ORGANISM COMMUNITIES AND BOTTOM FACIES, GREAT BAHAMA BANK

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INTRODUCTION

Accurate interpretations of past sedimentary environments form a central problem in historical geology. These interpretations are based mainly on the meager and frequently equivocal evidence of fossil organisms and their enclosing rock matrix. Any inquiry into past conditions and past events is necessarily deductive in method, as the past cannot be observed. But logical, and frequently quite detailed, inferences of high probability about the past may be drawn with the aid of analyses of present environments and their sedimentary products. Consequently, historical geologists, heeding Hutton's dictum that "the present is a key to the past," occasionally study observable processes and conditions in the perennial search for answers to questions about the past.

The present contribution is a report on the results of a reconnaissance field study of living marine bottom organisms and sedimentary conditions of one of the few remaining tropical "limestone seas," the Great Bahama Bank. This area and adjacent shoal platforms to the southeast of Florida (fig. 1) are covered by shallow shelf seas similar to those that were widespread in the past and responsible for deposition of great amounts of limestone. The waters of the Bahamas are warm, locally very clear, and they are completely free from terrigenous clay and quartz. All of the abundant sedimentary materials are composed of calcium carbonate. In this regard, the Bahamian platforms resemble oceanic atolls.

Our field work, undertaken during late May and June in 1955, 1956, and 1957, was based at the Lerner Marine Laboratory, a field station of the American Museum of Natural History, situated on Bimini, about 60 miles east of Miami, Florida (pl. 58). In keeping with the large size of the area studied, about 15,000 square kilometers, field mapping and sampling were generalized for small-scale reproduction. Somewhat more detailed field studies and mapping were undertaken around Bimini and the cays to the south, an area that is covered by aerial photographs of the United States Hydrographic Office. The sea floor in this area generally is visible on the photographs.

Regional studies by Black (1930), Cloud (1955), Field (1931), Illing (1954), Newell and Rigby (1957), C. L. Smith (1940), Thorp (1936, 1939), and Vaughan (1913, 1918) had prepared the way and provided an understanding of some of the salient geological and biological problems of the area.

Except for aid from specialists that is acknowledged below, we are responsible for the identifications of organisms cited herein. The present work does not include a quantitative census or even an enumeration of all the common benthonic species. The Bahamian fauna and flora are not well known, and long-sustained effort by many collectors and taxonomic specialists is required before the specific composition of the bottom biota can become really well known. We have, however, made an effort to record accurately the most conspicuous and distinctive species, the indicator organisms, on which the communities are based. In common with the communities ("zones") described long ago by Edward Forbes, our communities are distinguished "by association of the species they severally include. Certain species in each are found in no other; several are found in one region which do not range into the next. . . . Certain species have their maximum of development in each zone, being most prolific in individuals in that zone in which is their maximum, and of which they may be regarded as especially characteristic. Mingled with the true natives of every zone are stragglers, owing their presence to the secondary influences which modify distribution" (Forbes, 1843).

SAMPLING METHODS

The work near Bimini was done from small open boats of the Lerner Marine Laboratory. The long traverses were made, however, in the two cabin cruisers of the Laboratory, the 30-foot "Research," powered by twin gasoline engines, and the 40-foot "Wild Goose," with twin Diesel engines. The cabin cruisers were gifts to the Laboratory from Mr. D. H. Braman and Mr. Ferdinand Eberstadt, respectively.

General observations of the substrate and bottom communities were made in shallow dives with simple face plate or Scuba equip-

ment at many hundreds of localities and recorded in the descriptions of field stations. The localities were plotted on tracings of aerial photographs or on the United States Hydrographic Office Chart 26a, Great Bahama Bank, Northwestern Part (scale 1:286,367). Although this map dates from surveys of the British Admiralty made more than a century ago and contains numerous minor errors, it served excellently as a base for regional ecological studies.

Map stations were located by dead reckoning and boat-to-shore triangulation with a sextant. Systematic observations and samples taken at approximately 90 stations along predetermined tranverses across the Bank (fig. 2)

provided most of the information from which the bottom conditions of the shelf lagoon were mapped (figs. 8, 9), but traverse samples obtained earlier by Henry Such Smith and described by Newell and Rigby (1957) supplied part of the control for the maps. Water samples were taken for salinity titrations at the Laboratory, and at a few stations an approximate measure of salinity was obtained with a G.M. sea-water hydrometer. Depth and temperature measurements were made at every station. Attempts to measure systematically the turbidity of the water by means of a Schulter submarine photometer were unsatisfactory because of strong light reflection from the shallow bottom, and unavoidable expo-

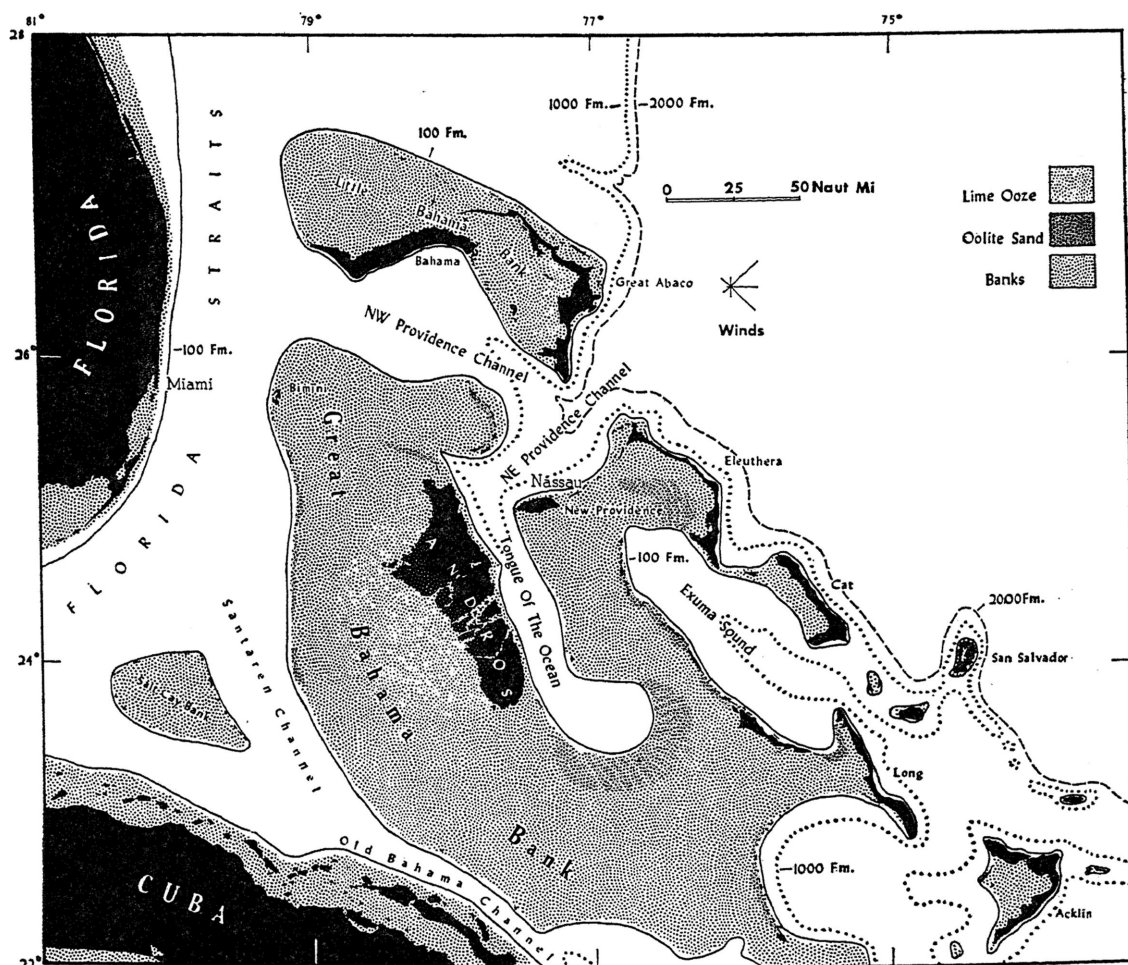FIG. 1. Great Bahama Bank and surrounding area. General form of channels and platforms and the location of principal deposits of lime ooze and oolite sand are indicated (Newell, 1955).
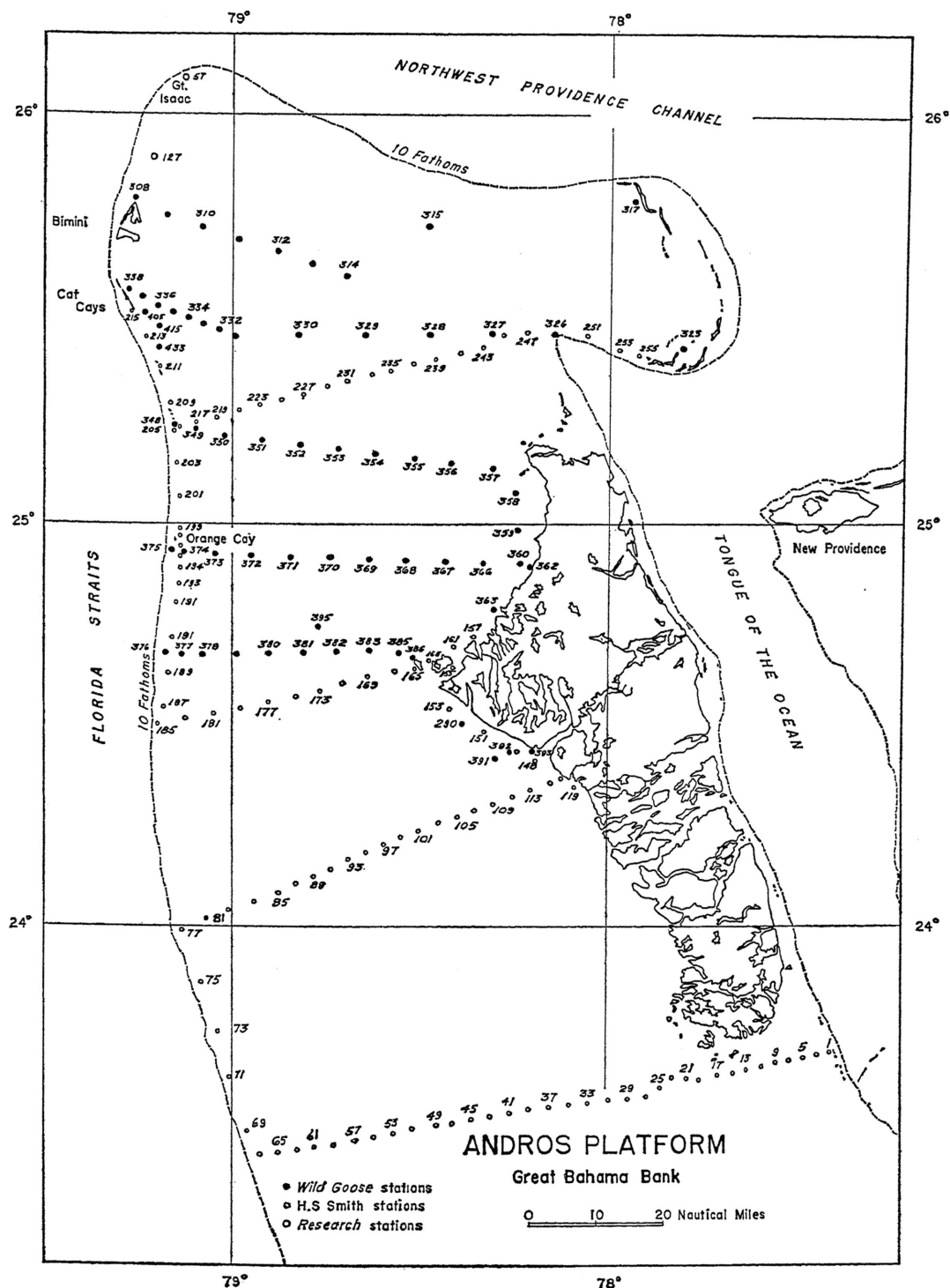
FIG. 2. Location of samples and traverses on Andros platform. H. S. Smith and "Research" samples are sediments only; "Wild Goose" samples include sediments and biological material collected by sieving and trawling.

sure of the control box to sea spray made most of the observations unreliable. Nevertheless, useful data on turbidity were obtained. A commercial glass-electrode pH meter (photovolt model 125), waterproofed against spray, was used for pH measurements. Current velocities and directions were measured with an Ekman current meter of the Gulf Research and Development Company.

At each of the traverse stations three methods of observing bottom conditions were used, and the data obtained were recorded. First, a dredge haul was taken at slow speed for five minutes. Next, the epibiota and substrate were observed directly from the surface or by means of shallow skin dives. Then a bottom sample was obtained with a Van Veen grab sampler. A small part of the unwashed sediment was collected for laboratory study, and the remainder (about 2 cubic feet) was passed through a one-quarter inch sieve and the coarse fraction examined for megascopic organisms. The community maps are based on living examples, but the distribution of dead skeletons was found to be in close agreement with the living forms. The results of these collecting methods were satisfactory. Doubtless the techniques employed explain the success in sampling organisms in areas that often have been described as relatively sterile.

ACKNOWLEDGMENTS

GENERAL PHYSICAL CONDITIONS ON THE GREAT BAHAMA BANK

LOCATION AND CLIMATE

THE ANDROS PLATFORM of the Great Bahama Bank lies southeast of Florida, beyond the Florida Straits (fig. 1). The area covered in this study lies within the belt of the trade winds between approximately latitude 23° 30' N. and latitude 26° N. It is bathed by tropical currents in which the mean surface temperatures range between around 24° C. in February, the coldest month, and 28.5° C. in August, the warmest month (Fuglister, 1947).

When air temperatures drop well below normal during winter storms, the inshore shallow waters are quickly chilled, and there is extensive mortality among certain fish of the bays and estuaries. The cold spells are not known to be particularly harmful to the fish wherever moderate depths and free circulation prevent extreme cooling of the water. There may be some damage to the shallowest reef corals, mollusks, and crustaceans at these times, but we have no records of such damage.

Climatic conditions that now prevail in the Bahamas permit occupancy of the region by the tropical West Indian biota. However, only a few thousand years ago the temperature was several degrees (6° C., according to Emiliani, 1958) cooler, and doubtless the region was occupied then by a very different biota of temperate type.

TOPOGRAPHY

The Great Bahama Bank is the largest of several submerged limestone plateaus or platforms that extend the continental shelf southeastward from Florida to the Greater Antilles. Each of the platforms is surrounded by deep water, and the Great Bank itself is divided by deep troughs (fig. 1) into a number of salients which may be conveniently specified as follows: the western lobe, between Florida Straits and Tongue of the Ocean, is the Andros platform; the Bank area between Tongue of the Ocean and Exuma Sound is the Exuma platform; and the names of the islands Eleuthera, Cat, and Long may be given to the platforms on which they rest. The southeastern extremity of the Great Bahama Bank has long been known as Columbus Bank.

The Andros platform is depressed to shallow depths generally less than 3 or 4 fathoms below sea level, and it is bordered by a barrier rim of limestone islands and cays formed, in part, of old beach ridges and dunes of Pleistocene age and modern sand ridges or bores (pl. 59). Along the eastern, or windward, margin there also are living coral reefs associated with the barrier rim. The shallow basin of the platform, termed shelf lagoon, is the site of accumulation of a thin blanket of recent calcium-carbonate sediments (fig. 3).

The basin-like form of the Andros shelf lagoon is interrupted by an inconspicuous broad shoal, the Bimini axis, which extends across the Bank in a west-northwest direction from northern Andros Island to Bimini (fig. 4). This is interpreted as a tectonic flexure of relatively recent, but otherwise uncertain, age. Another low ridge extends westward some 30 miles from the middle of Andros Island. This is Billy Island axis. The sediment cover apparently is thin over these structural features.

Outside the barrier rim is a narrow shelf, or outer platform, which is marked by drowned parallel beach ridges and erosional terraces (Newell and Imbrie, 1955). The outer platform slopes seaward from a depth of about 1½
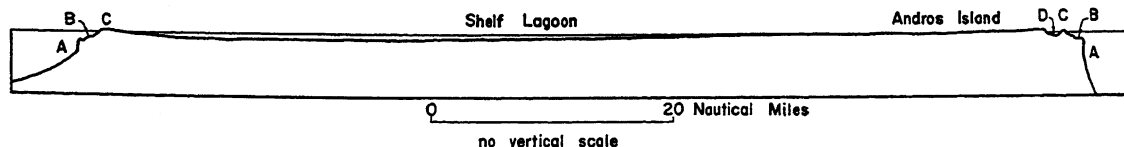
FIG. 3. Generalized west-east profile across Andros platform, showing major topographic elements.
A. Marginal escarpment. B. Outer platform. C. Barrier rim. D. Windward lagoon.
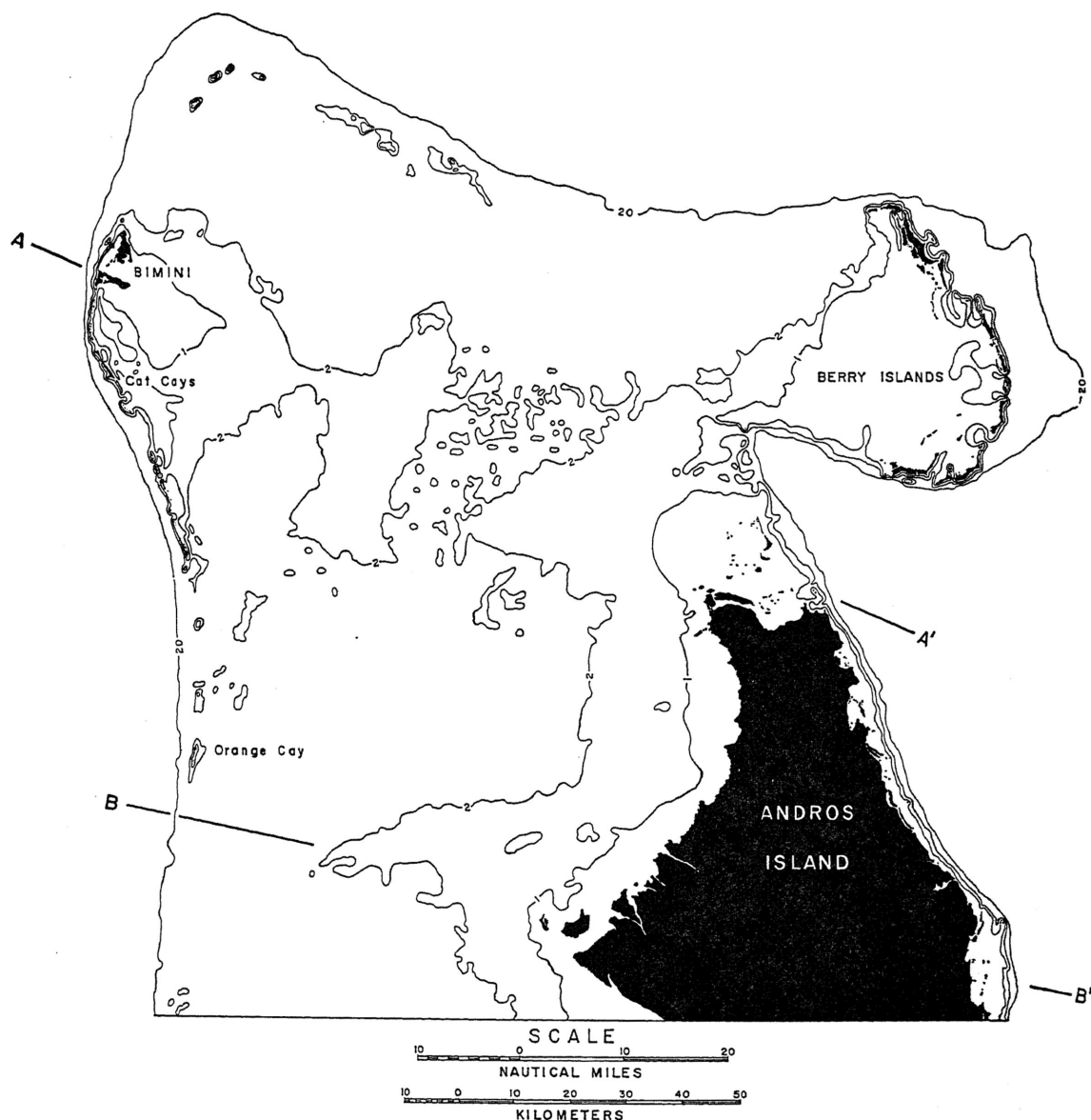
FIG. 4. Generalized hydrographic map of northern part of the Andros platform. Two low, east-west, submarine ridges are indicated, the Bimini axis (A–A') and the Billy Island axis (B–B').

to 2 fathoms at or near the shore to 16 to 20 fathoms at the outer margin where it is interrupted by a precipitous marginal escarpment (fig. 3). The latter has been interpreted as a drowned coral reef of Tertiary age (Newell, 1955).

