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FOUR SOUTHWESTERN CARIBBEAN ATOLLS: COURTOWN CAYS, ALBUQUERQUE CAYS, RONCADOR BANK AND SERRANA BANK

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by John D. Milliman [2]

ABSTRACT

The environment and ecologic zonations of four southwestern Caribbean atolls (Courtown Cays, Albuquerque Cays, Roncador Bank, Serrana Bank) are discussed. Although the atolls vary in size and configuration, the same general zonations are present at each.

Fewer than 10 species constitute more than 95 percent of the reef corals; the small number of species, however, is somewhat balanced by the different growth forms of several major species. Although coral and algae are abundant, other fauna and flora are sparse. The absence of starfish and scarcity of marine grasses is notable.

The ecologic zonations of the four atolls are similar to other Caribbean reefs, but have a luxuriance reminiscent of Indo-Pacific reefs. The emergent *Millepora* zone (comprised primarily of *Millepora alcicornis*, *Palythoa mammillosa* and red algae) on the outer edge of the windward reef flat appears to be the ecologic equivalent of the Indo-Pacific algal ridge. The lack of massive red algal encrustations on the reef flats is the main character differentiating these Caribbean atolls from those of the Indo-Pacific.

Most oxygen uptake by the reef waters occurs on the outer reef, probably the outer 50 to 100 m; trapping of oxygen by crashing waves accounts for a significant amount of this. Primary plankton productivity apparently contributes very little oxygen to the reef flat waters.

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INTRODUCTION

Darwin (1851) believed that there are no true atolls in the Atlantic. However, by defining an atoll as a geomorphic form (rather than by origin, as Darwin did), Bryan (1953) listed 27 Atlantic atolls, 26 of which are in the Caribbean. A more reasonable estimate might be 15. Prior to 1966, five Caribbean atolls had been extensively studied: Alacran Reef (Kornicker and Boyd, 1962; Hoskin, 1963), The British Honduras atolls, Lighthouse Reef, Glover's Reef and Turneffe Islands (Stoddart, 1962), and Hogsty Reef (Milliman, 1967a, 1967b).

In May and June, 1966, the Caribbean Reef and Atoll Program (CRAP) cruise conducted aboard the R/V GERDA, Institute of Marine Science, University of Miami, visited four other Caribbean atolls. These atolls, Courtown Cays, Albuquerque Cays, Roncador Bank, and Serrana Bank, are located in the Southwestern Caribbean, east of the Miskito Bank (Figures 1 and 2). In many respects these atolls bear close climatologic, oceanographic, and geologic resemblance to many Pacific atolls: 1) the climate is tropical and being 200 km windward of the Central American mainland, has little seasonal change (see below); 2) the windward fetch is more than 2,000 km; 3) the atolls are surrounded by deep water (deeper than 1,000 m) and may be the only atolls in the Caribbean with volcanic basement (Milliman and Supko, 1968).

This paper presents a discussion of the morphology, ecology and oceanography observed on the atolls during the cruise.

Acknowledgements

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Regional setting

Courtown Cays (12°24'N, 81°25'W) (Figure 3) and Albuquerque Cays (12°10'N, 81°50'W) (Figure 4) are two small atolls, lying about 200 km east of Nicaragua, seaward of the continental shelf. Both atolls belong to the Republic of Colombia, and are within the jurisdiction of San Andres (12°29'N, 81°43'W), an uplifted limestone island. The longitude of Courtown Cays is listed as 81°28'W (U.S. Hydrographic Office, 1952). Radar bearings from the R. V. GERDA, however, showed Courtown Cays as being 33 km (or 18' longitude) east of San Andres. Assuming that the coordinates of San Andres, having a commercial airport, are accurate, the longitude of Courtown Cays is 81°25'W.

Roncador Bank (13°34'N, 80°04'W) (Figure 5) is about 200 km northwest of Courtown Cays and 140 km west of the volcanic island, Providencia. Serrana Bank (14°16'N, 80°20'W) (Figure 6), the largest of the four atolls, lies about 70 km north of Roncador. Both atolls are under joint ownership by Colombia and the United States.

All four atolls appear to have volcanic foundations. However, in some cases the depth to volcanic basement may be considerable (Milliman and Supko, 1968). Whether this volcanism was related to Tertiary volcanic activity on the Nicaraguan mainland (McBirney and Williams, 1965) is not known.

Climate and Oceanography

Climatic values from the oceanic quadrant 10-15°N, 80-85°W (U.S. Hydrographic Office, 1952) are used since there are no recorded observations for any of the four atolls. The mean annual air temperature is 26.7°C, with a 1° range in monthly values. Winds are primarily from the E-NE, with mean monthly velocities varying from 3.2 to 6.2 m/sec. The atolls are relatively "wet," the measured rainfall on nearby San Andres averaging about 175 cm/yr (Parsons, 1956). Assuming that the rainy season coincides with that on the mainland, most rain falls from June through December.

The sea surface temperature averages 27.3°C, with a 2° range of mean monthly values. Ocean currents and waves like the wind are predominantly out of the E-NE. Tides on the atolls are mixed with a strong diurnal component. Tidal ranges are small, averaging .3 to .6 m. Changes in wind and barometric pressure often cause variations in water level greater than those caused by normal tides. A mean increase in water level of 6 cm occurs during the period of August through November, and a mean decrease of 9 cm occurs during March (U.S. Naval Oceanographic Office, 1965, personal communication).

History

The exact dates of discovery of these atolls are not known. Parsons (1966) wrote that Serrana Bank was "discovered" by (and subsequently named for) Pedro Serrana, a Spanish sailor who was ship-wrecked on its shores sometime prior to 1520. Judging from Spanish shipping activity in the area, the locations of Albuquerque, Courtown and Roncador probably were known long before the end of the 16th century.

None of the sand cays on the atolls had sufficient land to warrant colonization. But the neighboring islands of San Andres and Providencia, with rich soils and stragetic location, were the object of many colonial exploits. The islands were first settled by English puritans in 1631; their colony lasted only 10 years before it was overthrown by the Spanish. From 1641 to 1822 the islands fluctuated between Spanish and English rulers, with an occasional conquest by Jamaican pirates. Although the islands have been under Colombian rule for the past 150 years, most islanders (mainly descendents of African slaves) speak English and are Protestants. The complex history and sociology of San Andres and Providencia Islands are discussed by Parsons (1956) and Newton (1914).

Courtown and Albuquerque Cays have been visited by San Andrean and Providencian natives for many years. Fishermen remain at these atolls for several months, collecting both fish and turtles. Shacks and lean-tos are located on Sand, East and Middle Cays at Courtown, and on North Cay at Albuquerque. While Cayman islanders have hunted turtles on both Roncador and Serrana Banks, the main interest in these two atolls was the guano deposits on their cays. In the mid 19th century, with the increased need for fertilizer, the United States claimed possession of Serrana and Roncador Banks, on the pretense that James W. Jennett had "discovered" these cays during the civil war (Parsons, 1956). Although Colombia also laid claim to the atolls, pointing out that they had been discovered 300 years before (see above), the dispute continued until most all the guano had been removed by American companies. In 1928, the United States and Colombia agreed to joint ownership to the atolls, provided that Washington maintain lights at both atolls. Parsons (1956) discusses this history further.

Previous Studies

Although San Andres and Providencia had been visited by the U.S. Steamer ALBATROSS (U.S. Comm. Fish and Fisheries, 1886), the Pinchot South Sea Expedition (Pinchot, 1930), the Fifth George Vanderbilt Expedition (Vanderbilt, 1944), and the Catherwood-Chaplin West Indies Expedition (von Ripper, 1949), only the Vanderbilt expedition stopped at the neighboring atolls. The visits at each atoll were brief, a total of three days at Serrana and Roncador, and one day at Courtown and Albuquerque. Published observations include reports on the birds (Bond and DeSchauensee, 1944), the fish (Fowler, 1944) and crustaceans (Coventry, 1944) collected at these atolls.

Numerous other cruises have passed these atolls, taking various oceanographic observations. But to the best of the writer's knowledge, no other cruise had studied these atolls.

Methods

In order to gain insight into the ecology, oceanography, and geology of these atolls, the following data were collected: 1) sediment samples; 2) environmental distribution within the atolls; 3) bathymetry within the atoll; 4) meteorologic and hydrographic measurements within the atoll; 5) bathymetric and magnetic profiles and rock dredges on the outer slopes.

The dates spent at each atoll were: Courtown Cays, May 12-19, Albuquerque Cays, May 20-24, Roncador Bank, June 4-7, Serrana Bank, June 8-13. Additional data were collected at San Andres, May 28-29 and at Providencia, May 31-June 1. The data collected should be viewed in light of the limited time available at each atoll. This is especially true for the ecologic observations, which should be treated as preliminary.

While sediment samples were being collected (mainly by skin diving) the nature and depth of the bottom, together with prominent species of coral, algae and other organisms, were noted. The clarity of the water also allowed us to observe general changes in the bottom morphology and communities from an outboard skiff.

Several hydrographic stations within the lagoon of each atoll were occupied by the R. V. GERDA (Figure 7). Various hydrographic and meteorological measurements were taken hourly. Most stations were occupied for one day, although some for much longer or shorter durations.

Current velocities at the surface, mid-depth and 1/2 m above the bottom were measured by a Savonius rotor, registered on a digital meter. In shallow depths only surface and bottom readings were taken. Current directions were estimated from both the ship's head and the wire angle. A thermistor, attached to the current meter, was used to measure water temperature. Unfortunately the thermistor broke during the first hydrographic station at Courtown Cays. Thereafter a standard "bucket" thermometer, with an estimated accuracy of 0.5°C, was used.

Concurrent with these oceanographic observations, air temperature (in the shade) and wind velocity and direction were measured. The wind velocities observed during this cruise were generally greater than normal (see above), suggesting that the currents may have been somewhat faster than normal. The wind (and current) direction (except for Roncador) and air and water temperatures, however, did seem normal.

At Courtown Cays salinity samples of the surface and bottom waters were taken twice daily, at noon and midnight. At Albuquerque Cays and Serrana Bank one set of salinity samples was taken at each station. No samples were taken at Roncador Bank.

ATOLL ECOLOGY

General

Each atoll has the same basic environments: the reef front, windward reef flat, lagoon (together with patch reefs), and leeward reef flat (figure 8). To save space, these environments are discussed, followed by a discussion of the unique characteristics of each atoll.

Reef Front

The windward reef front drops steeply to a depth of about 5 m, gradually slopes to about 18 to 20 m, and then again steepens. The width of this reef front varies, but is generally less than 500 m (Figure 8). Because of the high surf conditions at Roncador and Serrana, only the reef fronts at Albuquerque and Courtown Cays were studied; even there surf limited the time spent on the reef front.

Montastrea annularis is the most prominent coral in depths exceeding 5 m. In shallow depths *Acropora palmata*, oriented into the surf, grows profusely. The prominence of this coral is characteristic of the shallow reef fronts of most Caribbean reefs (Shinn, 1963, and other references cited below). Other corals include Agaricia agaricites and Acropora cervicornis, the latter usually found in depths greater than 2 m. The hydrocoral, Millepora alcicornis, is prominent in shallow depths. Red algae, primarily Goniolithon, encrust reef rock and loose coral rubble.

Reef pinnacles, composed mainly of M. annularis and A. palmata, are common just windward of the surf zone at the northeast corners of both Courtown and Albuquerque cays. These pinnacles, rising from depths of about 5 m often break the surface.

Aerial photographs indicate the presence of buttresses and grooves oriented normal to the reef flat. Although these features were neither well-developed nor continuous on those parts of the reef front investigated, their prominence on the outer reef flat (see below) infers that the buttress-groove zone is present on much of the reef front, although probably not as well-developed as at Jamaica (Goreau, 1959).

Windward Reef Flat

Outer Margin: Reefs on the windward reef flat are best developed on the north and northeastern sides of each atoll, where waves and currents are greatest. The southeastern reefs tend to be less well-developed.

The northeastern and eastern reef margins of all atolls are penetrated by a series of surge channels, 1, to 2 m deep, oriented normal to the reef front. Crashing surf forces swift currents through these channels onto the reef flat. The sides of the channels are lined with massive Diploria, Montastrea annularis and Porites astroides, the latter, in places, assuming a flat, sheet-like form. Porites porites and the green alga, Halimeda opuntia form large masses. Branching red algae, Amphiroa and Goniolithon are common and the pink conch, Strombus gigas, is locally abundant.

Growing on the buttresses (and on most of the outer reef pavement not penetrated by surge channels) is the prolific assemblage of Millepora alcicornis, the soft coral Palythoa mammillosa, and encrusting red algae (Porolithon and Goniolithon); Agaricia agaricites and Halimeda opuntia are often present in this community (Plate 1). This feature, here termed the Millepora zone, grows up to 40 cm above the low tide level, and occupies a near continuous zone, 15 to 20 meters wide, along the outermost margins of the windward reef flat (Plate 2). It is most thoroughly developed on the northeastern sides of the atolls where high surf continually splashes and washes the emergent colonies. Concentrations of M. alcicornis and zoanthid corals on reef crests have been noted at other Caribbean reefs (Goreau, 1959; Lewis, 1960; Kornicker and Boyd, 1962), but at none are they reported emergent at low tide.

The Millepora zone seems to be the ecologic equivalent of the leeward portions of the algal ridge and Acropora cuneata zone found on Pacific atolls (Wells, 1954). In each area plate-like corals are encrusted with red algae and zoanthid corals, and are exposed to low tide (see Tracey, Ladd and Hoffmeister, 1948, Plate I, Figure 2; Emery, Tracey and Ladd, 1954, Plate 19, Figure 2). The zone, however, cannot really be called an algal ridge because massive red algae do not actually form the basic structure. Rather algae and the soft corals encrust emergent colonies of Millepora.

Just leeward of the Millepora zone is an environment of prolific coral growth, 20 to 50 m wide, termed the "Diploria zone," because of the abundance of that genus, especially D. clivosa; Lewis (1960) has described a similar zone at Barbados. Depths range from a few cm to over 1 m. The massive growth form of Montastrea annularis is prominent with lesser amounts of A. palmata (also in massive growth form), Millepora alcicornis, Porites astroides and P. porites. Thickets of Acropora cervicornis are present on the more leeward portions of the Diploria zone. Corals of every major hermatypic species, plus many species of algae, grow up to 1/2 m above low tide level (Plate 3). Although these organisms are exposed above mean low tide level for relatively long durations, they are able to survive by means of intermittent surf splash.

