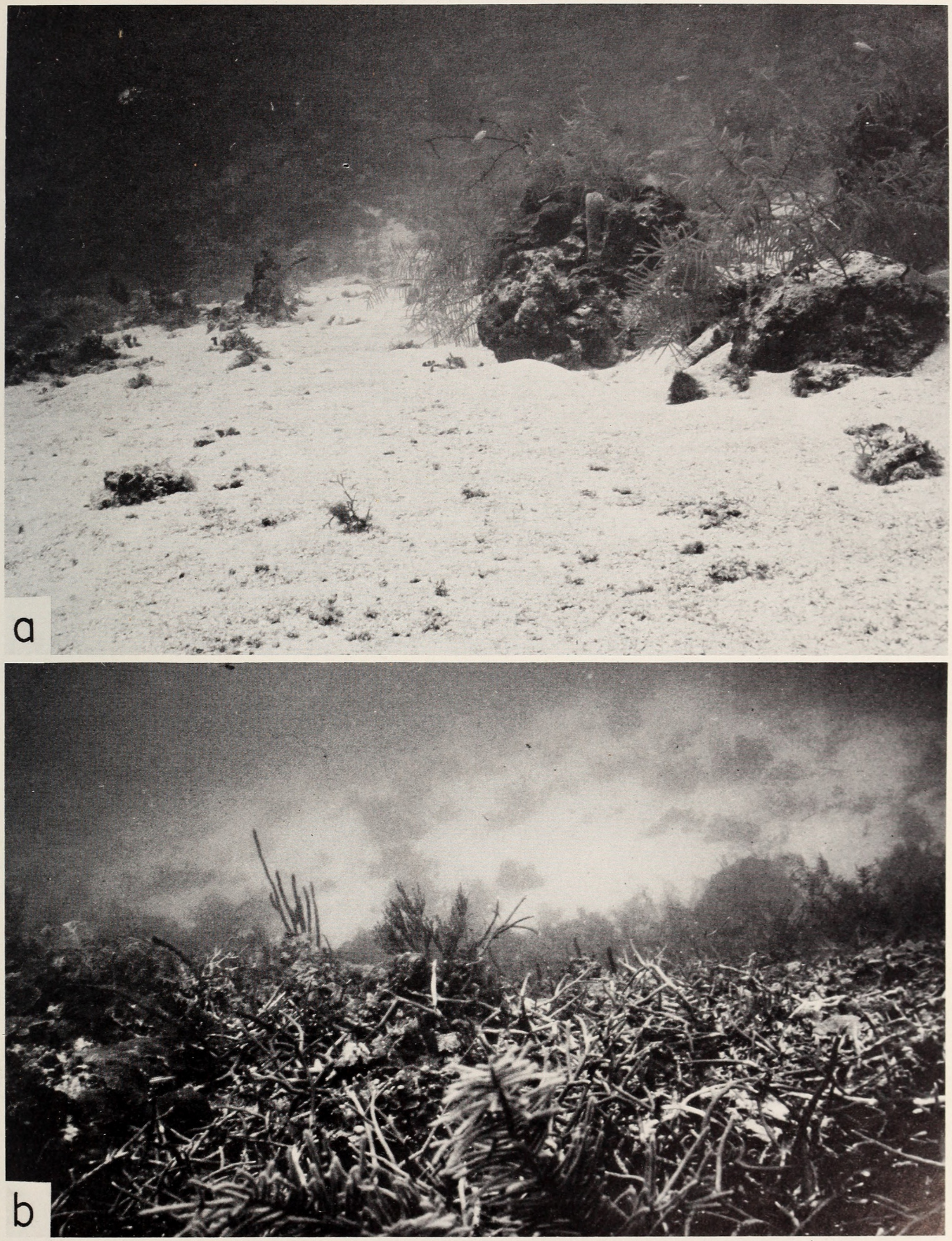


FIGURE 22.—Sand trough: *a*, isolated coral patches at the base of inner reef slope, 23 m deep; *b*, view from the top of the outer ridge over *Acropora cervicornis* thicket, 12 m relief.