The depth range over the platform of the Bahamas is so slight that, excepting amphibious intertidal species, many, perhaps most, of the benthonic organisms are reported to extend to greater depths than the marginal escarpment. Consequently, small local variations of depth over the Bank affect bottom communities mainly through turbulence and related factors. Very probably similar conditions prevailed in the shallow epeiric seas of the geologic past.[1]

[1] Elias (1937), in a very stimulating study of the paleoecology of the Permian Big Blue series, has concluded that water depth was the chief factor responsible
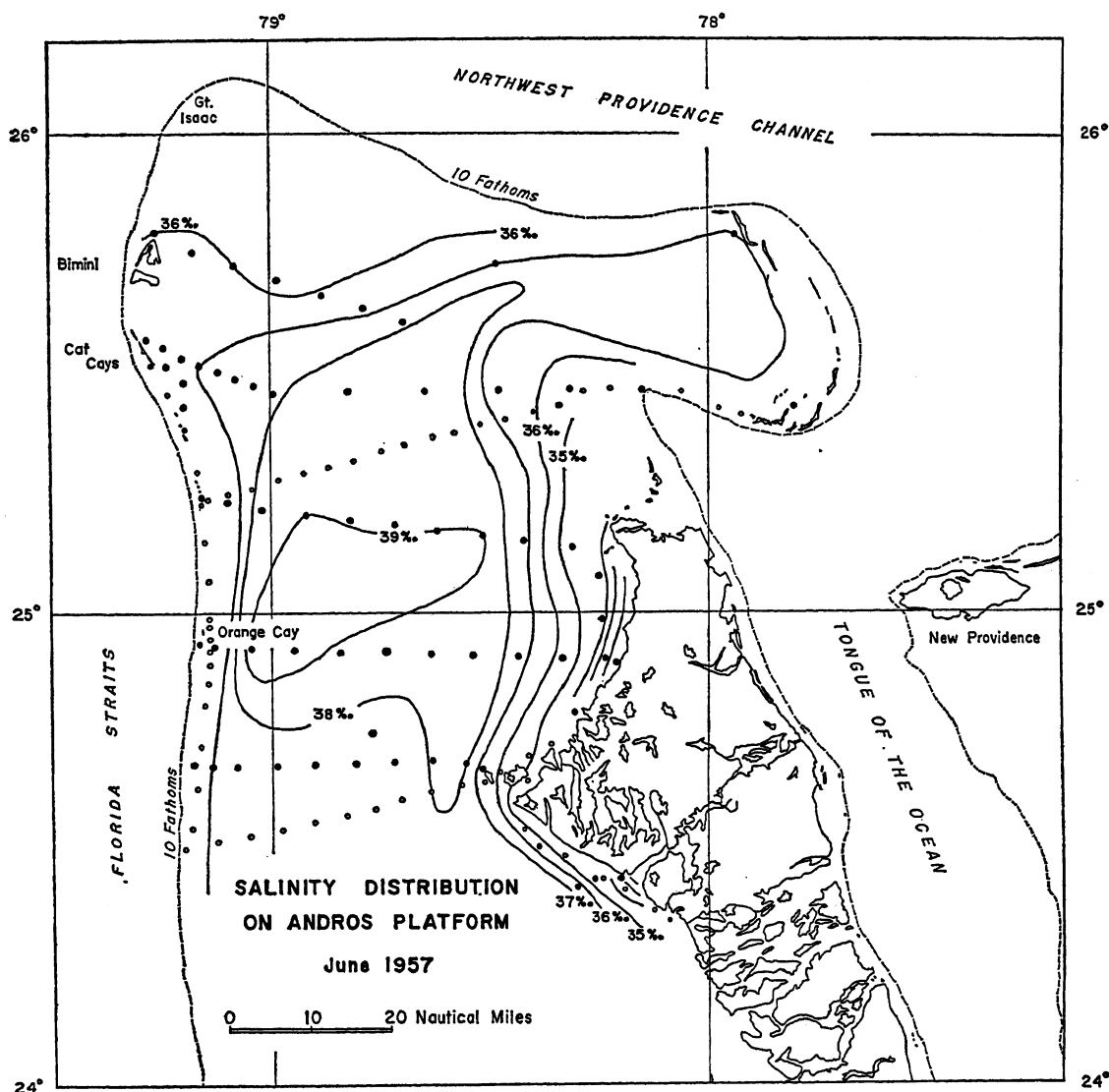
FIG. 5. Salinity distribution on northern Andros platform, June, 1957.

SALINITY OF THE BANK WATERS

Studies on the Great Bahama Bank by Black (1933) and Smith (1940, 1941) have shown that there are distinctive water masses on the Bank that change somewhat with the seasons. Smith concluded that the area in the lee of Andros Island characteristically is

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for the present stratigraphic distribution of benthonic organisms. It seems to us more probable that the chief ecological factor in the Big Blue sea was the same as that in the Bahamas to be described, i.e., the principal direct control of bottom milieu by turbulence.

occupied by waters of high salinity (40–42°/oo) and that the prevailing easterly winds caused a tongue of high salinity to extend over the Bank towards the west. He failed, however, to account for the fact that the distribution pattern showed marked changes towards the end of the year. Observations by Cloud (1955) and our own studies (fig. 5) tend to confirm Smith's results.

All existing records indicate a remarkably stable mass of hypersaline water concentrated by exaporation in the middle of the Bank west of Andros Island. This is trapped in a

tidal eddy; consequently, it has a slow rate of mixing with ocean water. It is said to be rather poor in plankton (Charles Fish, *in* Field, 1931). Evidently, the hypersaline water is rarely swept off the Bank, but it moves about somewhat under the influence of the winds. Black (1933) showed that the area of high salinity may at times be displaced a few miles to the south by northerly winds during the winter, but ordinarily it maintains a fairly constant location regardless of rainfall. A very slight concentration of magnesium in the bottom sediments has been reported by Newell and Rigby (1957, fig. 13) in the general area of high salinity.

During normal years most of the rainfall (40–60 inches) occurs from May to September. Our observations on salinity during the summer months of 1957, a year normal for precipitation, showed that there was considerable freshening of water of the mangrove swamps. As a result, drainage of rain water onto the Bank produced narrow, near-shore belts of depressed and variable salinity. This effect was particularly evident along the western shore of Andros Island where the salinity dropped below 35 parts per thousand. In contrast, during the dry months, as shown by Smith (1940, 1941), hypersaline waters extend to the western Andros shore. The waters of these poikilohaline areas (Dahl, 1956) fluctuate greatly between brackish and hypersaline conditions, and consequently they support only the most tolerant organisms of the *Cerithidea* community described below. From time to time the pattern of water masses may be broken up by northerly winds which introduce new supplies of sea water onto the Bank.

Conclusions that may be drawn from available data on salinity on the Bank are: (1) there is usually an area of high salinity in the north central part of the Bank west of Andros, with a maximum of about 43 to 46 parts per thousand, and (2) salinity along the west coast of Andros Island varies from brackish to hypersaline, depending on seasonal variations in rainfall and irregularities in the configuration of the shore line.

MEASUREMENTS OF pH

The normal daytime pH of Bank and Gulf Stream water is 8.0 ± 0.1. Even the water of the mangrove swamps of western Andros Island is not appreciably different. Furthermore, the water from near the sediment surface on the Bank is not very different from surface water. The pH of interstitial water in the sediment was consistently lower, probably because of bacterial activity, but the actual values are uncertain because of dilution by Bank water while the sediments were being collected. A sample of ground water from a newly dug trench on East Bimini gave a pH value of 7.7.

High pH values around 8.24 were encountered locally in the Bimini lagoon; these are correlated with elevated salinity. One series of hourly pH measurements (table 1) indicates that there may be a drop in pH shortly before dawn, but additional confirming data were not obtained, and from car-

TABLE 1

MEASUREMENTS OF pH AT NIGHT, IN BIMINI LAGOON, LERNER MARINE LABORATORY DOCK, JUNE 28–29, 1957

Sample	Hour	Temperature (Degrees Centigrade)	pH Water	Sediment pH
122	1600	30.80	7.98	7.30
123	1700	30.02	8.07	7.56
124	1800	29.87	8.10	7.30
125	1900	29.50	8.09	7.30
126	2000	29.02	8.08	7.49
127	2100	28.80	8.08	7.49
127A	2200	28.70	8.08	7.50
128	430	27.50	7.70	7.42
129	748	28.60	7.92	7.48

TABLE 2

Bank Measurements of pH During Daylight, July, 1957
(Temperature ±0.04, pH ±0.10)

| Station | Surface water | | Bottom water | | Sediment pH |
	Temperature (Degrees Centigrade)	pH	Temperature (Degrees Centigrade)	pH	
348	29.90	8.00	29.72	8.05	8.00
349	29.35	8.23	29.36	8.10	7.92
350	29.62	8.00	29.80	8.00	7.75
351	29.70	8.00	29.70	8.00	7.70
352	30.10	8.00	30.00	7.90	7.69
353	29.90	8.00	30.09	7.99	7.86
354	29.90	8.00	30.00	8.01	7.59
355	29.70	7.95	29.82	7.95	7.51
356	29.71	7.90	29.80	7.97	7.70
357	29.12	7.90	29.10	8.00	7.67
358	29.49	8.00	29.65	7.95	7.79
359	29.72	7.99	29.80	7.92	7.60
360	29.98	8.01	30.23	8.00	7.70
362[a]	—	8.08	—	—	7.35
363	29.60	7.95	30.08	7.91	—
364[a]	—	8.29	—	8.15	—
366	30.09	8.01	30.09	7.91	7.50
367	30.04	8.01	30.10	7.90	7.70
368	29.90	7.96	30.00	7.91	7.40
369	29.80	8.00	29.87	7.90	7.45
370	29.49	7.95	29.45	7.95	7.40
371	29.60	8.00	29.55	7.97	7.41
372	29.61	8.01	29.57	7.90	7.59
373	29.82	8.01	29.81	8.01	7.60
374	29.60	8.09	29.60	8.01	7.70
375	—	—	—	—	7.81

[a] Mangrove water.

bonate equilibrium considerations this probably does not greatly affect the environment.

ORGANIC MATTER AND E_H

Measurements of oxidation-reduction potential were not undertaken in this survey. Many Bank sediments characteristically produce a slight odor of H_2S for a few centimeters below the surface, indicating reducing conditions below the sediment-water interface. Well-sorted sands of the Bank margin, however, are characterized by oxidizing conditions, probably because they are more or less constantly being winnowed. The bottom waters apparently are well oxygenated everywhere except in the more sheltered mangrove areas. Kornicker (in press) found that organic carbon makes up as much as 2.9 per cent of the surficial sediments in and near the mangrove swamps of Bimini. The proportion of organic detritus drops rapidly away from the mangrove to an average of about 0.50 per cent on the Bank east of Bimini. It is not clear that the mangrove detritus is consumed directly by bottom animals, but it certainly supports a flora of bacteria that may be utilizied by detritus feeders. In this connection, it may be noted that the sediments of the Bimini lagoon, rich in organic matter, harbor an unusually diverse biota.

IT SEEMS THAT the present distribution of both bottom communities and sediments is of quite recent origin, dating from the time when melting of the continental glaciers raised the seas of the world to a level about 2 or 3 fathoms below the present level, and the interior of the Bank was flooded by rising water. Our studies, summarized below, indicate that this date could hardly have been more than

Pleistocene epoch. To what extent tectonic movements, of the sort indicated by the Bimini and Billy Island axes, have been a contributing factor is, of course, uncertain. Presumably, the rate of subsidence always has been negligible as compared with eustatic fluctuations in sea level. The old shore lines are approximately horizontal, and it seems probable that the area is now as stable di-
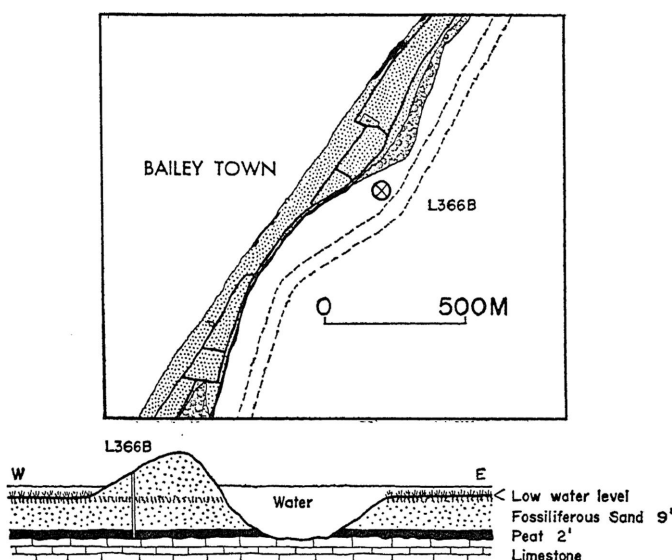
FIG. 6. Peat layer exposed in Lyon's channel, Bimini. *Above*: Index map of a portion of North Bimini showing location of bore-hole sample L-366B just west of channel. *Below:* Cross section showing bore hole and peat layer; no vertical exaggeration.

5000 years ago. The barrier reef in somewhat deeper water east of Andros Island could not have originated before sea level had risen to about the present 6- or 7-fathom line, the lower limit of the reef.

In the Bahamas, there is abundant topographic evidence in drowned sinkholes, submerged shore lines, and elevated coral reefs of great changes in the relative level of the sea with respect to the platform (Newell and Rigby, 1957). These changes are thought to have resulted from (1) long-continued slow subsidence of the basement, probably still in progress, and (2) comparatively rapid eustatic changes in sea level caused by alternate advances and melting of glaciers during the

astrophically as any comparable area elsewhere.

Just how ancient are the existing distributions and ecological situations? In 1956, during dredging operations in the Bimini lagoon, a thin bed of mangrove peat with *in situ* roots extending into underlying weathered bedrock was encountered 9 feet beneath low-water level (fig. 6). The position of the peat below the unconsolidated strata was determined at a point immediately west of the channel by means of a soil auger and sampler. Radiocarbon analysis of the peat by Dr. Wallace Broecker at the Lamont Geological Observatory gave a date of 4370 ± 110 years.

Several radiocarbon dates of between 3000

and 5000 years have been obtained in recent years from samples of buried fresh-water peat beds overlying Pleistocene limestones in southern Florida. These peat deposits probably were formed at levels ranging from low tide to a few feet above sea level and represent a change from well-drained to poorly drained conditions associated with the final phase of the post-Wisconsin rise in sea level. The available data on peat samples are given in table 3.

and we can find no evidence of a post-Pleistocene higher sea level.

Differential crustal movements of very small magnitude have affected the area, probably before deposition of the recent sediments, as indicated by the character of the Bimini axis (fig. 4). The warping of the exposed Pleistocene rocks has been very slight, resulting in slopes of not more than a few inches per mile.

Visible rocks in the Bahamas consist of ele-

TABLE 3
RADIOCARBON DATES OF LOW-LEVEL PEAT DEPOSITS

	Sample Number	Locality	Age in Years
Analyzed by Kulp and Broecker, Lamont Geological Observatory			
	L-141A[a]	Everglades, Florida, approximately 8 feet above mean sea level	4900±200
	L-141B[a]	Everglades, Florida, a few inches higher than L-141A	3800±200
	L-141C	10 miles south of Lake Okeechobee, approximately same elevation as L-141B	5050±200
	L-366B	Lyon's Channel, Bimini, 9–10 feet below low-water level	4370±110
Analyzed by Suess and Rubin, U. S. Geological Survey			
	W-149	Crane Key, Florida, 6–8 feet below low-water level	3330±110

[a] Elevations and other data were supplied by Mr. John C. Stephens of the Soil and Water Conservation Research Branch of the United States Department of Agriculture.

In addition to sample W-149 in table 3, Rubin obtained radiocarbon dates of 450±200 years (sample W-448) for aragonite mud about 0.2 meter below the bottom and 2490±400 years (sample W-447) for aragonite mud 2.0 to 2.1 meters below the sediment-water interface on the platform west of Andros Island, where the sediment cover above the bedrock is less than 10 feet thick over a large area (Cloud, 1955).

Altogether, these dates suggest that the rising sea first flooded the interior of the platform about 4000–5000 years ago, initiating marine and swamp sedimentation after the long emergence of the Wisconsin stage. Elevated in situ corals and mollusks of recent age are unknown in the Bahamas and Florida,

vated coral reefs, marine shell beds, and somewhat younger consolidated beach ridges and shore dunes of reworked marine calcareous sand, mainly, but not entirely, oolite. The lithified beach ridges and dunes are thought by us to belong mainly to a late, or regressive, phase of the interglacial (Sangamon) stage just prior to the Wisconsin emergence (Newell and Rigby, 1957). Summits of elevated in situ reef corals and reefs of the eastern border of the Andros platform on Fraziers Hog Cay and Andros lie at about 5 to 8 feet above low tides. These lie at about the same level and probably are about the same age as certain of the elevated reefs of the Florida Keys (Key Largo limestone), Jamaica, Cuba, and elsewhere. Radiocarbon

TABLE 4

RADIOCARBON DATES OF BAHAMIAN ROCKS BY KULP AND BROECKER,
LAMONT GEOLOGICAL OBSERVATORY

Sample Number	Locality	Age in Years
L-140A	Coral specimen (*Acropora cervicornis*), fossil reef 7 feet above lowest tides, Coakley Town, Andros Island	25,000+
L-321B	Clam shell (*Glycimeris pectinata*), fossil, north shore of South Bimini, near windmill	27,000+
L-366H	Calcarenite near high-tide level, blast hole, Till Hotel, Bimini	27,000+
L-321D	Oolite dune rock, about 8 feet above high-tide level, Till Hotel, Bimini	13,200 ± 400

dates of the rocks of the Andros platform show that they are much older than the unconsolidated sediments.

Confirmation for the last date in table 4 is needed from additional samples, as explained below. Fossil dune and beach ridges of the Andros platform are preserved as chains of elongate cays that mark an old shore line a few feet below the present level of the sea (pl. 59). Modern sand beaches are narrow and very limited in the Bahamas, and active dunes are unknown on most of the islands. If sea level were 3 or 4 fathoms lower than the present level, however, very extensive sand flats formed of fresh sediments would be exposed to wind and waves by the advancing shore, and broad beaches would be formed.

Cloud has obtained core samples of limestone immediately below the unconsolidated sediments of the shelf lagoon. Radiocarbon dates of this limestone, as determined by Rubin and Alexander (1958), range from 12,400 ± 600 to 21,300 ± 1000 years. We do not believe, however, that the limestone is actually so young.

According to many recent estimates, the cold cycle responsible for the Wisconsin glaciation began about 100,000 years ago.

After a glacial climax, warming and the melting of the glaciers resulted in an irregular rise in sea level that began about 18,000 years ago (Emiliani, 1958). Thus, until very recently, sea level must have been low, probably well below the platform rim, gradually rising to the present level.

It seems unlikely that marine sediments or beach ridges and rectilinear chains of dunes could have formed on the Andros platform only 13,000 to 20,000 years ago, when sea level must have been well below the level of the platform rim. The dominantly aragonitic limestones have undergone appreciable recrystallization and cementation. Consequently, it may be that the radiocarbon dates are appreciably lower than might be obtained on unaltered rock samples. On theoretical grounds the original sediments of which these rocks are composed should be 100,000 years or so old.

The western one-third of Andros Island is low and marshy and contains innumerable tidal estuaries, ponds, and mangrove swamps containing sea water. Except for scattered low areas of outcrop, the Pleistocene limestone is covered by a blanket of fine calcium-carbonate mud identical with that of the
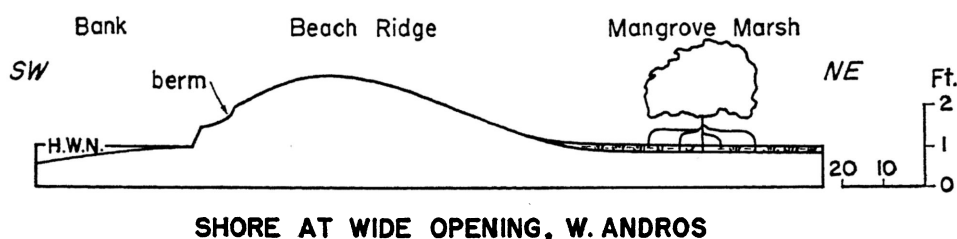
SHORE AT WIDE OPENING, W. ANDROS

FIG. 7. Shore profile at Wide Opening, western Andros Island. Level of high water neap tide shown (H.W.N.)

Bank to the west. The mud forms low levees along the estuaries (pls. 66, 67) and storm beaches locally several feet high along the most exposed shores. In places the waves have cliffed the storm beaches. These cliffed shores have given the erroneous impression that the mud flats slowly are being cut away by marine erosion (fig. 7), but the net effect seems to be extension of the shores by accretion.

Several investigators have been intrigued by the possibility that bacterial activities in the mangrove swamps were responsible for precipitation of the calcium-carbonate mud of the Andros swamps (Bavendamm, 1932; Black, 1933; Drew, 1914; Kellerman and Smith, 1914). They have thought that the muddy sediment is perhaps forming mainly within the island and gradually being transferred to the shelf lagoon by tidal currents and wave erosion.

As a means of testing the theory that the mud is now forming in the mangrove swamps of Andros, a 2½-foot core (A3) was taken within a mangrove swamp behind the beach ridge about ½ mile from the mouth of Deep Creek (east of station 363). The top of the core was approximately at high-tide level. After being freed from plant debris the calcium carbonate from the bottom and top was analyzed for radiocarbon at the Lamont Geolocial Observatory by Broecker, with the following results:

MUD CORE, ANDROS ISLAND	AGE IN YEARS
Top 3 inches, L-418D	2330 ± 100
Bottom 3 inches, L-418E	2660 ± 100

The material of the core contained scattered Foraminifera and marine gastropods. Rubin and Alexander (1958) obtained ages of 1025 ± 400 years and 1675 ± 200 years for two samples of lime mud taken from the 2-foot shore bluff at the extreme western point of Andros Island. These ages may reflect a mixing of younger Bank mud with older sediment of the mangrove swamps.

This evidence indicates that there is little or no deposition of new lime mud taking place at present in the swamps. It appears that the western part of Andros Island has been gradually growing by mangrove accretion at the expense of the shelf lagoon (pl. 66, fig. 1; pl. 67, fig. 2). The mud deposits in Andros Island are reworked; hence they are older than those of the shelf lagoon. Comparable changes in geography conceivably might have been caused by a drop of a few inches in sea level, but in that case accretion ridges might not be so numerous or so conspicuous.

BOTTOM FACIES AND COMMUNITIES, GENERAL CONSIDERATIONS

THE MEANING OF FACIES

EXPERIENCED STRATIGRAPHERS since the days of Cuvier and William Smith have been impressed by a tendency for fossil assemblages to change with variations of the enclosing rocks. This familiar relationship, among others, long ago impelled the Swiss geologist Gressly (1838) to formulate his concept of stratigraphic facies. Gressly explained inter-related variations of rocks and fossils in terms of common environmental controls at time of deposition. It is implicit, or stated, in the writings of many geologists (e.g., Gressly, *ibid.*) and biologists (e.g., Buchanan, 1958) that the texture and petrographic nature of the substrate determine the distribution of bottom organisms. However, even when the correlation is very good between community and substrate, there usually are reasons for the assumption that there are many environmental and historical factors that play a part in organism distribution. It is helpful for an understanding of the nature of stratigraphic facies to regard both benthos and substrate as products of an interacting complex of ecological variables. Not all environmental factors, however, affect organisms and substrate to the same degree. It is useful, therefore, to distinguish between factors responsible for a particular sediment and those that satisfy the requirements of a particular bottom community. For the most part they are not the same.

Many critical factors of aquatic environments, such as temperature, salinity, turbidity, predation, biologic competition, and biogeography, generally leave little or no record in the sediments, but variations in any of these factors greatly influence the character of bottom communities. Thus, contrary to Gressly's belief (1838 p. 12), a single type of substrate may support a variety of unlike communities in separate areas.

Characteristic modes of preservation tend to relate certain kinds of fossils to particular rock types. This is illustrated by the preferential association of black shales with fossil spores, conodonts, and graptolites. In such a case, it is probable that the association is an effect of special conditions of sedimentation and of preservation, but the life and depositional environments probably had little in common.