Halimeda opuntia, growing in large mounds, is a prominent sediment contributor. The sea urchin, Diadema antillarum, is also common, especially in holes and crevices. At some transects the windward reef flat is almost devoid of coral, the reef pavement and any available rubble being covered with encrusting algae. Red algae form large hemispherical masses, up to 25 cm in diameter. Many have hollow interiors, where they probably once encrusted dead coral.

Inner Reef Flat: The inner reef flat is defined by a sudden increase in depth leeward of the outer reef flat. Depths commonly increase from less than a few tens of cm to more than 1 m (Plate 4). The inner reef flat is largely devoid of coral although there are some Porites astroides, Montastrea annularis and Siderastrea, mainly in encrusting growth form. Covering large portions of the bottom are green algae (Halimeda, Penicillus, Rhipocephalus, Udotea, Padina), brown algae (Dictyota and Turbinaria) and red algae (Porolithon, Goniolithon, Amphiroa). Red algae are the most common type on the inner reef, encrusting much of the rubble that has been washed in from the windward reefs. The gastropods Strombus gigas and Astrea phoebia are locally common.

Lagoonward Margin: The leeward margin of the reef is generally 1 to 2 m deep, with occasional small reefs, primarily Montastrea annularis, Acropora cervicornis and A. palmata breaking the surface. Alcyonarians, very sparse on the outer reef, are somewhat more prominent in this zone. Green and brown algae are common. The marine grasses, Thalassia, Halodule, and Syringodium, are completely lacking, except in sheltered spots leeward of some cays. This contrasts with the abundance of reef flat grasses on Alacran Reef and the British Honduras atolls (Kornicker and Boyd, 1962; Stoddart, 1962). Green algae, especially Halimeda, and brown algae (Dictyota and Turbinaria) are the dominant plants on the lagoonward margin. Near the sand cays, Halimeda is especially prolific, as is evidenced by the widespread Halimeda sands on the cay beaches.

A common leeward feature of the lagoonward margin is a "sand cliff," which drops abruptly from the reef flat into the lagoon (Figure 10). Vertical relief is as great as 10 m, with slopes up to 35°. Similar steep slopes have been reported at Alacran Reef (Kornicker and Boyd, 1962) and Glover's Reef (Stoddart, 1962) in the Caribbean, and at Ifaluk Atoll (Tracey, et al., 1961) and Midway and Kure atolls (Gross, et al., 1968) in the Pacific. This steep slope may be formed by transport of reef flat sediment into the lagoon, suggesting a fore-set slope, or it may be a karst remnant of earlier Pleistocene low sea levels (MacNeil, 1954).

Lagoon

A large portion of the lagoon bottom at each atoll is covered with patch reefs. About 1/3 of the lagoon reefs are emergent, or come within a few meters of the surface. The rest are low-lying, rising no more than a few meters above the bottom (Plate 5). The massive and columnar growth forms of Montastrea annularis are prominent in shallow depths. The columnar (Lewis, 1960, p. 1143), pinnacle (Plate 6) and foliose forms are more characteristic of deeper patch reefs. Thickets of A. cervicornis are common on both shallow and deep reefs. There are also varying amounts of Diploria, A. palmata, P. porites, Siderastrea, and Agaricia. Alcyonarians, which are sporadic on the shallow reefs, are abundant on many of the deeper patch reefs.

Most of the lagoonal organisms live on, in, or near these reefs. Green algae (Penicillus, Rhipocephalus, Halimeda) are locally common near reefs, but otherwise generally lacking. Polychaete tubes, emerging from the bottom, grow thickly in the vicinity of patch reefs. In deeper parts of the lagoon, sponges are common and reach large size. Judging from the number of mounds, burrowing organisms may play an important role in the ecology of the lagoon bottom. The portion of the lagoon floor not covered with reef is generally bare, except for occasional conchs (Strombus gigas), algal patches, and fecal mounds.

Leeward Reef Flat

At all atolls the leeward peripheral reefs are ill-defined and discontinuous. They appear to have been formed by the coalition of patch reefs. The reef organisms are similar to those on the windward reefs, but less abundant; also, the marked zonations seen on the windward reefs are generally absent. In places the reefs are dead, with Dictyota and other brown algae encrusting the reef flat bottom.

Courtown Cays

Courtown Cays (12°24'N, 81°25'W) is a lenticular atoll, 8-1/2 km N-S and 3-1/2 km E-W. The windward reef flat is indented in two places, giving the atoll an unusual bowed shape (Figure 3). Aerial photographs show that surge channel lineations are most conspicuous in the indented portions of the outer reef. The area of most prominent lineations is labelled "Buttress-Groove Zone" in Figure 3. The surge channels in this area have relief of 1/2 to 1 m, and extend into the reef front as a buttress-groove system. Depths shoal to about 1 m on the outer reef;

no sign of the emergent Millepora zone or other reef organisms was seen. The generally deep, reef-less bottom in this indented area is difficult to explain; perhaps it is related to the swift currents that seem to continually flow through this area.

The leeward reef at Courtown Cays is interrupted by a 2 km gap, resulting in a lagoon open to the NW. Sounding profiles showed no lagoon sill. Lagoon depths average about 12 m, although depths locally reach 16 m.

A large patch of sea grass, both Thalassia and Syringodium, extends some 100 m leeward of East Cay. The echinoid Tripneustes esculentus is particularly common in this grass patch.

Patch reefs cover only about 10 percent of the lagoon bottom. The reefs that break, or nearly break, the surface are usually located within the 10 m isobath (Figure 3). Coalescing patch reefs have nearly isolated the southern third of the lagoon.

Courtown Cays has five small cays and one rocky spit. Sand Cay is about 200 m by 25 m with a maximum height of about 1-1/2 to 2 m. The windward beaches are covered with encrusted reef rubble. A sand spit extends about 20 m south of the cay. Two prominent plant species grow on the cay: Tournefortia shrubs, with heights up to 1 m, and a low creeping vine (Euphorbia ?). A few coconut palms are also present. One unoccupied thatched hut, about the size and shape of a pup-tent, was found on the central part of the cay.

East Cay is the largest cay at Courtown Cays, being about 300 m by 100 m. Four bands of beachrock, paralleling the eastern shoreline, extend windward on the reef flat. The rock bands, about 20 m apart, probably represent previous shorelines, and suggest the lagoon migration of the cay (Plates 7, 8). The distinguishing feature on East Cay is the tall stand of coconut palms (Plate 7). Large Scaevola bushes grow on the lagoon side. Several other plant types were noted but not identified. A shack, on the lagoonward side of the cay, was occupied by a San Andrean fisherman and his dog.

A small rocky spit, composed of massive coral debris, lies at the southern tip of the peripheral reef. Wave refraction around the southern end of the atoll results in crashing surf from both the southeast and southwest. Nestled in between the large coral rubble were the nets of several frigate birds. No living land plants were seen on the spit.

Three small cays, Middle Cay, West Cay, and a sand spit, sit on patch reefs that collectively form the leeward peripheral reef. Only Middle Cay was visited. Most of the cay is surrounded by emergent patch reefs. The central vegetated portion of the cay is bordered by Tournefortia and Scaevola bushes. Low-lying, unidentified creepers cover most of the cay's interior. Several Providencian natives were living on the cay.

Viewed from an outboard skiff, West Cay apparently had vegetation similar to that on Middle Cay. The sand spit appeared to lack any plant life.

Four hydrographic stations were occupied in the Courtown Cays lagoon (Table 1). Air temperatures averaged about 28°C. Water temperatures were somewhat lower averaging 27.5°C, with small daily ranges. While the thermistor was operative little difference was noted in the surface and near bottom water temperatures at Station C-1. Salinities were between 36.1 and 36.4 o/oo. Definite salinity variations were noticed at Station C-1, where the salinity on the second day was more than 0.2 o/oo higher than the first day (Table 1).

Northeast winds seldom dropped below 7 m/sec. Current direction coincided with the wind. At C-1 current velocities averaged 5 cm/sec. Current velocities at the other three stations averaged 16 to 21 c/sec at the surface and 10 to 14 cm/sec near the bottom.

Albuquerque Cays

Albuquerque Cays (12°10'N, 81°50'W) is a nearly circular atoll, about 6-1/2 km E-W and 5 km N-S (Figure 4). Leeward peripheral reefs grow on a shallow, wide sand flat, which forms the lagoon sill. The sand flat deepens from about 3 to 5 m at the leeward reefs, to 10 to 15 m 3 km to the west. The flat is covered with small, low-lying patch reefs. Two navigable channels on the southwest and northwest broach the flat into the lagoon.

Lagoon depths are as much as 18 m but generally about 10 to 15 m. Patch reefs cover an estimated 20 percent of the lagoon bottom. These reefs are especially prominent in the northern half. Anastomosing patch reefs, corresponding to those described by Kornicker and Boyd (1962) as "cellular reefs," were seen in the northeastern parts of the lagoon.

The only sea grasses found on this atoll are strands of *Halodule* and *Syringodium*, on the northern and southern sides of North Cay.

Two islands, North Cay and South Cay, rise above the windward reef flat. North Cay measures 350 m N-S and 125 m E-W, and stands about 2 m high. South Cay, about 250 m to the south, is a smaller version (180 by 70 m) of North Cay.

Beachrock is present on the eastern shorelines of both cays (Plate 9). Several other bands extend windward, in a similar manner to those at East Cay on Courtown. Another beachrock outcrop, standing 1/2 to 1-1/2 m above sea level is located on the northern sides of North and South Cays. This elevated beachrock apparently continues across both cays; a soil pit dug in the interior of South Cay exposed a layer of beachrock, about 1/2 m thick and about 1-1/2 m above present sea level, overlying an unconsolidated *Halimeda* sand. Carbon-14 dates have not

Station	WIND Duration (hours)	Velocity* (m/sec)	Direction*	Air Temp. (°C)	Water Depth (m)	CURRENTS Velocity* (cm/sec)	Direction*	WATER Temp.* (°C)	Salinity (o/oo)
1	35	9 (7-12)	55	27.4 (26.7-29.5)	10	5 (4-9)	235	27.6 (27.2-27.9)	(36.135-.347)
						5 (3-8)		27.6 (27.2-27.8)	
						5 (2-10)		27.5 (27.3-27.7)	(36.006-.390)
2	25	10 (8-12)	60	27.9 (27.0-29.5)	5	21 (6-30)	240	27.5 (27.3-27.7)	(36.236-.241)
						16 (5-29)			
						14 (4-28)			(36.193-.245)
3	25	10 (8-12)	53	27.9 (27.2-30.2)	12	16 (9-23)	233	27.4 (27.1-27.8)	(36.184-.187)
						15 (9-22)			
						12 (7-21)			(36.111-.179)
4	20	8 (7-11)	47	27.9 (27.1-28.9)	15	19 (13-23)	227	27.5 (27.2-27.8)	(36.291-.330)
						15 (11-19)			
						10 (4-17)			(36.205-.299)

Table 1. Hydrographic data collected at Courtown Cays, May 12-19, 1966. Asterisk (*) signifies that values presented are averages; numbers in parentheses represent the range in values.

		WIND				CURRENTS		WATER	
Station	Duration (hours)	Velocity* (m/sec)	Direction*	Air temp.* (°C)	Water Depth (m)	Velocity* (cm/sec)	Direction	Temp.* (°C)	Salinity (o/oo)
1	28	5 (3-8)	60	27.9 (27.0-30.4)	10	10 (4-17)	240	27.8 (27.2-28.3)	36.372
						7 (3-12)			
						5 (2-11)			36.791
2	6	7 (6-7)	75		5	10 (6-12)	255	27.7 (27.4-27.9)	36.350
						8 (5-11)			
						5 (0-9)			36.359
3	25	6 (2-8)	60	28.0 (26.9-29.5)	5	8 (4-19) [16]	240 [145]	27.7 (27.4-27.9)	36.382
						7 (3-12) [18]			
						6 (2-11) [4]			36.481

Table 2. Hydrographic data collected at Albuquerque Cays. Asterisk (*) signifies that values presented are averages; numbers in parentheses represent the range in values. For station 3, dominant average current values are given first; bracketed values represent average velocity and direction of tidal reversals.

been run on the rock or underlying sediments, so that the age and origin of this formation is open to speculation.

Coconut palms, Ficus trees and Scaevola shrubs are the prominent plants. The interior portions of both islands are so heavily wooded that little sun penetrates (Plate 10). On both cays the trees are lowest on the windward side and highest on the leeward side, giving the cays a swept-wing appearance. Because of the heavy, lush vegetation, the soils are more rich and loamy than at other atolls. When visited, four fishermen from Providencia were living on North Cay.

Bond and DeSchauensee (1944) reported nine species of birds on the two cays. Most were migratory birds, but some were boobies and terns. One species, a hummingbird (Anthracothorax prevostii hendersoni), is apparently a permanent inhabitant (Bond and DeSchauensee, 1944).

Three hydrographic stations, ranging in duration from six to 28 hours, were occupied at Albuquerque Cays (Table 2). Air and water temperatures were similar to those measurements taken at Courtown Cays. Salinity values were around 36.35 o/oo, somewhat higher than at Courtown Cays.

Winds were between 5 and 7 m/sec from the northeast. Surface currents at Stations A-1 and A-2 rarely exceeded 15 cm/sec, and averaging about 10 cm/sec; bottom currents were less, 5 cm/sec. Current direction, like wind, was in a westerly direction. The currents at Station A-3, at the southwestern lagoon entrance, reversed and flowed into the lagoon for a period of four hours. It is assumed that this current reversal was tidal.

Roncador Bank

Roncador Bank (13°34', 80°04'W) resembles the shape of a fish hook, being about 11 km long and 3-1/2 km wide (at its widest part) (Figure 5). The windward peripheral reef is better developed than at any of the other atolls. The Millepora zone, when visited during spring low tides, extended up to 50 cm above the water (Plate 2). The back reef, often awash at low tide, is considerably shallower than at the other atolls.