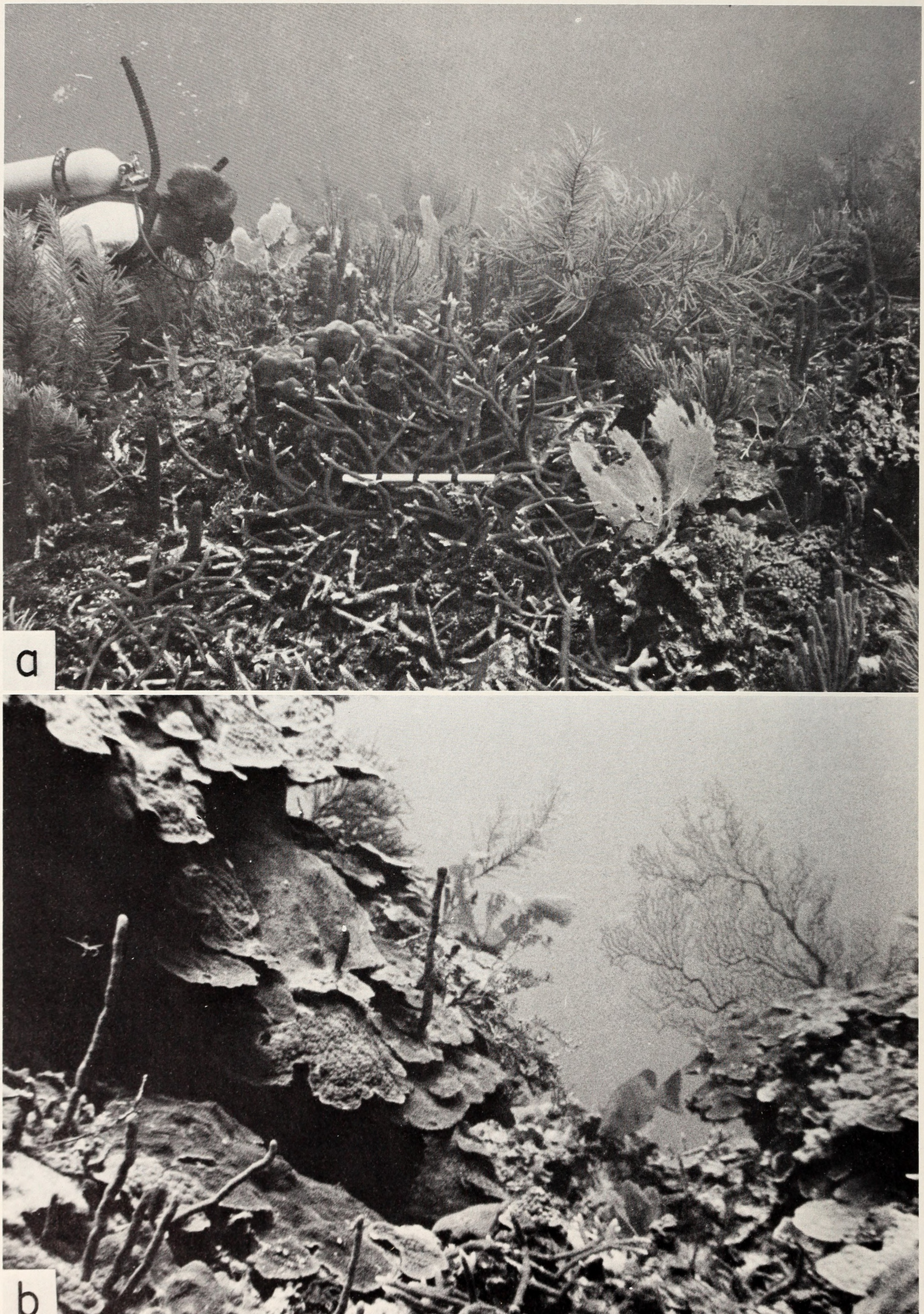

a
b

FIGURE 24.—Fore-reef slope: *a*, looking up sand shoot from 25 m; *b*, platy coral-octocoral community on transect at 30 m.

local accumulations of *Montastrea annularis*, *Agaricia agaricites*, *A. tenuifolia*, and *Madracis mirabilis* (Duchassaing and Michelotti). Fleshy green algae, and sponges of the genera *Aplysina*, *Verongula*, *Callyspongia*, *Xestospongia*, and *Agelas* are common associates (Plate 4: *center right*). Poorly sorted, very fine sand to gravel-sized sediments that are rich in *Halimeda* plates occur in small, 1 m deep depressions scattered along the crest of the ridge. An identical shelf-edge ridge occurs off South Water Cay (James and Ginsburg, 1978).

Approximately 645 m along the transect, the fore-reef slope (Figure 24) drops at an angle of 50°–70° from depths of 14 m down to 30–60 m,

FIGURE 23.—Outer ridge: *a*, coral community dominated by *Acropora cervicornis* on transect line, 12 m depth; *b*, platy *Montastrea annularis* and *Porites astreoides* framework 100 m south of transect, 14 m depth. (Scale = 40 cm.)

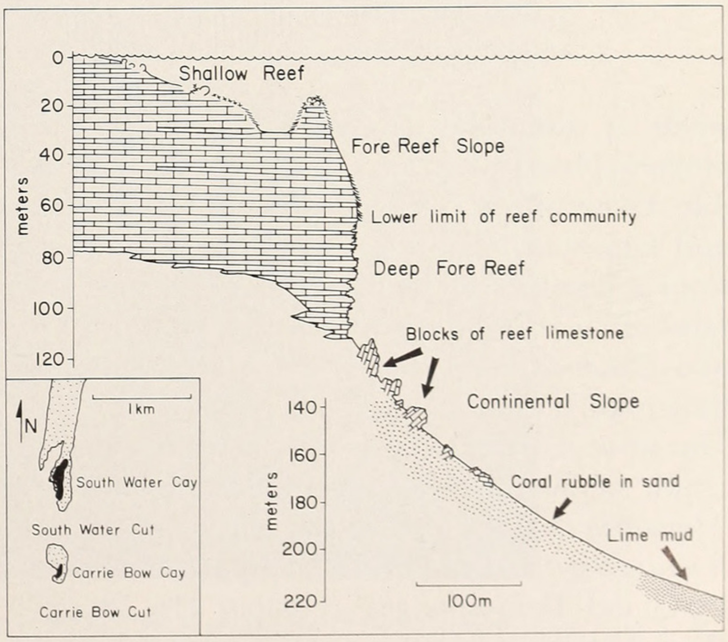


FIGURE 25.—Profile and dominant sea-floor characteristics of fore reef off South Water Cay (adapted from James and Ginsburg, 1978).