There is still much confusion with respect to facies terminology (e.g., Longwell, 1949); therefore, our own usage is herewith defined. We follow Moore (1949) in defining "stratigraphic facies" as "any areally restricted part of a designated stratigraphic unit which exhibits characters signicantly different from those of other parts of the unit." We agree, furthermore, with Krumbein and Sloss that "the expressions of variation in lithologic aspect are *lithofacies* and the expressions of variation in biologic aspect are *biofacies*" (Krumbein and Sloss, 1951). Moore (1949) regards fossils as primary constituents of fossiliferous sedimentary rocks; therefore, he considers them to be elements of lithofacies. It seems to us, however, that the biological aspects of fossils are something quite beyond and apart from their mineralogical composition, shapes, or their grade-size characteristics. Hence, to us, biofacies pertains not so much to the fossils themselves as sedimentary constituents, but to the information that they give us about past communities of organisms. The terms "organism communities" and "bottom facies" are employed here as approximately the modern counterparts, respectively, of biofacies and lithofacies of the stratigraphic record. However, many of the significant characteristics of bottom communities and facies are not preserved in the rocks. The communities and bottom facies, together with other environmental factors, make up the habitats of individual organisms, and they are different aspects of those habitats.[1] Because of the multiplicity

[1] The term "biotope" is sometimes used as a synonym of "habitat," but it is in no way superior to the latter, which is established firmly and is fairly well understood. The word "biotope" appears only once in the text of Allee and others (1949), and it is not used at all by Simpson, Pittendrigh, and Tiffany (1957) in a recent comprehensive treatise on biology. Wells (1957), feeling the need for a cognate term with which to describe the rock record of past environments, coined the word "lithotope." Many subsequent writers have misunder-

of facies terms, many of which have been of little practical value, and because of lack of uniform usage, it is now necessary for each writer to explain carefully his own application of any of these terms.

BENTHONIC HABITATS

The habitat, as understood here, may be defined as the normal external environment of the individual organism, or the community, including biological as well as physical factors. It should be emphasized that benthonic organisms modify their own environment and create many of the characteristics of the substrate and the bottom milieu. In turn, the substrate strongly influences the characteristics of the community, and both are subject to many factors not at all related to the substrate.

In a penetrating analysis Thorson (1957, p. 466) has summarized the broad ecological differences between hard and soft marine substrates. The former are characterized by numerous microhabitats and are not rapidly modified by waves and currents. Inherent stability of the hard substrate permits development of a diverse biota of anchored plants and animals, and these provide varied shelter and support for others, whereas the soft bottoms are available only to those that can cope with problems of sedimentation and insecure anchorage. Because of the ecological advantages of rocky substrates, their communities are relatively more diverse than those of sediment bottoms.

Thorson has used the term "level bottom" for areas of unconsolidated sediments, but this term is not appropriate for the Bahama region, and it might be equally misleading for other comparable areas. We therefore recognize two sorts of level bottoms in this report: rock pavements and sediment bottoms. It probably is true that the sediment-water interface usually is characterized by

stood, or have disagreed with, the original definition, and it has become virtually synonymous with "lithologic character." In such a sense it is clearly superfluous. The most appropriate application of "lithotope," if intended as the paleoecological equivalent of "biotope," is "the inferred depositional and diagenetic conditions under which a sedimentary rock has been formed." The term "phase" has been used for sedimentary rock type by R. S. Allan (1948) and Newell, Rigby, Fischer, and others (1953).

subdued topography as compared to current-swept rock surfaces, but there are many exceptions to the rule. There are broad areas of level rock pavement around each of the Bahamian platforms. This kind of bottom undoubtedly characterized portions of epicontinental seas in the geologic past, if we may judge from the plane character of many extensive disconformities, for example, the contact between middle Silurian and middle Devonian limestones over hundreds of thousands of square miles in the central United States. Soft sediments of intertidal mud flats may be, on the other hand, deeply furrowed by drainage channels, as in the Bay of Fundy and Dutch waddens.

Petersen (1913) recognized important distinctions between the modes of life of the epifauna and the infauna. The former is somewhat dependent on the bottom flora and includes many grazers and browsers as well as filter feeders, scavengers, and carnivores. On the other hand, the infauna is mainly, but not entirely, microphagous and is less dependent directly on the character of the bottom flora. Petersen was concerned almost entirely with indicator animals of sediment bottoms, and he gave but little attention to the associated plants or to the organisms of hard bottom.

Thorson regards the plants of the "level-bottom" areas as unimportant, possibly because he has in mind vast areas of ocean bottom that lie below the euphotic zone. "On the level bottom the animals are associated only with other animals and directly with the physical-chemical conditions" (Thorson, 1957, p. 466). Such a situation is not at all true for the Bahamas, and we think that bottom plants must play a dynamic role in all biocoenoses of very shallow marine benthos.

We are unable to class our communities with any of Thorson's (1957) level-bottom communities. The differences may be attributed to the fact that his examples, unlike the Bahamian communities, are derived from areas of terrigenous sedimentation and are taken mainly from cold and temperate waters.

THE COMMUNITY CONCEPT

The term "community" is used in this paper in its most general sense to indicate any defined group of organisms living to-

gether. Depending on the point of view, three sorts of communities can be recognized: the habitat community, the organism community, and the biocoenose. The habitat community is a natural association of organisms set apart according to certain defined features of the environment. In the Bahamas, for example, we can recognize as the rock-bottom community all those benthic organisms that inhabit rock bottom. The rock-bottom community can, in turn, be subdivided into the coral-reef community, the intertidal rocky-shore community, the community of infra-tidal rocky prominences, and the rock-pavement community.

A second approach to community analysis is to focus attention on the organisms themselves and to define a community as a regularly recurring combination of certain types of organisms (Molander, 1930, p. 4). Such a community, delineated without regard to habitat characteristics, is here referred to as the organism community, or biotic community. It has also been designated the Petersen community in reference to the classic work of Petersen. Seeking to describe the distribution of benthic animals in Danish waters, Petersen tried at first to delineate animal association on the basis of physical characteristics of the bottom alone, but he was forced to conclude that although "much has been gained along these lines we do not hereby come to the kernel of the matter, namely, the occurrence of the generally distributed animals, which alone can tell us where a certain animal community belongs, even though the depth and other conditions may vary" (Petersen, 1918, p. 1).

In the Bahamas appropriately defined habitat communities show close correspondence with organism communities. Thus our experience supports the general conclusions of nearly all students of marine bottom communities that the character and distribution of the communities are closely correlated with the substrate character. The correlation is, however, never exact, and in some cases there is little or no evident correlation. This point can be made clear by reference to figures 8 and 9. The map of bottom types (fig. 8) also may be considered as a map of habitat communities differentiated principally on the basis of sediment texture, and including a muddy-sand and mud community, a pellet-sand community, and so on. Figure 9, however, is an organism community map designed to show the known or inferred distribution of species combinations determined empirically and independently. Boundaries of the two sorts of communities correspond closely in some respects but not at all in others. The following points should be particularly noted:

1. The principal boundary between areas of muddy and pellet sand coincides in general with the boundary between the *Didemnum* and *Strombus costatus* communities. Along the traverse 18 miles south of Orange Cay, however, it may be noted that there is a discrepancy of several miles, which indicates that the diagnostic elements of the *Didemnum* assemblage are found here on sand bottoms. From the general correspondence in the two maps, we are led to conclude that the muddy sediment itself, as well as correlated habitat characteristics such as sediment Eh, turbulence, turbidity, and salinity, plays a major role in determining the mutual boundary between the *Didemnum* and *Strombus costatus* communities.

2. An isolated area of clean sand sampled at station 395 (also indicated on United States Hydrographic Office Chart 26a) supports not the *costatus* but the *Didemnum* community. This relationship, as well as that noted above, probably indicates that continuous invasion of the sand area by larvae originating on muddy bottoms to windward is more important ecologically than local edaphic factors.

3. Detailed field observations in an area of unstable oolite near Brown's Cay indicate that a close correspondence between this habitat and the *Tivela* community is the rule, and this community is unable to take advantage of other available substrates. Boundaries of the *Tivela* community are, therefore, mapped to correspond with those of unstable oolite areas.

4. Although there is a clear distinction between the *Cerithidea* and *Didemnum* communities, especially with regard to their molluscan constituents, no comparable habitat boundary can be mapped with certainty. We suspect that the poikilohaline nature of the inshore waters is at least in part responsible for the biotic change.
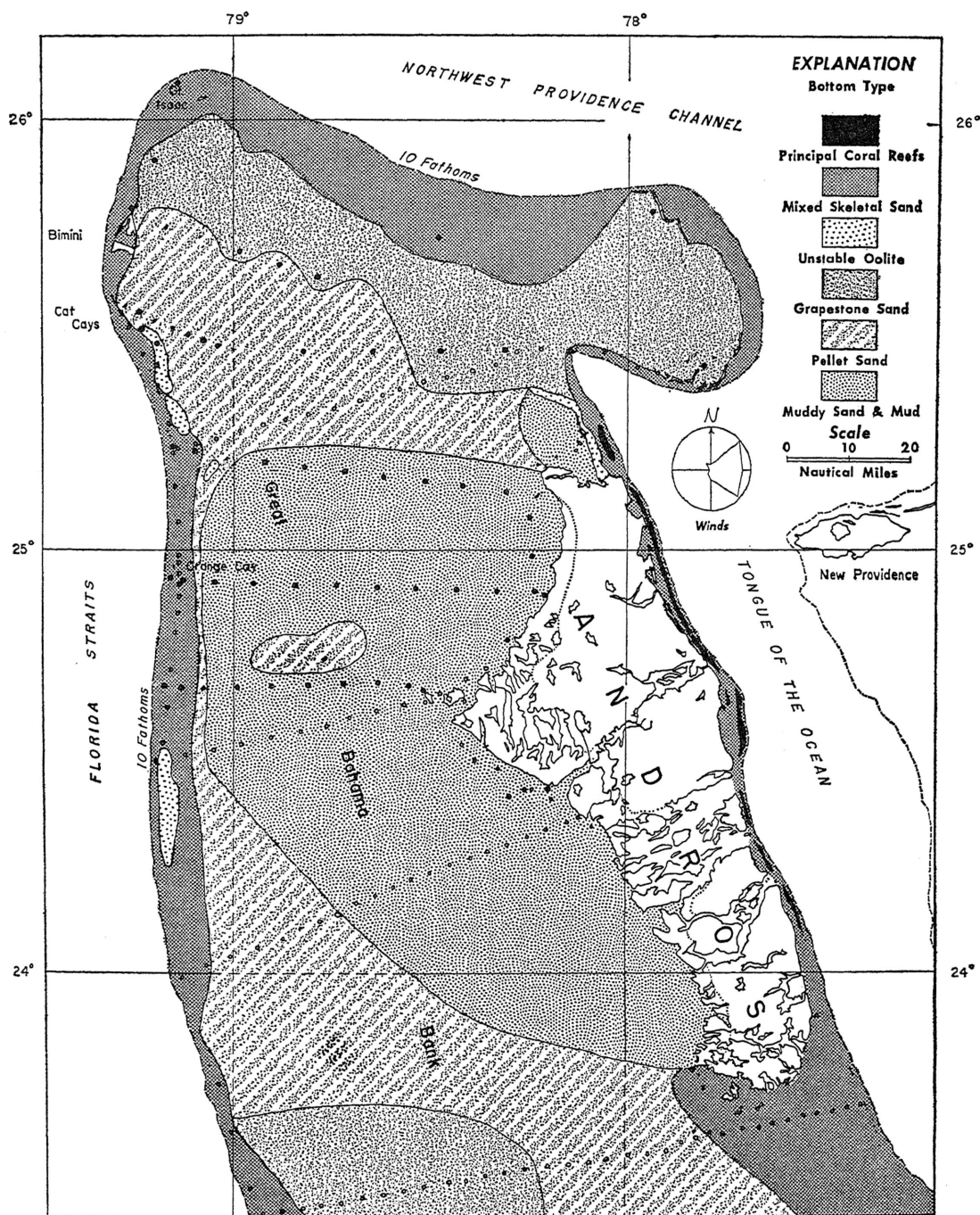
5. Correspondence between the rock-pave-

FIG. 8. Reconnaissance map of bottom types on the Andros platform. Nature and index numbers of control samples explained on figure 2.

ment habitat and the plexaurid community is very close. Wherever we have sampled the areas mapped as rock pavement on figure 17, they are covered with a dense growth of plexaurid and associated organisms living on a rock pavement that is either bare or covered with a thin blanket of migrating sand.

Bodenheimer (1938, pp. 113–142) has given an excellent analysis of the relationship between habitat and biotic communities. He concludes that although external factors of the habitat may be sufficient . . . "to give a good idea as to the general character of the environment of every zone, they are certainly insufficient to 'explain' the distribution of the species. . . . Zones or conditions of optimum, favorable, unfavorable, and impossible environments have been circumscribed and hold good in rough outlines when compared with the facts. But optimal zones remain where the species is absent or has a low population level due to obscure causes . . . [and] . . . there are impossible zones where a moderate population is constantly maintained" (pp. 128–129). The reasons for this imperfect correspondence between physical and biological aspect of the sea bottom are undoubtedly complex. In part it must be attributable to inadequate habitat analysis, but Bodenheimer believes that short-term intraspecific adaptations play a major role. Our observations cited above suggest that biogeographic factors may be important locally.

Both habitat and organism communities essentially are empirical statistical concepts in which the community is viewed as the simple sum of all of the organisms living in a particular place without regard to any of the complex inter-species relationships that may exist. In a third, or dynamic, concept of ecological communities, emphasis is given to the mutual dependence of animals and plants which not merely exist in geographic proximity but are bound together by their ecological functions. For this sort of community, the term "biocoenosis" (Möbius, 1877) is properly employed. This dynamic approach is not suited to regional studies, such as this investigation of the Great Bahama Bank, and it rarely is applicable to paleontologic work.

Paleontologists have not generally been aware of the dynamic nature of the biocoenosis, and this term frequently is inappropriately applied by them to associations of fossil skeletons thought to be more or less *in situ* and only moderately distributed by scavengers, gravity, and currents. However, even the best fossil assemblages are very imperfect records of living communities. A majority, commonly more than 95 per cent, of the species of a local biota are incapable of being preserved by the ordinary processes of fossilization. Even the *in situ* skeletons of a fossil coral reef, numbering at most a few dozen species, cannot provide the data needed for a reasonably complete reconstruction of the living reef community which may have included thousands of species of organisms (Wells, 1957). In the Bahamas very few of the shallow-water species are recognizable among the skeletal remains of the sediments.

Fossils provide a basis for inferences about past habitat communities, but they are in no sense the communities. Under exceptional conditions valid inferences may be drawn from fossils about dynamic interrelations of long dead organisms. The paleontologist, however, commonly has in mind the organism community or the habitat community rather than the biocoenosis.

PRINCIPAL LIMITING FACTORS

"The presence and success of an organism or a group of organisms depends [sic] upon a complex of conditions. Any condition which approaches or exceeds the limits of tolerance is said to be a limiting condition or a limiting factor" (Odum, 1953, p. 28). The most outstanding result of our efforts to determine and record the mutual distributions of bottom facies and indicator organisms of the Bank is the conclusion that both the communities and bottom facies are closely dependent on regimens of waves and currents.

Bottom conditions strongly influence the character and distribution of benthonic communities, Many investigators (e.g., the classical works of Davis, 1923, 1925; Petersen, 1913; Verrill and Smith, 1874) have demonstrated that the marine substate exerts sensitive control over bottom communities. Furthermore, conditions of sedimentation clearly determine the chemistry, stability, firmness, texture, and nutritional content of the bot-
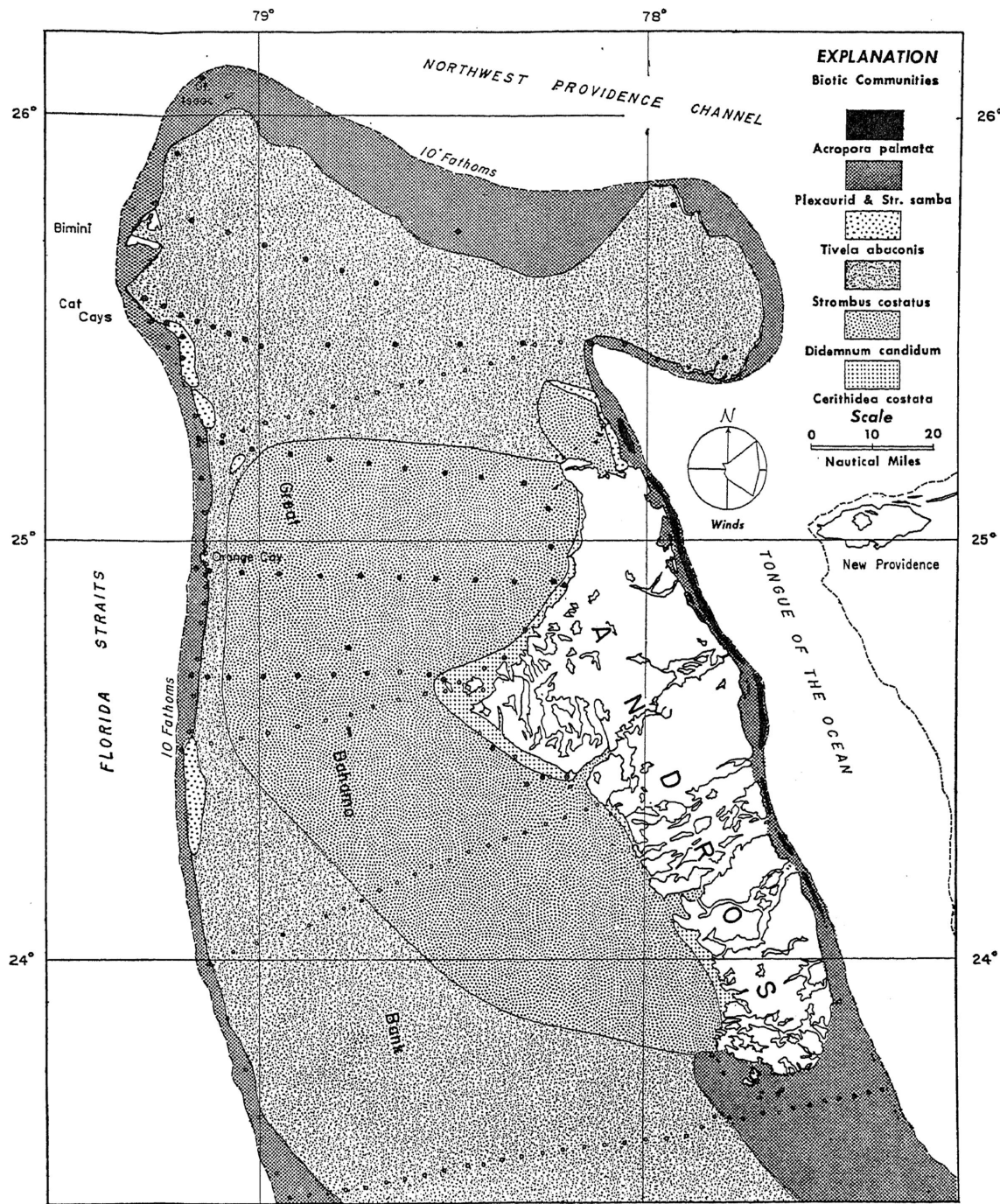
FIG. 9. Reconnaissance map of biotic communities on the Andros platform. Nature and index numbers of control samples explained on figure 2.

tom. The intimate interrelationship between benthonic communities and edaphic conditions of the substrate is further emphasized by the fact that sediment feeders ingest and modify, "condition," or even create the substrate, which consequently acquires distinctive properties that tend to be associated with particular communities.

The factors that relate a benthonic community to a particular bottom type clearly are complex, and it is not at all surprising that the correlation between community distribution and substrate rarely is perfect. Communities are sensitive to edaphic conditions, but the organisms play such an important part in the creation of those conditions that only under special circumstances are we justified in concluding that there is a one-way causal relationship between edaphic conditions and community type. Very frequently important characteristics of the bottom are produced, or determined, by the communities that live on or in it, and we do not believe with F. M. Davis (1925) or Buchanan (1958) that bottom communities always are mainly dependent on such edaphic factors as grain size of the sediments.

The organism communities of the Bahamas that occupy characteristic bottom facies tend to be sharply delimited or are joined by very narrow transitional zones (ecotones). Some community boundaries are in places better defined than corresponding bottom facies boundaries. The integrity of the communities thus is not solely an effect of substrate differences. Probably the narrowness of edge zones on the Great Bahama Bank is a result of competition and other threshold effects of biotic factors of the environment. Characteristic uniformity of the bottom over great areas and community distinctness have enabled us to prepare useful distribution maps of the greater part of the northwestern Great Bahama Bank (figs. 8, 9).

In the shallow shelf seas of the Bahamas, variations in depth, temperature, pH, and salinity are negligible over wide areas, and the most conspicuous variables are substrate, turbidity, and turbulence. Of these, turbulence clearly bears a dominant relationship to the others. The nature of sedimentation on the Great Bahama Bank results in large part from the kind and intensity of agitation of

water, and the major cause of turbulence, of course, is the kinetic energy of waves and tidal currents which, applied to the particular topography of the Bank, clearly is mainly responsible for the observed distribution of both bottom facies and organism communities (figs. 8, 9). A summary of our views on the complex web of relationships among the major ecological variables is given in figure 10.

Exposed marginal areas of the Bank are characterized by rocky platforms and unstable shifting sand. The sediments of finest grain form the bottom in quiet waters to the west of Andros Island, where currents are weak and the Bank is sheltered from the trade winds (fig. 1).

The abrupt demarcation between deep and shallow waters of contrasting energy characteristics is especially noteworthy, and the edge of the platform establishes the form and distribution of the habitat areas which are roughly parallel to it. Current velocities are greatest in shoal areas of the barrier rim where maximum flood-tide velocities of about 1.5 feet per second are encountered during
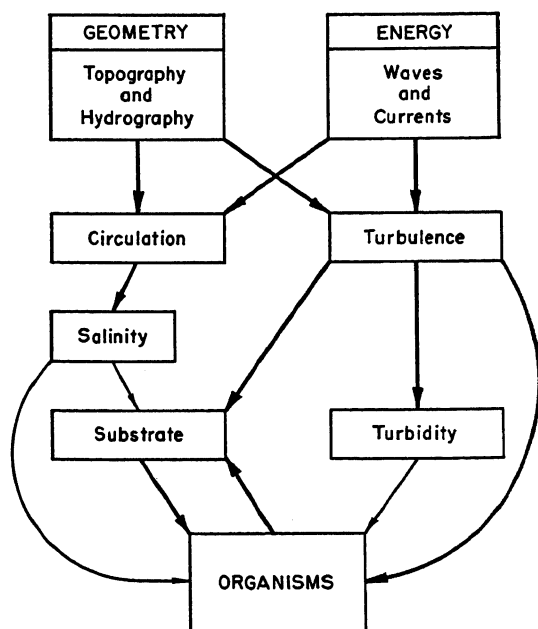

FIG. 10. Diagram illustrating an interpretation of causal relationships existing among major ecological variables in the Bahamas. Weight of arrow proportional to relative magnitude of influence.

normal weather. The velocity diminishes towards the interior of the Bank to about 0.5 foot per second. During extreme spring tides and at times of heavy winds, much greater current velocities undoubtedly occur.

