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Ecology of a Caribbean Coral Reef. The *Porites* Reef-Flat Biotope: Part I. Meteorology and Hydrography

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Abstract

Observations on certain conditions of the physical environment and plankton ecology of a Caribbean coral reef form the subjects of a two-part study. Here, physical factors are considered, with special attention directed to their influence on the *Porites* reef-flat biotope. Meteorologic (temperature, precipitation, wind) and hydrographic (temperature, salinity, tide, sea level, current) conditions are examined in order to determine their influence on water movement over the reef and correlation with seasonal variations in plankton abundance. Shoal-water circulation is characterized with reference to patterns of movement, origin, and volume flow. A relationship between wind velocity and direction to volume flow is examined in order to describe the interaction of these parameters. The effects of low tidal exposures and storms on the dominant coral species *Porites furcata* Lamarck are also examined. Observed mortalities and physical alterations due to these factors are shown to be significant, resulting in relatively rapid modifications of the reef-flat habitat. A chief overall objective of this study is to obtain a quantitative assessment of drifting net plankton crossing the reef-flat environment, and to evaluate its contribution as a food source to the shoal-reef biota. Integration of the physical observations with the plankton ecology will form the subject of a forthcoming publication.

Introduction

The present study was conceived to provide long-term observations on the physical environment and plankton ecology of a Caribbean coral reef. An integrated approach was followed to help understand the interaction of physical factors with the resident reef populations (in the sense of limiting factors), and their influence on the drifting plankton community, chiefly from the point of view of facilitating transport over the reef. In this paper, certain physical conditions are characterized for a coral reef in Puerto Rico, and contrasted with other reefs in the tropical Atlantic region, particularly those in the marginal Florida-Bahamas area. Seasonal variations in the current regime are also described in detail to provide a frame of reference for a forthcoming paper on the plankton ecology.

It is now recognized that a variety of unpredictable physical events can have marked effects on shoal-reef populations. All reefs present in the Caribbean Sea and at higher latitudes in the western Atlantic region (except for a narrow zone along the northern coast of South America) are subject to hurricane disturbances. Detailed accounts are available of framework destruction in British Honduras (Stoddart, 1962, 1963; Vermeer, 1963), Puerto Rico (Glynn *et al.*, 1964), and in south Florida and the Bahamas (Ball *et al.*, 1967; Perkins and Enos, 1968). Coral populations have been observed to suffer heavy mortality and gross alterations in shoal and emergent reef structures, with some effects persisting for several years (Stoddart, 1965, 1969a).

With the growing recognition that drying reef flats are a common feature of coral reefs in the Caribbean (Glynn, 1968, and in press), more attention is now being given to the catastrophic effects of low tidal exposures. Mid-day tidal exposure of shoal-reef populations has been described in the Palao Islands (Motoda, 1940), at Eilat in the Red Sea (Loya, 1972), and in the Caribbean Sea in Puerto Rico (Glynn, 1968), Jamaica (Jackson, 1972), and Panamá (Birkeland *et al.*, 1971). Shoal populations succumb through physical stress resulting from an abrupt seasonal shift in the timing of low water, e.g. in Puerto Rico, or by a sudden modification of the local tidal regime by meteorologic influences, a condition observed in Panamá. Data presented in this paper extend the tide-related mortality of echinoids and other reef-flat organisms to corals, particularly *Porites furcata* Lamarck[1]. Since vertical reef growth appears to have reached a limit on many Caribbean reef flats, we may be witnessing the results of a relatively sensitive stage in reef proliferation (i.e., the controlling effects of maximum Holocene sea-level transgression) where lateral growth is beginning to assume a greater role.

All workers interested in the trophic relations of coral reefs have attempted to measure the rate of water movement over reefs (e.g. Sargent and Austin, 1949; Odum and Odum, 1955). On western Atlantic coral reefs, circulation systems have been investigated in several areas, e.g. at Bermuda (Boden, 1952), in Florida (Jones, 1963), the Bahamas (Storr, 1964), and

[1] All coral nomenclature follows Goreau and Wells (1967). Specimens of *Porites furcata* are deposited in the U.S. National Museum, Division of Echinoderms (Accession No. 45613).

in Puerto Rico (Odum *et al.*, 1959) and off Nicaragua (Milliman, 1969) in the Caribbean. Jones' (1963) findings, that current velocity and direction are closely controlled by the local wind regime, are of particular interest in the present study. This relationship is examined further, taking into account tidal effects, seasonal variations in sea level, and other conditions necessary to describe the annual patterns of circulation over the reef. Thus, a basis will be developed for evaluating the abundance of drifting net plankton and its relation to the marine climate, rate of supply over the reef, and utilization by the suspension feeding component of the reef-flat biotope.

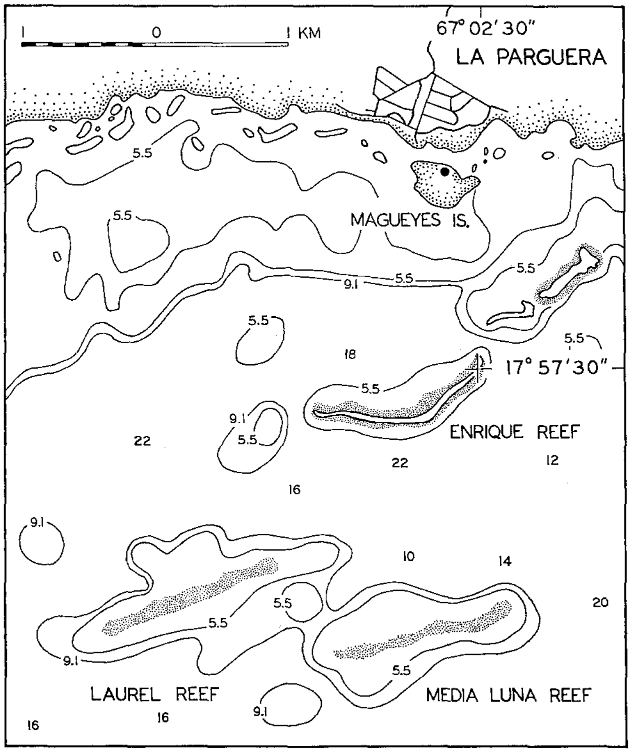

Fig. 1. Location of Laurel Reef off southwestern coast of Puerto Rico. Solid circle: location of weather station on Magueyes Island. Map from Parguera Quadrangle (see U.S. Department of the Interior, Geological Survey, 1957). Shoreline is approximate line of mean high water; datum for depth curves (m) is mean low water

The reef flat selected for study contains a high population density of the digitate coral *Porites furcata*, usually oriented in patches parallel to the long axis of the reef. Shoal *Porites* assemblages are a common feature on the lee margins of Caribbean reefs. The chief advantages for study offered by the reef-flat environment include: (a) shallow depth, permitting on-site observation even during adverse sea conditions; (b) relatively uniform bottom relief; (c) predominantly unidirectional water movement.

Materials and Methods

Atmospheric temperatures and precipation were observed daily at the weather station on the north side of Magueyes Island, at an elevation of ca. 3 m (Fig. 1). Long-term wind data are from the summit of Magueyes Island (26 m), and were obtained with a continuously recording anemometer (Triple Register No. 300, G. P. Friez & Son, Inc.).

Inshore hydrographic data were obtained at the tide station on the west side of Magueyes Island; these included sea-surface temperatures, salinity (computed from density), and continuous tidal records. Sea-surface temperature and salinity data were also obtained approximately weekly on the eastern limb of Laurel Reef. Salinity was determined by the high-precision Mohr titration (Strickland and Parsons, 1960). The locations of the principal sampling stations are shown in Fig. 2.

Water-soluble fluorescein marker dye was used to map current movements. The depth was measured at 5 m intervals along the current path, and wind velocity and direction were recorded every 5 min. Two anemometers were employed: Velometer Jr. with an attached compass indicating wind direction, and a Dwyer wind meter. Additional comments on methodology appear in the appropriate sections on current studies.

Observations largely embrace the period May, 1959 through 1967, with nearly continuous surveillance from 1963 to 1965.

Study Area

Regional Considerations

The principal study reef, locally known as Cayo Laurel (Laurel Cay) and also Arrecife Coral (Parguera Quadrangle topographic map, 1957; U.S. Coast and Geodetic Survey shoreline ms T-13120 and T-13121), is located on the insular shelf off the southwestern coast of Puerto Rico, approximately 3.5 km SSW of La Parguera, at a position centering near 67°03′45″ W; 17°56′30″ N (Figs. 1 and 2). The long axis of Laurel Cay (1.5 km), like six nearby coral reefs, is oriented approximately parallel to the coast, in an east-west direction. Relative to the prevailing E-SE trade winds, this location results in a nearly constant current, which moves diagonally over the reef.