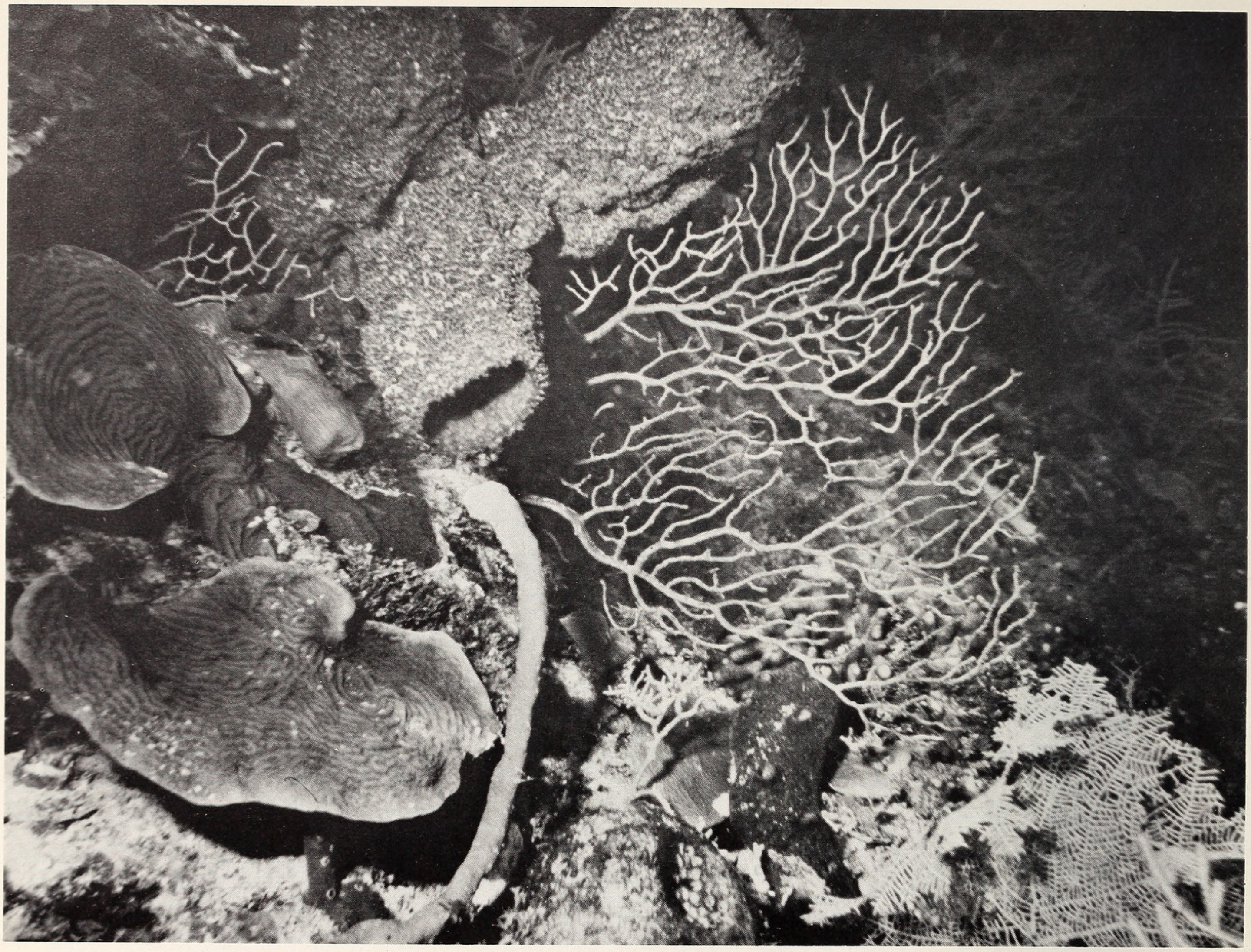


FIGURE 26.—Close-up view of representative fore-reef slope community of sponges, corals, and octocorals, including (clockwise from center bottom) *Cinachyra kuekenthali*, *Amphimedon compressa*, *Agaricia lamarcki*, *Mycale* sp., *Iciligorgia schrammi*, *Porites porites*, *Pseudopterogorgia* sp., and encrusting *Millepora* sp. (Depth: 30 m.)

where it diminishes to 40°–50°. According to previous observations from the research submersible *Nekton* off nearby South Water Cay (James and Ginsburg, 1978), a vertical wall continues from a depth of 60 m to about 110 m where a talus of large reef limestone blocks, coral rubble, and *Halimeda* sand grades into a gently sloping lime-mud bottom at about 200 m (Figure 25). Our surveys, which were restricted to a maximum depth of 30 m, show an abundance of platy *Montastrea cavernosa* and *M. annularis*, Gorgonacea, *Agaricia fragilis*, *Leptoseris cucullata* (Ellis and Solander), and Demospongea (Figures 24*b*, 26, 27; Plate 4: *bottom left*, *bottom right*). Commonly associated are *A. agaricites*, *A. lamarcki* Milne Edwards and Haime, *Porites porites* forma *furcata* Lamarck, *Diploria labyrinthiformis*, *Colpophyllia natans* (Houttuyn), and *Mycetophyllia danaana* Milne Edwards and Haime. Abundance of gorgonians decreases with depth whereas that of sponges increases. A conspicuous gorgonian under 20 m is *Iciligorgia schrammi* Duchassaing (Figure 27). Quantitatively important sponges are rope-shaped species of *Aplysina*, *Niphates*, and *Haliclona*, tubular *Agelas* sp. and *Verongula* sp., massive *Ectyoplasia ferox* (Duchassaing and Michelotti) and *Cinachyra kuekenthali* Uliczka, and coral-eroding *Cliona delitrix* Pang and *Siphonodictyon coralliphagum* Rützler. *Hal-*

FIGURE 27.—Vertical fore-reef slope with platy development of *Montastrea cavernosa* and abundant sponges and octocorals. (Depth: 40 m.)

TABLE 2.—Abundance of various benthic components (major substrates and predominant functional groups) compared by habitats of the barrier reef transect and the lagoon (number of counting points beneath zone names; +++ = very common; ++ = common; + = less common; +− = rare; − = not in samples; average abundance values (%) from point counts, if available, in parentheses; * = >100% total because corallines and their rock and rubble substrate were recorded separately)

Benthic components	*Barrier reef transect*					*Off-transect lagoon*		
	Lagoon 176	*Back reef* 368	*Reef crest** 272	*Inner fore-reef** 640	*Outer fore-reef* 480	*Seagrass flats* 0	*Mangrove* 0	*Patch reefs* 320
SUBSTRATE								
Mud	−	−	−	−	−	+	+++	−
Sand	+++ (55.7)	+++ (15.4)	+ (2.2)	+++ (12.0)	++ (9.6)	+++	+	+++ (28.2)
Rubble, boulders	++ (6.8)	+++ (17.4)	+++ (10.3)	+++ (18.8)	+ (4.2)	+−	−	+ (1.9)
Rock	−	+++ (14.7)	+++ (47.8)	+++ (16.3)	+++ (14.2)	−	−	+++ (14.7)
Mangrove roots	−	−	−	−	−	−	+++	−
FUNCTIONAL GROUP								
Marine grasses	+++ (22.2)	+− (0.5)	−	−	−	+++	+++	++ (8.5)
Fleshy macro-algae	+++ (13.6)	++ (8.2)	+ (3.7)	+− (0.9)	+ (3.8)	++	++	−
Calcareous macro-algae	+− (0.6)	++ (6.8)	+ (2.6)	+ (1.9)	+ (1.7)	++	++	−
Crustose Corallinacea	−	++ (5.2)	+++ (35.6)	++ (5.6)	+ (2.1)	−	−	−
Massive Demospongea	−	−	−	+ (2.7)	+++ (12.7)	++	+++	++ (8.5)
Excavating sponges	−	+ (3.0)	−	+ (5.0)	+ (2.5)	+	−	+− (0.6)
Hermatypic corals	+− (0.6)	+++ (24.5)	+++ (31.6)	+++ (35.9)	+++ (30.0)	+−	−	+++ (17.2)
Gorgonacea	−	++ (3.8)	+ (1.1)	++ (6.1)	+++ (18.5)	+−	−	+++ (19.7)
Others	+− (0.6)	+− (0.5)	+− (0.7)	+− (0.5)	+− (0.8)	+−	+	+− (0.7)

imeda-rich, very fine sand to gravel-sized sediment occurs in pockets or small ledges between the living cover of this slope. Other components of this sediment include mollusks, echinoids, corals and benthic foraminiferans.