Along the margin of the Bank there is an intimate relationship between the fine details of sedimentary patterns and the force and prevailing directions of tidal currents, which are disposed radially with respect to the edge of the platform. These currents are modified and reënforced by storm waves which have a centripetal effect on sedimentation. Newell and Rigby (1957, p. 56) have shown that sedimentary conditions are approximately in

equilibrium with ordinary winds and tides, and hurricanes probably have only minor and ephemeral effects on the substrate patterns. Driving tangentially across the outer edge of the platform, great storm waves periodically sweep sediments inward from the outer platform, preventing loss of the marginal sand bores to deep waters (pl. 60). Tidal currents, on the other hand, produce radial furrows, deltas, and levees across the barrier bar. The ebb currents, which are appreciably weaker than those of flood tides, are unable in most sectors to prevent the local accumulation of sand which rises in places to the level of the lowest tides.

TABLE 5

SOME INDICATOR ORGANISMS OF SEDIMENT-BOTTOM COMMUNITIES, GREAT BAHAMA BANK

	A	B	C	D	E
Plexaurid community	7				
Plexaura spp.		7	100	7	100
Spheciospongia vesparia		7	100	7	100
Strombus samba		2	29	7	29
Clypeaster rosaceus		3	43	8	37
Oreaster reticulatus		2	28	9	23
Tivela community	3				
Mellita sexiesperforata		3	100	14	21
Tivela abaconis		3	100	3	100
Oreaster reticulatus		3	100	9	33
Strombus costatus community	19				
Strombus costatus		5	26	7	71
Glycimeris undata		6	32	6	100
Tellina radiata		4	21	4	100
Cerithium litteratum		4	21	4	100
Oreaster reticulatus		4	21	9	44
Clypeaster rosaceus		3	16	8	38
Mellita sexiesperforata		9	47	14	64
Didemnum community	29				
Didemnum candidum		19	66	19	100
Verongia fistularis		10	34	10	100
Pitar simpsoni		13	45	13	100
Echinaster sentus		6	21	6	100
Caulerpa spp.		14	48	14	100
Batophora spp.		12	41	12	100
Clypeaster rosaceus		2	7	8	25
Cerithidea community	6				
Cerithidea costata		5	83	5	100
Pseudocyrena colorata		4	67	4	100

A, number of stations in the community.
B, number of occurrences in the community.
C, per cent of frequency in the community, 100×(B/A), index of characterization.
D, total occurrences in cited communities.
E, per cent of frequency in all communities cited, 100×(B/D), index of ecological restriction.

TABLE 6

COMMUNITY INDICATORS OF THE SHELF LAGOON

Station Number	Community[a]	Bottom Type[b]	Batophora spp.	Cantharus multangulus	Caulerpa spp.	Cerithidea costata	Cerithium litteratum	Clypeaster rosaceus	Didemnum candidum	Echinaster sentus	Glycimeris undata	Mellita sexiesperforata	Oreaster reticulatus	Pitar simpsoni	Tivela abaconis	Plexaura spp.	Pseudocyrena colorata	Spheciospongia vesparia	Strombus costatus	Tellina radiata	Verongia fistularis
308	P	r	—	—	—	—	—	—	—	—	—	x[c]	—	—	—	x	—	x	—	—	—
309	S	s	—	—	—	—	x	—	—	—	—	x	—	—	—	—	—	—	—	x	—
310	P	r	—	—	—	—	—	x	—	—	—	—	—	—	—	x	—	—	—	—	—
311	P	r	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	x	—	—	—
313	S	s	—	—	—	—	—	x	—	—	—	x	—	—	—	—	—	—	x	—	—
314	S	s	—	—	—	—	—	x	—	—	x	—	—	—	—	—	—	—	—	—	—
315	S	s	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	x	—
323	S	s	—	—	—	—	—	—	—	—	—	—	x	—	—	—	—	—	—	—	—
327	P	r	—	—	—	—	—	x	—	—	—	—	x	—	—	x	—	x	x	—	—
328	P	r	—	—	—	—	—	—	—	—	—	—	x	—	—	x	—	x	—	—	—
329	P	r	—	—	—	—	—	x	—	—	—	—	—	—	—	x	—	x	x	—	—
330	P	r	—	—	—	—	—	—	—	—	—	—	—	—	—	x	—	x	—	—	—
331	S	s	—	—	—	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—
332	S	s	—	—	—	—	—	—	—	—	—	x	—	—	—	—	—	—	—	—	—
333	S	s	—	—	—	—	—	—	—	—	—	x	—	—	—	—	—	—	x	—	—
334	S	s	—	—	—	—	—	—	—	—	x	x	x	—	—	—	—	—	x	—	—
336	S	s	—	—	—	—	—	—	—	—	—	x	x	—	—	—	—	—	—	—	—
337	S	s	—	—	—	—	—	—	—	—	—	—	x	—	—	—	—	—	—	—	—
338	S	s	—	—	—	—	—	—	—	—	—	x	—	—	—	—	—	—	—	—	—
348	S	s	—	—	—	—	x	—	—	—	—	—	—	—	—	—	—	—	x	—	—
349	S	s	—	—	—	—	x	—	—	—	—	x	—	—	—	—	—	—	x	—	—
350	S	s	—	—	—	—	—	—	—	—	—	x	—	—	—	—	—	—	—	—	—
351	D	ms	—	—	—	—	—	—	—	—	—	—	—	x	—	—	—	—	—	—	—
352	D	ms	—	—	x	—	—	x	x	—	—	—	—	x	—	—	—	—	—	—	—
353	D	ms	—	x	x	—	—	x	x	—	—	—	—	x	—	—	—	—	—	—	—
354	D	ms	—	—	x	—	—	—	x	—	—	—	—	x	—	—	—	—	—	—	x
355	D	ms	—	—	x	—	—	—	x	—	—	—	—	x	—	—	—	—	—	—	x
356	D	ms	—	x	x	—	—	—	x	x	—	—	—	x	—	—	—	—	—	—	x
357	D	ms	—	—	x	—	—	—	x	x	—	—	—	x	—	—	—	—	—	—	x
358	D	ms	—	—	x	—	—	—	x	—	—	—	—	x	—	—	—	—	—	—	—
359	D	ms	—	—	—	—	—	—	—	—	—	—	—	x	—	—	—	—	—	—	—
360	D	ms	—	—	—	—	—	—	x	x	—	—	—	—	—	—	—	—	—	—	—
361	C	m	—	—	—	x	—	—	—	—	—	—	—	—	—	—	x	—	—	—	—
362	C	ms	—	—	—	—	—	—	—	—	—	—	—	—	—	—	x	—	—	—	—
363	D	ms	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
364	C	m	—	—	—	x	—	—	—	—	—	—	—	—	—	—	x	—	—	—	—
365	C	m	—	—	—	x	—	—	—	—	—	—	—	—	—	—	x	—	—	—	—
366	D	ms	—	—	x	—	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—
367	D	ms	x	—	—	—	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—
368	D	ms	—	—	x	—	—	—	x	—	—	—	—	x	—	—	—	—	—	—	—
369	D	ms	x	—	—	—	—	—	x	x	—	—	—	x	—	—	—	—	—	—	—
370	D	m	—	—	x	—	—	—	—	—	—	—	—	x	—	—	—	—	—	—	—
371	D	ms	x	—	—	—	—	—	—	—	—	—	—	x	—	—	—	—	—	—	—
372	D	ms	x	—	—	—	—	—	x	—	—	—	—	x	—	—	—	—	—	—	—

TABLE 6—(*Continued*)

Station Number	Community	Bottom Type	*Batophora* spp.	*Cantharus multangulus*	*Caulerpa* spp.	*Cerithidea costata*	*Cerithium litteratum*	*Clypeaster rosaceus*	*Didemnum candidum*	*Echinaster sentus*	*Glycimeris undata*	*Mellita sexiesperforata*	*Oreaster reticulatus*	*Pitar simpsoni*	*Tivela abaconis*	*Plexaura* spp.	*Pseudocyrena colorata*	*Spheciospongia vesparia*	*Strombus costatus*	*Tellina radiata*	*Verongia fistularis*
373	D	ms	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
374	S	s	—	—	—	—	x	—	—	—	x	—	—	—	—	—	—	—	—	—	—
375	S	s	—	—	—	—	—	—	—	—	x	—	—	—	—	—	—	—	—	x	—
376	S	s	—	—	—	—	—	—	—	—	x	—	—	—	—	—	—	—	—	x	—
377	S	s	—	—	—	—	—	—	—	—	x	—	—	—	—	—	—	—	—	—	—
378	D	s	—	—	—	—	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—
379	D	ms	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	x
380	D	ms	x	x	—	—	—	—	x	—	—	—	—	—	—	—	—	—	—	—	x
381	D	ms	x	—	—	—	—	—	x	—	—	—	—	—	—	—	—	—	—	—	x
382	D	ms	—	—	—	—	—	—	—	x	—	—	—	—	—	—	—	—	—	—	—
384	D	ms	x	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
385	D	ms	x	—	—	—	—	—	—	—	—	—	—	—	—	—	x	—	—	—	x
386	C	ms	—	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
390	D	m	x	—	x	—	—	—	x	x	—	—	—	—	—	—	—	—	—	—	—
391	D	ms	—	—	x	—	—	—	x	—	—	—	—	—	—	—	—	—	—	—	x
393	C	ms	—	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
395	D	s	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	x
405	T	o	—	—	—	—	—	—	—	—	—	x	x	—	x	—	—	—	—	—	—
415	T	o	—	—	—	—	—	—	—	—	—	x	x	—	x	—	—	—	—	—	—
433	T	o	—	—	—	—	—	—	—	—	—	x	x	—	x	—	—	—	—	—	—

a *Symbols:* C, *Cerithidea* community; D, *Didemnum* community; P, plexaurid, sea-whip community; S, *Strombus costatus* community; T, *Tivela* community.

b *Symbols:* m, fine mud; ms, muddy sand; o, unstable oolite sand; r, rock pavement; s, stable sand bottom.

c *Symbol:* x, live examples, "Wild Goose" survey, 1957.

In the following discussion it has been convenient to designate the community habitats by the location and salient characteristics of the prevailing edaphic facies, but we do not mean to imply that the physical characteristics of the bottom alone constitute the habitat.

Eleven major habitats may be distinguished. These are designated rocky shore (midlittoral and supralittoral), ledges and prominences of country rock (infratidal), reef, pavement, unstable-sand, stable sand, muddy-sand, mud, mangrove, and sand beach. The sand beach habitat was not critically examined in this study. It is relatively unimportant in the Bahamas because of the limited extent of beaches. In each of the studied habitats both infauna and epifauna are recognized. These, of course, are not really separate faunas but represent community exploitation of zones or microhabitats within a major habitat. Under each of the habitat designations the general physical setting, the bottom facies, and our general observations on the community characteristics are described.

ROCK-BOTTOM HABITATS AND COMMUNITIES

THE MARINE SUBSTRATE in the Bahamas generally consists of limestone, sand, muddy sand, and mud, all composed of nearly pure calcium carbonate. Pebbles and cobbles resulting from the destruction of corals and the erosion of shoals and rocky shore are quickly reduced to fine sediment by the action of rasping and boring animals, by perforating filamentous algae, and by mechanical abrasion. Consequently, extensive deposits of gravel do not accumulate, and gravel bottom is not quantitatively significant. There are broad areas of rock bottom around the outer margin of the platform where strong turbulence prevents the accumulation of sediments.

Four distinctive communities are recognized on the rock substrate. The most evident environmental differences among them pertain to conditions of exposure, turbulence, and turbidity. They are: (1) rocky shores, (2) infratidal prominences, (3) coral reefs, and (4) rock pavements of submerged marine terraces.

The rock-bottom habitats provide firm anchorage and shelter for attached, burrowing, and boring plants and animals, and quite a number of species are equally at home in ledge, reef, and pavement situations. Nevertheless, there are conspicuous qualitative differences in the biotic associations, and these permit convenient field discrimination in advance of extensive faunal and floral determinations. The mollusks and coelenterates form characteristic associations in each of the rock-bottom habitats, and they provide a number of community indicator species.

THE ROCKY SHORE

ROCKY-SHORE HABITAT

Physical and ecological characteristics of rocky shores in the Bahamas exhibit striking uniformity from place to place. Significant variations from the usual pattern do occur (often correlated with differences in exposure), but these are never so impressive as the over-all similarities. The following description of the community of the rocky shore is based on detailed observations taken along a single transect off Rabbit Cay Point, South Bimini, but it illustrates also the essential

features of observations made at more than a dozen localities scattered along the northwestern margin of the Andros platform from Orange Cay to East Isaac.

The littorine community occupies the upper surface and notched face of a limestone terrace (pl. 63) from its landward extremity down to the level of mean low spring tides (figs. 11, 12). The upper surface of the terrace, although extremely irregular and jagged in detail has a gentle and uniform seaward slope (pl. 63, fig. 1). There are four zones characterized by conspicuous surface-color differences that can be distinguished.

In descending order they are the white, gray, black, and yellow zones. These zones have been described in many parts of the
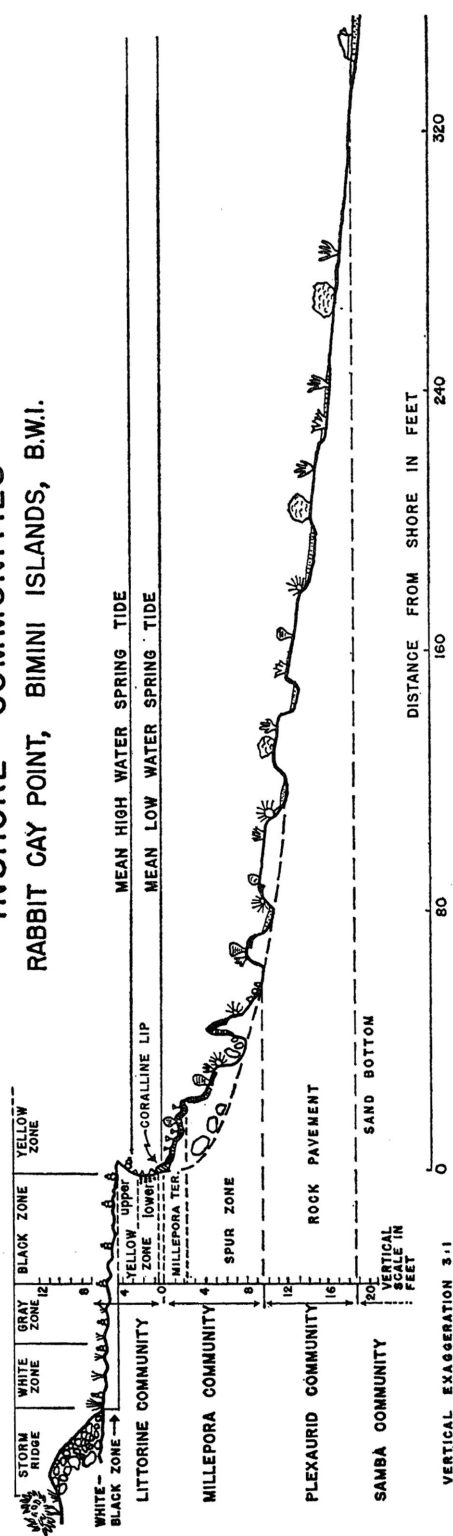
ROCKY SHORE PROFILE, BIMINI AREA
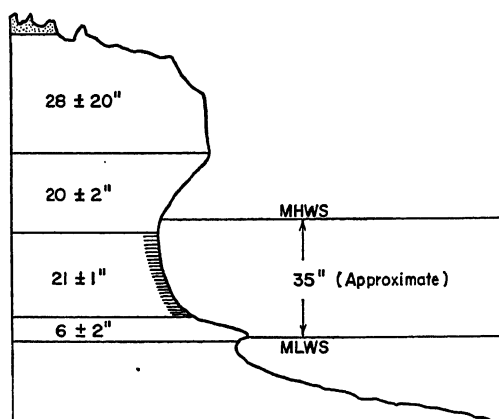
Extreme spring tide range	3.2 ft. (approx.)
Minimum neap range	1.4
Average spring range	2.9
Average neap range	1.6
Variation in MSL	0.4 ±

FIG. 11. Diagram of relationship between shore profile and sea level as inferred for the Bimini area. Pattern of small dots indicates lowermost extremity of black zone. Hachured portion of profile represents zone of *Lithotrya*. Center of coralline lip is approximately at mean low water spring.

FIG. 12. Shore profile and communities. Rabbit Cay Point, Bimini, showing vertical distribution of some of the most distinctive indicator organisms. Sand and gravel flooring depressions in spur zone and rock pavement indicated by standard symbols. Dashed line indicates base of grooves in spur zone.

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world by numerous observers and provide a convenient frame of reference for describing the vertical distribution of phenomena in the shore zone.

Along the seaward margins of the terrace surface the black and yellow zones are broadly gradational and overlapping. Here the black zone is developed on level areas around the yellowish surfaces of tide pools, splash rills, and other depressions that dissect the general surface. The yellow zone is well expressed along the steep and undercut terrace face (pl. 63, fig. 2). Vertical distribution gradients of many conspicuous organisms are so well marked within the yellow zone that it is convenient to recognize a lower and an upper yellow zone. The upper yellow zone is characterized by the alga *Bostrychia*, the barnacle *Chthamalus*, and the gastropod *Nerita versicolor*. The most striking feature of the lower zone is the abundance of two organisms, a vermetid gastropod, *Spiroglyphus*, and a boring barnacle, *Lithotrya*.

Immediately below the lower yellow zone, the face of which is either vertical or slightly concave seaward, a 6-inch interval is occupied by a dense growth of the encrusting coralline alga *Porolithon pachydermum*. As a result of the protection from erosion afforded by the deposits of this plant, the *Porolithon* zone commonly stands in relief as a cornice several inches thick in vertical dimension just above the level of low spring tides. This is the coralline lip (fig. 12), a feeble counterpart of the algal ridge of Pacific coral reefs.

The profile below the lip is submerged. It exhibits a number of variations correlated with degree of exposure of the coast to wave action. At Rabbit Cay Point (fig. 12) the rock surface below the coralline lip may drop away steeply, or it may jut out to form the *Millepora* terrace (pl. 64). Along parts of the inner shore of Great Isaac, however, extensive undercutting has produced a conspicuous reëntrant immediately below the coralline lip.

LITTORINE COMMUNITY

All the species encountered in the littorine community are narrowly restricted in their vertical distribution, a phenomenon that has so intrigued marine ecologists that there exists a large and complex literature devoted to its description and analysis. Judging from a recent review by Doty (1957), students of this problem are agreed only on the generalization that the observed biotic zonation results from various environmental gradients developed in relation to the water-air interface.

The list below and figure 12 record our observations on the vertical distribution on the common species of plants and animals in the littorine community.

Shore zones of the Florida Keys (Stephenson and Stephenson, 1950) are closely similar to those of the Great Bahama Bank. In general these similarities are greatest in the white, gray, and black zones (the supralittoral fringe) and become less impressive at successively lower levels. The following comments will serve to point out some of the conspicuous differences between the Florida and Bahamian expressions of the littorine community but should not obscure the many impressive similarities that exist.

The small cerithid gastropod *Batillaria minima*, common in the black zone of the Florida Keys, is entirely lacking on Bahamian rocky shores, although the taxonomically similar *Cerithium variable* (also present in Florida) and the rare *Cerithium biminiense* (endemic to parts of the Bimini islands) are found in the black zone of Bahamian shores. *Batillaria minima* is found in abundance, however, on protected intertidal mud flats in the Bahamas.

Three gastropod species are common in the Bahamian yellow zone but are absent or rare on rocky shores of the Florida Keys: *Acmaea jamaicensis*, *Livona pica*, and *Petaloconchus* aff. *nigricans*. The boring barnacle *Lithotrya*, a characteristic inhabitant of the lower yellow zone in the Bahamas, is not reported by the Stephensons from the Keys, but it does in fact occur there in abundance (Ginsburg, 1953). The coralline lip seems to be absent from the Florida Keys. In fact, judging from observations of Stephenson and Stephenson 1950), encrusting coralline algae in general are sparse on rocky intertidal surface, their growth being restricted essentially to positions "under movable rocks or on dead coral, especially at low levels." This contrast may originate in differences in exposure to storm waves. Western and northern rocky shores of the Andros platform are exposed to the

open waters of the Florida Straits and the Northwest Providence Channel, whereas in the Florida Keys and eastern Andros Island the offshore reef tracts offer a measure of protection to the shores, and the coralline algae are inconspicuous along those shores. The coralline lip is more conspicuous on the inner rocky shores of cays around the Great Bahama Bank.

The main indicator organisms of the littorine community (rocky shores and intertidal and spray zones) are given in the following list (species marked by an asterisk are especially abundant):

White zone
Gastropods
*Tectarius muricatus
Littorina ziczac
Nodolittorina tuberculata
Echininus nodulosus

Gray zone
Gastropods
*Tectarius muricatus
*Littorina ziczac
*Nodolittorina tuberculata
*Echininus nodulosus

Black zone
Algae
Perforating green and blue-green (e.g., Entophysalis deusta)
Gastropods
Not in tide pools
*Littorina ziczac
Littorina mespillum
Littorina meleagris
Tectarius muricatus
Nodilittorina tuberculata
*Echininus nodulosus
Tide pools
Puperita pupa
Nitidella ocellata
Planaxis lineatus
Cerithium biminiense
Purpura patula
Lowest part of zone
*Nerita versicolor
*Nerita peloronta
Nerita tessellata
Crab
Grapsus grapsus

Upper yellow zone
Alga
Enteromorpha sp.?
Chitons
Chiton squamosus
*Acanthopleura granulata

Gastropods
*Littorina ziczac
Littorina mespillum
Littorina meleagris
Nodilittorina tuberculata
Echininus nodulosus
Livona pica
Purpura patula
*Nerita versicolor
Nerita peloronta
Nerita tessellata
Spiroglyphus "irregularis"
Siphonaria alternata
Acmaea jamaicensis
Diodora listeri
Sponge
Clione sp.
Barnacles
*Chthamalus angustitergum
*Tetraclita squamosa stalactifera (lower part of zone)

Lower yellow zone
Alga (green)
Valonia ocellata
Chitons
Chiton viridis
Chiton squamosus
Acanthopleura granulata
Gastropods
*Nerita tessellata
*Spiroglyphus "irregularis"
*Petaloconchus aff. nigricans
Thais rustica
*Livona pica
Purpura patula
*Acmaea jamaicensis
*Fissurella barbadensis
Pelecypods
Isognomon bicolor
Brachidontes exustus
Sipunculid
Phaseolosoma antillarum?
Barnacles
*Tetraclita squamosa stalactifera
*Lithotrya dorsalis

Coralline lip zone
Alga (encrusting coralline)
Porolithon pachydermum
Chiton
Chiton viridis
Gastropods
*Spiroglyphus "irregularis"
Thais deltoidea
Livona pica
Echinoid
Echinometra lacunter

INFRATIDAL SHOALS

LEDGES AND PROMINENCES
OF COUNTRY ROCK

Infratidal rock ledges and prominences are characteristic of exposed rocky shores in the Bahamas, where they form a characteristic substrate extending in a narrow band for hundreds of miles around virtually all the small cays and rocks of the Bank margin. These rock ledges are found also along rocky, mainly seaward, shores of Andros and Bimini, but generally they are absent along the inner shores of the larger islands which characteristically are low and muddy or sandy.