Large boulders, standing as much as 1-1/2 m above the reef flat, line extensive portions of the outer reef flat, especially near Roncador (Plate 11). The boulders are lenticular blocks, unlike either the negro heads found on Pacific reef flats or beachrock. Hopefully carbon-14 dates and petrographic study will shed light on the boulders' origin.

Leeward peripheral reefs at Roncador are the poorest developed of any of the four atolls. Except for a few large, but deep (2 to 3 m), patch reefs that define the peripheral reef to the south, the lagoon is open. Lagoon depths reach 18 m, but average between 10 and 12 m. Patch reefs dominate the lagoon's bottom. Almost the entire third of the lagoon is covered with low-lying reefs; interspersing sand patches probably account for no more than 30 percent of the bottom (Figure 9).

Roncador Cay is 400 m long and 150 m wide. Coral rubble covers most of the island. Walls of Montastrea and Diploria (Plate 12) perhaps were constructed by guano workers during the last century (see above). Vegetation is sparse; low-lying Tournefortia bushes and a creeping vine cover only small portions of the island.

This desolate rocky island is a far cry from the lush islands at Albuquerque Cays. Strangely enough, however, castaways have managed to survive on it. Newton (1914) writes that a ship carrying four men escaping from the Puritan rule on Providencia was wrecked on Roncador in 1636. In 1639 the sole survivor was rescued and returned to Providencia. As if living on this forsaken island for 2-1/2 years were not bad enough, after a Sunday evening service ". . . the rescued man was introduced (to the congregation) . . . to offer up public thanksgiving for his deliverance, to make confession for his vicious life, and to register a vow of future atonements." (Newton, 1914, p. 278). In the mid 19th century, an American ship was wrecked on Roncador, and the surviving crew remained on Roncador Cay for 10 days (Parsons, 1956).

Bond and DeSchauensee (1944) reported only three bird species, a hawk and two boobies, at the atoll. During our cruise Roncador Cay was covered with boobies and terns. These sea birds apparently migrate to Roncador and Serrana Banks during the spring months to nest (Parsons, 1956). Parsons (1956, p. 63) quotes the estimate that 25,000 sea bird eggs are annually removed from Roncador Bank by natives from San Andres and Providencia.

A sand spit, about 15 m in diameter, lies on the inner reef flat of the northeastern peripheral reef. The beaches are strewn with coral debris and Strombus shells. Another sand spit, also about 15 m in diameter, lies on the southern peripheral reef flat. No vegetation was seen on either spit.

During the stay at Roncador Bank, winds were from the south-southeast, probably in response to Hurricane Alma, which was in the northwestern Caribbean. Wind velocities averaged 7 m/sec (Table 3). Lagoon currents were generally less than 15 cm/sec, averaging between 8 and 11 cm/sec at the surface and 6 to 7 cm/sec near the bottom. Current direction coincided with wind direction. Air temperatures averaged 27.9°C. Water temperatures were somewhat higher, averaging between 28° and 28.4°.

Serrana Bank

Although Serrana Bank (14°16'N, 80°20'W) (Figure 6) is large (32 by 16 km), its morphology and ecology are generally similar to the other atolls. The peripheral reef is well developed on three sides; the western side is completely open.

Vanderbilt (1944) reported a "deep hole" on the reef flat by Southwest Cay. We found this hole to be about 9 m deep, and to have gradual sandy slopes, with some Syringodium blades on the bottom. This was the only grass seen at Serrana Bank. No thermocline was noted in the hole.

Station	Duration (hours)	WIND Velocity* (m/sec)	WIND Direction*	Air Temp.* (°C)	Water Depth (m)	CURRENTS Velocity* (cm/sec)	CURRENTS Direction*	WATER Temp.* (°C)	WATER Salinity (o/oo)
1	25	7 (6-9)	145	27.9 (26.2- 28.9)	11	11 (7-16) 10 (6-17) 6 (5-10)	325	28.4 (28.0-28.8)	
2	25	8 (6-10)	130	27.8 (27.4- 28.6)	10	9 (3-15) 9 (4-12) 7 (3-13)	310	28.0 (27.8-28.4)	
3	22	7 (3-10)	165	27.9 (26.4- 28.6)	12	6 (5-14) 7 (4-12) 6 (4-10)	245	28.0 (27.4-28.2)	

Table 3. Hydrographic data collected at Roncador Bank, June 4-7, 1966. Asterisk (*) signifies that values presented are averages; numbers in parentheses represent the range in values.

Two bands of patch reefs, one extending north from East Cay, the other extending south from the northern peripheral reef towards Little Cay, effectively divide Serrana lagoon in half (Figure 6). While lagoon water flows over these extensive reef complexes, water depths are too shallow for anything larger than a small skiff to pass over. The eastern string of patch reefs shoals rapidly from depths exceeding 15 m. Alcyonarians and gorgonians, together with Monastrea heads and scattered clumps of green algae, dominate the deeper bottom (Plate 13). As the reef shoals, Acropora cervicornis and Monastrea annularis increase in abundance. In depths shallower than 4 m, Acropora palmata oriented into the currents and Millepora alcicornis are prolific. The reef flat, up to 100 m wide, is generally 1 to 2 m deep. Most common corals on the reef flat are M. annularis, Diploria, Acropora palmata, A. cervicornis and alcyonarian corals. The encrusting coral, Porites astroides, is common throughout the patch reef.

A. cervicornis exhibits three distinctive growth forms on the patch reefs. On the reef front, in deeper water (5 to 10 m), the colonies are small and fragile; at shallower depths (1 to 3 m) on the reef front, the colonies are longer and thicker, but with few branches. On the reef flat, A. cervicornis is smaller, but with many thick branches.

The nature of the bottom and the zonation of the corals on these coalescing patch reefs are similar to the windward peripheral reefs. With an open lagoon fetch of some 3 to 5 km, considerable surf can crash onto these shallow reefs. In contrast to the windward peripheral reefs alcyonarians are more common, red algae less common, and the emergent Millepora zone and surge channel lineations are absent.

The second, leeward coalescing patch reef, while having similar zonations to the eastern patch reefs, lies on a broad sand bank, that extends some 2 km leeward of the reefs. Depths on the bank are seldom more than 3 or 4 m. It is difficult to conceive that this reef has produced that much sand; rather, the reefs probably have grown on the sand flat.

Lagoon depths east of the patch reef bands reach 20 m, but average about 15 m. An estimated thirty percent of the bottom in the eastern lagoon is covered with patch reef (Figure 10). Leeward of the linear reef bands is a broad shallow flat; depths seldom are greater than 10 m (Figure 6). In contrast to the eastern lagoon, only about 5 percent of this flat is covered with patch reefs (Figure 10).

Six cays are located on Serrana Bank. East Cay is a small islet covered with coral and mollusk (Astrea sp.) rubble. Tournefortia is the only plant present.

South Cay is about 150 m long and 25 m wide. Beachrock lines the seaward beach; the rest of the cay is composed of rubble and sand. The three species of plants present (Tournefortia, Ipomoea and Euphorbia were all sparse.

Little Cay lies on the southern edge of a linear reef band (see above) and forms the apex of an equilateral triangle with South and Narrow Cays. The cay is less than 100 m in diameter. Rubble lines the seaward (south and east) beaches, and beachrock is present on the south and west sides. The rest of the island is fine sand; no vegetation was seen.

Narrow Cay west of South Cay is essentially a rubble pile. The entire reef flat west of the cay is covered with beachrock and rubble. This may indicate the former position of the cay.

Southwest Cay is the largest island on any of the atolls visited. Its dimensions (about 500 m long, 200 m wide) contrast with five small cays on this atoll. Although most of the island is only a few m high, sand dunes on the south and west sides reach heights greater than 10 m.

For an island of this size there are surprisingly few plant species. A creeper vine covers much of the low-lying part of the cay. Several species of shrubs grow on the dunes. Two dilapidated huts are located in a small grove of coconut palms. These huts may belong to Cayman Brac natives who, according to Vanderbilt (1944), live on Serrana Bank most of the year, collecting guano and hunting turtles. No natives were seen during our visit.

Bond and DeSchauensee (1944) reported eight species of birds at Serrana. At the time of our visit large colonies of boobies and terns were nesting; we estimated about 100,000 birds on the cay. It is not hard to see why Parsons (1956) reports that 300,000 bird eggs are collected annually by Jamaicans, nor to understand why guano accumulated in such large quantities.

North Cay, located at the northern edge of the peripheral reef, is composed of sand and rubble. Three species of plants, *Tournefortia*, *Ipomea* and the small species of creeper seen at Southwest Cay were noted.

Five hydrographic stations, ranging in duration from 17 to 24 hours, were occupied at Serrana Bank (Table 4) at the first station, S-1, wind was from the southeast with an average velocity of 4 m/sec. The wind direction then shifted to the east and velocities increased to about 8 m/sec. These winds continued for the rest of the stay at Serrana.

Currents in the interior parts of the lagoon (stations S-1, S-4, and S-5) followed the wind direction. Currents near the lagoon entrances (S-2 and S-3), however, were seldom coincident with the wind. Water flowed out of the lagoon (S-3) or westward (S-2) during ebb tide. During flood and slack tide, water would flow into the lagoon. Thus the average current flowed into the lagoon. The fastest currents measured during the entire cruise were at these lagoon entrances; at S-3, currents often exceeded 50 cm/sec.

Air and water temperatures were in near equilibrium; the daily average for each being about 27.9°C. Salinities ranged between 35.93 and 36.04 o/oo.

	WIND					CURRENTS		WATER	
Station	Duration (hours)	Velocity* (m/sec)	Direction*	Air Temp.* (°C)	Water Depth (m)	Velocity* (cm/sec)	Direction*	Temp.* (°C)	Salinity (o/oo)
1	23	4 (1-8)	140	28.1 (27.7-29.3)	8	8 (4-18) 5 (4-7) 4 (2-9)	320	28.0 (27.6-28.6)	35.937
2	24	8 (6-11)	93	28.0 (26.4-28.6)	18	15 (12-22) [10] 16 (15-25) [8] 14 (9-22) [10]	010 [270]	28.0 (27.4-28.6)	36.048
3	24	9 (7-11	87	27.9 (27.5-28.6)	10	34 (19-53) [36] 35 (18-52) [37] 26 (14-43) [26]	000 [160]	28.0 (27.8-28.8)	36.004
4	19	8 (6-10)	93	27.9 (27.5-28.6)	5	34 (19-52) 23 (12-39)	270	27.9 (27.4-28.3)	35.993
5	17	11 (9-16)	90	27.4 (27.6-28.7)	5	18 (14-23) 16 (12-25)	270	27.9 (27.5-28.2)	35.953

Table 4. Hydrographic data collected at Serrana Bank, June 8-13, 1966. Asterisk (*) signifies that values presented are averages; numbers in parantheses represent the range in values. For stations 2 and 3 dominant average current values are given first; bracketed values represent average velocity and direction of tidal reversals.

DISCUSSION

Similar ecologic zonations are present at Courtown Cays, Albuquerque Cays, Roncador Bank and Serrana Bank. The outer windward reef flat is characterized by an emergent *Millepora* zone and a leeward *Diploria* zone. The deeper (1 to 2 m) inner reef flat lacks the prolific reef growth; red, green and brown algae are most conspicuous. Steep sand cliffs mark the sudden transition from the inner reef flat to the lagoon. Patch reefs dominate the lagoons. The leeward reefs seem to result from coalescence of patch reefs.

Some differences exist between atolls: 1) Serrana Bank, being larger than the other three atolls, has a more complex lagoon. Bands of coalescing patch reefs have almost divided the lagoon in two. 2) Courtown and Roncador, lacking leeward reefs, have more open lagoons. 3) Lagoon patch reefs are especially dominant at Roncador Bank, where an estimated 40 to 50 percent of the bottom is covered. 4) The sand cays at Albuquerque Cays have a relatively lush foliage and rich soil compared to the pioneer strandline plant communities at the other three atolls. 5) Elevated beachrock is found on the two islands at Albuquerque; large reef blocks line the outer periphery of the windward reef flat at Roncador.

Other than the abundant corals and calcareous algae, the fauna and flora of these Nicaraguan atolls seem depauperate. The most important mollusk and echinoderm species (*Strombus*, *Astrea* and *Diadema*) are only locally common. Several species of ophiuroids were collected or observed, but only the ubiquitous black *Ophiocoma riisei* was common. Virtually no holothurians were seen except *Actinopyga agassizii*, locally abundant on the reef flat and at moderate depths in the lagoon. Crustacea also were poorly represented. Many of the surface dwelling fauna such as *Clypeaster rosaceus* and *Lytechinus variegatus*, were not seen. Signs of an abundant molluscan infauna, such as empty bivalve shells, were also lacking. Prolific alcyonarian growth was primarily limited to deeper lagoon reefs.

Not one starfish was found. The total absence of this group and the almost complete lack of marine grasses was surprising, especially since both are common on the leeward shores of nearby San Andres and Providencia islands. This might suggest that the high current energy environments on the atolls have effectively limited the starfish and grass populations. It is interesting to note that the few grasses at the atolls were always found in the most restricted, low-energy environments.

Fowler (1944) was impressed by the numerous fish at Courtown Cays. He also mentioned catching several lobsters (*Panulirus argus*). The present writer was impressed by the small number and size of fish species and individuals. Extensive skin diving did not reveal many lobsters. The discrepancy between Fowler's observations and ours may be due to the fishing activity of the natives.

NICARAGUAN AND PACIFIC ATOLLS

Caribbean reefs and atolls are considered pale images of their Indo-Pacific counterparts, lacking in: 1) number of coral species (about 50 versus about 700 in the Indo-Pacific), 2) the emergence of corals at low tide, 3) an algal ridge zone, and 4) general reef maturity (Wells, 1957; Newell, 1959; Yonge, 1963). These conditions are true in the northern Caribbean, where the fetch is often short and the annual range of air temperature may be great. Yet at the Nicaraguan atolls, whose environment closely parallels many Pacific atolls, most hermatypic coral species can live exposed between tides. While no true algal ridge occurs on the Nicaraguan atolls, the *Millepora* zone, emergent at low tide, appears to be its ecologic equivalent.