Lagoon Environment

Reef-forming organisms and other characteristic and quantitatively prominent associates observed on the barrier reef transect off Carrie Bow Cay are all sessile and require stable substrates to keep them from being washed away. In the protected lagoon fine sediments tend to bury such substrates and, by settling on organisms as well, constitute a selective stress factor for the living populations. Thus, we examined the lagoon within a radius of 2 km from Carrie Bow Cay in order to compare its characteristic benthic biota with those of the barrier reef (Table 2). A similar comparison of zooplankton is presented by Ferraris (herein: 143) and complemented by Rützler et al. (1980). Although seagrass flats and mangroves were surveyed only qualitatively, patch reefs were examined both quantitatively and qualitatively. The Carrie Bow Cay reef flat (between the cay and the reef crest) is the subject of a separate detailed study (Rützler, in prep.).

Seagrass Community.—An area of approximately 6 km^2 of lagoon bottom immediately due west of Carrie Bow Cay was found to be less than 6.5 m deep, commonly 4–6 m deep. More than 90 percent of this area is flat soft bottom covered by *Thalassia testudinum*; the rest consists of rubble, reef patches, and large sponges. Most of the rubble originates from the commercial conch *Strombus gigas*. The shells, abandoned by fishermen in large piles or fields, provide substrate for a variety of algae (for instance, *Amphiora fragilissima* (Linnaeus) Lamouroux), sponges (*Desmapsamma anchorata* (Carter)), hydrocorals (*Millepora* sp.), corals (*Porites* sp., *Siderastrea siderea*), gorgonians (*Plexaura* sp.), and many less conspicuous organisms. The dark interior of these shells constitutes a well-vented miniature cave habitat because fishermen puncture the spire near the apex where they cut the retractor muscle to remove the soft parts of the snail. Extent of colonization depends on exposure time and position of aperture relative to the sediment substrate. Small reef fishes, encrusting coralline algae, foraminiferans (*Homotrema rubrum* (Lamarck)), sponges (*Spirastrella* sp., *Clathrina* sp.), bryozoans and ascidians, as well as anemones (*Bartholomea annulata*), crabs (*Mithrax* sp.), and ophiuroids (*Ophiotrix* spp.) are common inhabitants. Several species of *Cliona* excavate the walls of old shells, some of which are occupied by the hermit crab *Petrochirus diogenes* (Linnaeus).

Distribution of living conchs is patchy and their depletion in large areas observed by us over a seven-year period indicates over fishing. On the other hand we noted concentrations near certain conch rubble patches comparable to those reported by Hesse (1979). Another large gastropod, *Turbinella angulata*, is a common associate. Sponges are quantitatively the most important organisms in the *Thalassia* meadows, even outside the rubble fields. In 1975 and 1978 many were found loose and only partly alive, together with gorgonians in similar condition (Muzik, herein: 303) and can be assumed to have been torn from the reef and washed into the lagoon by hurricane surge (Rützler and Ferraris, herein: 77). The presence of recently sunken coconut trees confirms this assumption. Other sponges, however, were healthy and attached to small pieces of rubble and seagrass (*Desmapsamma anchorata*, *Iotrochota birotula* (Higgin), *Aplysina fistularis* (Pallas), *Niphates erecta* Duchassaing and Michelotti) or, like some very large forms (5–40 l volume), were rooted in sand (*Spheciospongia vesparium* (Lamarck), *Ircinia* spp.).

Patch Reefs.—These lagoon reefs of low relief are clustered about 0.3–2.0 km to the west and southwest of Carrie Bow Cay (Figure 2). Favorable substrate conditions, together with tradewind and tide-induced currents passing through South Water and Carrie Bow cuts probably promoted the development of these structures that now exhibit a richness of reef fauna that is surpassed only by the outer barrier fore reef. Diversity and biomass of sponges, in particular, are higher than in any other habitat of similar depth because most species favor areas having a high rate of water exchange but lack resistance against