Kaye (1959) noted that coral reefs in Puerto Rico were best developed on the leeward side of the island; at other localities in the Caribbean and West Indies major reef formations are commonly present on windward shores. Kaye suggested that the following factors tend to discourage coral growth along the north coast of Puerto Rico: (a) river discharge, resulting in dilution and turbidity (the latter interfering with light penetra-

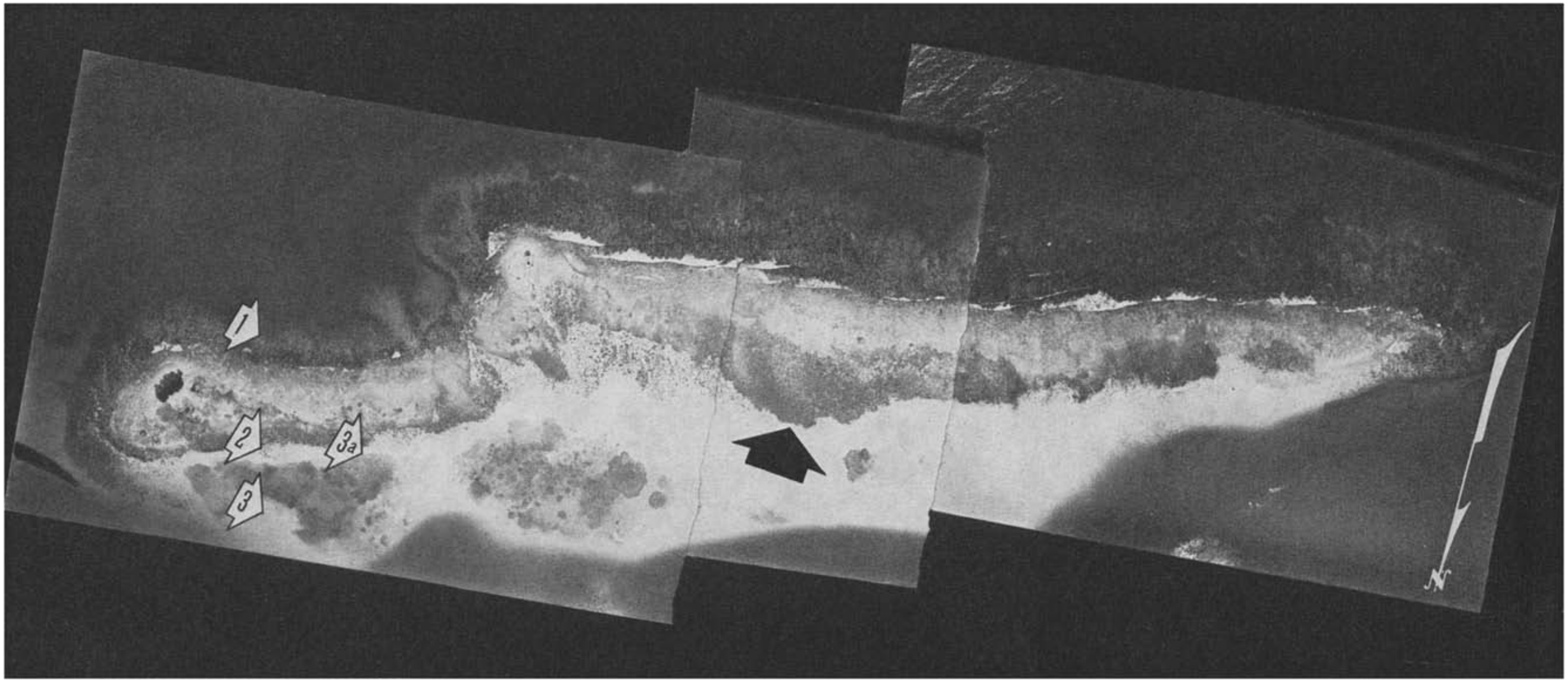

Fig. 2. Aerial view of Laurel Reef showing location of sampling stations across eastern limb of reef (March 4, 1965; 2000 m altitude). Dark patches adjacent to sand bottom on lee side of reef flat (black arrow) show location of living *Porites furcata* assemblage

tion); (b) sandy or muddy substrata combined with high waves, causing instability and sedimentation. Inspection of the bottom along the north coast shelf with SCUBA, to depths of 30 m, disclosed the presence of numerous hardpan areas which support the growth of small massive corals (e.g. certain members of the Faviidae and Mussidae). This suggests that an absence of shallow platforms raised above the bottom may also prevent the development of large reef formations along the north shore (Almy and Carrión Torres, 1963).

Present evidence indicates that the major geological features of the Parguera area today are a result of deformation of Upper Cretaceous limestones (with interbedded mudstones and volcanic rocks) into a WNW-ESE trending syncline whose axis passes through Magueyes Island (Almy, 1965). The northern limb of the syncline is represented by the Parguera hills, and possibly the southern limb by the trend of the coral reefs on the shelf. A longer exposure of the south limb of the syncline to attack by the surf zone at times of low sea level would result in a lower relief. With a rise in sea level following the end of the last Pleistocene glaciation (Wisconsin), the low limestone ridges on the shelf would have been gradually submerged, providing preferred sites for coral growth and subsequent reef formation.

Mitchell (1954) and Kaye (1959) are of the opinion that the reefs in this area have developed on drowned, calcarenite cuestas, which were formed as eolianite structures parallel to the shore during the Wisconsin glacial period. Data are not currently available to support either of these hypotheses.

Vaughan (1919a) noted that the earliest fossils of *Porites furcata* are of Pliocene age, from the Caloosahatchee marl in Florida (USA). It occurs commonly in Pleistocene deposits and "...is usual in the material behind elevated, sea-front reefs of the West Indies and eastern Central America, and it is one of the most abundant corals on the flats inside the living coral reefs in the same region and Florida." (Vaughan, 1919a, p. 499). Subsequent studies substantiate Vaughan's conclusions, and have extended the range of *P. furcata* to new localities in the Bahama Islands (Squires, 1958; Storr, 1964), Florida (Yonge, 1935; Stephenson and Stephenson, 1950) and Jamaica (Goreau, 1959). It also occurs in Barbados (Lewis, 1960), Curaçao (Roos, 1964, 1971) and Panamá (Porter, 1972). At several of these localities, *Porites* colonies were observed to grow in juxtaposition, forming dense thickets, patches, or belts. In Barbados, an unidentified variety of *Porites* was reported to cover acres of the bottom, as continuous patches at depths of 4 to 5 m (Nutting, 1919).

Reef Zonation

Although *Porites furcata* is the dominant coral of the reef flat, it is important to note its uneven distribution and to recognize the presence of other species. Six fairly well defined areas or zones can be identified at shallow depth ($\leq$ 3 m) on Laurel Cay. Some of these formations were briefly described for an inshore reef at La Parguera (Glynn, 1968).

Acropora palmata (Lamarck) is most evident on the seaward slope, where wave action and turbulence are greatest (Fig. 3A, foreground). As noted earlier (Glynn *et al.*, 1964), a spur and groove formation is not present on coral reefs in this area. The shoaling seaward slope normally gives way to a rigid framework of *Millepora complanata* Lamarck; this hydrocoral reaches close to the mean low water (MLW) mark, thus forming a sill on the seaward edge of the reef flat (Fig. 3A, background). Abundant dead colonies of *M. complanata* are present, in original growth position, and these are often overgrown and bound together by crustose coralline algae. This zone is often exposed during periods of extreme low water.

Leeward of the sill, the depth increases slightly, to around 0.5 m; shallow depressions with living *Porites furcata* are present here (Fig. 3B). The zone of greatest width (50 to 75 m) is shallow (20 to 40 cm below mean sea level) and composed largely of *P. furcata* rubble underlain by sand and silt (Fig. 2, light area behind breaker line). Patches of the phanerogam *Thalassia testudinum* König sometimes occur here. Eroded coral blocks of various sizes are often scattered over this area of the reef flat, and also behind the *Millepora complanata* sill. Bioclastic debris sometimes accumulates on the reef flat to form small islands. These may become colonized with mangroves (*Rhizophora* and *Avicennia*) and other strand vegetation.

The depth increases abruptly to 1 to 1.5 m on the lee edge of the coral rubble flat. *Porites furcata* is most dense in this area, often forming a framework 0.5 m in height as continuous patches 3 to 50 m in width (Figs. 2, 3C, D, E). Coral destruction is much in evidence where *P. furcata* borders the shoal flat. Some of the disturbed areas are a result of the destructive effects of hurricanes (see Glynn *et al.*, 1964 and "Cyclonic Disturbances", present paper). The deep edge of the *P. furcata* belt, 2 to 2.5 m deep, grades abruptly into a smooth sandy bottom (Fig. 3F, right-hand side). Fifty to 100 m beyond, *Thalassia testudinum* becomes abundant, often forming circular patches which extend to the edge of the slope. The leeward slope descends abruptly to approximately 15 to 20 m depth (Figs. 1, 2).

With reference to the patterns of zonation outlined above, the locations of the principal sampling stations are as follows: Station 1 was located over the seaward slope, above *Acropora palmata* and approximately 20 to 30 m from the reef crest; Station 2, along the deep edge of flourishing *Porites furcata*; Station 3, over the sand bottom dominated by *Thalassia testudinum*. In October, 1964, Station 3 was relocated to Station 3a, along the rear edge of the *P. furcata* assemblage (Fig. 2).