The lack of coral species does not seem to inhibit the prolific reef growth. As in other Caribbean reefs (Goreau, 1959; Lewis, 1960; Stoddart, 1962), *Montastrea annularis* is the basic reef framework builder, estimated to comprise more than 60 percent (by volume) of the total coral. If the various species of *Acropora*, *Porites* and *Diplora*, and the hydrozoan *Millepora* were added to this estimate, the figure is closer to 95 percent. These few species adapt to the various environments of the atoll by assuming different growth forms. Thus, for instance, *Montastrea annularis* has four basic growth forms: the massive (and most common) form is typical of the reef flat and shallow lagoon; the columnar form is found throughout the lagoon; the pinnacle and foliose forms are more typical of the deeper lagoon reefs. Similarly, *Acropora palmata*, *Porites porites* and *Millepora alcicornis* were noted to have several growth forms.

The main difference between Nicaraguan and Pacific atolls is the relative importance of encrusting coralline algae. Although algal encrustations cover portions of the Nicaraguan reef flats, and coat much of the reef debris, massive colonies of red algae such as *Porolithon* species that form the Pacific algal ridges are lacking. Thus the Caribbean equivalent to the algal ridge is mainly *Millepora* coral; coralline algae only encrust the emergent colonies. The general lack of red algae in the Caribbean has also been noted by Goreau (1959) and Fosberg (1962).

Perhaps it is this lack of profuse encrusting red algae that limits the development of an algal ridge and results in the general lack of reef cohesiveness that so many Caribbean reef workers have observed (Wells, 1957; Newell, 1959). This point should be one of future study.

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APPENDIX: REEF PRODUCTIVITY MEASUREMENTS

by John D. Milliman and Conrad V. W. Mahnken [1]

Oxygen Uptake on Reef Flats

Hydrographic observations were taken on transects across the reef flats of Courtown and Albuquerque cays. Three stations comprised the transect at Courtown (between East and Sand cays); four stations comprised the Albuquerque transect (south of South Cay). Each station was marked by two anchored buoys, placed at approximately equally spaced intervals across the reef flat. The outermost station (referred to as Station 1) of both transects was about 75 m leeward of the outer reef margin; the innermost (Station 3 at Courtown, 4 at Albuquerque) was on the leeward margin of the inner reef (Figure A-1). Observations were taken at approximately three-hour intervals for 25 hours at Courtown Cays (23-24 May). The outer reef stations were not sampled at night due to hazardous navigation; values, however, could be inferred from sunset and pre-dawn values.

Water and air temperatures were measured with a "bucket" thermometer, the accuracy being about ± 0.5°C. Current direction and velocity were estimated by measuring the direction and time for a partially submerged small float to traverse a distance of 10 m. Salinity and oxygen samples were taken; the oxygen samples were then "pickled," using the standard Winkler technique, and stored in a dark, cool place until return to the laboratory.

Temperature, salinity and oxygen variations over the outer and inner reef flats of Courtown and Albuquerque cays are shown in Figures A-2 and A-3. The ranges of oxygen and temperature values generally were greater at the inner stations (higher values in daytime, lower at night). Salinity remained more or less constant, indicating the relatively rapid passage of water over the reef flat. Currents on the reef flat stations at Courtown Cays ranged from 26 to 36 cm/sec and at Albuquerque Cays, from 13 to 15 cm/sec.

Oxygen change in flowing waters is expressed as the product of mean current velocity, mean water depth, and the difference in oxygen concentrations between the up- and down-stream stations (Sargent and Austin, 1954). In calculating the oxygen uptake on the outer reef

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	NET OXYGEN GAINED (ml/cm/day)	NET OXYGEN LOST	NET OXYGEN GAIN (ml/cm/day)
Total reef flat (sta. 4 - ocean sta.)	69,000	8,200	60,900
Outer reef flat (sta. 1 - ocean sta.)	83,000	0	83,000
Inner reef flat (sta. 4 - sta. 1)	9,800	30,600	-20,800
ALBUQUERQUE CAYS			
Total reef flat (sta. 3 - ocean sta.)	75,000	7,300	67,700
Outer reef flat (sta. 1 - ocean sta.)	67,300	0	67,300
Inner reef flat (sta. 3 - sta. 1)	37,200	36,400	-800
COURTOWN CAYS			

Table A-1. Computation of oxygen gain and loss on the reef flats of Albuquerque and Courtown Cays.

		REEF STATIONS			
	OCEAN	1	2	3	4
Courtown	----	2.87	3.15	3.18	----
Albuquerque	----	2.37	2.23	4.47	5.38
Western Caribbean	2.21				

Table A-2. Twenty-four hour mean surface carbon fixation (g/Carbon/m^3/day) at stations across the windward reef of Courtown and Albuquerque Cays and oceanic waters of the western Caribbean.

flat, open-ocean and outer reef flat values represent up- and down-stream values, respectively [1/]; for the inner reef, outer reef and inner reef values represent up- and down-stream values. Oxygen uptake across the entire reef flat is reflected by the difference in open ocean (up stream) and inner reef (down stream) oxygen values. The calculated oxygen changes in the reef waters at Courtown and Albuquerque Cays are shown in Figures A-4 and A-5. Integration of the area above the zero lines quantifies the net gain in oxygen; similarly, the area below the line represents the net loss. These values (for 24 hours) are given in Table A-1.

At Courtown Cays most of the oxygen uptake occurred on the outer reef; the net oxygen gain on the inner reef flat was negligible. At Albuquerque Cays, waters flowing across the inner reef flat actually lost oxygen; the entire oxygen uptake occurred on the outer reef.

If the oxygen influx had been strictly due to biologic activity, a net loss of oxygen would have been expected at night. The fact that incoming ocean waters continually gained oxygen on the outer reef suggests that oxygen is entering from a non-biologic source. Blanchard and Woodcock (1957; cf. Gordon and Kelly, 1962) showed that the trapping of air bubbles by breaking waves can cause oxygen saturations up to 115 percent. With surf almost constantly crashing on the outer reefs of both atolls, oxygen can be continuously forced into the incoming waters.

Without a proper measure of the amount of oxygen physically put into the outer reef waters, no measure of reef productivity can be made. However, these observations lend support to the opinion that most oxygen uptake takes place on the outer edge of the reef (Gordon and Kelly, 1962).

Plankton Productivity

At each station the plankton productivity of the ambient reef waters was determined by measuring the C-14 uptake (Steeman-Nielsen, 1952). Dark and light bottles were inoculated with C-14 and incubated *in situ* in a series of short-term experiments corresponding in time to the periods between oxygen sampling. The bottles at each station were hung from lines attached between two buoys. Upon retrieval, the water in each bottle was filtered through an HA Millipore filter (0.45 μ pore opening). The individual filters were stored and later counted at

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[1/] In these calculations it is assumed that open ocean water approaching the atoll is in equilibrium with the atmosphere (that is saturated with oxygen). Indeed, oxygen values in the upper 20 m of nine oceanographic stations occupied by the U.S. Fish and Wildlife service GERONIMO during October 1965, in the vicinity of Courtown Cays, are essentially at saturation levels (101 - 1 percent; 4.45 ± 0.01 ml/1), with a diurnal range of hundredths of a ml/1 (unpublished data).

the U.S. Bureau of Commercial Fisheries Radiobiological Laboratory, Beaufort, N.C.

Two trends of plankton productivity are apparent at both atolls: there is a marked diurnal variation in carbon fixation, and there is a net increase in carbon fixation from the windward to leeward stations across the reefs (Figures A-6, A-7; Table A-2). Because no synoptic oceanic measurements were taken for comparison, we have used a mean production estimate of five ocean stations occupied in October 1965, by the F. W. S. GERONIMO, along a section extending 700 km to the windward of Courtown and Albuquerque Cays. Since light inhibition is characteristic of shallow surface waters at all five ocean stations (maximum productivity is at 10 to 15 m) (unpublished data) the strong light must also tend to inhibit planktonic productivity on the shallow reef stations at the two atolls. Consistent with this assumption is the similarity between mean surface carbon fixation rates for the oceanic and windward reef stations (Table A-2). The successive increase in carbon fixation across the reefs in the direction of flow therefore may not be attributed to planktonic algae, but instead may be related to the presence of benthic algae, torn loose from the reef flat, which are not inhibited by high irradiance. The reef water possibly accumulates more benthonic fragments as it passes across the reef, accounting for the increase in net carbon fixation at the innermost stations. Thus the relative contribution of planktonic forms to the overall productivity of the reef flat is probably nil; Odum and Odum (1955) reached a similar conclusion.

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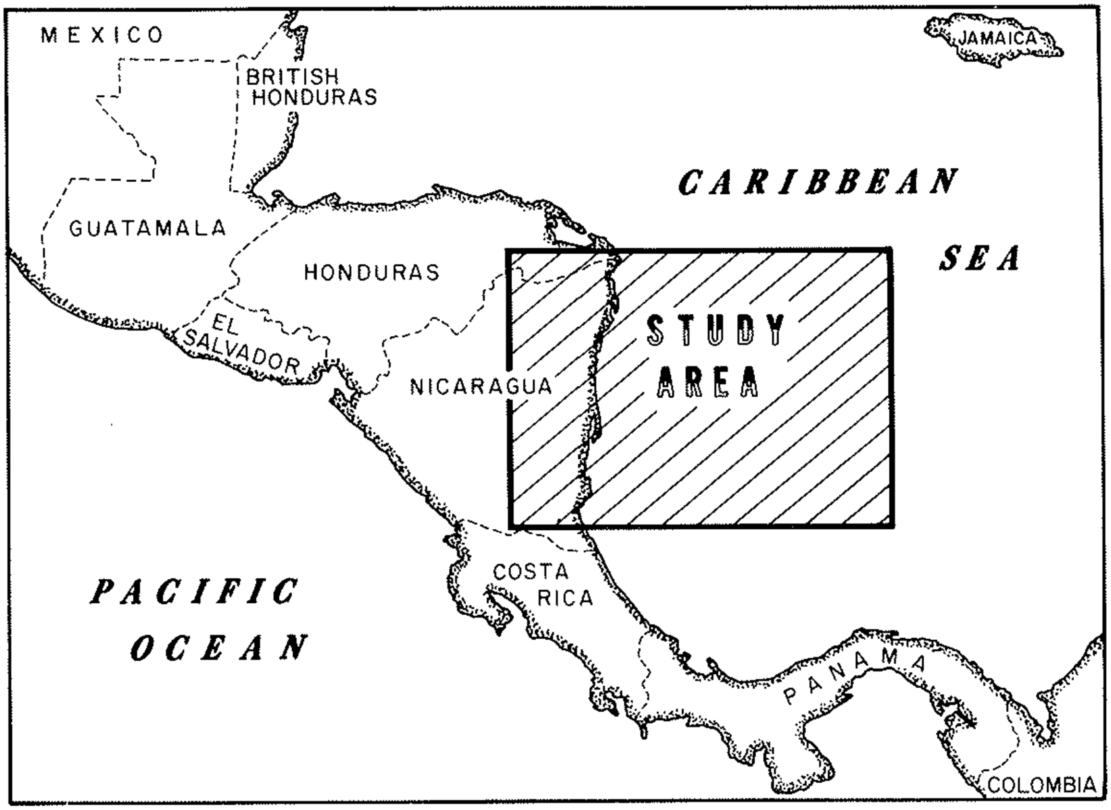
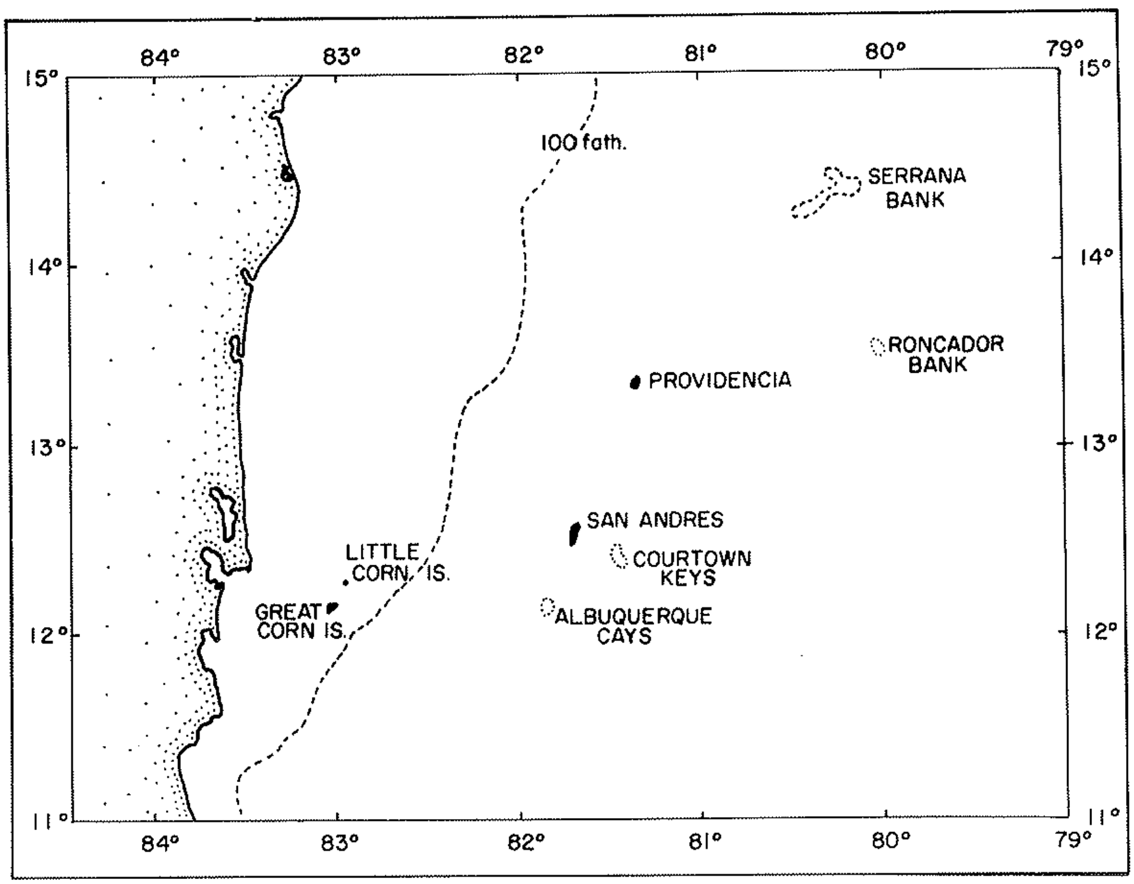
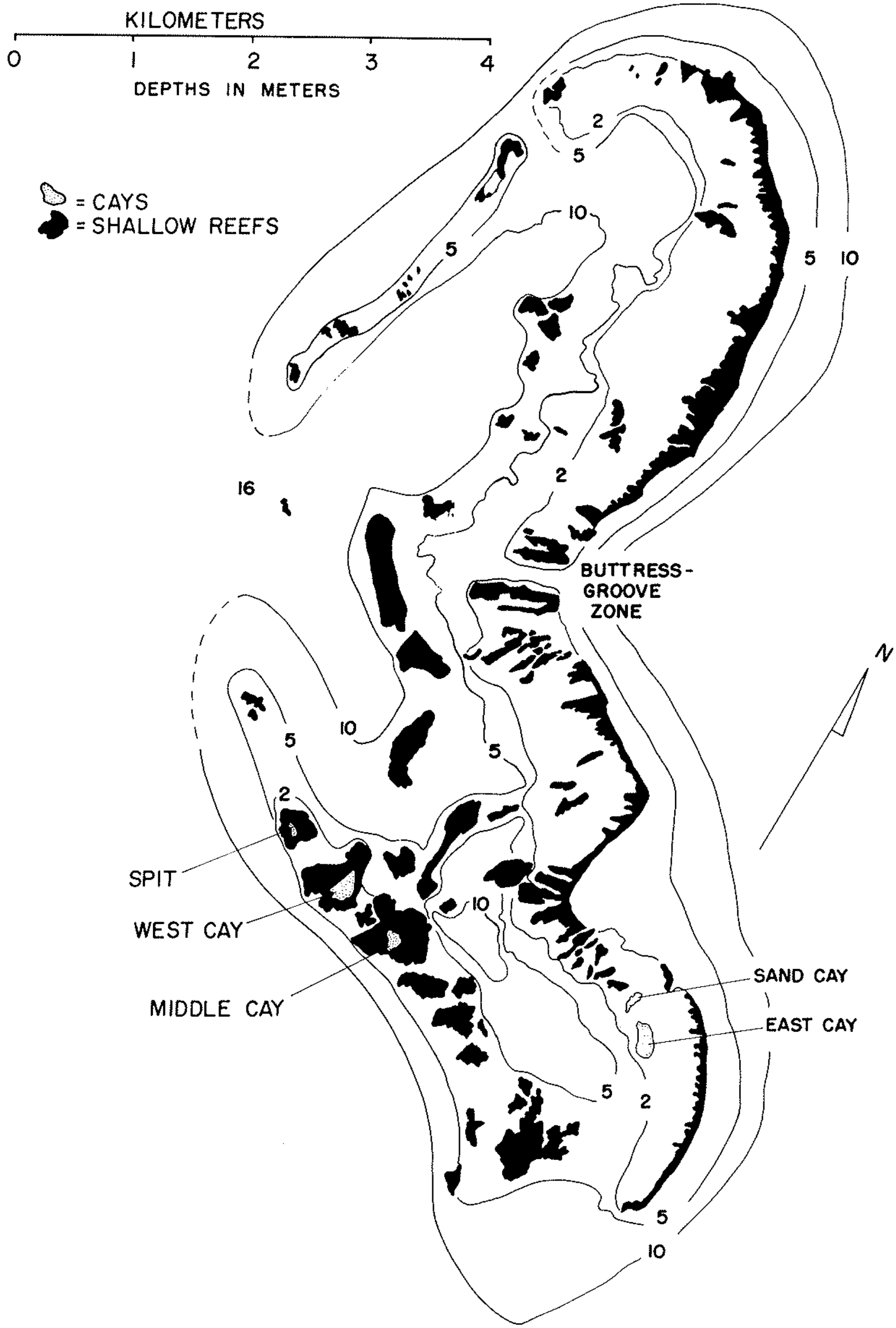