At many places along the rocky shores the *Millepora* terrace slopes gently seaward from the coralline lip (fig. 12; pl. 64). The maximum width of the platform thus formed is about 15 feet, but in most places it is either narrower or not developed at all, being removed by storm waves as it is formed. The surface of the platform is quite irregular, maximum depths below mean low stage ranging from about 2.5 to 5.0 feet. The lowest spring tides expose only the shallower portions of the terrace surface. We interpret this as an erosional remnant remaining after the *Porolithon* deposits have been stripped back, leaving the surface protected by encrusting corals and *Millepora*.

Immediately seaward of the upper surface of the terrace the bottom slopes away steeply as a wave-cut cliff that drops 12 feet or so to the gently sloping pavement of the outer platform (fig. 12). The submarine scarp usually is undercut, with an overhang ranging from a few inches to 6 feet or more (pl. 64, fig. 1). Scattered potholes formed by gravel scour lie at the foot of the cliff. This part of the profile is judged to be an effect mainly of present mechanical and organic erosion on the soft country rock (Newell and Imbrie, 1955). Encrusting calcareous organisms that might retard erosion are almost absent at these depths.

Conspicuous rocky spurs similar to those of Pacific coral reefs project at right angles from the shore along the seaward margin of the terrace face. A short distance offshore irregular erosion remnants rise here and there a few feet above the bottom. Parallel grooves, likewise reminiscent of the toothed margin of

Pacific reefs, are cut in the rock floor between the spurs and pinnacles.

Millepora COMMUNITY

Projecting rock ledges and prominences along the shore beneath the level of the lowest tides and above the sediment-scoured pavement support a community that has several of the characteristic elements of the coral reefs, but the majority of species are either soft-bodied epibiota or inbiota. Lime-secreting forms are subordinate here, and the environment is dominantly one of erosion by wave impact and strong turbulence. The most distinctive organisms are algae, sponges, a yellow gorgonian fan, *Millepora alcicornis*, and a host of rock-boring and burrowing organisms, including low forms of perforating algae (pl. 64, fig. 2). These are part of the *Millepora* community. The community composition is strikingly different from that of the amphibious littorine community above, but it exhibits a gradual transition to the plexaurid community of the rock pavement below. Characteristic species are listed below and are indicated on figure 12. At shallower depths many of the surfaces are covered with incrustations of the hydrocoralline *Millepora alcicornis*. In slightly deeper water this species commonly produces castellated, labyrinthine structures. *Porolithon* occurs in fair abundance over the inner surface of the terrace, but it becomes inconspicuous below low-tide level. Where the terrace is well developed, there is usually an abundance of small brown algae, especially *Turbinaria turbinata* and *Padina sanctaecrucis*.

Topographically and ecologically the *Millepora* terrace has many features in common with the "lower platform" described by the Stephensons (1950) from the Florida Keys. Among the conspicuous organisms of the *Millepora* community reported by the Stephensons from their lower terrace are: algae, *Valonia ocellata*, *Halimeda opuntia*, *Laurencia papillosa;* anemones, *Bartholomea annulata*, *Phymanthus crucifer*, *Condylactis gigantea*, *Zoanthus sociatus*; and *Echinometra lacunter*. However, a number of the characteristic elements of the Bahamian *Millepora* terrace are not reported in this position in the Keys, notably species of *Porolithon*, *Turbinaria*, *Padina*, *Millepora*, *Siderastrea*, and

Gorgonia. In all, the differences are about as impressive as the resemblances.

The characteristic species of the *Millepora* community (infratidal rocky prominences in turbulent waters) are as follows (asterisks denote the abundant species):

Algae
  Green
    Valonia ocellata
    Cladophoropsis membranacea
    Halimeda opuntia
    Caulerpa paspaloides
  Brown
    Turbinaria tubrinata
    Padina sanctaecrucis
    Zonaria zonalis
    Sargassum polyceratium ovatum
  Red
    Laurencia papillosa
    Corallina cubensis
    Goniolithon solubile?
    Jania capillacea
    Galaxaura subverticillata
Sponges
  Ircinia strobilina
  Ircinia fasciculata
  Tedania ignis
  Cliona vastifica
  Callyspongia vaginalis
  Chondrilla nucula
  Spongia officinalis
  Verongia fistularis
  Encrusting brown sponge
Anemones
  Bartholomea annulata
  Phymanthus crucifer
  Condylactis gigantea
  Stoichactis helianthus
  Zoanthus sociatus
Hydrocoralline
  Millepora spp.
Gorgonians
  Gorgonia flabellum (yellow variety)
  Plexaurids
Corals
  Palythoa sp.
  Diploria clivosa
  Diploria strigosa
  Siderastrea radians
  Siderastrea siderea
  Montastrea annulata
  Porites asteroides
  Porites porites
  Isophyllastrea rigida
  Agaricia agaricites
Echinoderms
  Echinometra lacunter

  Diadema antillarum
  Eucidaris tribuloides
  Ophiuroids, spp.
  Synaptus sp.
Gastropods
  Nitidella nitidula
  Columbella mercatoria
  Cyphoma gibbosum
  Coralliophila sp.
  Astraea tecta
  Livona pica
  Thais rustica
  T. deltoidea
  Fissurella fascicularis
  Conus mus
  Diodora listeri
  Morula nodulosa
  Thais deltoidea
  Leucozonia ocellata
Pelecypods
  Lithophaga bisulcata
  Lithophaga nigra
  Musculus coralliophagus
  Gastrochaena hians
  Isognomon radiata
Barnacle
  Lithotrya dorsalis
Crabs
  Panulirus argus
  Galappa flammea
Sipunculids

CORAL REEFS

REEF HABITAT

In Florida and the Bahamas, coral reefs generally are limited to shoals along the windward, or eastern, margins of submerged platforms where they are best developed a few hundred yards from the shores of larger cays and islands. Typically, the reefs encrust shoals and offshore cays of non-reef country rock, forming reef barriers outside shallow windward lagoons (fig. 8). Fringing reefs along the inner shores of these lagoons are virtually unknown, probably because of an abundance here of shifting calcareous sand, but patch reefs are common along the outer margin of the lagoons.

Reef corals generally are absent from the shelf lagoon of the Great Bahama Bank, but they are well represented in favorable places around the margins of the platforms, even in leeward areas. For example, although coral reefs are lacking along the western and northern margins of the Great Bahama Bank,

a majority of the known corals of the Bahamas, about 25 species, are recognized by Squires (1958) near Bimini. Most of these occur on rock bottom west of the cays, where they are bathed by clean ocean water of the Florida Current. These scattered colonies may be considered as pioneers in the colonization of the less favorable leeward margin of the Great Bahama Bank.

The climate of the Bahamas has been cited as marginal with respect to coral reefs (W. M. Davis, 1928), but several of the Bahamian coral species form thriving reefs at Bermuda, where the mean temperature for the coldest month is about 18.5° C. (Fuglister, 1947), or 5.5° C. lower than that of the Great Bahama Bank.

According to Vaughan and Wells (1943, p. 55), the optimum temperatures for reef growth lie between 25° C. and 29° C., with a minimum endurable temperature of about 18.5° C. Temperatures suitable for reef corals certainly prevail around the margins of the Great Bahama Bank. Winter temperatures cooler than those of the water surrounding the Great Bahama Bank occur for hundreds of miles along the Great Barrier Reef of Australia south of about latitude 12° S. (United States Hydrographic Office, 1944), but the biota of the Great Barrier Reef is much richer, and coral growth is more vigorous, than in the Bahamas. Differences in the reefs of the two regions certainly cannot be logically attributed to present differences in temperature.

It was long ago demonstrated in the tropical western Pacific that the prevailing wind has a marked influence on the growth and form of coral reefs and that windward reefs generally are more vigorous and better developed than leeward reefs. In the Bahamas coral reefs are limited almost entirely to the windward margins of the platforms, although hermatypic species are widely distributed around the leeward as well as windward edges. The factors responsible for characteristic differences between the windward and leeward coral communities undoubtedly are complex and are still debated. They have been attributed to variations in turbidity, turbulence, oxygenation, and abundance of animal plankton. Yonge (1940, p. 382) believes that the relative transparency and consequent stimulation of windward reefs by sunlight are mainly responsible for their greater vigor.

The distribution of hermatypic corals and coral reefs in the Bahamas not only indicates that the shallow bottom of the interior of the platforms is unfavorable but strongly suggests that the waters that return to the sea from the shelf lagoons during ebb tides also are deleterious to the hermatypic corals. The reef association is best developed on the seaward sides of islands, cays, and rocky shoals where the reefs are protected from Bank waters. The Bank waters are more variable than normal sea water in temperature and salinity. They are poor in plankton (Charles Fish *in* Field, 1931), and they may be appreciably depleted with respect to plant nutrients.

Water of the Great Bahama Bank is usually turbid. A large area of muddy deposits in the lee of Andros Island is covered by shallow waters in which the bottom generally is invisible in water more than 2 or 3 feet deep. On the other hand, small objects sometimes can be clearly seen in the water on the seaward side of the coral reefs east of Andros Island at a depth of 15 fathoms and more. Intermediate conditions of transparency exist along the western and northern margins of the Bank, where small objects are rarely visible at depths greater than 8 or 10 fathoms during calm weather. The shallowest bottoms of leeward areas become invisible in rough weather when fine sediment from the Bank is stirred up. At such times greenish waters spread beyond the platform, contrasting markedly with the deep blue waters of the ocean (pl. 58, fig. 2).

The precise effect of turbidity on corals is not well understood. The filtering of light by turbid waters probably is deleterious for the corals, as suggested above, but this cannot be decisive in the Bahamas because the correlation between transparency of the water and the observed depth for each coral species is only imperfect. Possibly, the finest-grained sediments have a smothering effect on the corals, especially branching, porous forms such as *Acropora*, that cannot remove sediment efficiently from the surface of the corallum.

Low air temperatures may affect corals of

the leeward margins of the Bahamian plat-forms more than those of windward areas. During winter storms, the air temperatures in the northern Bahamas occasionally drop to 50° F., causing extensive mortality among fishes of the shallowest waters. Observations are lacking, but it is probable that some damage occurs to the highest branches of the reef corals at these times. The majority of reef corals probably cannot live more than a few hours at temperatures below 62° F. (18° C.). The effects of exceptionally low winter temperatures may be greatest leeward where the Bank water, chilled to lower tem-peratures than those of the open ocean, tends to drift with the wind across the edge of the platform. Infrequent low temperatures in the northern Bahamas (e.g., the Abaco area) may limit upward growth of the corals to depths a few feet below the lowest tides.

The Andros barrier reef has been described by Newell and Rigby (1957). It is composed of discontinuous thin accumulations of dead and living corals on a submerged beach ridge of oolitic limestone dating from a stage in the Pleistocene when sea level was a few feet lower than the present level. To the south and north of Andros, where the barrier reef is bathed by Bank waters, it breaks down into patch reefs and scattered massive colonies, and the elkhorn coral (*Acropora palmata*), characteristic of the climax reef community, drops out. The lagoon patch reefs are bio-logically similar to the outer reef.

Acropora palmata COMMUNITY

The Bahamian reefs are characterized by an association of about 30 species of herma-typic corals, of which only a few are suf-ficiently abundant to be considered primary reef formers. The most important of these are:

> *Montastrea annularis*
> *Montastrea cavernosa*
> *Siderastrea siderea*
> *Diploria labyrinthiformis*
> *Acropora palmata*
> *Acropora cervicornis*
> *Porites porites*

Coralline algae play a role in cementation of the dead coral skeletons and foraminiferal sand, but they are much less important bind-ing agents than they are on many Pacific reefs. The minor role of the Corallinaceae and the lack of a marginal algal ridge in the Baha-mas are reflected in the loose texture of the reefs and the free circulation of sea water through, instead of over, the reefs (pl. 62, fig. 1). The intertidal reef flat so characteristic of Pacific reefs generally is lacking in West Indian reefs because of the lack of a protect-ing algal ridge (Newell and Imbrie, 1955).

The most conspicuous coral species of the Andros reefs is the elkhorn coral (*Acro-pora palmata*), a magnificent tree-like species that not infrequently attains a height of 10 feet or so, with a trunk 1 foot in diamter (pl. 61, fig. 1). This species characterizes depths that range from the surf zone down to a maximum of about 25 or 30 feet, and the tops of the branches in places grow upward into the lower part of the intertidal zone.

Seaward, the elkhorn coral is replaced by patches of the staghorn *Acropora cervicornis* and *Porites porites* (fig. 13). The outer and deepest parts of the reef are dominated by massive heads of *Montastrea annularis* (pl. 61, fig. 2), *Montastrea cavernosa*, *Siderastrea siderea*, and *Diploria labyrinthiformis* which cap buttresses and scattered knolls down to a depth of about 60 feet. The outer edge of the barrier reef usually lies in not more than 35 to 40 feet of water.

Visual inspection of the rock pavement outside the reef barrier below 60 feet shows only scattered massive colonies and much rarer coral knolls. Where the reefs are well developed, the reef ridge rises shoreward above the limits of *Acropora palmata*, with a crest near the lagoonal margin of the reef (fig. 13). Wherever the ridge rises above the water to form linear series of cays and rocks, it is seen to consist of oolitic limestone of drowned beach ridges of Pleistocene age. These have become encrusted on the seaward side by coral reefs and thin deposits of *Mil-lepora alcicornis*. The shoal rocks above the limits of *Acropora palmata* generally are being eroded. They lie in the zone of *Millepora*.

The reefs include a rich biota of rock-dwell-ing animals and plants which find shelter among the corals. In addition, there are many of the boring and burrowing worms and clams that also inhabit the *Millepora* zone.

ROCK PAVEMENT

PAVEMENT HABITAT

Among the distinctive features of the Great Bahama Bank are extensive level rocky bottoms or rock pavements. These are particularly well developed in marginal areas of the Andros platform, where waves and currents sweep the underlying country rock clear of sediment (fig. 17). They are particularly characteristic of the outer platform and the windward lagoon of Andros Island. Detailed studies of pavement areas in the vicinity of Bimini show that many of the rock-bottom areas represent submerged erosional terraces (Newell and Imbrie, 1955). Although pavement is most extensive in these marginal areas, there also are isolated small patches over the Bimini axis where currents prevent permanent accumulation of loose sediments. These areas support some of the "sponge reefs" formerly important to Bahamian economy and differ in important details from the more exposed outer platform.
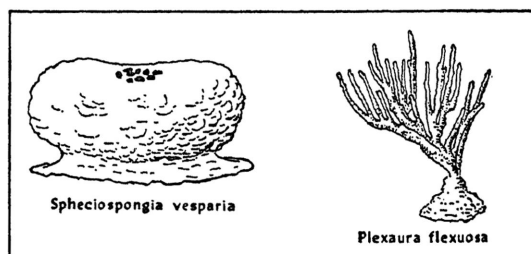
PLEXAURID COMMUNITY

The inner, shallow margin of the outer platform is subjected to vigorous gravel scour and wave impact (Newell and Imbrie, 1955). The pavement in these places supports a sparse cover of low algae and a few scattered sponges and massive corals of *Montastrea* and *Diploria*. These become somewhat larger and more numerous seaward below the depths of most frequent attack by storm waves. The most characteristic animals of this habitat, however, are sea whips of the family Plexauridae (fig. 13; pl. 62, fig. 2).

An ephemeral thin blanket of sand is spread over much of the rock surface occupied by the plexaurid community. This sediment cover is shifted about constantly by waves and currents, and the attached organisms are alternately buried and subjected to sediment scour. Once established, the gorgonian association can withstand scour and accumulation of sand to a depth of several inches, but pioneer larvae probably survive only in areas that are for a time free of sediments. Wherever the sediment cover exceeds about 6 inches in thickness, the pavement community is replaced by anchored
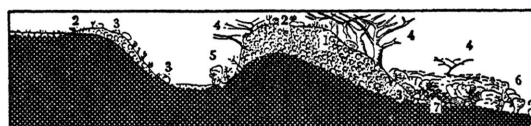
Acropora palmata Community

Plexaurid Community
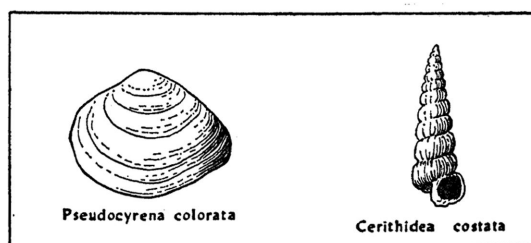
Cerithidea Community

FIG. 13. Characteristic organisms of the *Acropora palmata*, plexaurid, and *Cerithidea* communities. In the upper figure a cross section of the Andros barrier reef shows the community growing on reef rock (light pattern) which in turn overlies oolitic limestone (dark pattern). 1. *Millepora.* 2. Gorgonians. 3. *Diploria.* 4. *Acropora palmata.* 5. *Siderastrea.* 6. *Montastrea.* 7. *A. cervicornis.* Not shown to scale.

plants, vagrant organisms, and the infauna characteristic of sediment bottoms.

The most conspicuous elements of the plexaurid community (level rock pavement, with sand veneer) are as follows:

Algae
    Green
        Udotea flabellum
        Udotea cyathiformis
        Halimeda tridens
        Halimeda opuntia
        Halimeda scabra
        Halimeda incrassata
        Cladophoropsis membranacea
        Penicillus capitatus
        Penicillus pyriformis

    Penicillus dumetosus
    Rhipocephalus phoenix
Brown
    Sargassum sp.
Red
    Laurencia intricata
Grasses
    Cymodocea manatorum
    Thalassia testudinum
Sponges
    Spheciospongia vesparia
    Ircinia fasciculata
    Ircinia strobilina
    Spongia officinalis
    Callyspongia vaginalis
    Encrusting brown sponge
Bryozoan
    Schizoporella pungens[1]

[1] Restricted, apparently, to the shelf lagoon.

Gorgonaceans
    Gorgonia flabellum, purple variety
    Gorgoniids, many species
    Plexaurids, many species
Corals
    Montastrea annulata
    Siderastrea siderea
    Diploria strigosa
    Agaricia agaricites
    Porites porites
    Favia fragum
Echinoderms
    Ophiuroids, spp.
    Synaptus sp.
Pelecypod
    Chama congregata
Gastropods
    Cyphoma gibbosum
    Coralliophila sp.

SEDIMENT-BOTTOM HABITATS AND COMMUNITIES

THE SEDIMENTS OF THE Andros platform, as noted elsewhere in the Bahamas by Illing (1954), consist of several distinctive kinds of calcareous grains mixed in varying proportions. In terms of texture they are mainly medium-grained sands with varying mixtures of silt and clay-sized particles. The coarser fraction of the mixed sediment is rather well sorted. The grains include particles of skeletons of plants and invertebrates (pl. 69, fig. 3), but fish teeth and bones are either completely lacking or are extraordinarily rare. Other constituents are oolitic sand (pl. 68, fig. 3), ellipsoidal pellets, in large part calcified fecal pellets (pl. 68, fig. 1), grapestone lumps (pl. 68, fig. 2), and clay-sized particles that are irregular or acicular in shape (pl. 69, fig. 4). If contained water and organic matter be disregarded, the sediment is everywhere composed of nearly pure calcium carbonate mainly in the mineral form aragonite, with a minor proportion of calcite tests of Foraminifera and coralline algae.

Visual estimates of the percentage of each of the constituent kinds of grains in approximately 350 sediment samples has enabled us to construct a rough map of bottom facies (fig. 8). Extrapolation of facies boundaries are judgments based on topography and indications of bottom types on United States Hydrographic Office Chart 26a. Further sampling undoubtedly will require adjustments in the placement of the boundaries, but the broad patterns probably will not be modified greatly through additional work. It should be noted that identification of sediment type for the purpose of this study is based solely on external appearance; preliminary inspection of a few thin sections indicates that there are several subfacies within the major types enumerated here. Detailed description and evaluation of the sediments are being undertaken now by Edward Purdy for publication in the future.

The sedimentary facies show more intergradation than do the communities. Nevertheless the boundaries are real. They were selected objectively and without reference to the organisms.

The communities of the sediment bottoms include many burrowing mollusks, worms, and crustaceans of the infauna, not well represented in our sampling, but there also are many species of plants and invertebrates that are adapted to life on the surface of loose sediments. In protected marginal areas the plants form a protective cover that conceals 50 to 100 per cent of the area of the bottom. The majority of plants, both grasses and algae, of the soft bottoms are well anchored by means of holdfasts. They either penetrate the sediments or cling to anchored host plants. Some of the green algae, for example the Codiaceae (*Halimeda, Penicillus*), extend root-like processes deep into the substrate. These enmesh and cement with calcium carbonate the sand grains around the buried rhizomes, thus forming heavy cylindrical holdfasts that serve as efficient anchors (pl. 69, fig. 2). These plants serve not only as hosts for many commensals (pl. 69, fig. 1) and provide shelter and possibly food for animals, but they form a protective cover over the soft bottom, stabilizing the substrate and making it habitable for many of the species of the infauna that otherwise would be dispossessed with each storm. The main grasses, *Thalassia testudinum* and *Cymodocea manatorum*, are quantitatively by far the most important plants of the shallow Bank waters. In places, especially near the Bank margin, they form heavy carpets, which contrast markedly with the sparse plant cover characteristic of the interior of the shelf lagoon.

Seven sediment-bottom communities are recognized in this work, four of which are shown on the regional community map (fig. 9). They are: a beach community, *Strombus samba* (outer platform unstable sand), *Tivela* (unstable oolite), *Strombus costatus* (shelf lagoon stable sand), *Didemnum* (muddy sand), *Cerithidea* (near-shore mud), and mangrove (intertidal mud) communities. The following tabulation indicates the observed relationship between bottom facies and organism communities.