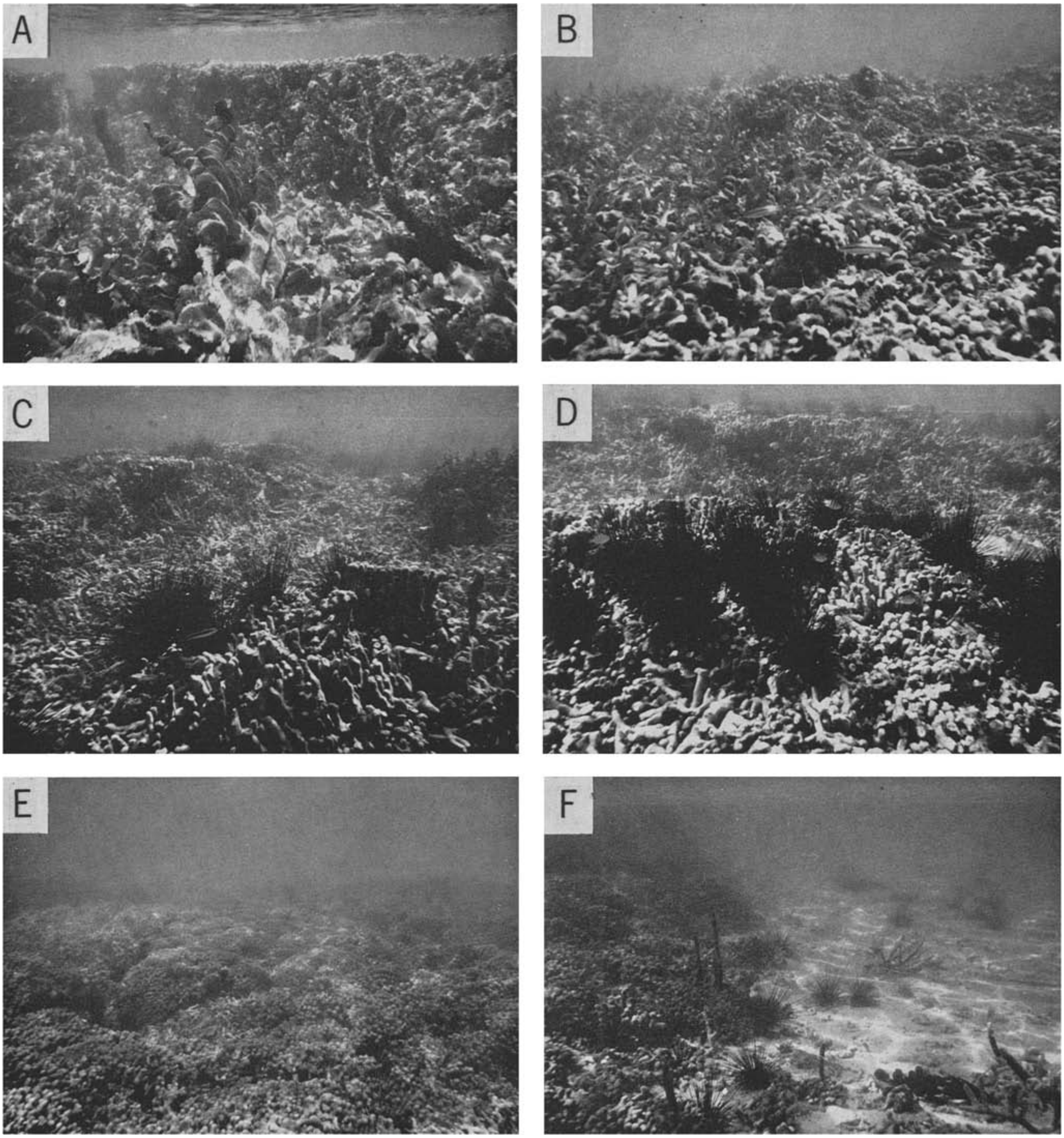

Fig. 3. Subsurface views across eastern limb of Laurel Reef from seaward slope to sand bottom bordering *Porites furcata* assemblage on lee side (December 13, 1967). (A) Seaward slope, view toward reef flat; *Acropora palmata* in foreground, *Millepora complanata* sill in background (greatest depth ca. 2 m below mean sea level). (B) Fore-reef flat depression with loose coral debris and sparse growth of *Thalassia testudinum* and *P. furcata* (ca. 0.5 m). (C), (D) Leeward reef-flat slope showing tracts of damaged *P. furcata* and echinoid *Diadema antillarum* Philippi (ca. 1 m). (E) Flourishing assemblage of *P. furcata* (ca. 1.5 m). (F) Deep edge of *P. furcata* assemblage bordering leeward sand bottom (ca. 2 m)

Porites furcata communities similar to that described in the study area occur on most coral reefs near La Parguera and at other localities along the south coast of Puerto Rico, including the SE sector of Culebra Island. In most cases, abundant coral growth was found on a substratum of coarse-grained sand or rubble subject to good circulation, but protected from strong wave action. Goreau (1959), however, found *P. furcata* best developed in the buttress zone of the Ocho Rios Reef on the north coast of Jamaica. The preferred bathymetric range of *P. furcata* at this locality is 6 to 20 m (Goreau and Wells, 1967). My observations in Puerto Rico support the findings of Almy and Carrión Torres (1963), namely that *P. furcata* is most abundant in shallow, relatively calm water on the back sides of reefs; *P. porites* (Pallas) is normally found as independent colonies in deeper water (3 to 10 m) on the seaward slope, and *P. divaricata* Lesueur usually occurs as separate colonies or forms a continuous cover at 0.5 to 1.0 m depth closer to the coastline.

Meteorological Conditions

Atmospheric Temperature

Although Puerto Rico, located at a position approximately 5° latitude below the Tropic of Cancer, is influenced by a maritime climate and is exposed to the easterly trade winds throughout the year, regular seasonal variations in temperature are clearly evident. This is seen in the atmosphere as well as the shallow coastal waters. The greatest seasonal difference observed in monthly mean atmospheric temperatures at La Parguera was nearly 6 C°; temperatures ranged from 25.2 °C (January, 1965) to 31.0 °C (August, 1966) over a 7 year period (Fig. 4). A nearly 19 C° difference in extreme air temperatures was recorded over the same period (16.1 °C in February, 1965 and 34.6 °C in August, 1966).

Recurring seasonal fluctuations are readily apparent in the monthly mean and extreme mean temperature records. Mean temperatures equal to or exceeding 29 °C occurred in May or June, and persisted at this high level until September or October. The sun is at its zenith over La Parguera during mid May and again in early August (U.S. Naval Observatory, Department of the Navy, 1967). A slight decline in mean temperature sometimes occurs during the summer; this was noted in June, 1962, August, 1963, and July, 1966. This phenomenon is probably a result of the sun's position at a lower elevation from the horizon as it approaches the summer solstice, in combination with local meteorologic effects. The low and variable rainfall at La Parguera would seem not to be an important factor in causing the mid-summer thermal depression. Possibly greater cloud cover during the summer months also contributes toward this condition (Smedley, 1961).

From October through December, atmospheric temperatures declined rapidly to a mean value between 26° and 27 °C, which persisted until about March. From April through May, temperatures increased steadily to the high summer values. Extreme maximum temperatures normally occurred in the late summer (August-September) and extreme minima in the winter (December-March). This thermal regime is consistent for regions exposed to the easterly trades of the Atlantic Ocean, which interact to produce "oceanic"-type temperature curves with late summer maxima and late winter minima (Riehl, 1954).

During cyclonic disturbances in the summer or fall, exceptionally low temperature spells are experienced. A minimum temperature of 16.5 °C was recorded at the weather station (09.00 hrs) on September 27, 1963, when Hurricane Edith passed the south coast of Puerto Rico (approximately 49 nautical miles from La Parguera). On the same day, immediately preceding and during transit of the storm, temperatures of 16.0° and

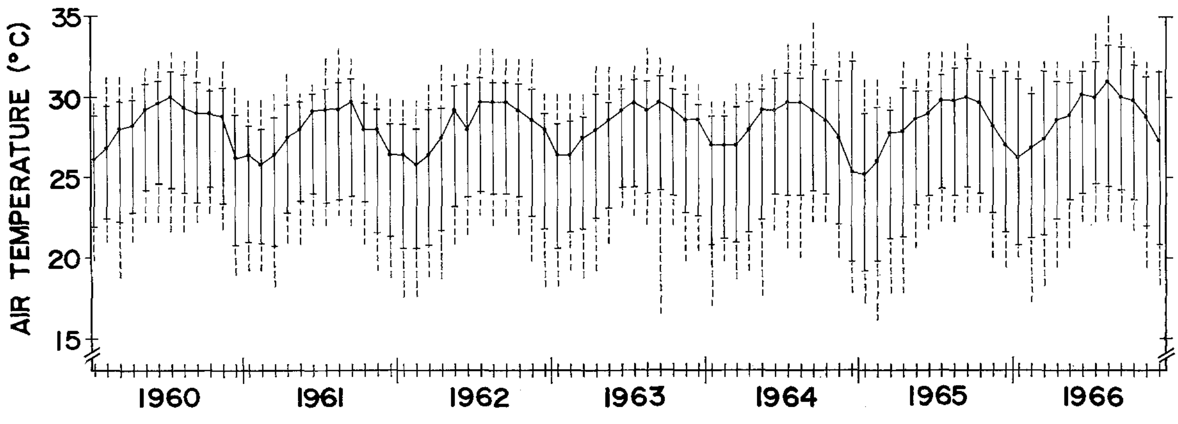

Fig. 4. Dry bulb air-temperature records observed at approximately 09.00 hrs, Magueyes Island, La Parguera, 1960—1966. Solid curve joins monthly mean values, vertical lines indicate range of mean maxima and minima, and broken vertical lines extreme maximum and minimum observations