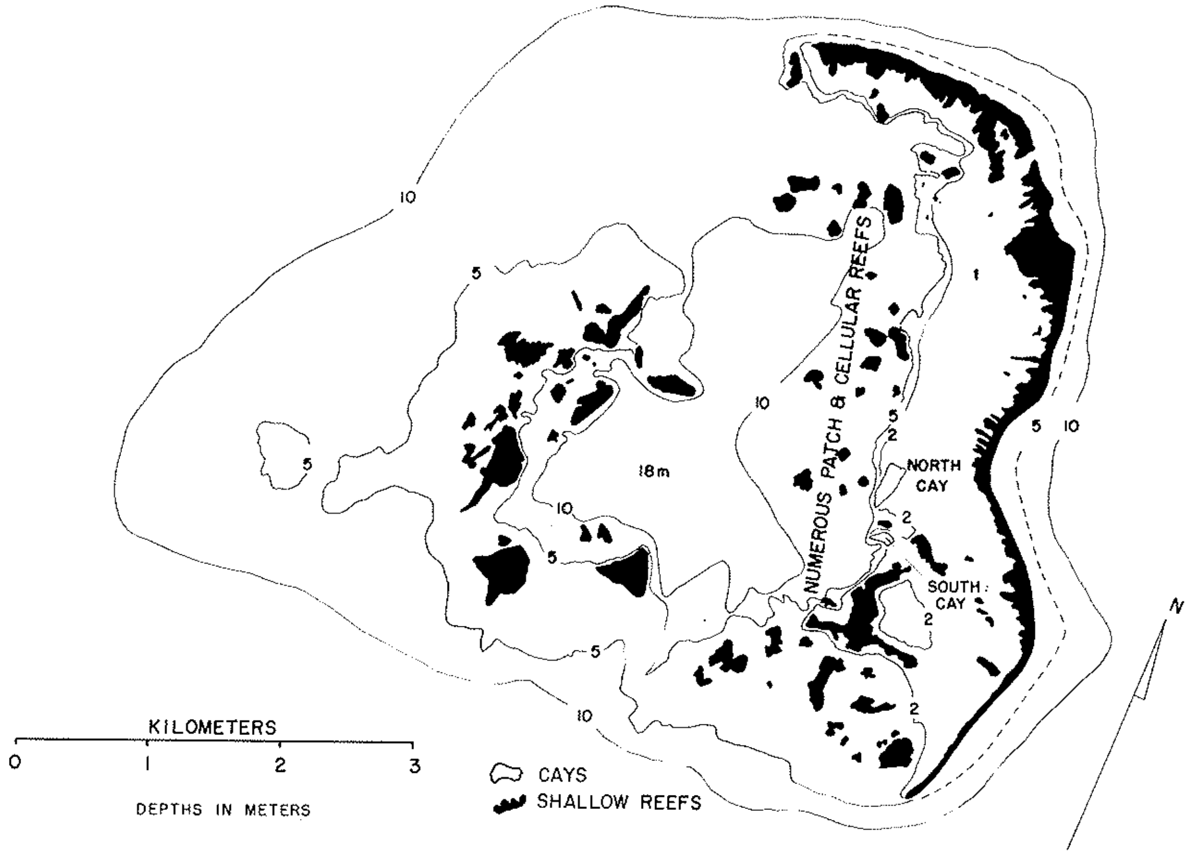
1. Chart of western Caribbean and Central America.



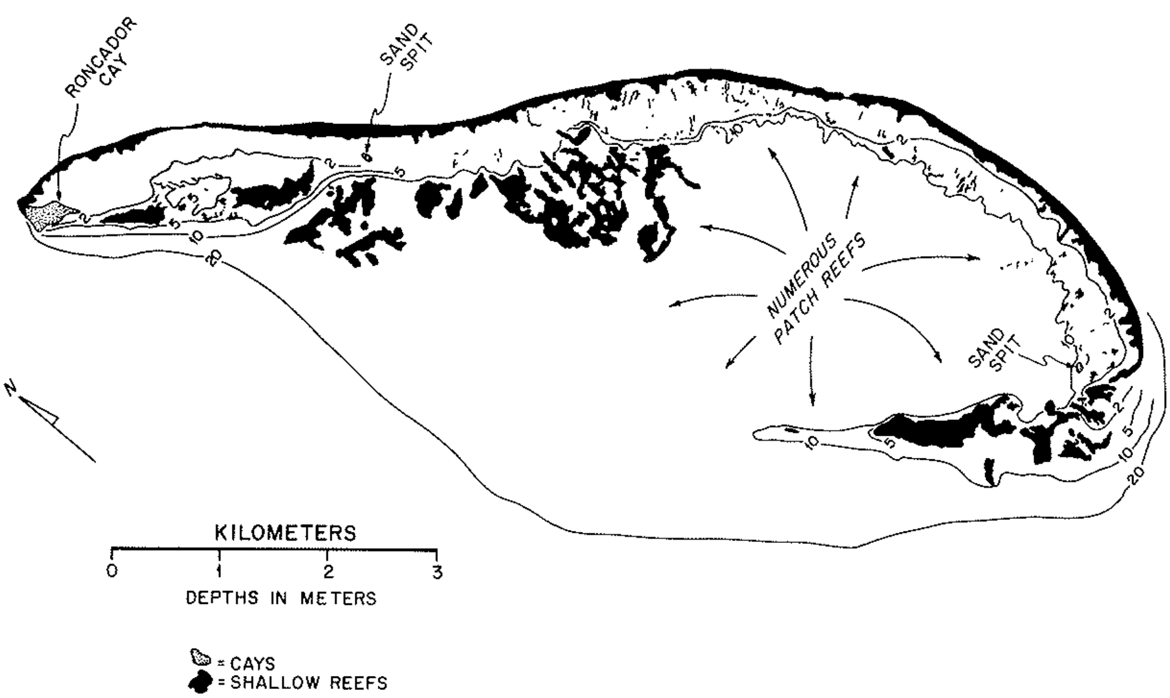
2. Study area chart.



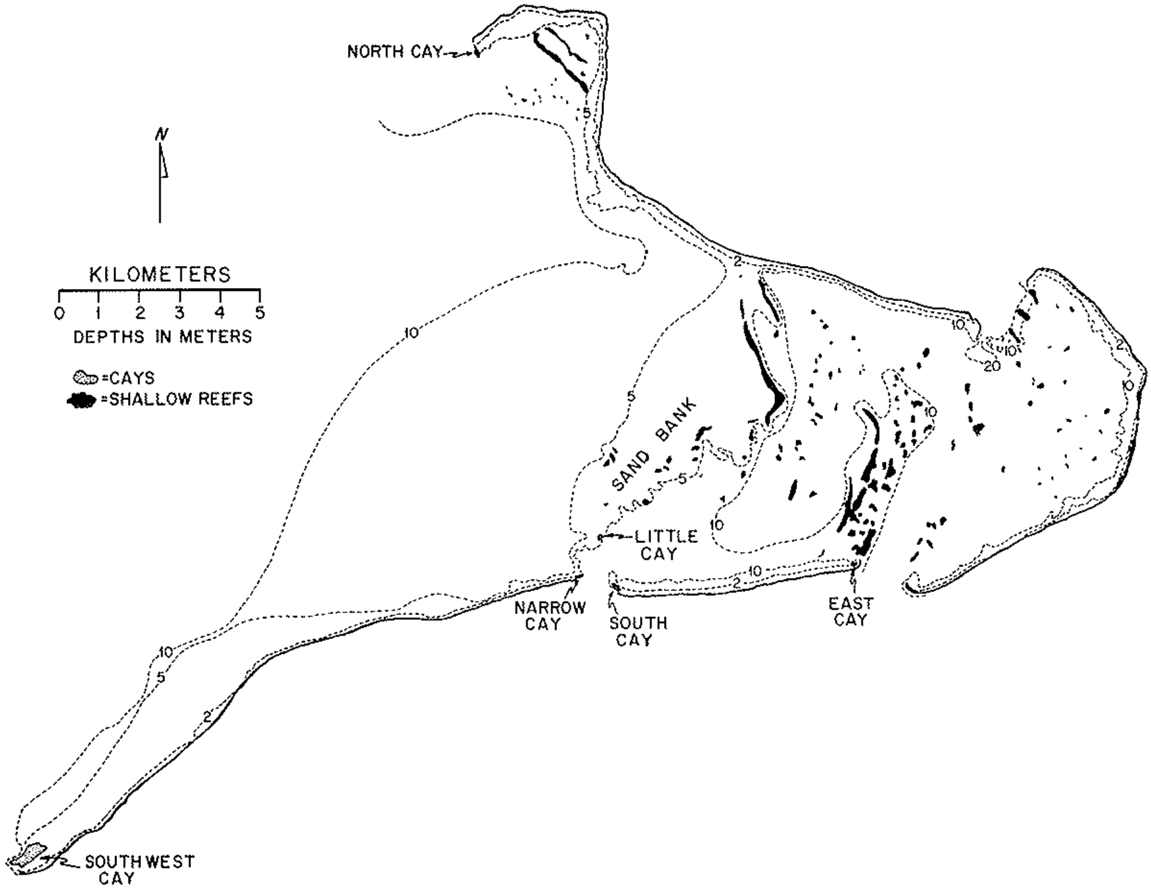
3. Chart of Courtown Cays, based on aerial photographs, H. O. Chart 2077, and observations made during the cruise.