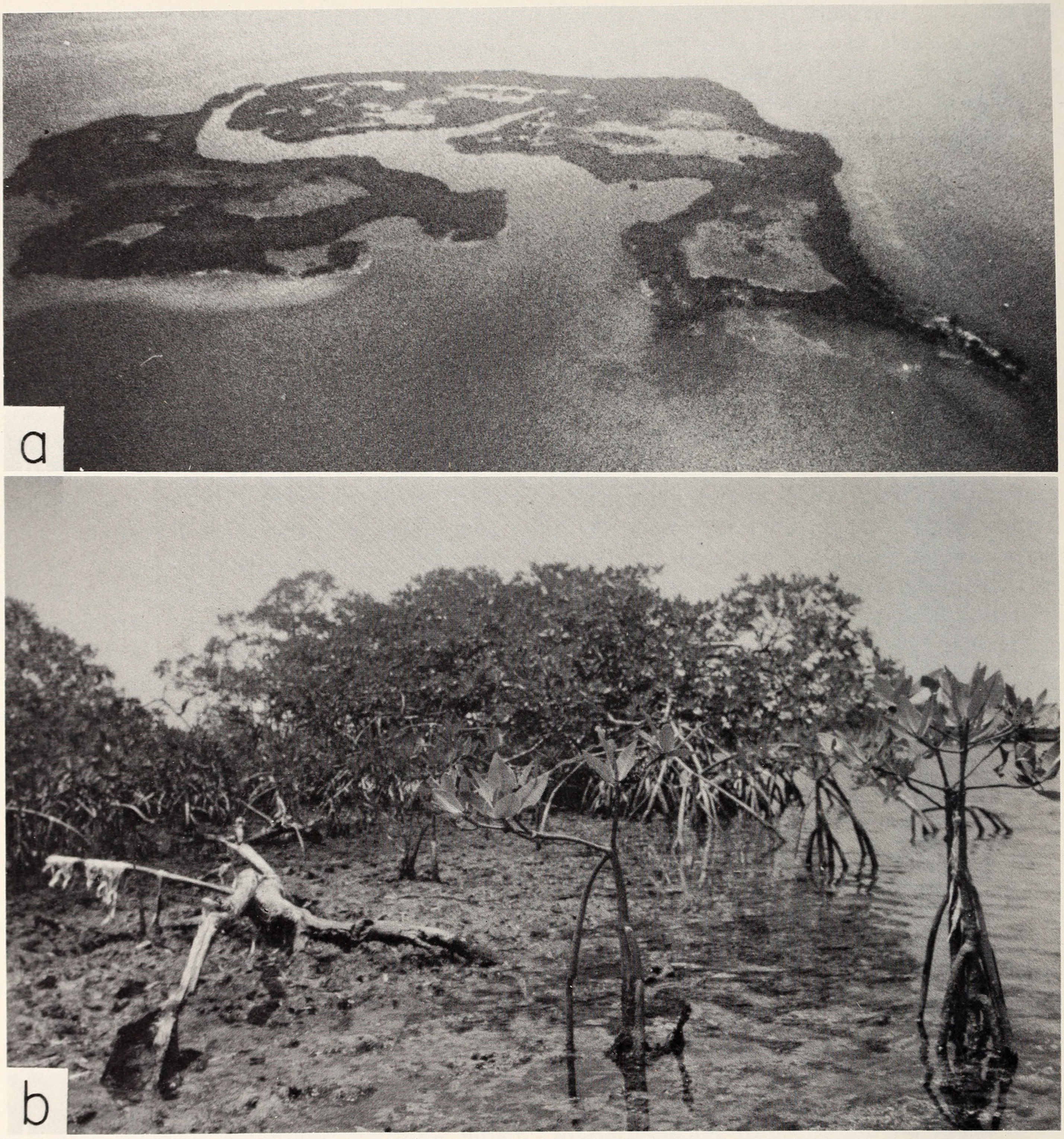


FIGURE 28.—Twin Cays: *a*, aerial view of mangrove island showing channel and intertidal mud flats behind red mangrove fringes; *b*, red mangrove (*Rhizophora mangle*) on mud bank bordering channel.

detachment from substrates by undulating water movement. The patch reefs are circular or oval, some are arranged in string-of-pearl fashion, 5–60 m in diameter and raised 0.2–1.0 m above the surrounding flat sand and *Thalassia* bottom in depths of 3–6 m. Abundance data were derived from two perpendicular transects across a characteristic patch reef, named "Spaghetti Reef," after a new species of stringy sponge of the genus *Ulosa* (Rützler, 1981). Sand and coral rock make

FIGURE 29.—Seagrass community of the shallow lagoon at the entrance to Twin Cay channel: *Thalassia testudinum*, *Halimeda incrassata*, and *Manicina areolata*. (Depth: 1 m.)

up 45% of the surface area. Gorgonians are the most abundant organisms (20%), followed by corals and milleporids (17%), sponges (9%), and *Thalassia* seagrass (on sand, 9%). Large algae are notably absent. *Gorgonia ventalina* and *Pseudopterogorgia* spp. are the most conspicuous octocorals on the patch reefs. Massive forms dominate among the corals (*Siderastrea siderea*, *Diploria labyrinthiformis*, *D. strigosa*, *Montastrea annularis*), the most common hydrocoral is *Millepora alcicornis*, which encrusts numerous gorgonian skeletons. Sponges, although they score comparatively low in the point counts, contribute most to the standing crop. The principal species are *Ircinia* spp., *Xestospongia* sp., *Iotrochota birotula*, *Desmapsamma anchorata*, *Amphimedon compressa* Duchassaing and Michelotti, and *Callyspongia* spp. (Plate 5: *center left*, *center right*).

MANGROVE.—Toward Twin Cays from the southeast a belt of shallow (1 m) *Thalassia* flat grades into the larger entrance of the channel that divides this island (Figure 28*a*). The flat is a transition zone between the more agitated deeper lagoon and the protected mangrove where moderate tidal currents control water exchange. Most abundant among the *Thalassia* are some algae (for instance, *Penicillus capitatus*, *Halimeda incrassata* (Ellis) Lamouroux), sponges (*Tedania ignis* (Duchassaing and Michelotti), *Oligoceras violacea* (Duchassaing and Michelotti), *Haliclona viridis* (Duchassaing and Michelotti)), and the coral *Manicina areolata* (Linnaeus) (Figure 29). *Millepora* sp. encrusts large surface areas of submerged wood. Some more sponges, *Aplysina fulva* (Pallas) and the large loggerhead *Spheciospongia vesparium*, and numerous starfish (*Oreaster reticulatus* (Linnaeus)) occur on the bottom of the channel entrance.

The meandering channel is 0.5–2.0 m deep and is lined by red mangroves, *Rhizophora mangle* Linnaeus, which grow on intertidal mud banks and extend their arched prop roots into subtidal water (Figure 28*b*). In places the mud banks are washed out to form vertical walls and even overhangs and caves. Mud caves, probably of similar origin, are found outside the present mangrove margin just north of Twin Cays. They extend horizontally into mud banks surrounding 4 m depressions in the seagrass floor. The caves are large enough to harbor 2 m long sharks.

Mangrove roots offer the only substrates that are not subject to accumulation of fine sediments. In this habitat strong competiton for the limited space takes place among diverse flora and fauna (Figure 30). On the light-exposed roots and bank edges, clusters of the algae *Caulerpa verticillata* J. Agardh and *Halimeda* spp. compete with the sponges *Tedania ignis*, *Ircinia felix* (Duchassaing and Michelotti), and *Lissodendoryx* sp. (Figure 30*a*,*b*; Plate 5: *bottom left*, *bottom right*). The walls of the shaded overhangs are dominated by the sponge *Ulosa ruetzleri* Wiedenmayer and, at the north entrance of the channel, by *Mycale* sp. Also, locally important in biomass are the anemones *Bartholomea annulata* and *Condylactis gigantea* (Weinland), the tunicates *Ecteinascidia turbinata* Herdman and *Ascidia nigra* (Savigny), and sabellid polychaetes. The intertidal parts of the mangrove roots are dominated by the oyster *Crassostrea* sp., whereas the *Thalassia* mud bottom supports a dense population of Scyphomedusae (*Cassiopea* spp.), with specimens of *Oreaster reticulatus* interspersed (Figure 30*c*). Mud caves and roots provide hiding places for a diverse fish fauna (Figure 30*b*).