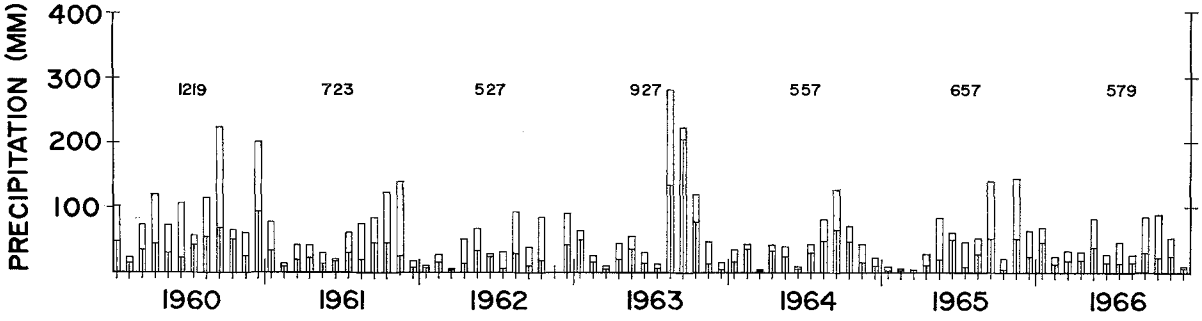

Fig. 5. Rainfall records from Magueyes Island, 1960—1966. Bars: total precipitation for each month; vertical lines: maximum daily observations. Yearly totals appear above each 12-month period

30.0 °C were also observed (Glynn *et al.*, 1964). This represents a marked short-term excursion, approaching the maximum yearly extreme temperature records. It is expected that continuous temperature records would disclose daily and annual ranges significantly in excess of 14° and 25 °C, respectively.

Precipitation

Because precipitation is largely due to an orographic influence in this area, the southwestern coastal plains (located on the leeward side of the central mountain range) are subject to a rain-shadow effect, resulting in a semi-arid climate. As Smedley (1961) pointed out, the topographic slope of the mountain range toward the south is much steeper than on the northward side of the island. This causes a relatively abrupt decrease in rainfall on the south side of the ridge. Doerr (1955) reported a 635 mm isohyet roughly skirting the shoreline along the extreme southwestern corner of Puerto Rico.

Wet and dry seasons are evident, but do not recur with any marked regularity. The period of greatest rainfall has its origin in easterly waves, which usually prevail from May through November; the driest time of year extends from about December through April. Substantial precipitation occurs infrequently in the dry season, when cold fronts move in from the north (Smedley, 1961). The wettest and driest months are usually September or October and February or March, respectively.

Annual rainfall records from Magueyes Island show total precipitation values in the order of 500 to 1200 mm (Fig. 5). An unusually high amount of rain fell in August and September, 1963, resulting in the relatively high annual total of 927 mm. The total monthly rainfall in September of this year amounted to 222 mm. This was due to Hurricane Edith, which resulted in a downpour of 203 mm in a 12 h period (Glynn *et al.*, 1964). Nearly two times the normal rainfall was recorded in 1960 (1219 mm). Much of this was due presumably to the influence of cold fronts, since a total of 510 mm, or about 43% of the yearly total, fell over the period January-April and in December.

Wind

The local wind system, including diel and seasonal patterns, will now be examined in detail to establish a basis for its effects on the current regimen and, hence, rate of supply of suspended materials over the reef. Unfortunately, only incomplete wind records were available from the Magueyes Island weather station — 28 monthly observations out of a possible 60 over the period 1959 to 1963. The location of Puerto Rico relative to the high-pressure belt ("subtropical highs") over the eastern Atlantic Ocean, however, places it well within the influence of the steady trade winds throughout the year. Therefore, once the local wind field has been characterized, it is seen that a similar annual pattern recurs with fair regularity.

The wind records disclose a strong SE component, which frequently prevailed 30 to 40% of the time at a velocity of 15 to 25 km/h (Fig. 6). Weaker E winds of 10 to 15 km/h occurred more frequently, often 30 to 50% of the time. The combined mean annual frequency of the SE and E components amounted to 81.1% (Table 1). Winds from the N or NE were next in importance; together they prevailed at a frequency of 12.1%, but usually did not exceed 10 km/h. Winds from the S, SW, W and NW quadrants were relatively unimportant. Periods of calm occurred most often in October and November, with mean frequencies of 6.0 and 6.2%, respectively. The period of least air movement occurred in November, 1961; no wind was registered for 13% of the time in this month.

The mean wind velocities from the 4 dominant directions illustrate well the more significant seasonal variations (Fig. 7). Winds from the SE showed two yearly velocity maxima. The strongest of these occurred in the late spring and summer (May-August), with mean velocities in excess of 21 km/h; moderately strong winds, equal to about 20 km/h, were also observed in January and February. The SE winds

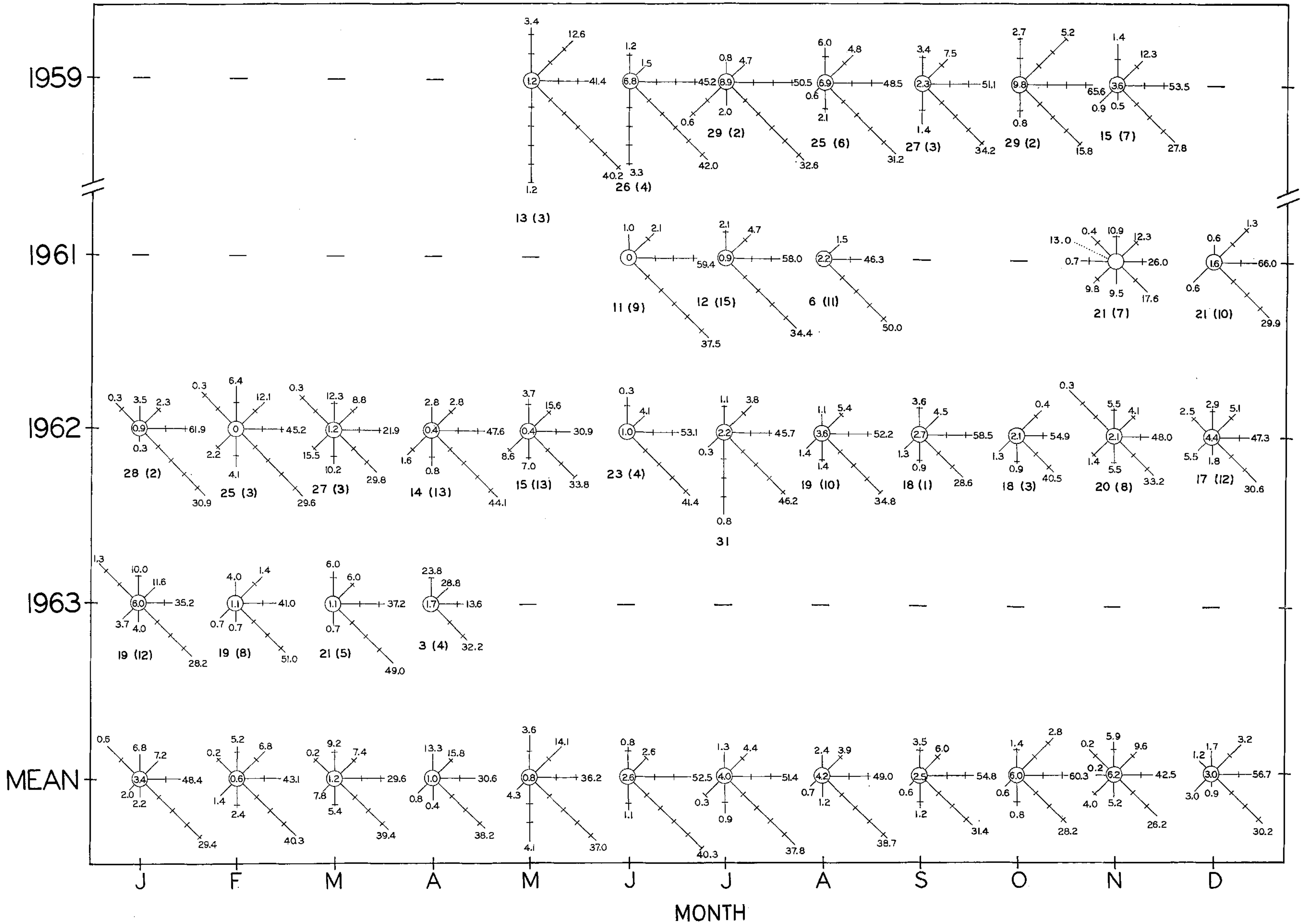

Fig. 6. Wind records from Magueyes Island, 1959—1963. Numbers at origin of each vector indicate percent time wind blew from a particular quadrant; wind velocities are scaled at intervals of 5 km/h. Frequency of calm spells is noted at center of each wind-rose. Larger-sized numbers denote days of complete and incomplete (in parentheses) records

Table 1. *Wind directions and mean frequencies observed at Magueyes Island weather station (computed from records in Fig. 6)*

Wind direction	Frequency (%)
N	5.1
NE	7.0
E	46.3
SE	34.8
S	2.2
SW	2.1
W	< 0.1
NW	0.2
Calm	3.0

or SE. The trade-wind circulation is thereby enforced, and its velocity increases rapidly until about midday. Strong SE winds usually continue until the late afternoon or early evening, at which time the E component again comes into play. This diurnal pattern is an important aspect of the wind regime along the SW coast, and is interrupted only infrequently by light breezes from other directions. Gale-force winds also occur, but rarely with approaching cyclonic disturbances.