The relationship between substrate facies and organism community is as follows:

Mixed skeletal sand
    Strombus samba
    Strombus costatus

Unstable oolite
  Tivela
Stable oolite
  Strombus costatus
Grapestone sand
  Strombus costatus
Pellet sand
  Strombus costatus
Muddy sand and mud
  Didemnum
  Cerithidea
  Mangrove

Evidently there are environmental factors besides the characters of the substrate which determine the distributions of these communities. "Mixed skeletal" sand is found in extensive patches over the outer platform, but it is also the dominant bottom type in some areas just within the barrier rim (fig. 17). The skeletal sand areas of the outer platform are much more exposed than those within the shelf lagoon, and the hydrographic conditions on the two sides of the barrier rim are very different. These ecological differences are not reflected, however, in the gross character of the skeletal sediments. Thus two habitats are recognized with more or less identical substrate of skeletal sand. The grapestone sand, pellet sand, and stable oolite are physically unlike, but they characterize areas of stable bottom with a single distinctive biotic association, the *Strombus costatus* community. A muddy substrate is found in the areas of the *Didemnum*, *Cerithidea*, and mangrove communities. These communities were not distinguished by bottom type. There are, however, very evident dissimilarities in other factors of the physical environment. The *Cerithidea* community is found only in inshore areas of highly variable salinity, and the mangrove community extends into waters not deeper than about 3 feet at high tide. Field relations indicate that the *Cerithidea* community usually is found on areas having slightly higher mud content than the *Didemnum* community, but laboratory studies of the sediments have not yet been made to test this impression.

OUTER PLATFORM

UNSTABLE-SAND HABITAT

The several sand facies of the Bank margin are difficult to characterize. In this area the calcareous sand contains an appreciable proportion of skeletal grains, but it also usually contains a variety of other kinds of grains. Outside the barrier rim the skeletal content is greater than in other sands of the Great Bahama Bank. Skeletal grains are dominant in sediments of the windward lagoon and outer platform to the east of Andros Island (Newell, Rigby, Whiteman, and Bradley, 1951). It should not be inferred, however, that skeletal grains are in all places the dominant sediment constituent over the outer platform, for in places a mixture of oolite, pellets, and grapestone constitutes an estimated 90 per cent of the sediment. Hence the term "mixed skeletal sand" (pl. 69, fig. 3).

The inner, bankward, portion of the facies varies considerably in composition, and estimated percentages of skeletal material range from 10 per cent to nearly 100 per cent. In contrast, the seaward margin rather consistently contains more than 50 per cent of skeletal material. This variation in skeletal content apparently is the result of the dilution of skeletal grains by oolite pellets, and grapestone which migrate seaward from the Bank interior to the deeper water of the outer platform.

The mixed skeletal sand is limited largely to the windward lagoon (pl. 62, fig. 1) and to the outer platform between the marginal line of cays and shoals and the ocean. Where the marginal barrier is poorly defined, the inner edge of the facies tends to extend a short distance into the shelf lagoon.

The sand of this facies is characteristically thin, and extensive areas of bare rock pavement show through the thin cover.

Strombus samba COMMUNITY

This community is characteristic of relatively clear turbulent waters of the outer platform. The sand bottom is heavily rippled and relatively unstable; consequently, there is only very sparse vegetation, consisting mainly of patches of *Thalassia*. Our observations of this community are not so numerous as for communities of the shelf lagoon, but it was established that the black conch *Strombus samba*[1] (fig. 14) is highly characteristic of the

[1] This species is regarded by some authorities as invalid, pertaining to old individuals of *S. gigas*. In our

sands of the outer platform, and the bottom fauna contains a number of species, mainly pelecypods, not encountered in the many samples from shallower waters of the Bank interior.

The species characteristic of the *Strombus samba* community (outer platform, unstable-sand bottom, generally deeper than 2 fathoms) are:

Algae
  Green
    Udotea flabellum
    Halimeda spp.
    Acetabularia sp.
  Brown
    Padina sanctaecrucis
  Red
    Laurencia intricata

Grasses
  Cymodocea manatorum
  Thalassia testudinatum

Foraminifera
  Rotalia rosea

Polychaete worms

Echinoid
  Mellita sexiesperforata

Pelecypods
  Chione cancellata
  Laevicardium laevigatum
  Varicorbula operculata?
  Glycimeris undata
  Divaricella quadrisulcata
  Strigilla mirabilis
  Tellina radiata
  Lucina pensylvanica
  Verticordia ornata
  Chlamys benedicti
  Tellina interrupta
  Macrocallista maculata
  Irvilia sp.
  Gouldia cerina
  Pinctada radiata
  Musculus lateralis
  Plicatula gibbosa
  Anadara notabilis
  Aequipecten gibbus

Gastropod
  Strombus samba

experience the two forms favor very different habitats. They may represent ecophenotypes, or they may represent good subspecies. In any case, the form *S. samba* is an excellent indicator of the sandy bottom community on the outer platform.

OOLITE SAND SHOALS OF THE BARRIER RIM

UNSTABLE-OOLITE SAND HABITAT

Extensive sectors of the marginal barrier of the Andros platform are characterized by shallow ridges, or bores, of rippled, shifting, pure oolitic sand (pls. 60, 65) nearly devoid of animals and anchored vegetation. The extreme mobility of the substrate is demonstrated by observed continuous migration of small ripples and reversal of asymmetry of the megaripples with changes in tides. Megaripples with a maximum wave length of 100 meters and an amplitude of 0.5 meter are not exceptional in the areas of unstable oolite.

On the western side of the platform the unstable-oolite sand forms a relatively narrow, irregular, and discontinuous ridge a mile or so within the marginal escarpment (fig. 17). Wherever rocky cays occur along the oolite trend, the sand is concentrated entirely on the inner, or bankward, side of the cays, where it is somewhat protected from storm waves and tidal flow. On the eastern side of the Bank, oolite deposits occupy similar situations both north and south of Andros Island (Newell and Rigby, 1957), but the oolite facies is absent along the northern margin of the Bank, where it appears that water depths generally are too great for oolite formation.

In many places the oolite ridge just described rises to low-tide level and is conspicuously shallower than bottoms of adjacent facies. The margins of the oolite deposits are marked in places by steep slopes and are judged to correspond to fore-set accretions of tidal deltas. Oolite grains found mingled with other sediments immediately bankward of the ridge are in general smaller and less well sorted. They are interpreted as having been transported from the site of origin, the marginal oolite ridge.

The marginal distribution of the unstable oolite in very shoal areas of strongly agitated waters indicates that this sediment is forming at the sites of maximum accumulation at intertidal depths. Flood-tide water, saturated with respect to calcium carbonate, becomes heated and agitated, and the dissolved salts are further concentrated by evaporation on entering the Bank (Newell and Rigby, 1957).

Just why precipitation is in the form of concretionary layers around nuclei, rather than in the form of disseminated crystals, is not yet known. In any case, the youngest deposits of oolite known to us, as dated by radiocarbon means, are those of intertidal areas of the marginal bores.

Each ooid grain contains a great deal of mucilaginous organic matter and a tangled skein of microscopic filaments of blue-green and other algae (mainly *Entophysalis deusti*) which normally are perforating, rock-destroying forms. Although some of the colonies of algae clearly cut across the laminations, we do not believe that the over-all effect of these

animal life. This paucity of life is interpreted as the result of the extreme mobility of the substrate. A similar condition has been noted at the southern end of Lake Michigan where the sand substrate is " . . . much battered by waves . . . [and] the loose sand tends to be as bare of life as is a sandy desert during the heat of the day" (Allee and others, 1949, p. 161).

Even the distribution of the few hardy species adapted to this habitat (fig. 14) is governed by oolite mobility. The sparse growths of *Cymodocea* and, more rarely, of *Thalassia* and examples of the starfish *Oreaster* nearly always occur on the bankward

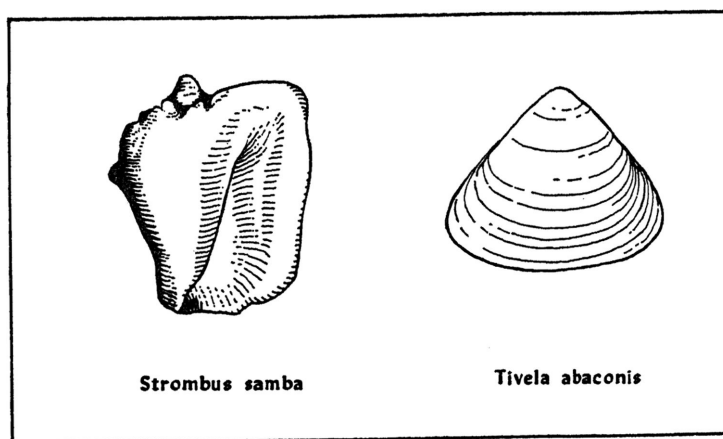**Strombus samba**   **Tivela abaconis**

FIG. 14. Characteristic organisms of the *Strombus samba* and *Tivela* communities. Not shown to scale.

plants is to destroy the ooid grains. In fact, the physical relationships as viewed in thin section strongly indicate that the calcium carbonate has been laid down around many of the filaments which originally must have adhered to the surface. As these are low forms of photosynthesizing plants, it is possible, but not certain, that they aid, possibly initiate, precipitation by elevating the pH locally over the surface. We are engaged in further studies of this problem.

Tivela COMMUNITY

No more striking example of the effect of substrate instability on marine life is to be found in the Bahamas than in the areas mapped as unstable oolite. In marked contrast to other Bahamian facies, the mobile oolite sands are relatively devoid of plant and

areas of the oolite belt, where the water is slightly deeper and, therefore, the tidal current velocity is less. This plant cover indicates comparative substrate stability.

As most starfish are carnivorous and feed chiefly on bivalves, it follows that the relative abundance of this asteroid in these somewhat stabilized, unsampled oolite areas is suggestive of a locally abundant pelecypod infauna. The species of the *Tivela* community (unstable-oolite sand bottom) are as follows (asterisks denote the most abundant forms):

Grass
   *Cymodocea manatorum
    Thalassia testudinum
Pelecypod
   *Tivela abaconis
Echinoderms
    Mellita sexiesperforata
   *Oreaster reticulatus

STABLE-SAND BOTTOM OF SHELF LAGOON AND MARGINAL LAGOONS

STABLE-SAND HABITAT

Bankward from the barrier rim there is a broad belt of fairly well-sorted calcareous sand in the range from fine-grained to medium-grained sand (fig. 8). This sand is heterogeneous in origin, as demonstrated by the variable content of skeletal grains, pellets, oolite, and grapestone. Evidently the prevailing conditions of disintegration and turbulence have resulted in nearly uniform texture over a vast area. Each of the several grain types is dominant in certain areas, which suggests different sources as well as different origins of the constituents, and these grain types have been separately mapped (fig. 8). The bottom in this part of the platform is sheltered from storm waves by the barrier rim, and the sediments are winnowed continuously by a fixed regimen of vigorous tidal flow and waves and currents caused by average winds. A protecting cover of vegetation, mainly grass, has stabilized the bottom in many places, particularly near the cays, where locally the grass cover becomes very heavy (fig. 17). This situation may reflect combined advantages of shelter and availability of fresh supplies of sea water rich in nutrients as compared with the depleted Bank waters of the interior. Rippling of the surface is not so common here as in the more exposed seaward zones. Andros windward lagoon and Bimini Bay contain large areas of stable-sand bottom similar to, but somewhat more protected than, the equivalent habitat in the shelf lagoon.

The pellet and grapestone sands require description, because these are poorly understood sedimentary types. The term "grapestone" is used for composite sand grains composed of small ooids and other grains cemented together to form botryoidal aggregates (Illing, 1954, p. 30). The grapestone facies replaces unstable oolite in some areas and may be a product of somewhat similar environmental conditions (pl. 68, fig. 2).

Sediment containing grapestone grains in excess of 30 per cent is indicated in the map (fig. 8) as grapestone, but the grapestone content of some samples runs as high as 95 per cent. In general, this facies seems to be characterized by stability, as indicated by the absence of ripple marks, the occasional presence of an organic film over the bottom, an abundance of the large mounds of burrowing organisms, and sparse to heavy vegetation. However, in the grapestone area of locality 323, where the water was very shallow, there was a notable lack of vegetation, and there were many coarse ripple marks.

The grapestone facies is most conspicuous in areas north and south of the latitude of Andros Island. The seaward margin of the facies is bounded by mixed skeletal sand or oolite, and the bankward margin is bounded by pellet sand.

Pellet sands are characterized by the presence of ellipsoidal grains in excess of 25 per cent (pl. 68, fig. 1). Many of these lack any trace of internal lamination. They have long been considered to be fecal pellets, and Cloud (personal communication) has evidence indicating that they may be formed mainly by a polychaete. The term is used here as a designation of prevailing ellipsoidal shape and carries no implication of origin. The maximum pellet content of the facies is about 80 per cent.

Our observations of the bottom indicate that the pellet sands in general are devoid of ripple marks, and they usually are covered by a brownish film composed of microscopic bits of living and dead organic matter. Many of the samples emit the odor of hydrogen sulfide. These characteristics indicate a general lack of mobility of the substrate. Because stabilized substrate is so characteristic of the pellet facies, we have mapped two areas of dominantly oolitic sediment (localities 314, 395) as pellet sand rather than adopt a separate map symbol for stabilized oolite sand.

The seaward margin of the pellet sand is bounded by any one of three bottom types: mixed skeletal sand, unstable oolite, or grapestone. In contrast, the bankward margin is consistently bounded by muddy sand.

Strombus costatus COMMUNITY

This is a rich and diverse community characterized especially by many echino-

derms and mollusks[1] living in a moderately heavy plant cover of grass and algae (fig. 15; pl. 59, fig. 1). Locally, in the sheltered, very shallow waters of Bimini and Andros lagoons, holothurians are abundant and conspicuous, but they are rare or absent over the shelf lagoon. *Goniolithon strictum*, a coralline alga, is abundant over shallow grass bottoms in protected places where locally it is an important sediment former. It is ecologically quite unrelated to the corallines of the reef community. A conspicuous element of the *Strombus costatus* community over the shelf

lagoon) communities, but the colonies are there smaller and less numerous.

The species of the *Strombus costatus* community (shelf lagoon and marginal lagoons, stable-sand bottom, generally less than 1.5 fathoms) are as follows (most abundant forms marked with an asterisk):
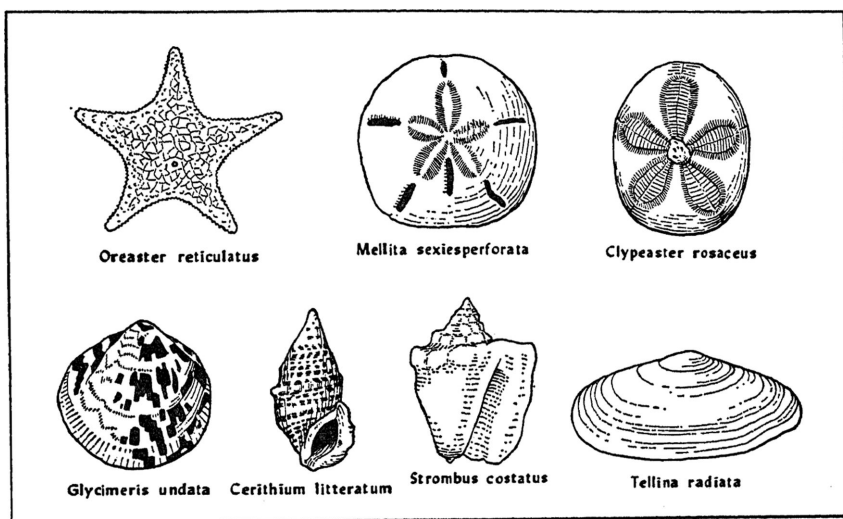
Algae
    Green
        Halimeda spp.
        Penicillus pyriformis
        Acetabularia crenulata
        Dictyosphaeria cavernosa

Oreaster reticulatus   Mellita sexiesperforata   Clypeaster rosaceus

Glycimeris undata   Cerithium litteratum   Strombus costatus   Tellina radiata

Strombus costatus Community

FIG. 15. Characteristic organisms of the *Strombus costatus* community. Not shown to scale.

lagoon is a commensal association of a branching cheilostome bryozoan (*Schizoporella pungens*) and species of *Halimeda* (pl. 69, fig. 1). The function of the plant seems to be that of providing an anchorage and growth nucleus. The whole structure is easily uprooted and rather fragile, and its occurrence in the pellet sand is additional evidence that points to the stability of this bottom facies and generally quiet waters above it. The *Schizoporella-Halimeda* combination is found also in the *Didemnum* and plexaurid (shelf

        Rhipocephalus phoenix
    Red
        Laurencia intricata
        Goniolithon strictum
Grasses
    Thalassia testudinum
    Cymodocea manatorum
Echinoderms
    Clypeaster rosaceus
    Mellita sexiesperforata
    Tripneustes esculentus
    Lytechinus variegatus
    Myoma ventricosa
    Oreaster reticulatus
Corals
    Porites furcatus
    Manicina areolata

[1] Although we did not encounter it in this community, Robert Robertson (personal communication) reports *Cantharus multangulus* as locally common in grassy areas.

Bryozoan
  Schizoporella pungens
Gastropods
  Strombus costatus
  Strombus gigas
  Cerithium litteratum
  Cerithium eburneum
  "*Olivella*" sp.
  Astraea phoebia
  Conus jaspideus
  Columbella mercatoria
  Nassarius ambiguus
  Bulla occidentalis
  Modulus modulus
  Terebra dislocata
  Prunum apicinum
  Natica canrena
  Calliostoma pulchrum
  Cantharus multangulus
Pelecypods
  Glycymeris undata
  Glycymeris pectinata
  Anadara notabilis
  Lucina pensylvanica
  Lucina nassula
  Codakia orbicularis
  Macrocallista maculata
  Crassinella lunulata
  Gouldia cerina
  Semele bellastriata
  Cumingia coarctata
  Musculus lateralis
  Tellina radiata
  Trigoniocardia media
  Laevicardium laevigatum
  Trachycardium muricatum
  Anodontia alba
  Diplodonta sp.
  Macoma sp.
  Pitar sp.?
  Pinctada radiata
  Aequipecten gibbus
Polychaete worm
  Arenicola cristata
Crab
  Petrochirus bahamensis

BIMINI LAGOON

In figure 9 Bimini lagoon has been mapped as part of the *Strombus costatus* community. This is an oversimplification of a faunally complex area which is justified only by the relatively small size of the lagoon. In the broadest sense the lagoon may be said to consist of three basic habitats: a northern area characterized by poikilohaline and, to some extent, intertidal conditions; a southwestern area characterized by relatively stenohaline conditions; and a southeastern area of intertidal flats (see Turekian, 1957, for a discussion of the salinities in the Bimini lagoon). In all three areas the proportion of rock bottom is small.

In the nothern part of the lagoon the most conspicuous constituents of the biotic community are the alga *Batophora* spp. and the gastropod *Batillaria minima*. Plexaurids generally are absent on small areas of rock substrate. The southwestern portion of the lagoon is characterized by an abundant and taxonomically diverse echinoderm fauna. Holothurians (*Holothuria mexicana*, *Stichopus badionotus*, *Actinopyga agassizi*) and echinoids (*Diadema antillarum*, *Tripneustes ventricosus*, *Lytechinus variegatus*, *Clypeaster rosaceus*, and *Mellita sexiesperforata*) are particularly abundant, and asteroids (*Oreaster reticulatus* and *Echinaster sentus*) and ophiuroids are common. Plexaurids, corals, and sponges colonize relatively small areas of rock substrate. Squires (1958, p. 229) has noted corals on the rock margins of a natural channel along the North Bimini shore near the lagoon entrance, an occurrence that he has attributed to vigorous current action and daily replenishment of new ocean water by the tides. The gastropods *Strombus gigas* and *S. costatus* frequently occur among growths of the marine grass *Thalassia testudinum*. The abundance and taxonomic diversity of the echinoderms suggest a closer degree of affinity to the *S. costatus* community than to any other recognized Bank community. The southeastern part of the lagoon is characterized chiefly by an abundance of worm mounds and by a general lack of flora.

MUDDY SEDIMENT OF THE SHELF LAGOON

MUDDY-SAND AND MUD HABITATS

The sheltered area west of Andros Island is characterized by muddy sediments in which there is 10 per cent or more of silt- and clay-sized particles of aragonite (pl. 69, fig. 4). In general, the proportion of fine particles increases towards the Andros shore where silt- and clay-sized particles compose up to 80 per cent of the sediment, and the sand constituents are pellets and skeletal grains. Stability of the substrate is indicated by bottom vegetation, fineness of the sediment, and

the almost complete absence of ripple marks.

The muddy-sand and mud facies is bounded on the north, west, and south by pellet sand, and on the east by Andros Island. The southern boundary of the facies was inferred from textural indications on United States Hydrographic Office Chart 26a.

Three well-defined habitats may be distinguished over the muddy substrate: (1) areas of normal to hypersaline waters (*Didemnum* community); (2) near-shore and estuarine areas of alternately low and high (poikilohaline) salinities (*Cerithidea* community); and (3) intertidal flats (mangrove community).

A frequently cited correlation between high salinity and bottom mud on the Bank is only an approximation. Many investigators have attributed the formation of the aragonite mud to evaporation and inorganic precipitation. The distribution of the fine sediment, however, seems to be an effect of shelter from currents.

Lowenstam and Epstein (1957) have offered evidence that the aragonite mud consists of needles secreted internally by various species of algae. In support of this idea they show that needles from experimentally grown control algae are not in equilibrium with respect to O^{18}/O^{16} under conditions of salinity and temperature assumed for the Bank waters. They compare the oxygen ratio of a mud sample from the west coast of Andros with that of Bahamian oolite which was found to be in equilibrium with the surrounding waters. Lowenstam and Epstein assumed an average salinity of greater than 40 parts per thousand for the water over their mud sample. However, if, as seems more reasonable, an average of 39 parts per thousand were assumed, the aragonite mud would appear to be in equilibrium, and hence, according to their argument, should be of inorganic origin. This possibility casts some doubt on their argument that the mud is largely, or entirely, of organic origin, and the whole matter needs further investigation.