Summary and Conclusions

This paper presents the first detailed description of the biological-geological zonation of the barrier reef complex off Belize. Despite some variation along the barrier reef (see Burke, herein), the zonation of the Carrie Bow Cay segment is typical of the entire reef platform (Figures 4, 31). Except for its large lagoon and greater distance from land, the Belizean barrier reef is comparable to well-investigated fringing barrier reefs off the north coast of Jamaica (Goreau, 1959; Goreau and Land, 1974).

Seaward of the *Thalassia*-dominated lagoon, the back reef occurs between an area of massive coral heads on rock pavement and the breakers of the reef crest (Figure 31). On our transect we did not consider this "reef flat" as part of the crest (Goreau, 1959:74) because, although this zone is intertidal, it is very narrow and almost always flooded by waves; instead, we defined "reef flats" herein as large intertidal areas between the eastern shores of South Water and Carrie Bow cays and their nearby crests (Larson and Larson, herein; Rützler, in prep.). Only the narrow intertidal breaker zone is included in the reef crest. The inner fore reef begins at this point with a spur and groove (= buttress) zone of high relief—which in Jamaica is considered a part of the crest (Goreau, 1959)—but it changes abruptly into a gently sloping terrace of spurs and grooves having low relief ("seaward slope" or "upper fore-reef terrace" in Jamaica). The outer fore reef on our transect has a steep inner reef slope, a perpendicular sand trough parallel to the reef crest, and an outer coral ridge where the fore-reef slope begins to drop off to the deep (vertical) fore reef. The comparable feature off Jamaica is a lower fore reef having a lower fore-reef escarpment. Both the trough and the ridge are missing in Jamaica (Goreau and Land, 1974).

Water movement (direction and force) appear to control the development of zonation patterns. Wave action determines not only reef types, by influencing coral zonation (Geister, 1977), but also influences the distribution of all other sedentary organisms, some of which—for instance, octocorals, sponges, and algae—have considerable ecological importance. The quantitative significance of many coral associates is undervalued by most field methods (point and chain-link counts, estimates of area coverage) because presence or surface area is measured but not biomass (massive sponges) or space occupied (swaying

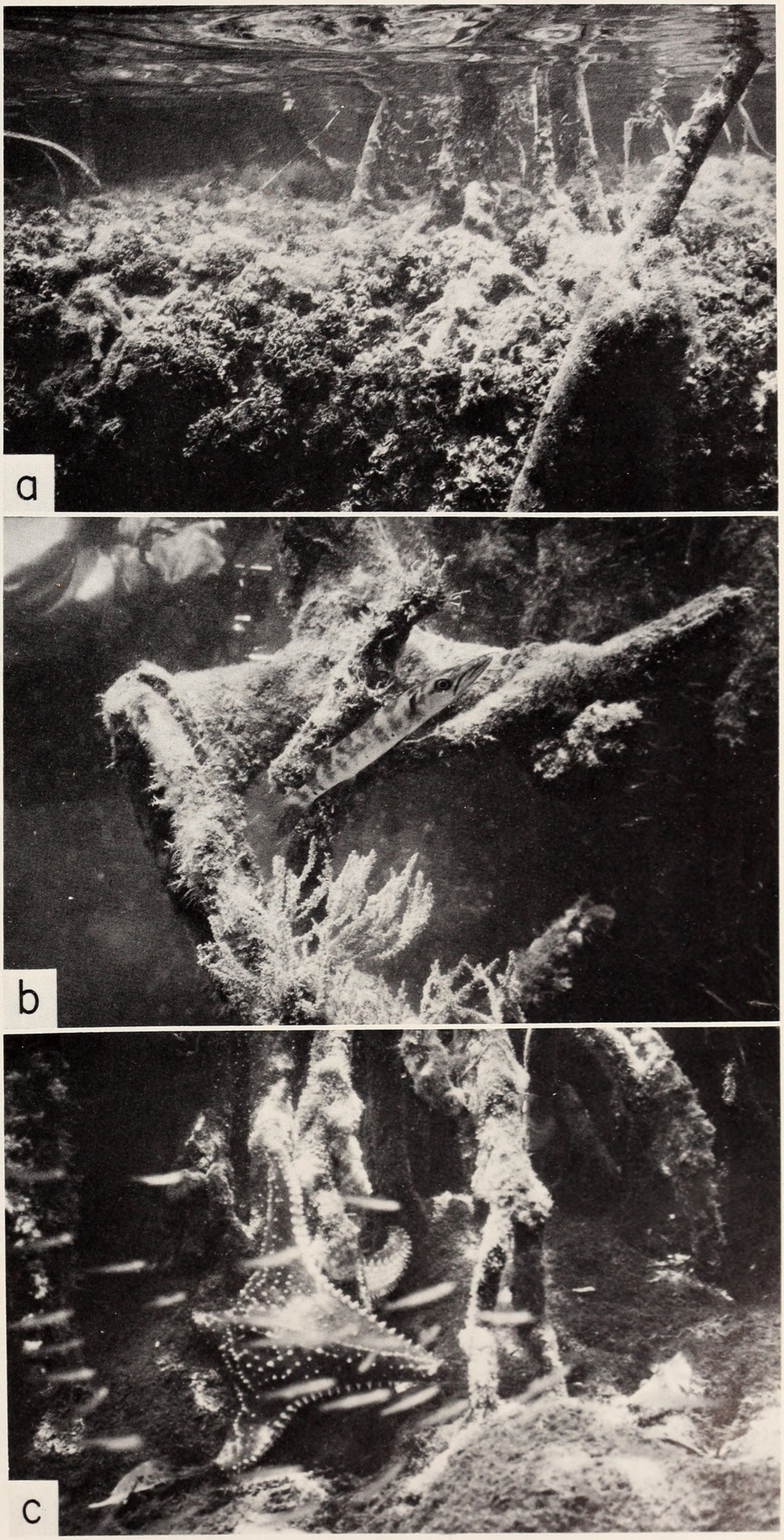


FIGURE 30.—Underwater views of mangrove root system at edge of Twin Cay channel: *a*, mudbank stabilized by rootlets and overgrown by *Halimeda* mat; *b*, juvenile barracuda finding shelter and food among the *Rhizophora* roots; *c*, *Oreaster reticulatus* on mangrove roots penetrating sediment bottom of the channel.