Because local wind data are far from complete, it is desirable to compare the regime observed at La Parguera with other areas in Puerto Rico under surveillance for longer periods of time. Long-term wind-velocity data from 4 localities are compared with

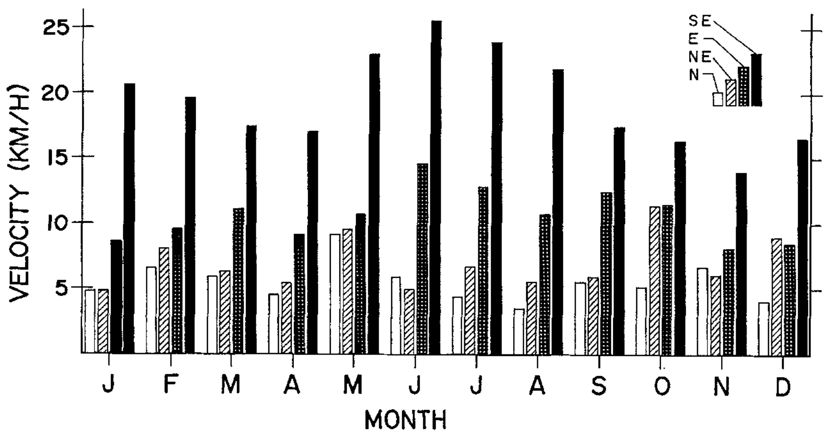

Fig. 7. Seasonal distribution of mean wind velocities at Magueyes Island (data from Fig. 6)

gradually diminished in intensity in March and April, and were least developed in the fall (October-November). Regular seasonal variations were less evident in E winds. As with SE winds, however, the highest mean velocities occurred in the summer (June-July) and the lowest in November and December. Winds from the N and NE prevailed less than 10% of the time, and usually with a mean velocity between 5 and 10 km/h through the year.

Long-term wind observations at sea (U.S. Naval Oceanographic Office, 1963) show that the surface circulation near Puerto Rico has a predominantly easterly direction from April through October. From November through March, the E and NE components are nearly equally well developed. In order to reconcile these data with the predominantly E and SE wind directions observed at La Parguera, it is necessary to consider the influence of sea breezes.

In the early morning hours, a light breeze frequently prevails from the E or NE. As the sea-breeze effect takes hold later in the morning, often after 07.00 or 08.00 hrs, the wind direction shifts to the E

the annual regime at Magueyes Island in Fig. 8. Total wind movement at Magueyes Island (Curve 4) and Lajas (Curve 5) showed a similar annual pattern. However, a pronounced difference in velocity is evident, with a more vigorous circulation near the coast. Data obtained from more distantly located stations also disclosed similar annual variations, i.e., a relatively high velocity during the first quarter of the year and in the summer, a slight decline in intensity during the spring, and a marked calm period in the late summer or early fall. Even the strong movement of the jet stream at 1,000 m altitude (Curve 1) exhibited marked seasonal differences, with a pattern similar to that observed at sea level. Surface winds over the open sea (Curve 2) and along the north coast of the island (Curve 3) consistently demonstrated higher mean velocities than observed at Magueyes Island.

Cyclonic Disturbances

Perhaps the most obvious physical factor affecting the survival of shallow coral growth and the geo-

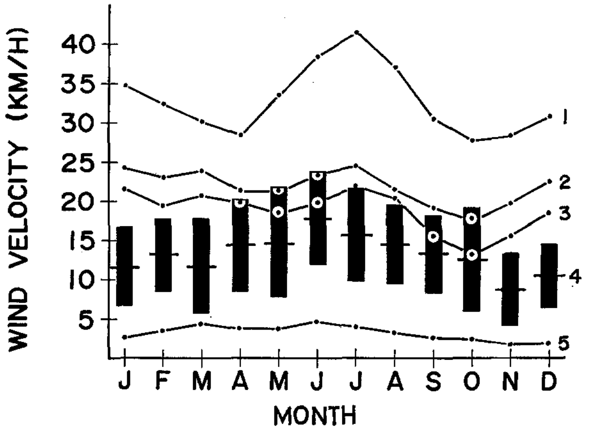

Fig. 8. Seasonal distribution of mean total wind-movement at different localities around Puerto Rico. 1: 1,000 m altitude (Fassig, 1933). 2: offshore ship observations (U.S. Naval Oceanographic Office, 1963). 3: San Juan, 32 year record (U.S. Hydrographic Office, 1951). 4: Magueyes Island, based on data from complete daily records; standard deviation represented by vertical bars. 5: Lajas (approximately 9 km north of Magueyes Island), based on data from nearly complete records for period 1960—1966, exclusive of 1964

of the reef. Particularly evident was a lateral movement of corals to leeward, including living colonies of *Porites furcata* and rubble; this resulted in a lateral displacement, 0.5 m in extent, on certain portions of the reef flat. If these deposits become stabilized, they should provide support for new coral growth, thus enhancing a leeward expansion of the reef flat.

Hydrographic Conditions

Sea-Water Temperature

The mean annual temperature curves of the atmosphere and sea surface are very similar in appearance (Figs. 4 and 9). Just as the highest atmospheric temperatures were observed in the late summer, marine temperatures also reached a peak in this season, with September frequently the warmest month. Similarly, the lowest temperatures usually occurred in January or February.

Temperatures recorded at Laurel Reef began to fall in October or November, and by January the temperature declined to near 26.5 °C and maintained this low level through March. The autumnal decline

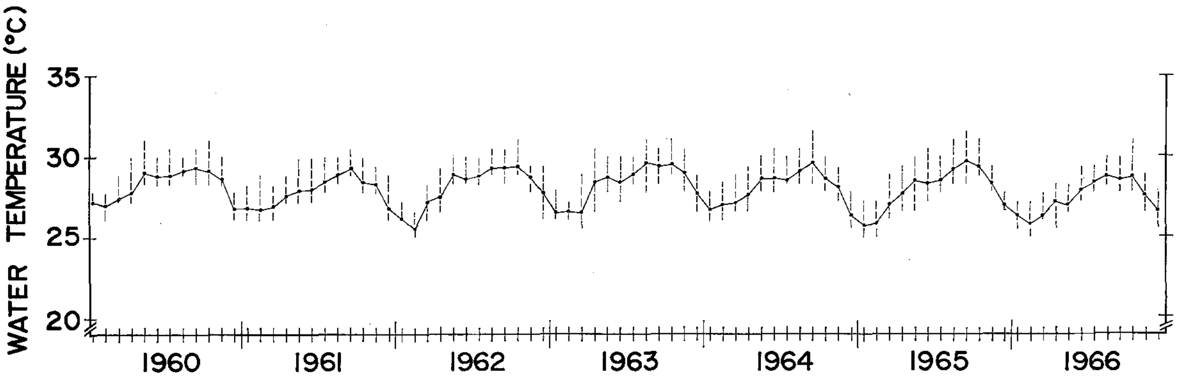

Fig. 9. Monthly mean and extreme sea-surface temperature observations recorded at Magueyes Island tide station, 1960 to 1966. Readings made daily between 08.00 and 10.00 hrs, and occasionally at 14.00 hrs. Vertical dotted lines: extreme ranges of temperature

morphology of emergent reef structures is the erratic and devastating effect of storm waves generated by hurricanes. Destruction of shallow-growing *Porites furcata* was observed after the transit of Hurricane Edith in 1963 (Glynn *et al.*, 1964). The movement of coral blocks across the reef flat produced a trenching effect in the *P. furcata* zone.

Four years later, Hurricane Beulah (September 10, 1967), approximately equal in intensity to Hurricane Edith, passed 80 to 100 km from the southwest coast of Puerto Rico. This storm generated waves exceeding 2 m in height which struck the windward face of Laurel Reef. Normally, the waves breaking on this reef are considerably smaller in size ($\leq$ 1 m). Extensive areas were affected on the windward and back sides

occurred over a steeper gradient (2 to 3 months) than did the spring warming period, which was gradual and of 4 month's duration. An early warming spell was evident in April, 1963.

Slightly higher mean temperatures, of the order of 0.5 C°, were regularly observed in shoal water over the reef flat (Station 2) although, during the fall and winter months, such differences were less evident. The highest temperature recorded on the reef flat during the regular weekly sampling schedule was 30.4 °C on September 13, 1963. Solar heating at shallow depths can be quite pronounced, however, especially on calm days at slack tide. Temperatures in the range of 35° to 40 °C were observed commonly on Caracoles Reef at La Parguera (Glynn, 1968).

On the reef flat, early evening temperatures ranged between 25.8° and 29.4 °C. Although a marked cooling is expected here before sunrise in the winter season, no data are available to indicate the magnitude of this. Because extreme atmospheric temperatures below 19 °C do occur with fair regularity (Fig. 4), it is possible that temperatures occasionally approach 20 °C in shoal water.

The long-term surface temperature data from Magueyes Island follow the same annual trend observed at Laurel Reef (Fig. 9). A relatively sharp decline in the thermal structure in the fall, compared with a gradual ascent through the winter and spring, is again evident. In similar manner, the inshore extreme maximum and minimum temperatures usually occurred in September or October and February, respectively.