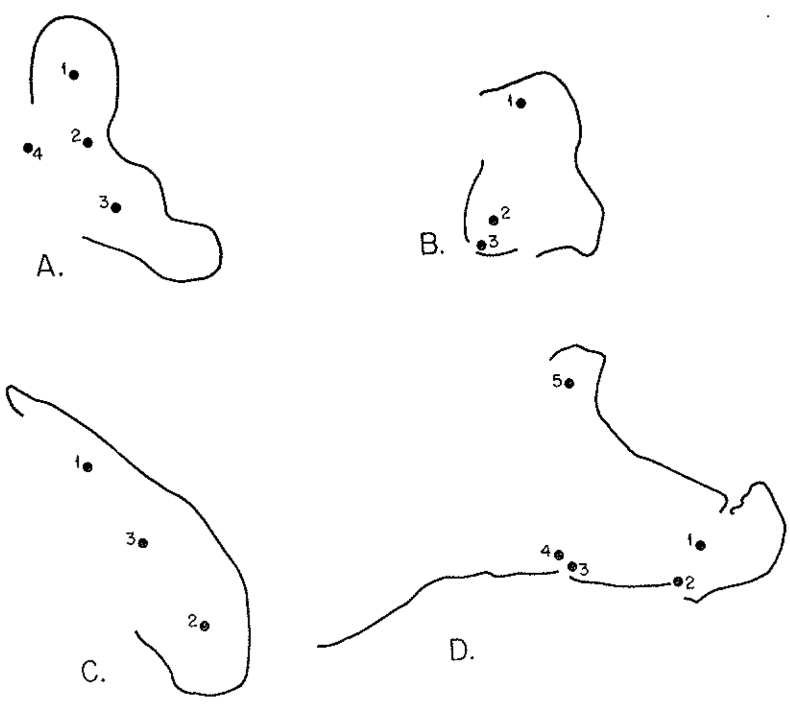
4. Chart of Albuquerque Cays, based on aerial photographs, H. O. Chart 2077, and observations made during the cruise.



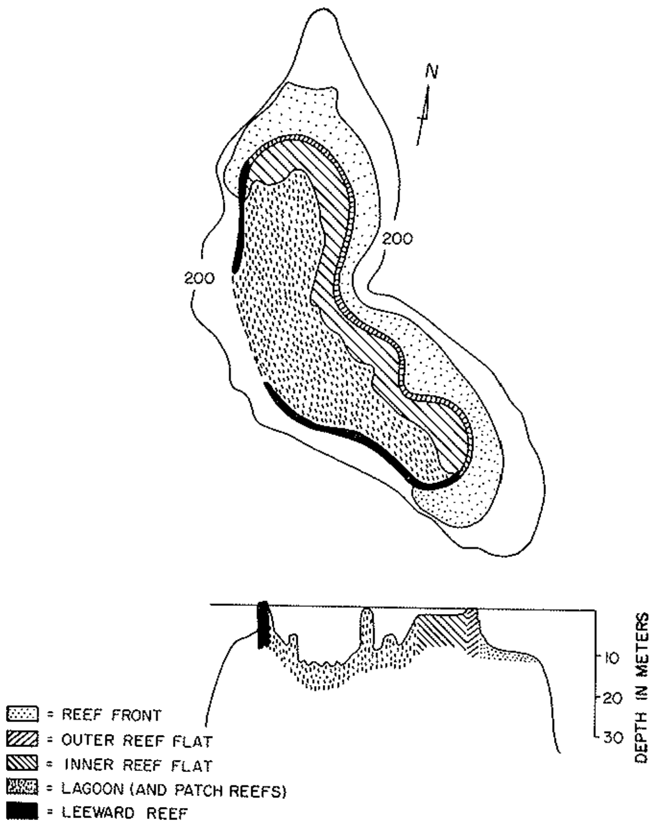
5. Chart of Roncador Bank, based on aerial photographs, H. O. Chart 1374, and observations made during the cruise.



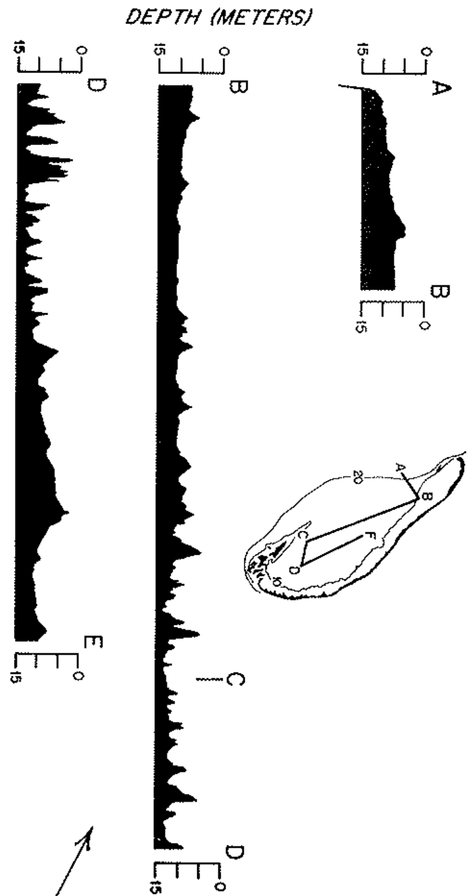
6. Chart of Serrana Bank, based on aerial photographs, H. O. Chart 1374, and observations made during the cruise.



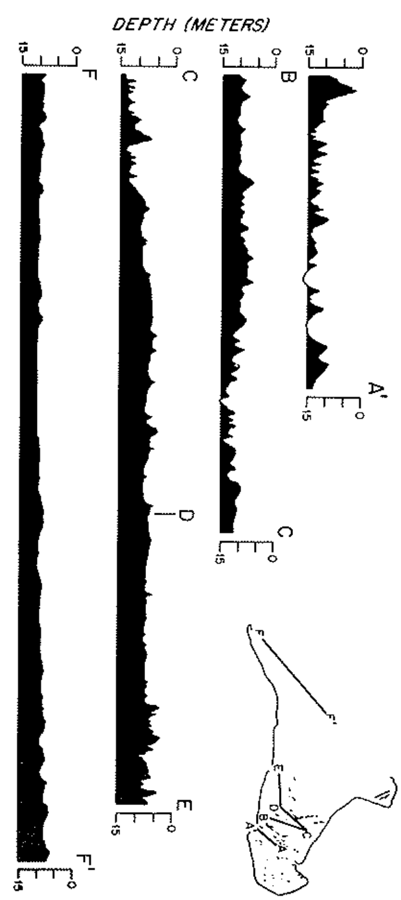
7. Locations of hydrographic stations occupied at Courtown Cays (A), Albuquerque Cays (B), Roncador Bank (C) and Serrana Bank (D).



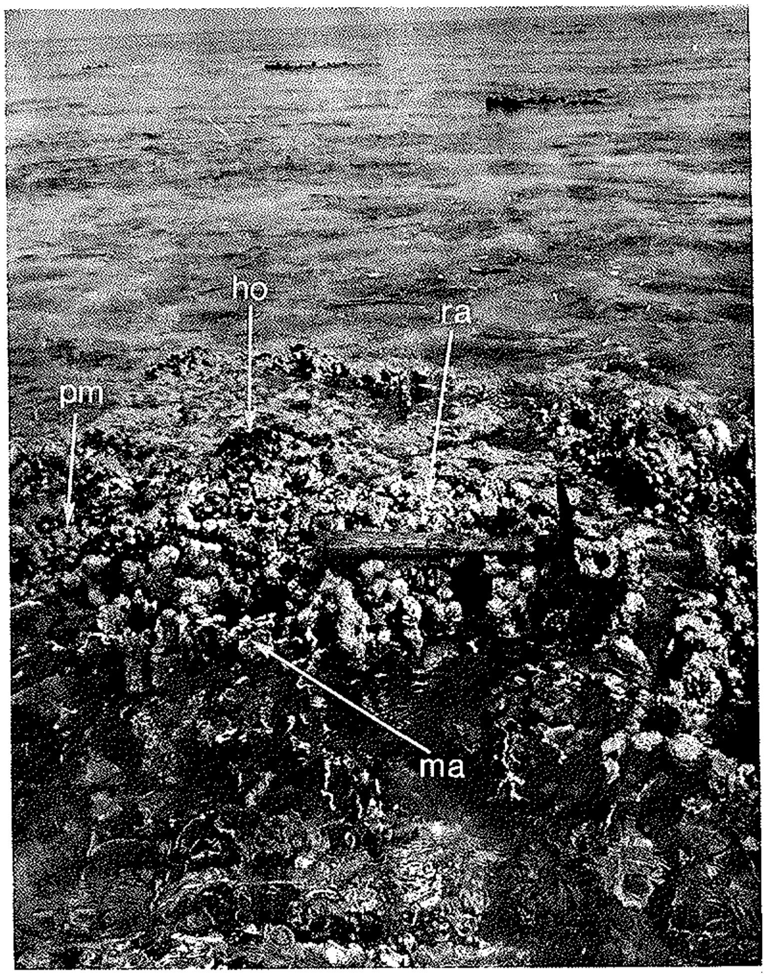
8. Idealized plan and cross sectional views of the ecologic zonations at Courtown Cays. The other atolls have similar zonations.



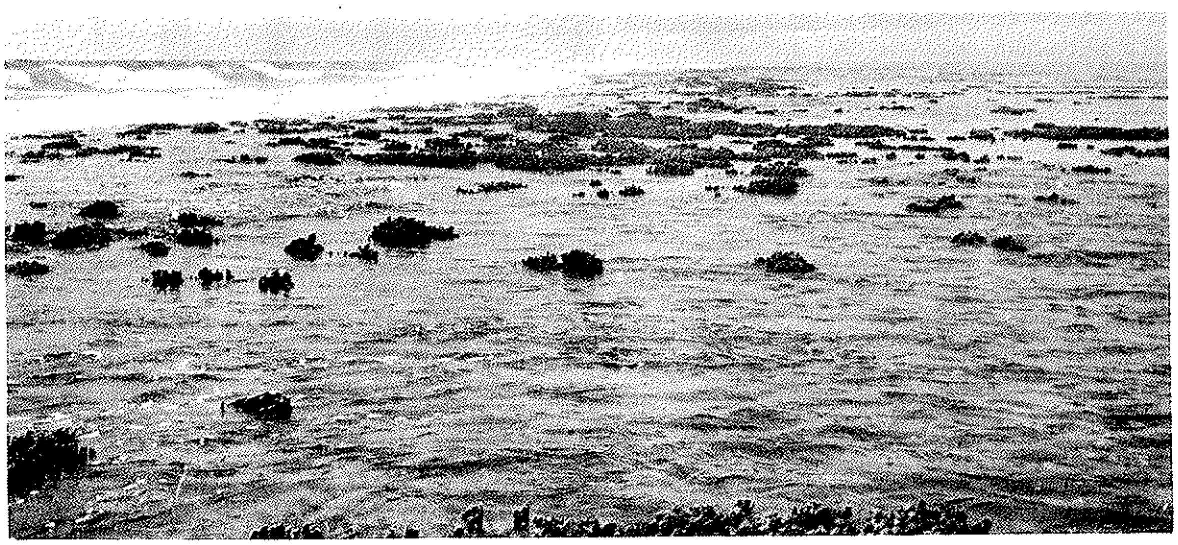
9. Profiles of the lagoon at Roncador Bank, based on soundings made during the cruise. These profiles depict the great number of patch reefs within the lagoon, and also show the lack of any apparent sill (profile AB).



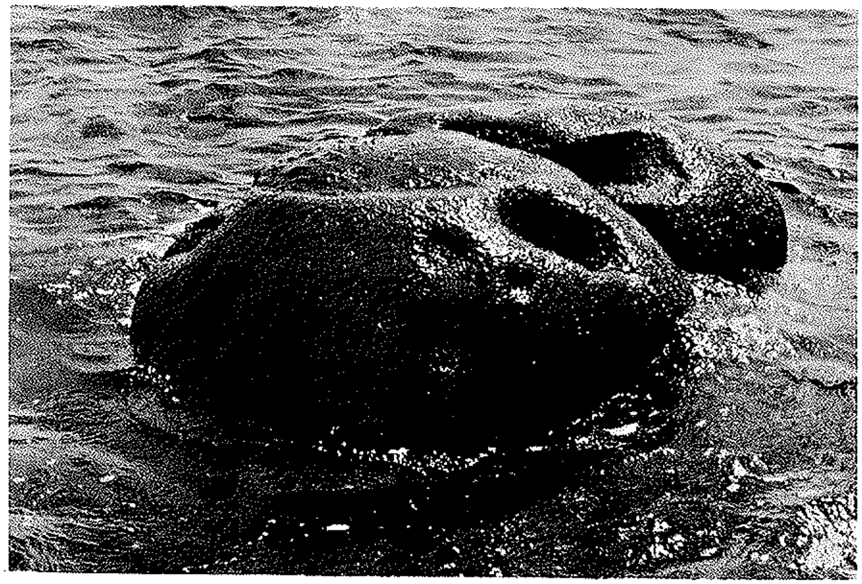
10. Profiles of Serrana Bank lagoon. These profiles show the contrast of the great number of patch reefs in the eastern part of the lagoon, and the relatively flat, shallow lagoon bottom to the west (profile FF').



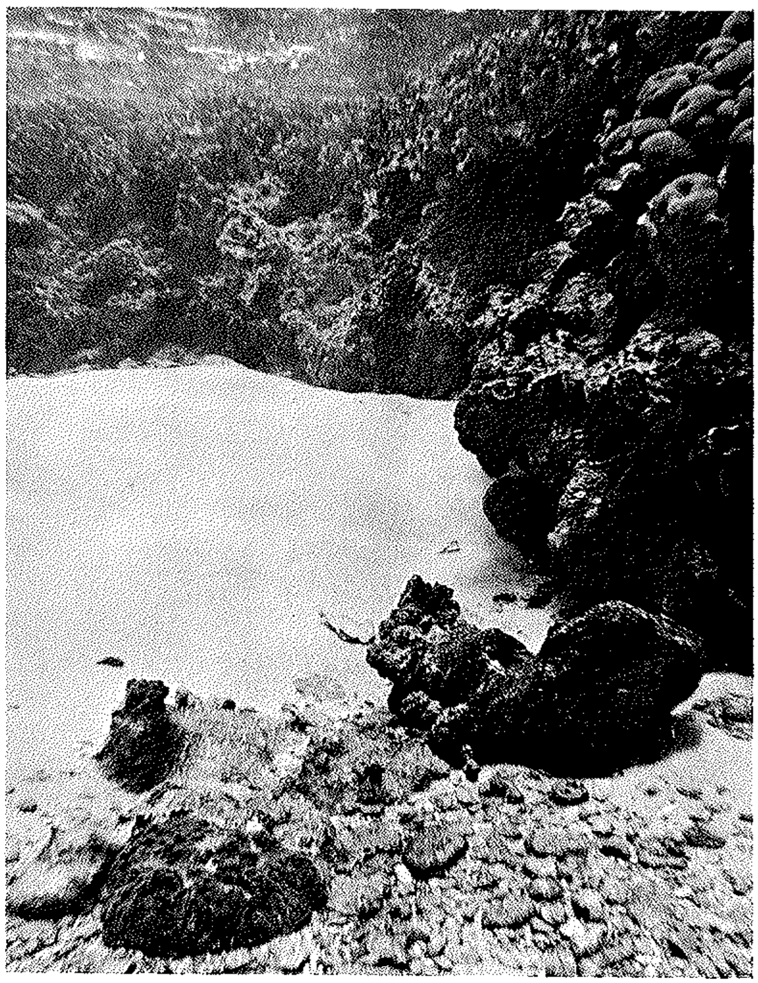
1. The Millepora zone, composed primarily of the flat hydrocoral Millepora alcicornis (labeled ma in picture), the soft coral Palythoa mammillosa (pm) and encrusting red algae (ra); Halimeda opuntia (ho) is also common.