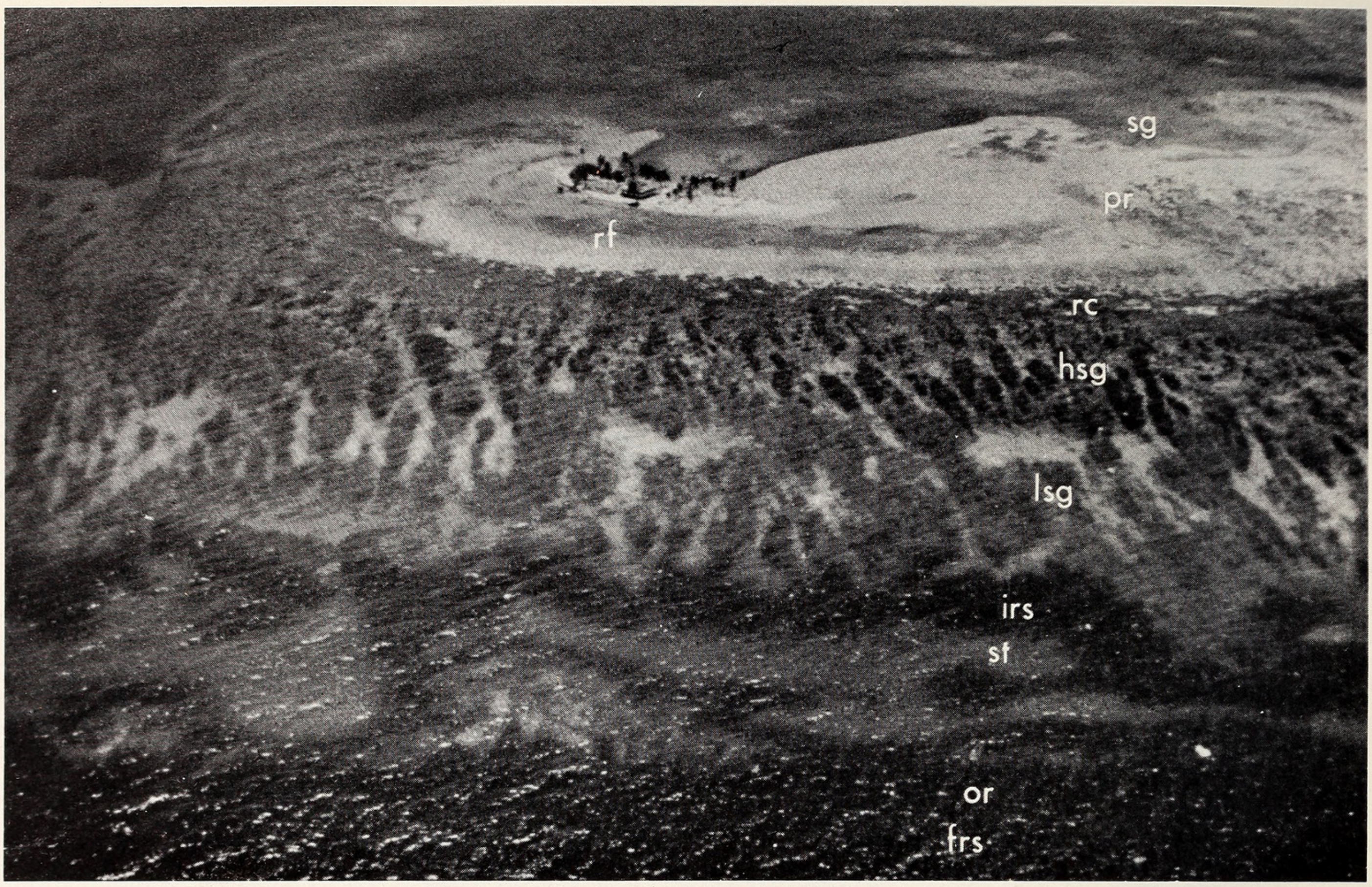
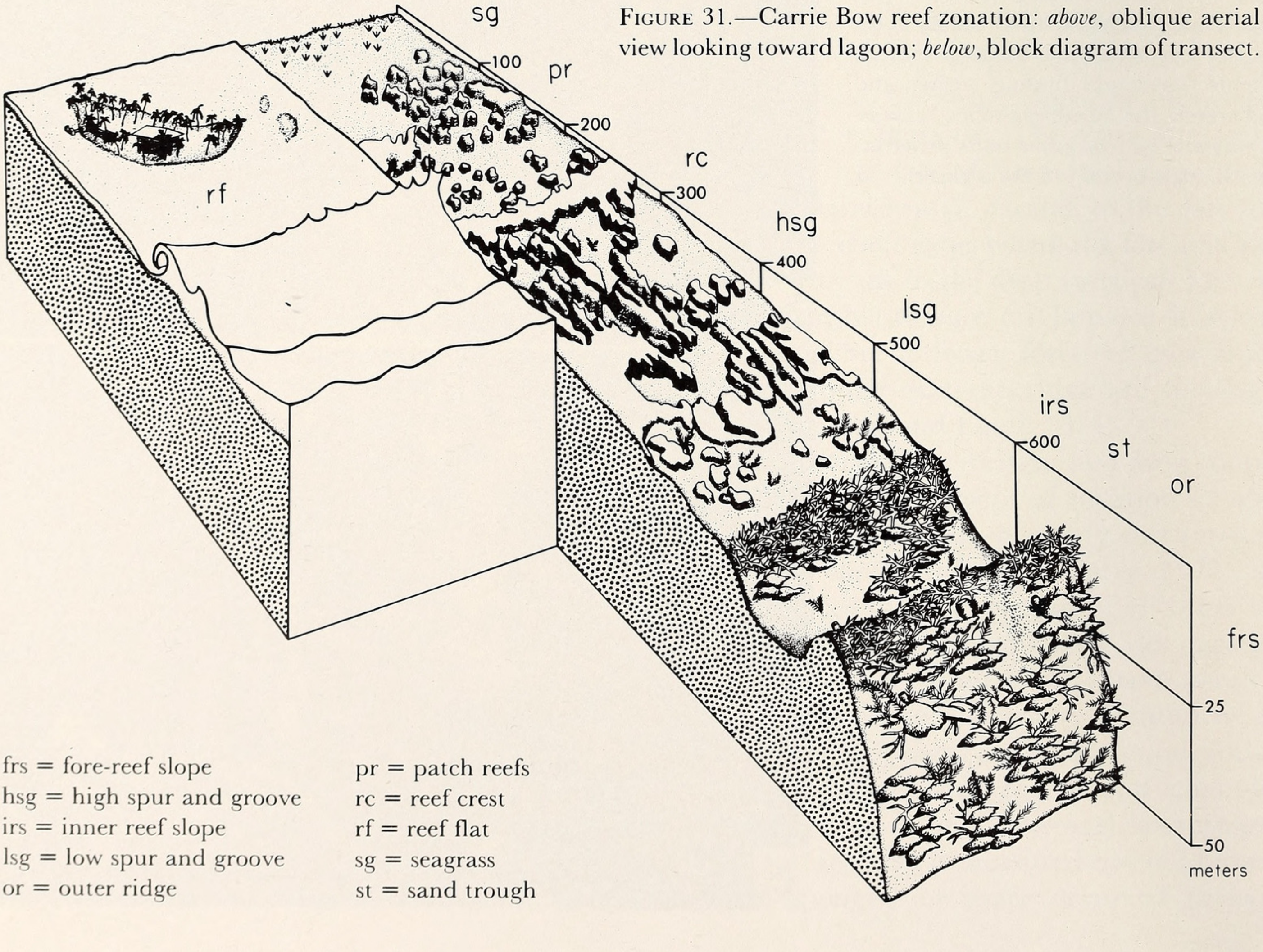