A causal relationship is suspected between the variations in surface temperatures and total wind movement. As noted above, exceptionally high temperatures were observed at Laurel Reef in April, 1963. At that time, an unusually low mean wind-velocity of 13 km/h from the SE was recorded. The records from Magueyes Island show a similar correlation. An abrupt rise in the mean sea-surface temperature in either April or May was followed by a slight decline in temperature a month later. Some specific examples follow. In May, 1962, the mean surface temperature rose to 28.9 °C at a mean wind velocity of 15 km/h from the SE. From April to May, 1959, the mean surface temperature declined by 0.5 C°; in May, the mean SE wind velocity was 31 km/h.

This trend was also evident in the sea-temperature data from Magueyes Island and the total wind movement recorded at Lajas. In general, the following correspondence was observed: low-velocity winds and rapid rise in temperature; high-velocity winds and an abatement or decline in surface warming. This relationship was especially marked in June and once in May over the period 1962 to 1966 (exclusive of 1964 because of lack of data).

Despite the inadequacy of this analysis, it does appear that the usual variations in wind movement in the spring may modify the surface thermal structure at this time of year. Day (1961) noted similar periods of cooling in the spring and fall at Mona Island (Puerto Rico), but was unable to relate these in a clear manner to the wind records obtained at San Juan and elsewhere. Maximum cloud cover in Puerto Rico occurs biannually, in May or June and again in September or October (Smedley, 1961). Reduced solar heating due to this factor, in May or June, does not seem too important because the temperature records disclose no corresponding response later in the year. Moreover, minimal cloud cover in March was not accompanied by a significant rise in temperature.

Salinity

The surface salinity at Laurel Reef and nearer shore at Magueyes Island did not vary appreciably through the year. A recurrent annual pattern was evident, however, which usually ranged between 33 and 37‰ S (Fig. 10). The extreme maximum and minimum values observed over a 7 year period were 37.5 and 31.9‰ S. Maximum salinities were most frequent in April or May, and lowest in October or November. The greatest range in values, particularly noticeable at Laurel Reef, occurred in August, September, and October.

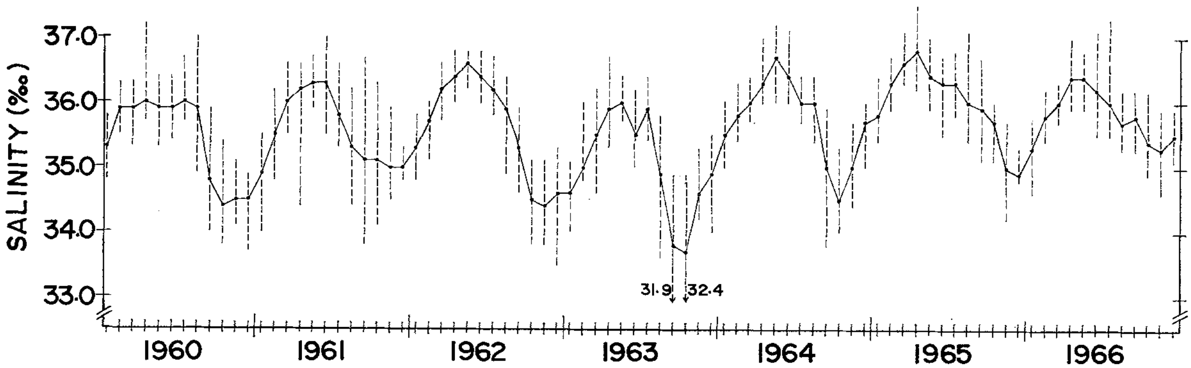

Fig. 10. Monthly mean and extreme sea-surface salinity observations recorded at Magueyes Island tide station, 1960 to 1966. Readings obtained daily with hydrometer between 08.00 and 10.00 hrs, and occasionally at 14.00 hrs

The excessive precipitation which accompanied Hurricane Edith in September, 1963 was clearly responsible for the lowest salinity value observed. Water along the shoreline at La Parguera, and up to 0.5 km seaward, was highly turbid from the extensive and rapid runoff on that occasion. The extreme minimum salinity on record for Magueyes Island — 9.8‰, 3 m from shore (Coker and González, 1960) — was observed in an enclosed area and was, therefore, presumably of limited influence.

Considering the seasonal irregularities in the rainfall records and great differences in total amount from year to year (Fig. 5), the observed uniform annual variations in salinity were unexpected. However, a strong correlation is evident between the monthly salinity minima and rainfall maxima. Since land drainage is slight in the immediate area of study, it is likely that rivers discharging to the east have an important effect. The prevailing coastal currents are strong, moving in an E-W direction.

Periods of relatively high salinity (> 37.0‰ S) and temperature (27° to 32 °C) were observed most frequently in April, and are probably the result of sea-surface evaporation preceding the rainy season and periods of calm with accompanying intense solar heating. Temperatures below 26 °C, at a relatively high salinity, were observed from December through March, and were most likely due to atmospheric cooling, diminished rainfall and continuing evaporation. Evaporation at Lajas, as elsewhere in Puerto Rico and the Virgin Islands, is high, with an annual mean value of 2,068 mm (Smedley, 1961). The influence of this factor on the surface salinity of inshore waters must be considerable; the annual loss of moisture through evaporation actually exceeds the gain from precipitation. If the rate of evaporation at La Parguera approximates that recorded at nearby localities, it would exceed the local annual rainfall by a factor of three or four.

It is possible that at least limited mixing between the surface and bottom waters of the shelf takes place when strong winds prevail in the late spring or early summer. Vertical temperature and salinity profiles failed to reveal any significant differences in these parameters throughout the water column. Lack of stratification would enhance overturn, allowing the entire water column to behave hydrodynamically as a neutral mass. Data obtained 13 km due south of La Parguera (González, unpublished manuscript, 1965) indicated some mixing between the surface and deeper strata in March and April, 1965. At this time, the discontinuity layer at 75 m had deteriorated, with an accompanying increase in surface salinity, concentration of phosphates and silicates, and primary production. (Similar conditions were not observed over the shelf on this occasion). The phytoplankton bloom which followed Hurricane Edith in 1963 further implies wind-induced mixing (Glynn *et al.*, 1964).

The temperature-salinity extremes observed at Laurel Reef are distributed within the bounds of the long-term records (~ 9 year period). Compared with other coastal environments (Hedgpeth, 1951), the temperature-salinity characteristics of La Parguera, as routinely observed at the Magueyes Island tide station, are indicative of a mild hydrographic climate. However, under certain conditions, such as low tidal exposures, thermal and other physical factors undergo brief but extreme excursions, which can result in extensive mortalities.

Tidal Regime and Variations in Sea Level

The major characteristics of tides at La Parguera, summarized tentatively by Coker and González (1960) for a 4 year period, have been substantially confirmed by subsequent observations. Briefly, the tides can be characterized as follows: (1) Slight vertical range (daily maximum 40 cm, yearly maximum 55 cm); (2) largely diurnal and irregular; (3) relatively abrupt seasonal shift in timing (with low-water stands occurring at night in the winter and during the day in the summer); (4) higher mean elevation of sea level in the late summer and fall.

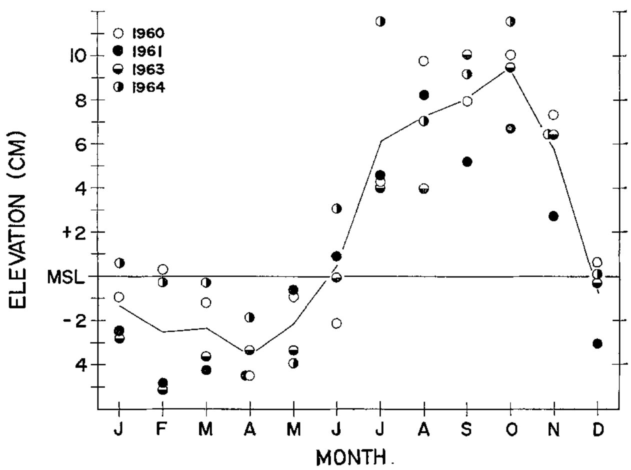

Fig. 11. Seasonal variation in mean sea level (MSL), Magueyes Island. Curve represents mean for 4 years. MSL (1.15 m or 3.78 ft) is that for 10-year period 1955—1964, exclusive of 1962

Recent data show that the mean monthly elevations in sea level vary in a regular manner from year to year (Fig. 11). Although the differences in elevation are small (maximum range 0.17 m), the records clearly demonstrate a relatively low stand from December through May, and a higher stand from July through November.

The mean annual elevation in sea level showed an irregular, although apparent, increase over the period 1955 to 1964. In 1955, the mean elevation was 1.11 m; in 1964, 1.19 m. This trend was interrupted in 1965 by a mean elevation of 1.12 m; in 1966, the sea level returned to 1.16 m. The differences in sea-level elevation over the first and last 5 year periods indicate a mean annual rise of 1.8 mm/year over the 11 year period. This agrees reasonably well with the 1.4 mm/year rise (applying a 2 mm/year correction for subsidence) for the Atlantic and Gulf coasts of the continental United States (Lizitzin, 1963).

A feature not emphasized earlier is the presence of a definite, although often irregular, daily time progression during periods of spring low-water tides. Daily progressions showing some regularity, observed at the tide station on Magueyes Island and at several reefs offshore, indicated a time difference of around 50 min on successive days. Progressive time differences between high tides were often shorter and less well defined. In general, the observed heights and timing of the tides usually conformed closely to the predicted schedules.