In some places the extensive mud deposits of the lakes and swamps of western Andros Island gradually are being eroded and redeposited on the Bank (pl. 67), and the inland deposits, as discussed above, may be many hundreds of years old. In any case, the mud probably is not forming by bacterial action

in the swamps under existing conditions as postulated by Bavendamm (1932), Black (1933), Drew (1914), and Kellerman and Smith (1914). From dates obtained by Rubin on samples taken on the Bank west of Andros, it appears that the average age of the surface sediment here is only a few hundred years. All the facts support the theory advanced by Vaughan (1918) and tested by C. L. Smith (1940) that most, but not necessarily all, of the mud is inorganically precipitated from sea water as it is concentrated by evaporation over the Bank.

Didemnum AND *Cerithidea* COMMUNITIES

The hypersaline water of the interior shelf lagoon is underlain by the distinctive *Didemnum* community. The area occupied by the community is more extensive, however, than the waters of high salinity. Consequently, there is only imperfect correlation of the distribution of this community with local conditions of salinity. The most conspicuous and distinctive surface-dwelling elements of this community are a green alga (*Caulerpa paspaloides*), a yellow candle sponge (*Verongia fistularis*), and especially a gray-white colonial tunicate (*Didemnum candidum*). In general, the epifauna is rather sparse, and it is only when the infauna is collected and considered that the diversity of the whole community is appreciated. Undoubtedly failure on the part of previous investigators to examine and sieve the bottom sediments is responsible for a widespread impression that the muddy areas of the Andros platform are nearly barren of life. The species identified in our survey are listed below (the most abundant marked by asterisks), and figure 16 illustrates a few of the most prominent forms.

Compared to the *Didemnum* community just described, the *Cerithidea* association is much less diverse. Our sampling of this community is very limited, however, and it is possible that additional work will alter this impression. *Batophora oerstedii* is particularly abundant, and two mollusks (*Cerithidea costata* and *Pseudocyrena colorata*) seem to be limited largely to this poikilohaline habitat (fig. 13). This is the only example that we can offer among Bank communities of salinity-controlled distribution.

Species of the *Didemnum* community (stable bottom, muddy sand) are:

Algae
  Green
    Halimeda spp.
    Penicillus pyriformis
    Acetabularia crenulata
    Dictyosphaeria cavernosa
    Rhipocephalus phoenix
    **Caulerpa paspaloides*
    Batophora oerstedii

MANGROVE HABITAT AND COMMUNITY

The mangrove community, as does the coral reef, modifies and dominates its environment. It characterizes sheltered marshes and intertidal mud flats where the interlocking prop and buttress roots of the mangrove plants form an efficient trap for fine sediment. Consequently, the mangrove community plays an important role in the extension of

Didemnum Community
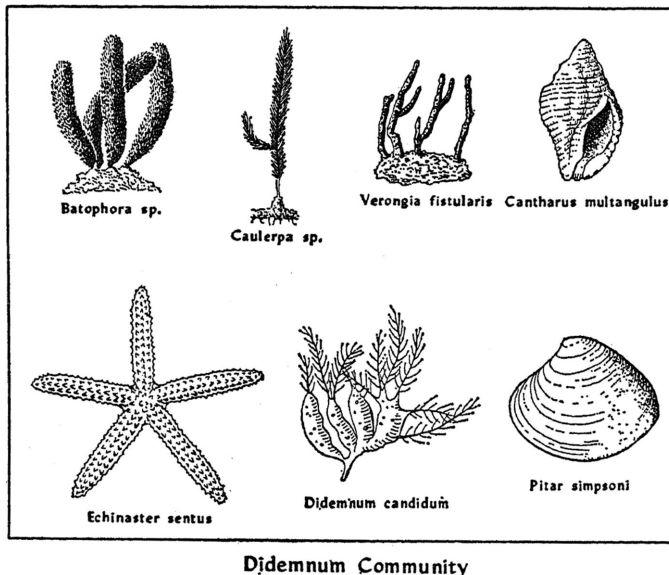
FIG. 16. Characteristic organisms of the *Didemnum* community. Not shown to scale.

Grasses
    Thalassia testudinum
    Cymodocea manatorum
Mollusks
  Pitar simpsoni
  Cantharus multangulus
Sponges
  **Verongia fistularis*
  Ircinia fasciculata
Bryozoan
  Schizoporella pungens
Coral
  Manicina areolata
Echinoderms
  Echinaster sentus
  Clypeaster rosaceus
Tunicate
  **Didemnum candidum*

island shores by means of sediment accretion (John H. Davis, Jr., 1940). The lagoon shores of Bimini and the marshes of western Andros Island are covered in places by mangrove thickets of rather low and stunted growth over alternating low ridges and swampy swales (fig. 7; pl. 66). As the ridges are more or less accordant and near high-tide level, it seems that they were all formed approximately at present sea level. The accretion ridges represent successive tidal levees and storm beaches which were quickly stabilized by the mangrove plants, especially the red mangrove (*Rhizophora mangle*) and the black mangrove (*Avicenna nitida*). Where offshore waters are very shallow, the pioneer man-
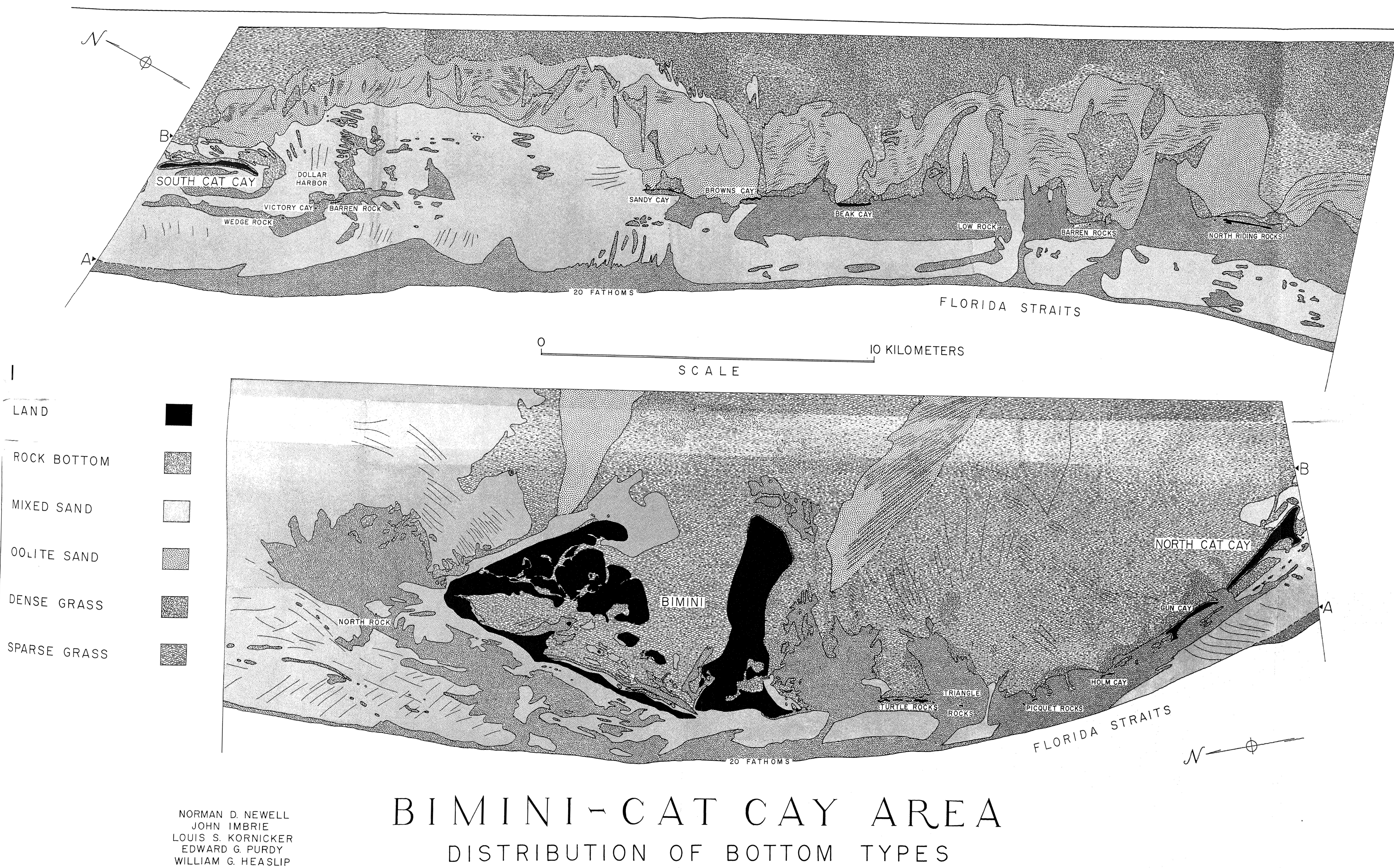
N

B

SOUTH CAT CAY

DOLLAR
HARBOR

VICTORY CAY   BARREN ROCK

WEDGE ROCK

A

SANDY CAY

BROWNS CAY

PEAK CAY

LOW ROCK

20 FATHOMS

BARREN ROCKS

NORTH RIDING ROCKS

FLORIDA STRAITS

0   10 KILOMETERS
SCALE

I

LAND

ROCK BOTTOM

MIXED SAND

OOLITE SAND

DENSE GRASS

SPARSE GRASS

NORTH ROCK

BIMINI

NORTH CAT CAY

GUN CAY

A

HOLM CAY

TRIANGLE
ROCKS

TURTLE ROCKS

PICQUET ROCKS

20 FATHOMS

FLORIDA STRAITS

N

NORMAN D. NEWELL
JOHN IMBRIE
LOUIS S. KORNICKER
EDWARD G. PURDY
WILLIAM G. HEASLIP

BIMINI-CAT CAY AREA
DISTRIBUTION OF BOTTOM TYPES

FIG. 17. Map of bottom types along the western margin of the Andros platform from Bimini to North
Riding Rock. Trends of megaripples, sand streaks, and small tidal channels shown by form lines.

grove plants (especially *Rhizophora mangle*) form a protective seaward fringe which effectively anchors the outer ridge, and, by trapping sediment, they gradually extend the shore until the community advance is checked temporarily by construction of a new storm beach beyond the mangrove (pl. 66). The black mangrove requires space and periodic exposure of the air-breathing roots. Consequently, it is most characteristic of the ridges, while the red mangrove dominates the swales.

The bottom sediments within and near the mangrove thickets are muddy and rich in organic detritus, most of which probably consists of the more refractory constituents of decaying mangrove vegetation. Kornicker (in press) has found that the sediment is rich in H_2S and contains as much as 2.19 per cent of organic carbon. The infauna is correspondingly poor and specialized for life in anaerobic sediments.

Many mollusks favor the peculiar conditions of life among filamentous algae on the mangrove roots. Several unidentified species of Foraminifera also were observed here. Some of the common species of the community are as follows (the most abundant marked by asterisks):

Algae
   *Batophora sp.
   *Filamentous algae, various spp.
Mangroves
   *Rhizophora mangle
   *Avicenna nitida
Gastropods

   *Littorina angulifera
   Meioceras nitidum
   Caecum floridanum
   Fasciolaria tulipa
   Persicula lavalleana
   Pedipes ovalis
   Cerithium litteratum
   Nitidella ocellata
   *Batillaria minima
   Cerithidea costata
   Modulus modulus
   Prunum apicinum
   Assiminia sp.
   *Cerithium variable
Pelecypods
   *Lasaea bermudensis
   Condylocardia floridensis
   Pseudocyrena sp.
   Brachydontes citrinus

The tidal creeks within the mangrove areas are floored with muddy sediment and patches of vegetation of *Thalassia testudinum*, *Dasycladus* sp., and *Laurencia* sp. The following mollusks were collected here by dredging:

Gastropods
   Cerithium eburnium
   Cerithidea costata
   Crepidula convexa
   Tricolia bella
   Rissoina cancellata
   Acteocina sp.
Pelecypods
   Cumingia coarctata
   Tellina iris
   Codakia orbiculata
   Chione cancellata
   Pseudocyrena sp.
   Transennella sp.

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Bimini Islands

General view looking north. The islands are composed of Pleistocene marine limestones and accretion ridges of Recent age. Dark patches to the left of Bimini are areas of submarine pavement of the outer rim. Black areas along the lagoon shores are mainly mangrove thickets. Lerner Marine Laboratory is ᵈ to the left of center

South Bimini and vicinity, looking north; Florida Straits on the left. Sediment-laden Bank waters form ᵃ counter current along the western shore. The peninsula at the left, Rabbit Cay Point, is bordered on ᵂard side by a narrow strip of rock bottom which supports a diverse fauna of gorgonians and corals ᵇᵏward by sand bottom. Foreground is mainly submerged rock pavement marked by thin strips of ˢkeletal sand

1

2

ISLANDS OF THE BARRIER RIM

1. View northwest across Beak Cay; Brown's Cay just visible in distance. Light-colored of oolite sand are accumulating on the Bank sides of these cays. Dark-colored bottom between are mixed sand with varying amounts of *Thalassia* grass cover

2. View northwest across Little Harbor Cay, Berry Islands; Ambergris Cays in the lagoon is separated here from deeper water of the outer platform (foreground) by a double cays are Pleistocene dunes and beach ridges of oolitic limestone. Note conspicuous the foreground

Ridge of the barrier rim, about 35 kilometers south of Bimini. Outer platform to left, shelf lagoon at right. Damming effect of barrier islands shown by festoon arrangement of light-colored oolite ridge. Part of extensive stippled area of the ridge is intertidal. It is bordered on both sides in most places by outward-facing delta scarps. Note narrow, east-west channel north of Sandy Cay doubly terminated by small deltas. Approximate scale: 1 cm. = 275 meters.   United States Hydrographic Office photograph
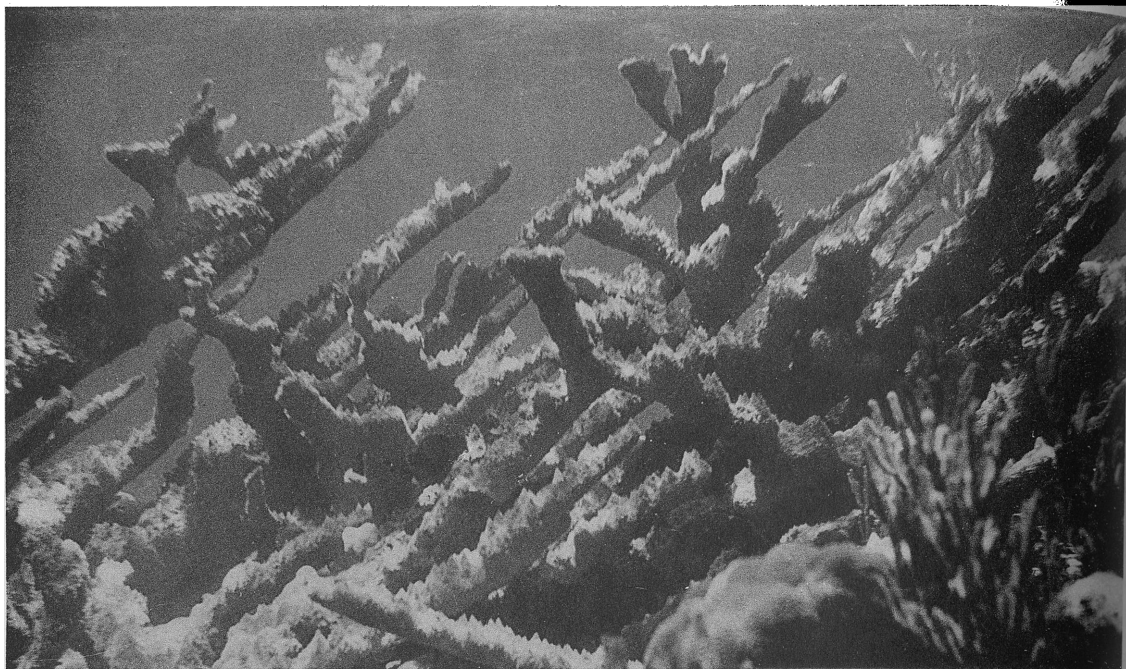
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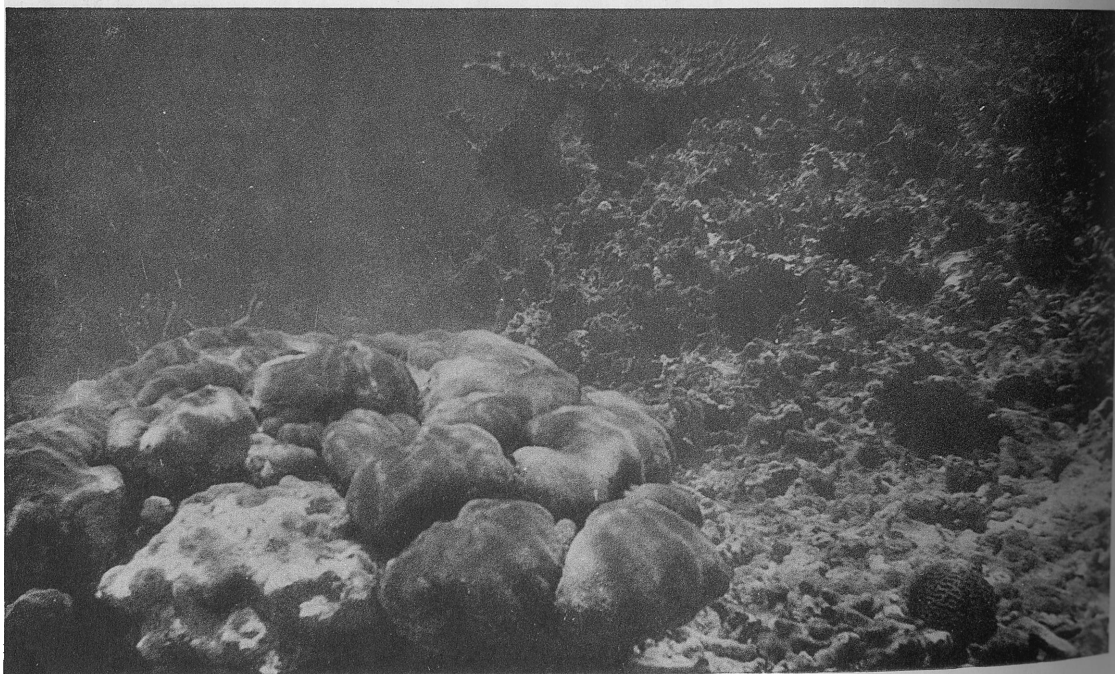
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CORAL REEF ZONES

1. *Acropora palmata*, species of the climax reef, near Long Cay, Andros Island. The
background is about 10 feet wide

2. *Montastrea annularis*, left foreground, a colony about 8 feet in diameter. This spe
outer and deeper margin of the reefs. The shallower corals in the background are *Acrop*
of the rubble visible belongs to this species

ROCK-BOTTOM COMMUNITIES

iculate rim of Andros barrier reef east of Mastic Point. Conspicuous colonies of *Acropora palmata*
just below low-water level. Deeper corals of *Montastrea* zone form indistinct spurs in the foreground
urid community of gorgonians, scattered corals, and algae; outer platform, Goat Cay, near Andros
ros Island

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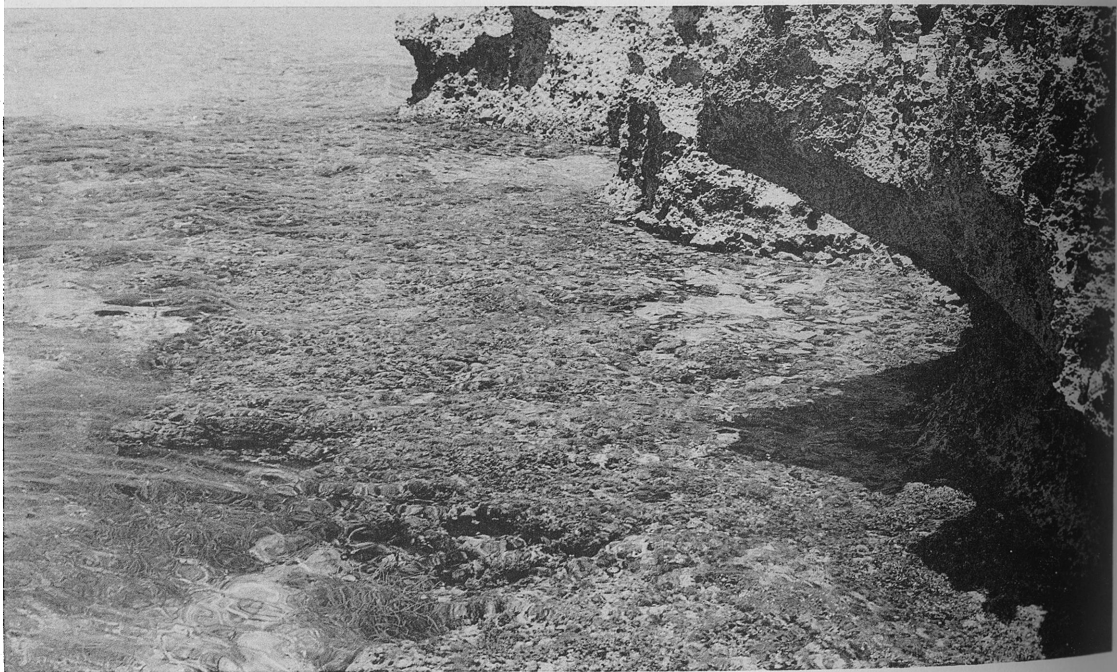
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ROCKY-SHORE PROFILES

1. Looking south along east side of Fraziers Hog Cay. Storm terrace cut in cross-bedded
The yellow and black zones to the left exhibit the hackly surface characteristic of erosion
along the inner part of the platform is encrusted by a caliche-like deposit