FIGURE 31.—Carrie Bow reef zonation: *above*, oblique aerial view looking toward lagoon; *below*, block diagram of transect.



frs = fore-reef slope
hsg = high spur and groove
irs = inner reef slope
lsg = low spur and groove
or = outer ridge

pr = patch reefs
rc = reef crest
rf = reef flat
sg = seagrass
st = sand trough

gorgonians). Objective evaluation of nonframe-building organisms is essential when comparisons are made between reef biota and nearby lagoon habitats that are not dominated by corals, or only partly dominated by them.

We documented an impressive proliferation of *Acropora cervicornis* in the back-reef and lagoon zones during the four years following the destruction caused by hurricane Fifi in 1974. Our spring 1979 survey indicated that destruction associated with hurricane Greta (September 1978) was mainly the breaking up and lagoonward transportation of the shallow-water *A. cervicornis*. Few colonies of the fragile branching coral escaped this movement and subsequent burial in the sand and rubble zone as well as in the patch reef zone. Almost all of this coral has been washed out of the rubble and pavement zone (Figure 11). Although many of the living and partly buried fragments will, in time, develop into large colonies, the number of living *A. cervicornis* in shallow water has been drastically reduced. This constant cycle of vigorous development, destruction, and resurgence gives rise to the commonly observed high proportion of *A. cervicornis* rubble in comparison to living *A. cervicornis* in many shallow-reef areas.

Although the branching corals *Acropora palmata* and *A. cervicornis* suffer extensive mechanical damage during hurricanes, the transportation and reestablishment of living fragments are significant factors in the distribution of these corals in the shallow-water environment (Plate 2: *center left*; Highsmith et al., 1980). Similar observations have been made in Florida (Shinn, 1972; Gilmore and Hall, 1976) and in Jamaica (Tunnicliffe, 1980) where the dispersal of *A. cervicornis* in these reefs was reported to be largely related to asexual reproduction by regeneration of broken and transported branches.

Our observations and those of James and Ginsburg (1978) have documented *Halimeda* as a major contributor to sediment in the Belizean barrier-reef complex. This calcareous green alga forms a major fraction of these sediments, extending from the shallow lagoon down to at least 200 m on the fore-reef slope, well below its living depth range (approximately 100 m). Commonly comprising the dominant component of the extremely coarse fractions (2–4 mm), the readily identifiable calcareous plates of *Halimeda* are more characteristic of reef-derived sediments than are the fragments of any other organisms, including the corals.

The narrow rock pavement that occurs directly shoreward of the reef crest off Carrie Bow Cay (Figure 4) is a characteristic substrate of shallow reef areas that are constantly having their sediment cover swept away by turbulent waters. The dates of 480±90 years and 534±90 years obtained from coral fragments embedded in a pavement off South Water Cay (James et al., 1976) indicate a long period of formation. These dates also support Macintyre's (1977) observation that submarine lithification is most highly developed in reef areas of high agitation and/or slow accumulation, where the substrate is exposed to normal marine conditions for long periods of time.

James and Ginsburg (1978) speculated that a shelf-edge ridge off South Water Cay is a submerged reef similar to the relict shallow-water, Late Holocene reefs described by Macintyre (1967, 1972), Adey et al. (1977), and Lighty et al. (1978). In contrast, Burke (herein) proposed that these ridges are active accumulations of the rapidly growing coral *Acropora cervicornis*. Burke points out that not only is *A. cervicornis* dominant on these ridges, but that the ridges along the barrier reef complex are restricted to areas protected from long-period storm waves by the outlying atolls. The difficulty with which we probed this ridge (an average penetration of 1 m, maximum of 1.5 m) in contrast to the ease of probing through *Acropora cervicornis* at Rhomboid Shoals near Victoria Channel (Macintyre et al., 1977) indicates that this ridge does not have a similar open-frame network. Our earlier observation that *Montastrea annularis* constructs most of the modern framework of the ridge south of our transect also indicates that this shelf-edge ridge is not merely an accumulation of *A. cervicornis*. Core samples of the internal structure are needed to establish the relative importance of relict and modern framework in the construction of this ridge system.

The reef off Carrie Bow Cay has a species composition and community zonation that is representative of the entire barrier reef system (Burke, herein). The structure of shallow zones of this central province reef, however, is somewhat more similar to that of the discontinuous reefs in the northern and southern provinces because current flow through South Water and Carrie Bow cuts influences the sediment and coral distribution patterns in the back reef and lagoon. The Carrie Bow Cay fore-reef structures, on the other hand, have a degree of development and flourishing coral communities that are characteristic of the central province.

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