Although *Porites furcata* mortalities have not been related directly to extreme low-water stands of the tide, the frequent occurrence of dead colonies at equal depth levels — in a natural growth position only a few centimeters below MLW — indicates the likelihood of mass kills during periods of low-water exposure. No living colonies were found shallower than 8 cm below MLW on the reef flat at Laurel Reef (Table 2). Most dead *P. furcata* occurred at depths between 3 and 7 cm. Dead *P. furcata* present at shallow depth often formed a continuous pavement, 1 to 2 m^2, composed of numerous individual colonies encrusted with coralline algae.

Table 2. *Porites furcata. Number of isolated colonies or clusters of dead and living specimens found at various depths below mean low water (MLW), Laurel Reef, December 13 and 15, 1967. Data based on tally of all coral encountered at minimum depth over a 500 m^2 section of reef flat. Depth measured from highest branch tips to surface. MLW = 9.7 cm below mean sea level*

Depth (cm below MLW)	Dead	Alive
3— 4	12	0
5— 6	10	0
7— 8	8	2
9—10	3	2
11—12	2	10
13—14	2	50
15—16	0	60
17—18	2	> 100
19—20	0	> 100
21—22	0	> 100
23—24	0	> 100

Extreme low tides occurred frequently during 1960 to 1966, and were exceptionally common in 1965, at a time of relatively low sea level. About 60% of the extreme low tides recorded in this 7 year period occurred in 1965 (Table 3); the low water level reached −18 cm on 22 days, and −21 cm on 2 days. These tides were diurnal in character, thus resulting in prolonged periods of exposure. Considering the local weather records and climatic regimen, the following conditions would be expected to have a detrimental effect on exposed corals: heating, chilling, desiccation, actinic damage.

Comparison of Tables 2 and 3 shows that *Porites furcata* at the −15 cm level was exposed commonly over the past 6 years, and most frequently in 1965 and 1966. The tidal records indicated 8 h exposure periods at the −15 cm level. Some of these occurred at night in December, 1965 and during the day in April, 1966, at times of expected extreme conditions. However, surveillance of Laurel Reef since 1960 failed to reveal any large-scale coral kills, indicating that the dead clusters of *P. furcata* probably resulted from low tidal exposures prior to this time. Considering the numerous extreme low tides that accompanied the low sea level of 1965 (Table 3), the 1955 to 1959 period of low seastand may well have been critical, and is here tentatively implicated in the recent mortality of *P. furcata.*

Current Characteristics and Volume Flow

General Circulation Pattern

At Puerto Rico's latitudinal position, the geostrophic surface currents offshore move in a westerly direction, at a velocity close to 1.5 km/h in the winter, January-March, and summer, July-September (U.S. Naval Oceanographic Office, 1965). The location and topography of the shoreline and insular shelf off La Parguera permit the inshore current system to follow a similar course, although apparently at a reduced rate. Thus, a nearly continuous and often vigorous surface current flows past the coral reefs in this area. Since water movement over Laurel Reef seemed to be influenced appreciably by wind and tide, these factors were measured over periods of varying current flow in order to determine the degree of correlation.

Most current measurements were carried out on the reef flat of Laurel Reef, across the central portion of the eastern limb of the reef (from reef crest to deep edge of *Porites furcata*, between Stations 2 and 3a, Fig. 2). Observations elsewhere on Laurel Reef, including the western limb, and on different reefs with a similar orientation relative to the prevailing currents (Media Luna and Margarita Reefs), showed that the location of the main sampling station was representative and should, accordingly, provide an indication of volume transport over the reef-flat biotope.

Water-soluble, fluorescein marker dye was introduced rapidly as a spot on the surface of the windward edge of the reef flat. The relatively small waves crossing this portion of the reef are usually of the solitary class. They are generated directly from advancing foam lines or bores, and are well formed along the lee side of the windward sill. The center of the dye spot, intensified midway along its course when necessary, was timed as it moved across the reef flat and over the *Porites furcata* assemblage in deeper water. Sketch maps were drawn of the course of water movement as the dye spot traveled across the reef.

Table 3. *Extreme low tides recorded at Magueyes Island tide station. Data from U.S. Department of Commerce, Coast & Geodetic Survey (1960—1966). Data for 1962 based on tide predictions. MLW: Mean low water; MSL: mean sea level*

Exposure (≥ 15 cm below MLW)	Time of day[a]	Month	Year	Frequency[b]	MSL (m)
—	—	—	1960	0	1.18
15	D	Jan.	1961	1	1.16
15	D	Dec.		1	
18	D	Jan.		1	
15	D	Jan.	1962	4	—
15	D	Feb.		5	
15	L	May	1963	1	1.16
15	D	Jan.		1	
15	L	May	1964	1	1.19
15	D	Dec.		1	
15	D	Jan.		7	
18	D	Jan.		4	
15	D	Feb.		12	
15	L	Feb.		4	
18	D	Feb.		4	
15	L	April		3	
15	L	May	1965	3	1.12
18	L	May		6	
15	L	June		6	
18	L	June		2	
15	L	July		1	
18	D	Dec.		1	
21	D	Dec.		1	
15	D	Jan.		3	
15	L	April		3	
18	L	April		3	
21	L	April	1966	1	1.16
15	L	May		1	
15	L	June		2	
15	D	Dec.		5	
18	D	Dec.		1	

[a] D: Predominantly dark (18.00 to 06.00 hrs); L: predominantly light (06.00 to 18.00 hrs).
[b] Number of occurences.

Wind velocity and direction were recorded where the dye was initially released. All data are summarized in Table 4.

Preliminary measurements of the velocity of surface currents immediately surrounding Laurel Reef indicated that water movement over the shelf is considerably less than on the open sea. For example, on December 12, 1967, the surface-current velocity on the lee side of Laurel Reef (2.4 m depth) was 4.5 m/min; surface water movement on the open sea is around 25 m/min (U.S. Naval Oceanographic Office, 1965). Observations of surface currents over depths of 18 m on the windward and leeward sides of the reef disclosed velocities in the range of 5 m/min. As water moves across the shoal-reef flat, however, the velocity increases markedly, until the current flow again reaches greater depths to leeward. This is evident in a lee velocity of 4.5 m/min, compared with a current velocity of 7.5 m/min (0.42 m mean depth) observed concurrently on the reef flat.

Origin of Shoal Water

Because the reef front is normally subject to moderate surf action, turbulent conditions usually prevail in this zone. This does not necessarily imply, however, that plankton and suspended matter at different levels in the water column have an equal opportunity of being transported over the *Millepora complanata* sill and across the reef flat. In order to gain some notion of the relative contribution from various depths in supplying suspended materials to the shoal areas of the reef, an attempt was made to determine the lateral water movements at different levels in this zone.

The procedure was as follows. A line was fixed vertically in the water column (from surface to bottom); 3 plastic bags were fastened to the line, each bag being filled with a packet of fluorescein dye. The line was positioned approximately 10 m seaward of the sill. The bags were secured to the line at the surface and at depths of 1.2 and 2.5 m. They were then

Table 4. *Summary of current data from Laurel Reef. Roman numerals in last column refer to circulation patterns in Fig. 12. Q: Volume flow of water over reef*

Observation No.	Date	Time (hrs)	Wind velocity (km/h)	Mean depth (m)	Current velocity (m/min)	Q (m^3/min)	Current type
1	20. I. 1965	15.41—16.20	29 SE	0.30	11.8	3.5	I
			29	0.29	10.4	3.0	
			29	0.28	10.4	2.9	
2	26. II. 1965	09.40—10.21	6 S	0.24	5.9	1.4	I
			8	0.24	6.3	1.5	
			8	0.23	5.9	1.4	
3	30. III. 1965	15.15—15.55	24 S	0.18	10.0	1.8	XII
			26	0.18	10.0	1.8	
			29	0.18	11.7	2.1	
4	30. IV. 1965	14.36—15.22	23 SE	0.24	8.5	2.0	I
			19	0.24	7.8	1.9	
			16	0.24	7.8	1.9	
5	25. V. 1967	10.10—12.15	16 SE	0.24	3.0	0.7	V
			16	0.22	2.7	0.6	
			16	0.20	3.0	0.6	
6	19. VI. 1967	14.12—15.19	26 SE	0.25	4.7	1.2	II
			26	0.26	6.7	1.7	
			26	0.28	5.9	1.7	
7	31. VII. 1964	10.00—11.30	29 SE	0.43	4.7	2.0	I
			29	0.43	4.7	2.0	
			29	0.43	4.5	1.9	
8	20. VIII. 1964	10.00—11.05	8 E	0.18	1.7	0.3	XIII
9	11. IX. 1964	10.00—11.15	19 E	0.30	2.4	0.7	I
			23	0.30	2.6	0.8	
			24	0.30	3.5	1.0	
10	23. IX. 1964	09.55—10.30	27 E	0.46	6.7	3.1	II
			27	0.46	6.7	3.1	
			27	0.46	6.7	3.1	
11	21. X. 1964	10.40—11.45	13 S	0.46	2.7	1.2	I
			14	0.47	3.5	1.6	
			16	0.48	3.6	1.7	
12	26. X. 1965	19.43—19.58	18 SE	0.30	6.7	2.0	III
13	5. XI. 1965	10.20—11.12	13 SE	0.37	3.9	1.4	I
			10	0.37	4.3	1.6	
			10	0.37	3.5	1.3	
14	15. XI. 1965	16.05—17.43	10 SW	0.46	1.2	0.6	VI
			8	0.47	1.2	0.6	
			8	0.48	0.9	0.4	
15	28. XI. 1965	15.30—17.00	8 SW	0.49	1.7	0.8	VII
			10	0.49	1.2	0.6	
			10	0.49	1.5	0.7	
16	8. XII. 1964	14.10—15.20	14 S	0.43	2.5	1.1	I
			8	0.42	3.2	1.3	
			16	0.41	2.8	1.1	
17	11. XII. 1967	08.55—09.32	24 E	0.44	8.3	3.6	II
18	11. XII. 1967	10.10—10.50	24 ESE	0.44	6.8	3.0	III
19	11. XII. 1967	14.30—15.35	26 ESE	0.45	7.9	3.6	II
20	11. XII. 1967	15.45—16.15	25 ESE	0.45	10.5	4.7	I
21	12. XII. 1967	07.20—07.50	19 E	0.42	5.5	2.3	III
22	12. XII. 1967	08.00—08.30	21 E	0.42	7.5	3.2	III
23	13. XII. 1967	05.38—06.07	9 NE	0.41	4.6	1.9	II
24	13. XII. 1967	06.15—06.50	9 NE	0.41	4.6	1.9	III
25	13. XII. 1967	07.15—07.50	2 NE	0.54	2.4	1.3	IX
26	13. XII. 1967	09.40—10.18	3 NE	0.46	2.7	1.2	IX
27	13. XII. 1967	11.00—11.30	17 SE	0.42	6.4	2.7	II
28	13. XII. 1967	11.40—12.10	21 SE	0.42	6.4	2.7	III