2. Intertidal nip and *Millepora* terrace along western shore of Rabbit Cay Point, South B
lip is here an inconspicuous ridge just at the water level. The *Millepora* terrace suppor
brown and red algae
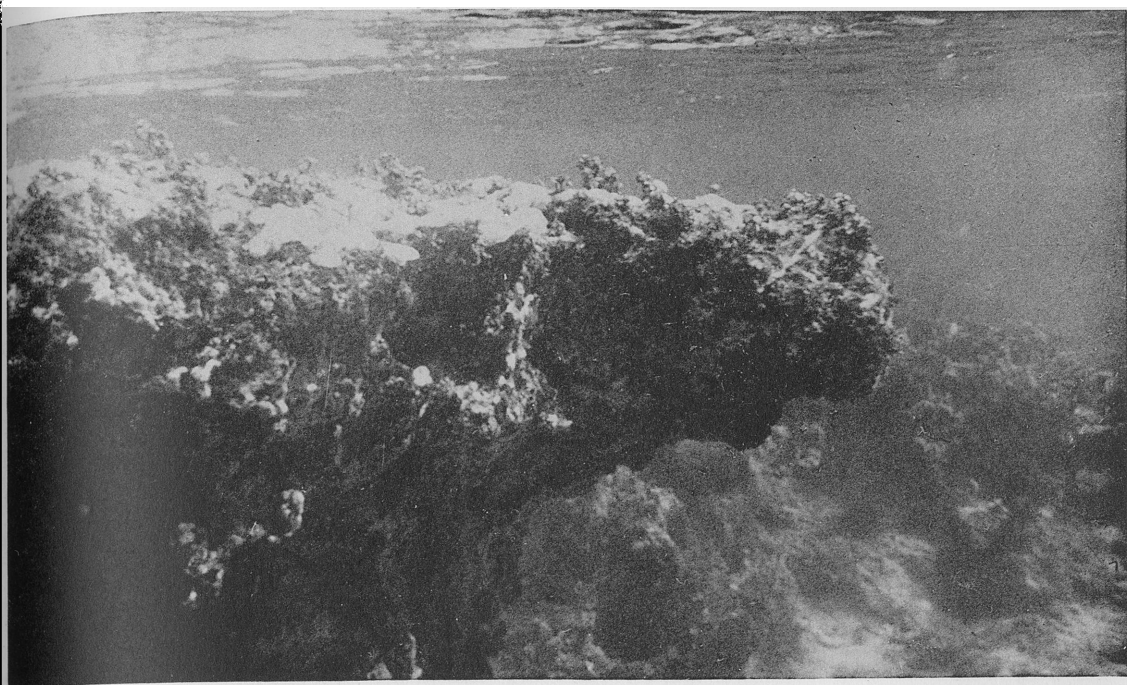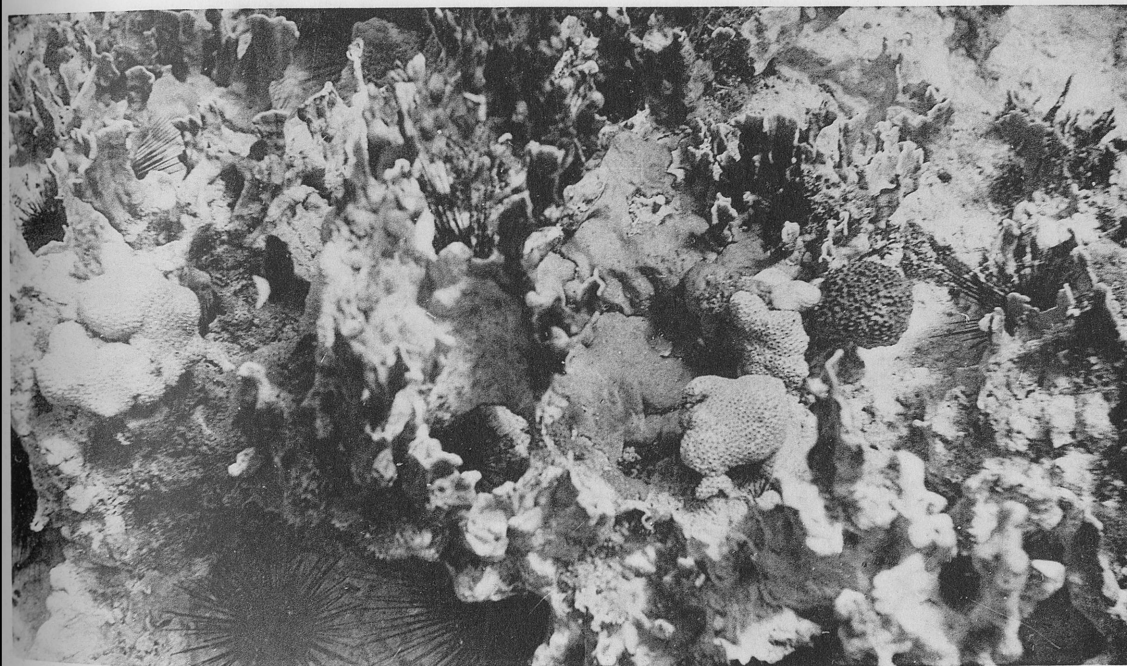
Millepora COMMUNITY AT RABBIT CAY POINT, SOUTH BIMINI

Under-water view looking south along overhanging face of Millepora terrace. Visible on the upper surface isolated tufts of brown algae and encrusting colonies of a light-colored soft coral

Close-up view of Millepora community. Dominant organism is the hydrocoralline Millepora alcicornis. Visible also the long-spined echinoid Diadema antillarum, a globose sponge, and lobate growths of soft coral
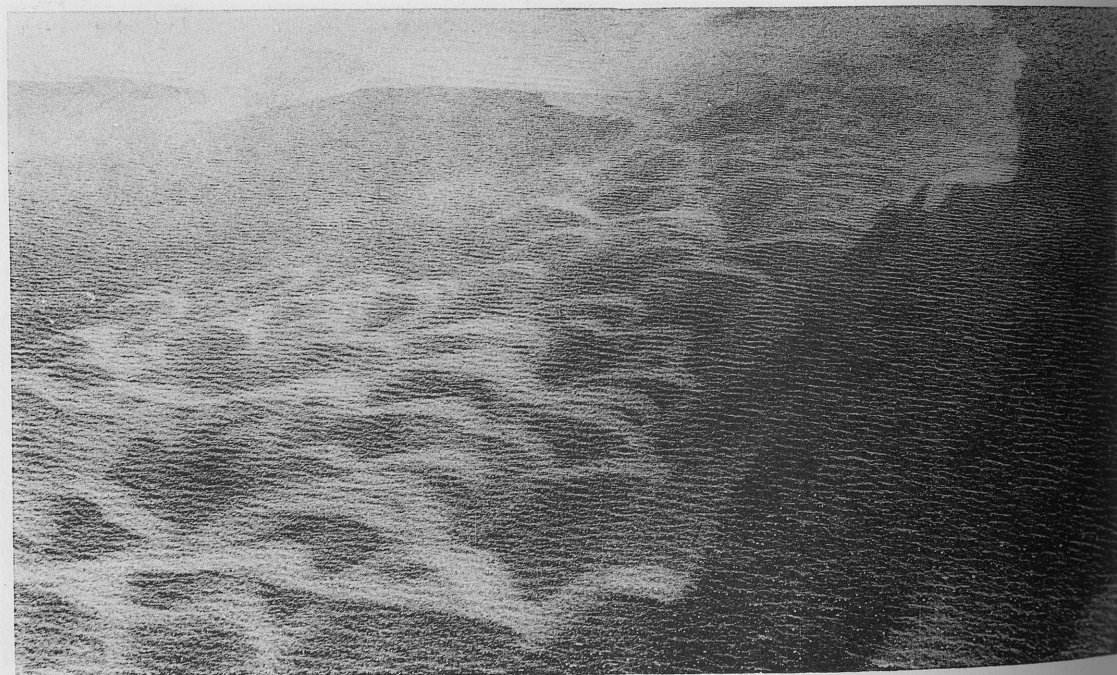
OOLITE BORES

1. View northeast across Sandy Cay. Light-colored bottom in middle distance is the
of extensive deposits of nearly pure oolite sand in a belt 3 kilometers wide along the edge of
of east-west trending ridges (bores) rise to intertidal depths. Dark-colored bottom between
channels, portions of which have become stabilized by carpets of *Thalassia* grass

2. Barchan-like deposits of oolite sand over rock pavement of Tongue of the Ocean.
to 100 feet wide
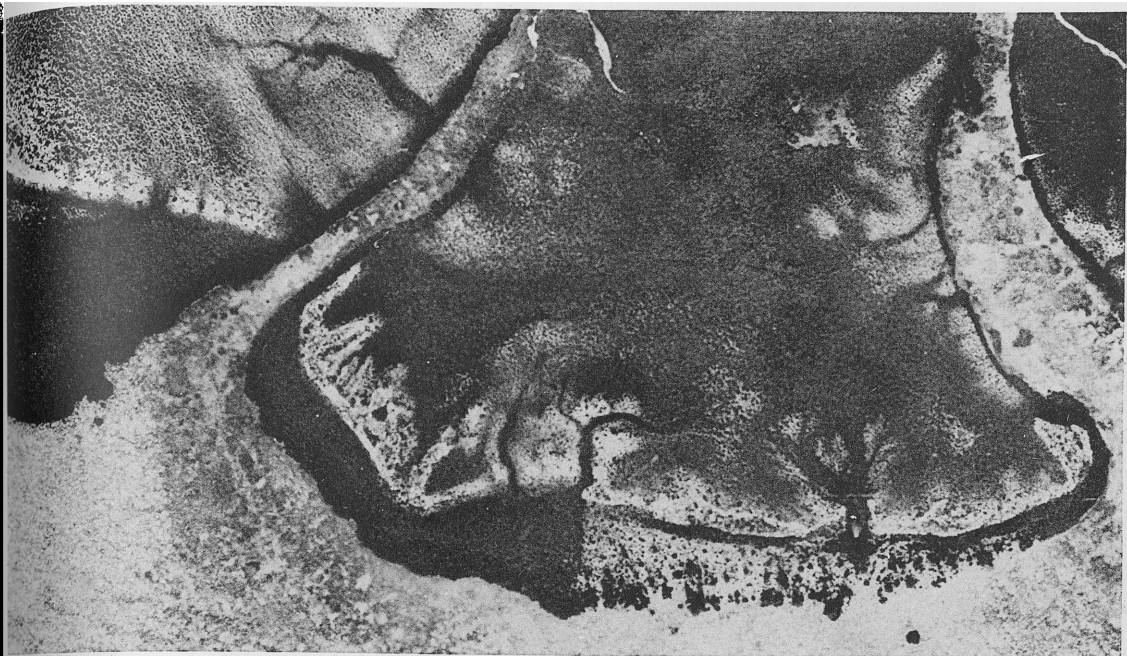
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ACCRETION TOPOGRAPHY

tical view of mangrove area west of Bone Fish Hole, East Bimini. Dark-colored areas are swamps of
grove; mottled areas, better-drained swales of black mangrove; and narrow, light-colored bands,
n and bypassed beach ridges. Note isolated offshore pioneer clumps of red mangrove
w looking north over Andros Island near its western shore, just visible at upper left. Narrow west-
dal creek in foreground is flanked by mangrove-covered natural levees. Interstream areas are a
of mangrove swamps, shallow lakes, and swales. The dark patch near the center of the photograph
y an erosion remnant of bedrock
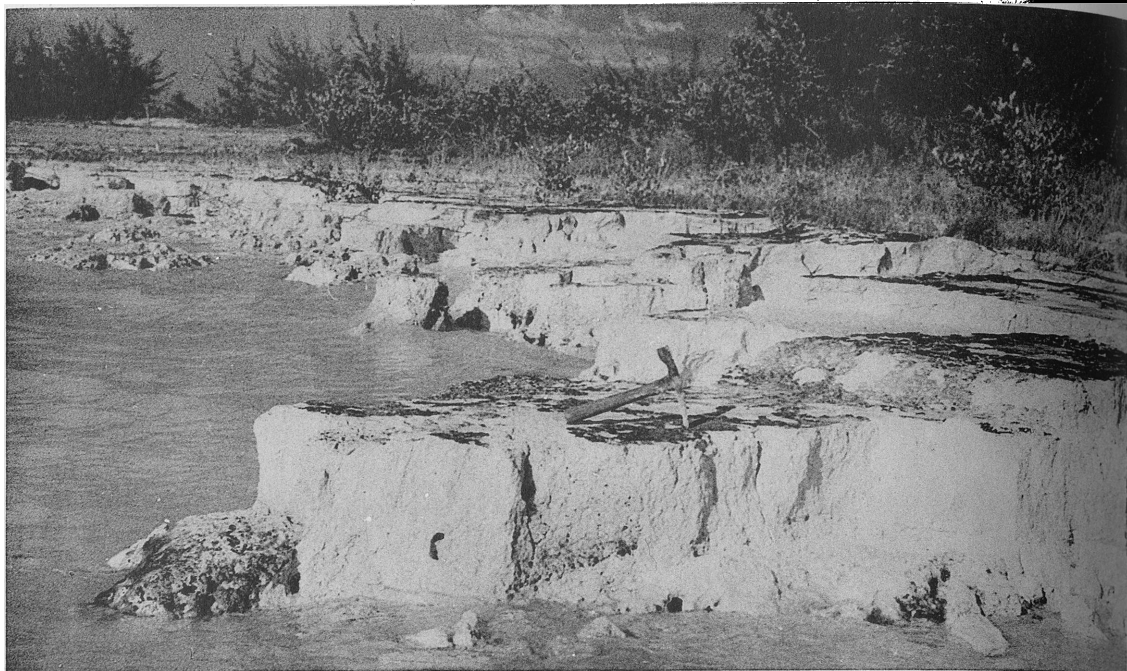
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MUD SHORES OF WESTERN ANDROS ISLAND

1. Low sea cliff cut in soft sandy mud. Beach ridge in background rises several feet above it separates extensive swamps from the shelf lagoon

2. View looking north towards the mouth of South Bight. Active beach ridges of sandy mud western shore and shores of the larger tidal inlets. The densest red mangrove colonies, such as the middle distance, occur in protected ponds of suitable depths
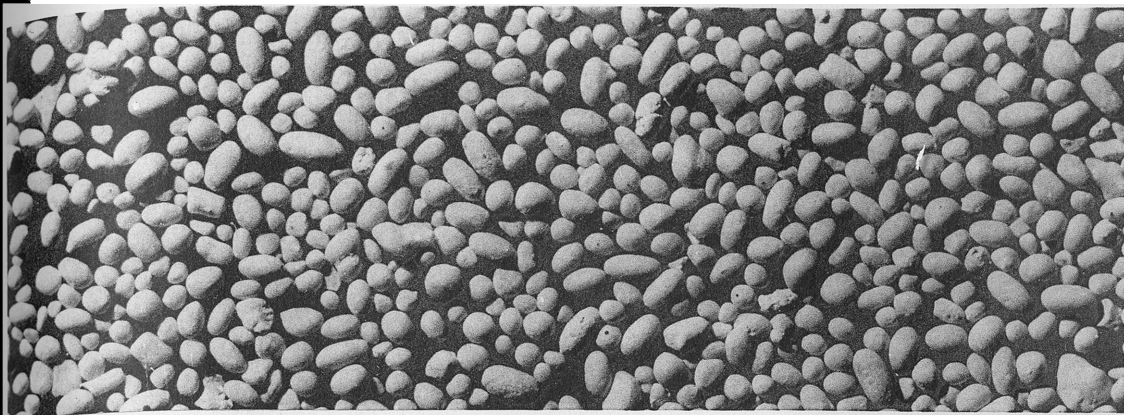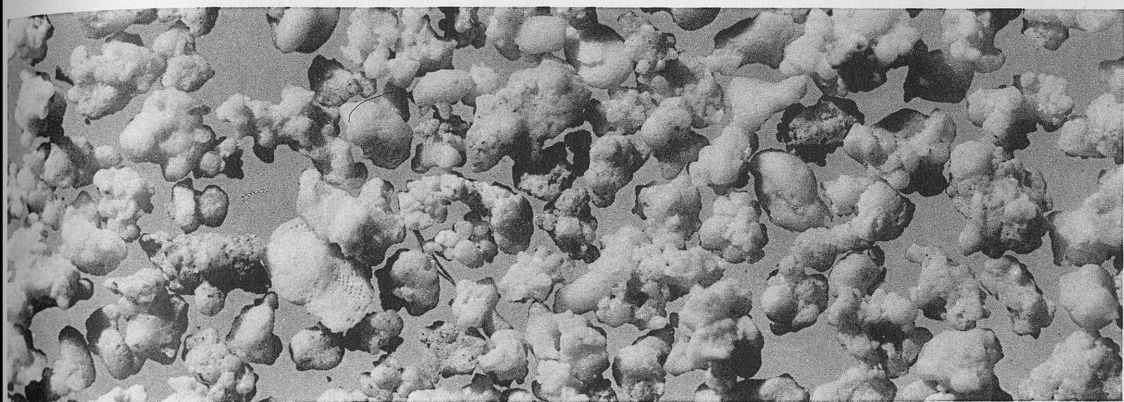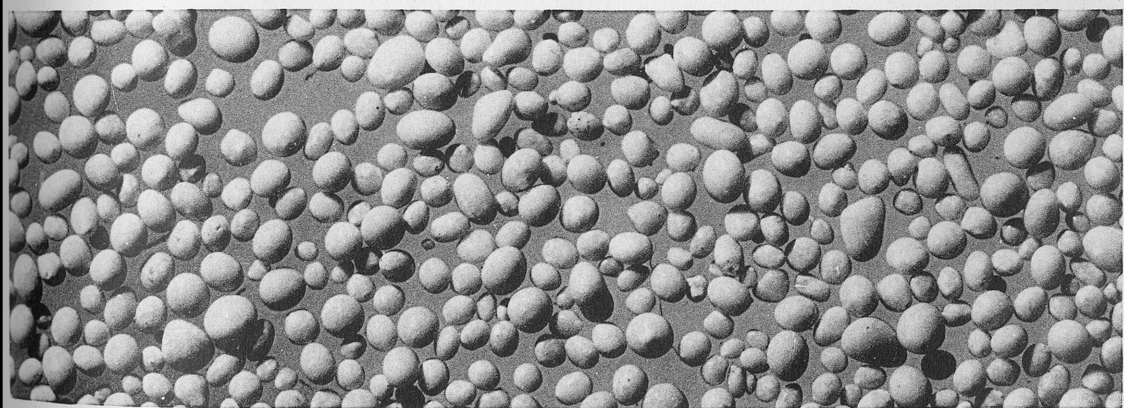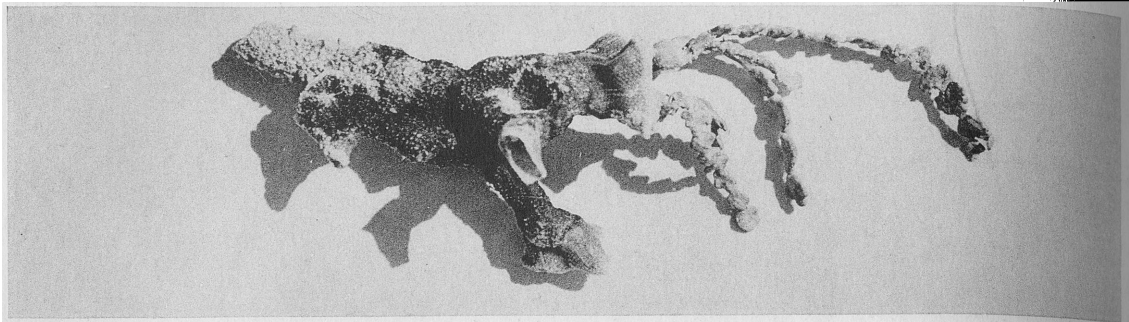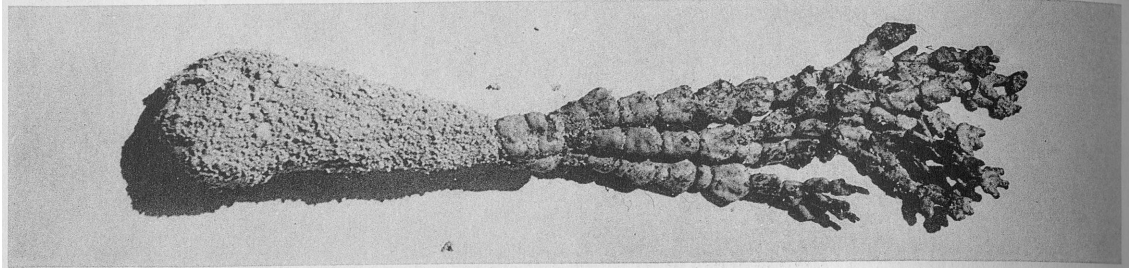
SEDIMENTS OF THE SHELF LAGOON

Pellet sand, about 8 miles east of South Riding Rock, near the western margin of the shelf lagoon (station
  Larger grains are ellipsoidal; smaller grains, subspheroidal; both have surficial, accretionary, aragonite
  s

Grapestone sand, 1 mile northeast of Fraziers Hog Cay, Berry Islands (station 323). Most of the grains
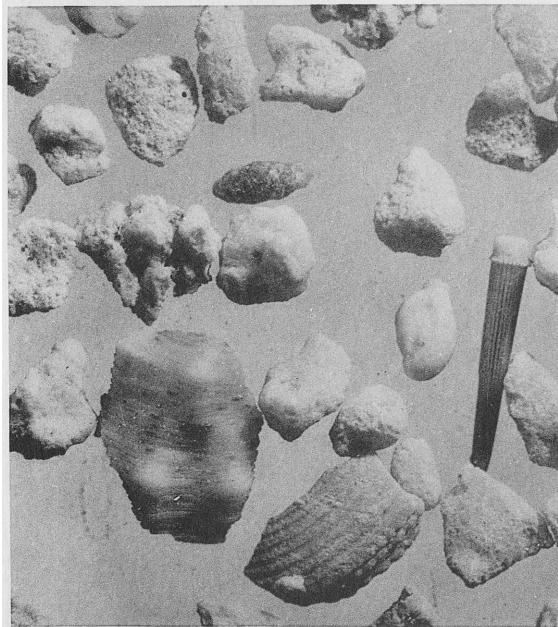 cemented aggregates of ooids or pellets
Oolite sand, from intertidal portion of oolite ridge near Sandy Cay, 35 miles south of Bimini (station 433).
  sorted, glossy, subspheroidal, concentrically laminated oolite grains
  are × 10
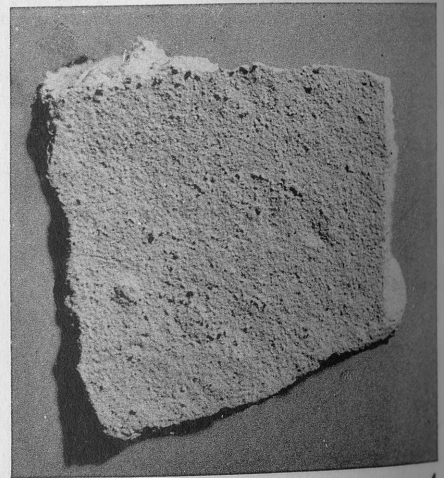
SEDIMENTS AND ORGANISMS OF THE SHELF LAGOON

1. *Halimeda*, with lower portion encrusted by the bryozoan *Schizoporella pungens*

2. The green alga *Halimeda*. The hold-fast at the base of the plant consists of cemented enmeshed sediment

3. Skeletal sand, from the barrier rim at Northwest Channel Light (station 326). Relative grains include an echinoid spine, a miliolid test, and gastropod fragments. Fusiform gr picture is a partly eroded alcyonarian spicule. Most of the remaining particles are co fragments. × 10

4. Calcareous mud, near western shore of Andros Island. Mud curl from laboratory dry sediment. × 10