2. A panoramic photograph of the Millepora zone in the heavy surf zone (left) of the outer windward reef. This picture was taken at Roncador Bank during spring low tides; similar, but somewhat less well-developed colonies are found at the other atolls.

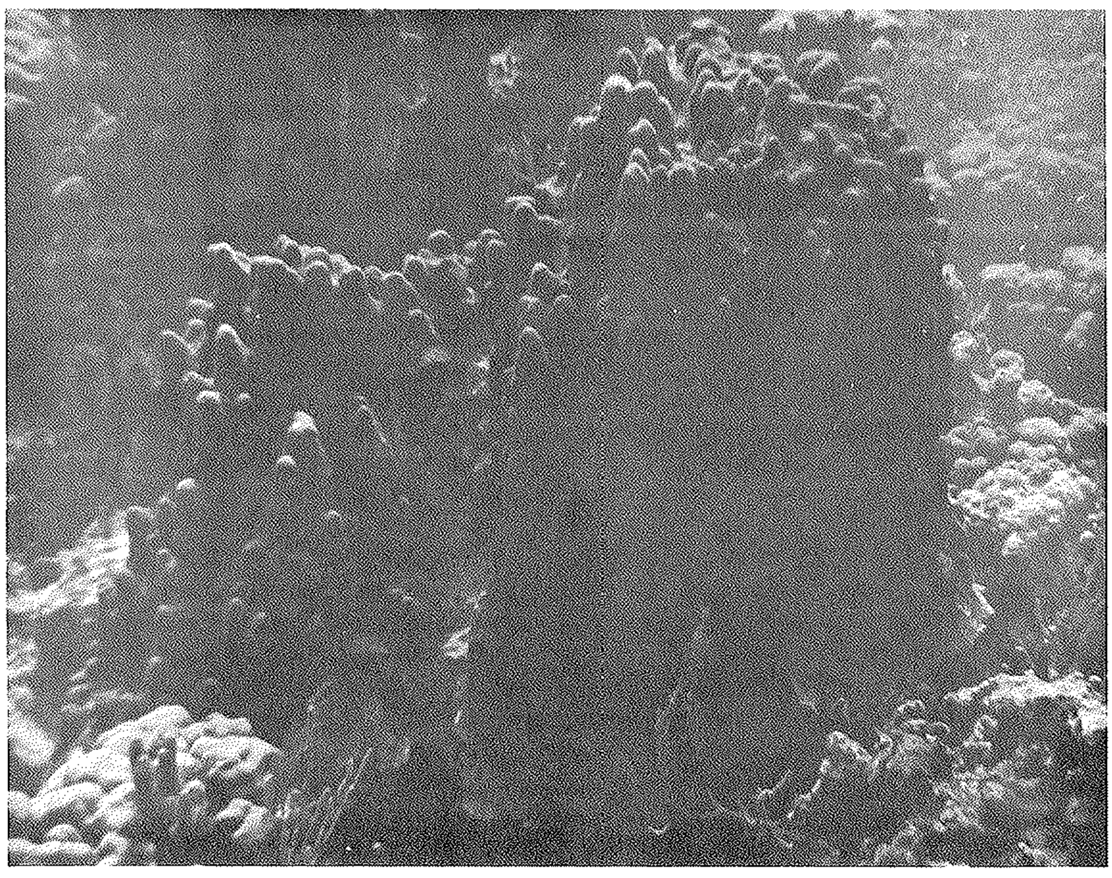


3. A large colony of Diploria, located in the Diploria zone on the outer reef, is seen exposed about 1/2 m above low tide. The upper 10 cm of the coral is dead, perhaps reflecting the limit to which normal waves can bathe it.

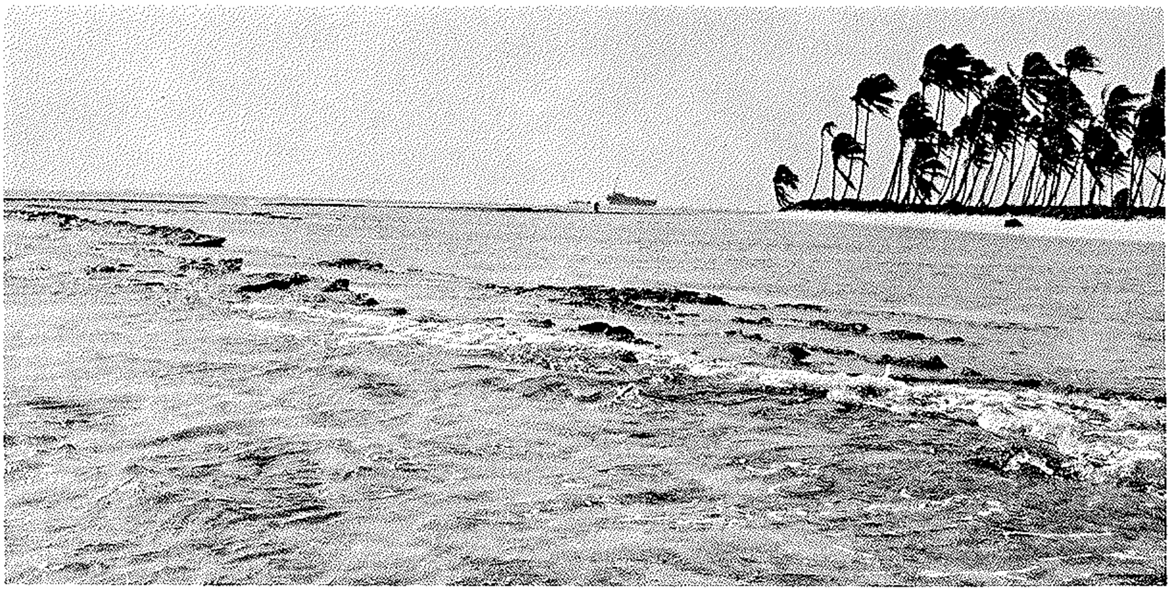


4. Depths in the inner reef flat (foreground) are significantly greater than on the outer reef flat (background).

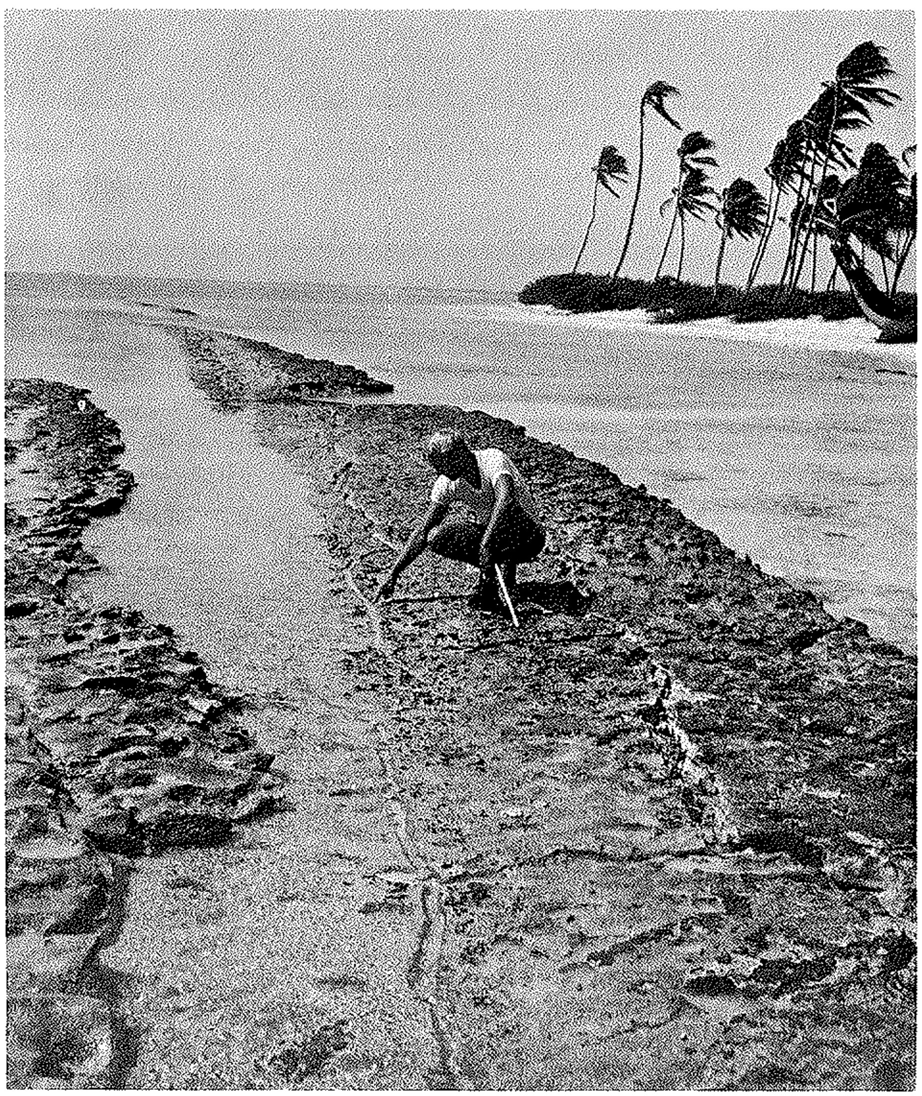
5. At all atolls the majority of lagoon reefs are scattered, low-lying patches. The bottom depth in this photograph is about 13 m; the diver is 5'10" tall.



6. Patch reefs often have an abundance of foliose and pinnacle growth forms of Montastrea annularis, the latter shown in the center of this picture.



7. Bands of beachrock extend windward from East Cay at Courtown Cays, seemingly indicative of the lagoonward migration of the cay. Tall palm trees characterize the vegetation on East Cay. In the background is the wreck of a Colombian ship, awash on the reefs.



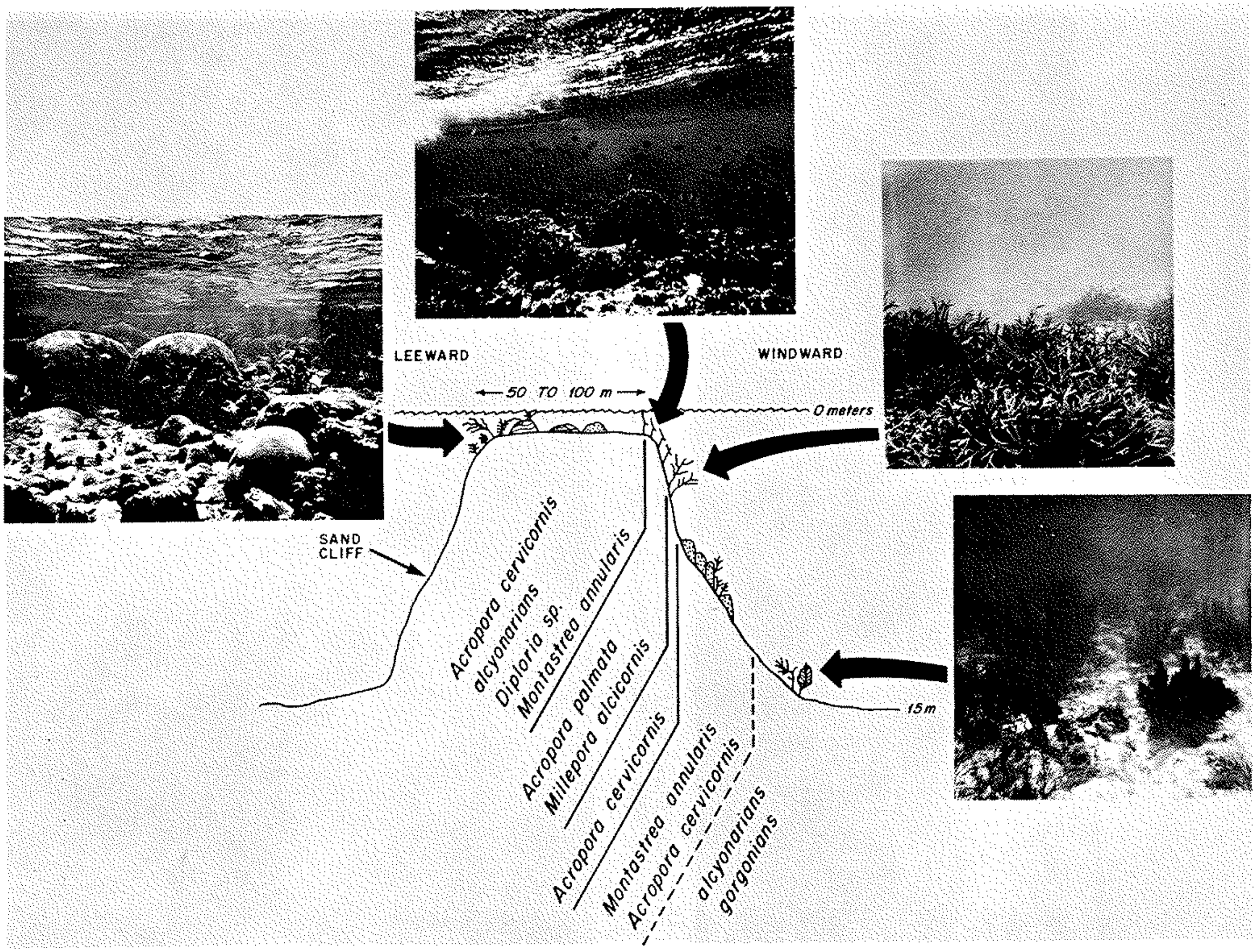
8. Close-up picture of the beachrock bands. Fissures are parallel and perpendicular to the strike of the rock.

9. Elevated beachrock at North Cay, Albuquerque Cays. Recent beachrock is in the foreground of the picture.

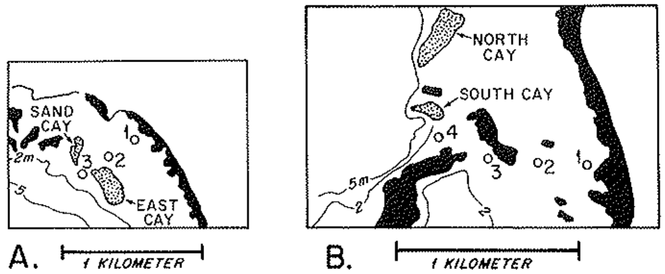
10. Dense Ficus **forest** at South Cay, Albuquerque Cays.

11. Rocks emergent at low tide line the windward rim of the outer reef at Roncador Bank. Roncador Cay is seen in the background.

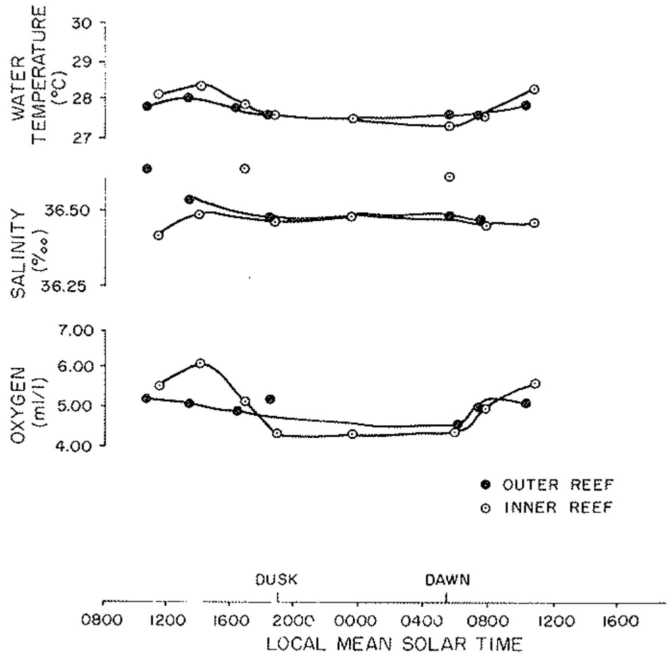
12. Roncador Cay is covered with a rubble of coral heads. Piles of these dead corals were once used as walls.



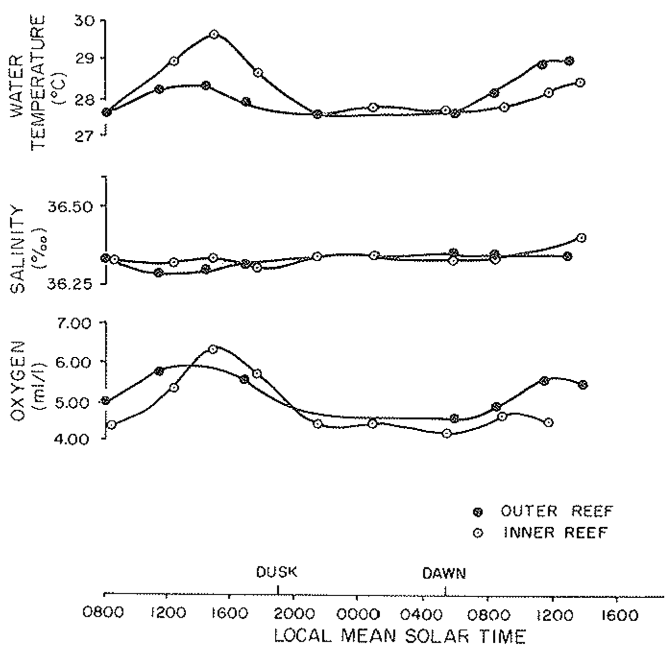
3. A cross-section of a lagoon patch reef at Serrana Bank. The photographs illustrate the various communities that characterize the different depths and environments.



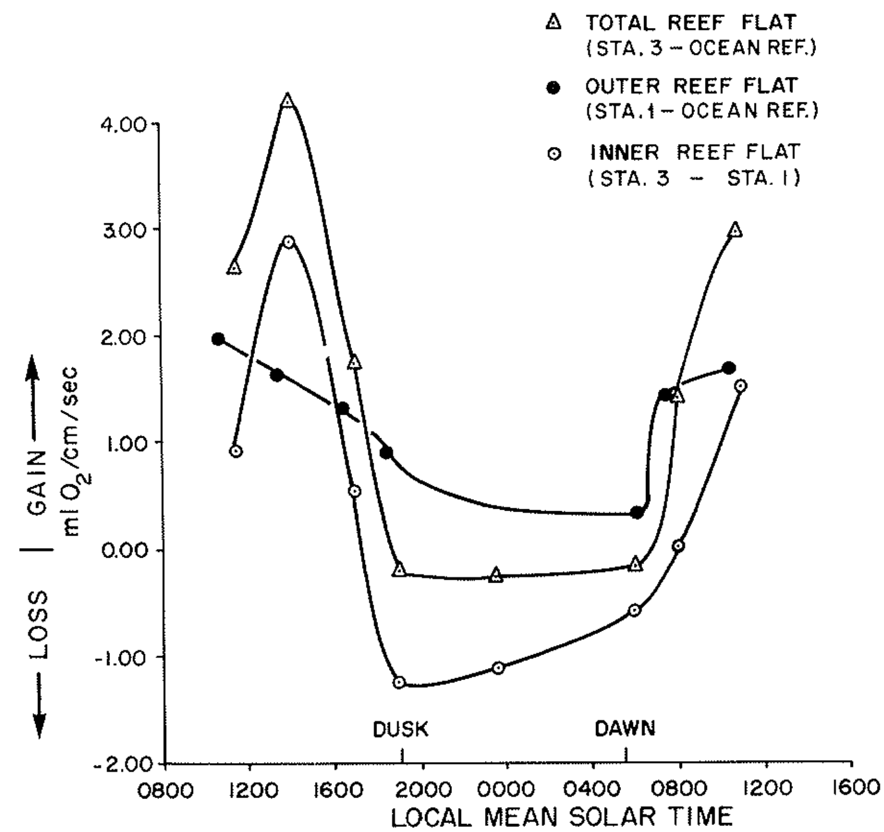
A-1 Locations of reef productivity stations at Courtown and Albuquerque Cays.



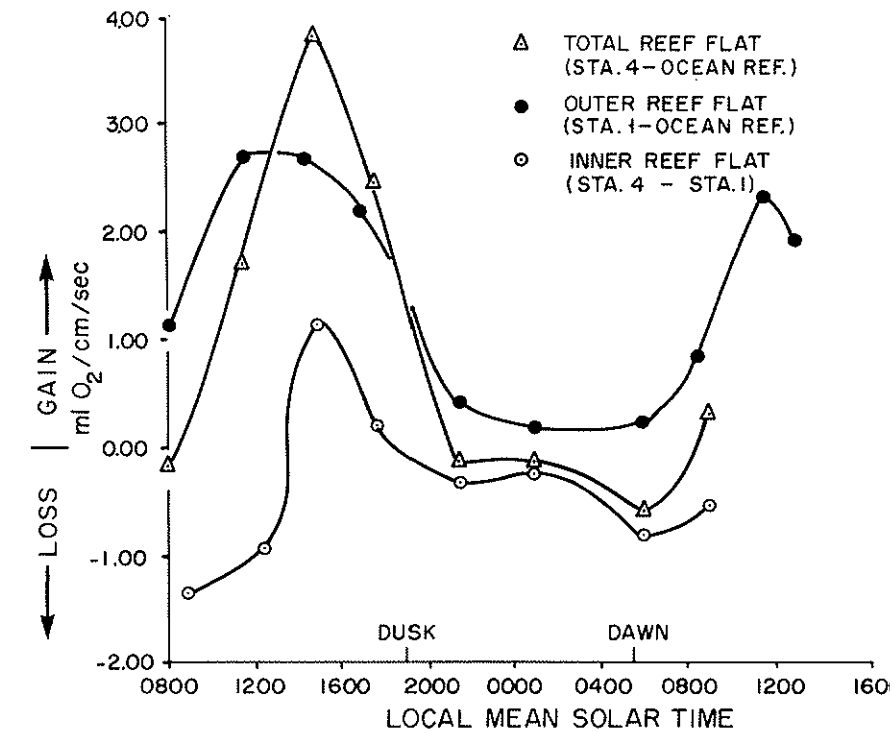
A-2. Time plot of temperature, salinity and oxygen variations on the reef flats of Courtown Cays.



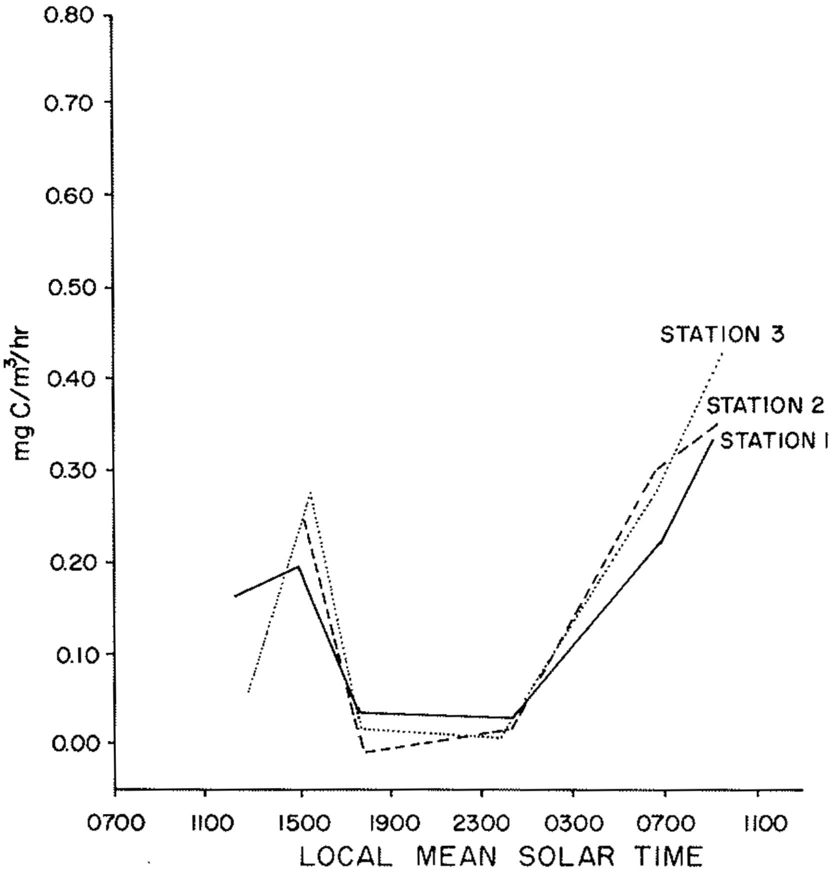
A-3. Time plot of temperature, salinity and oxygen variations on the reef flats of Albuquerque Cays.



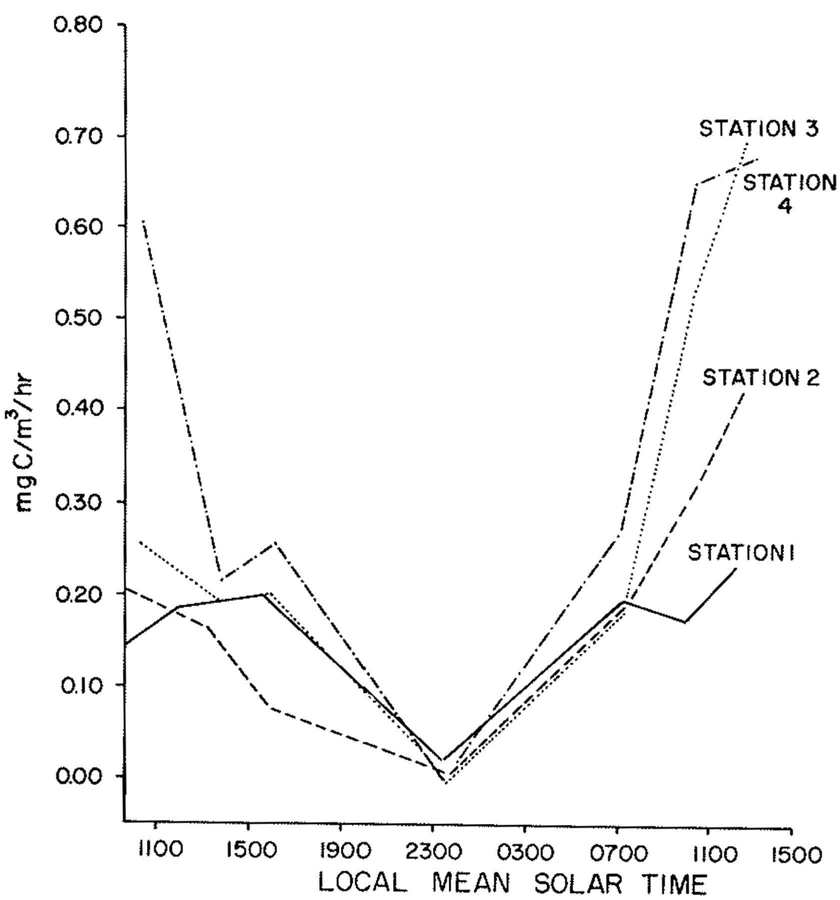
A-4. Calculated oxygen gain and loss on the reef flats of Courtown Cays.



A-5. Calculated oxygen gain and loss on the reef flats of Albuquerque Cays.



A-6. Carbon fixation rates across the windward reef flat of Courtown Cays.



A-7. Carbon fixation rates across the windward reef flat of Albuquerque Cays.