Table 4. (continued)

Observation No.	Date	Time (hrs)	Wind velocity (km/h)	Mean depth (m)	Current velocity (m/min)	Q (m^3/min)	Current type
29	14. XII. 1967	13.35—14.05	8 S	0.37	3.8	1.4	V
30	14. XII. 1967	14.25—14.55	9 SSW	0.34	3.7	1.3	III
31	14. XII. 1967	16.00—16.25	7 W	0.34	4.6	1.6	VIII
32	15. XII. 1967	08.30—09.00	6 NNE	0.59	0.9	0.5	X
33	15. XII. 1967	09.45—10.15	0	0.53	0.9	0.5	XI
34	16. XII. 1967	13.30—13.55	6 SSW	0.42	0.9	0.4	IV
35	17. XII. 1967	13.30—14.05	17 SE	0.48	3.9	1.9	III
36	17. XII. 1967	14.45—15.20	15 SE	0.44	3.2	1.4	III
37	17. XII. 1967	15.30—16.05	13 SE	0.38	3.0	1.1	III
38	28. XII. 1964	15.42—16.48	16 W	0.21	1.5	0.3	VI
			16	0.21	1.7	0.4	
			21	0.20	2.5	0.5	

punctured, and the dye issuing from them was observed underwater for $^1/_2$ h. The wind and hydrographic conditions which accompanied these observations are noted under Observation Nos. 30 and 31 in Table 4.

The dye tended to spread horizontally toward the reef flat, and most rapidly near the surface. Vertical mixing occurred, but not to the degree expected. A layering effect at the three levels was still discernible after 20 min. A seaward backwash, from the reflection of waves, was pronounced. The dye issuing from the bottom bag was especially affected by this movement. These initial observations, under calm sea conditions, suggest that the surface-water stratum probably supplies the bulk of suspended materials of windward origin washing over the reef.

Influence of Wind Regime

Under normal wind conditions (E-SE), a fairly consistent pattern emerged relative to the direction of the surface currents moving past Laurel Reef and the set assumed by the currents traversing the reef flat. If the direction of movement of the shoal current over the reef flat was from the SSE, then the surrounding current on the windward and lee sides of the reef would usually show a set from the SE or ESE, roughly a 30° to 40° displacement over the shoals. This is probably a result of wave refraction in shallow water.

The influence of wind direction on the various routes followed by the current is clearly evident (Fig. 12). Winds with strong E or S components (Patterns I to V) accompanied an oblique pattern of water movement over the reef towards the NW. Current flow in this direction was also observed in the early morning hours, with light NE winds of short duration. Light winds with a W component (SSW), or winds from this quarter of short duration, also tended not to disturb the usual current set to the NW. When N and W winds persisted for longer periods of time, and with greater force, the direction of circulation was observed to change. The effect of N winds was to oppose the normal trend in circulation toward the NW, resulting in partial (Pattern VI) or complete (Pattern VII) reversal seaward. On one occasion, under perfectly calm conditions following a period with a light NNE breeze, the direction of current flow reverted to a NW course, presumably in response to the set of the ambient current (Pattern VIII). When W winds prevailed, water movement over the reef flat shifted toward the N (Patterns IX to XI). At low tides with a mean depth of 0.18 m, a meandering movement was evident (Patterns XII and XIII), probably a result of non-linear irregularities in the vertical velocity distribution.

On numerous occasions, when the tides were near MSL (mean depth 0.43 m), and at various elevations of high water, sub-surface surveillance of the movement of dye indicated that the hypothetical, velocity-distribution curve best described conditions of turbulent flow ($k = 1.0$) throughout the entire water column. Rapid mixing occurred from the surface to the bottom, resulting in a down-wind movement of a more or less uniform dye front. By the time the dye spot was judged to be over the deep *Porites furcata* assemblage (viewed from the surface), underwater observations also showed that fairly thorough mixing had occurred to all depths. A short but undetermined distance to leeward, the shoal water streaming off the reef flat mingles with the main current stream (the ambient current) moving behind the reef. This mixing results in a lowering of the temperature and, most probably, a replenishment of plankton.

High-velocity winds moving in predominantly the

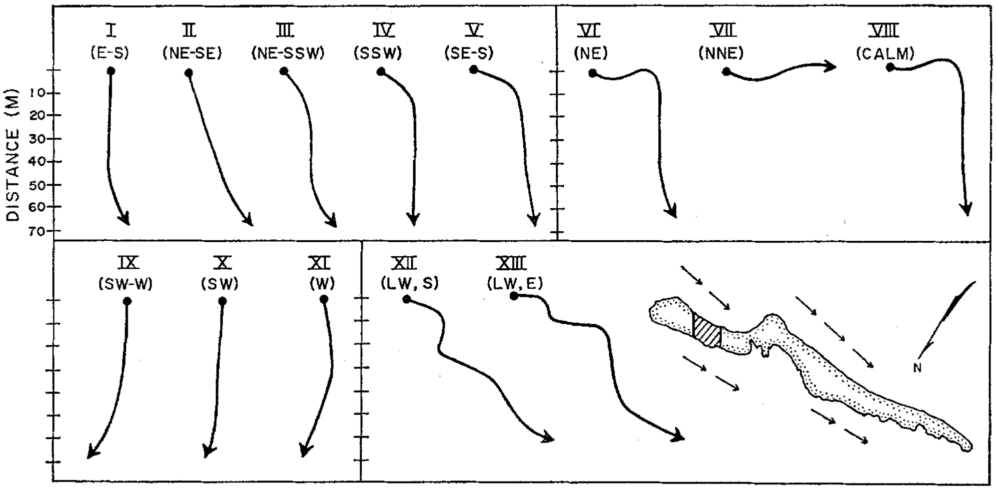

Fig. 12. Direction and distance of water movement across Laurel Reef under varying wind conditions. Circulation patterns XII and XIII observed at low water (5 cm below mean low water). Inset of Laurel Reef shows normal ambient current flow adjacent to shoals. Observations obtained primarily on eastern limb of reef in indicated area. For additional data see Table 4

same direction as the ambient current usually resulted in the greatest volume transport of water over the reef. An abatement of circulation often occurred during light and gentle E or SE breezes, or with winds which offered an opposing force to the usual direction of water movement. These observations necessitated a study of the interaction of wind and current in terms of the component forces which were thought to be involved. Analysis of these data disclosed a more rigorous relationship when volume flow (Q, m^3/min) was compared with wind velocity and direction rather than simply the current velocity (C, m/min).

The usual wind movement at La Parguera, from the E and SE quarters with an overall combined frequency of 81.1%, was found to have a decided driving effect on the currents traversing the reef flat (Fig. 13). A total of 37 observations was recorded with winds from the E and SE, and these demonstrated essentially the same response in the different seasons. Higher values of Q were observed at increasing wind velocities up to nearly 30 km/h. The regression equation describing these results is

$$Q = 0.545\ V^{0.024},$$

where $V = \log^{-1} V_w$. The correlation coefficient (r) in this case is 0.523. All but a single observation fall within the 90% confidence limits of the regression curve.

Southerly winds, moving at a greater angle from the main path of ambient current flow (or occasionally even perpendicular to it), were noted to have a much less marked effect on Q. The regression curve of 13 measurements made under these conditions, in 4 different months during the autumn and winter seasons, is characterized by a slightly positive exponent

$$(Q = 1.149\ V^{0.007};\ r = 0.64).$$

With SW and W winds, the ambient E-W current stream was opposed either obliquely or directly. At such times, water transport over the reef flat tended to be more substantial at lower wind velocities. The equation of the regression curve, based on only 12 observations, is

$$Q = 1.004\ V^{-0.020}.$$

The scatter in these data is considerable, with r equal to 0.430. A possible complicating factor in this case could arise from variations in the length of time SW and W winds prevailed; they occur only rarely, and are of relatively brief duration. In summary, the relationship of V_w and Q for all winds from the E through W quadrants, shows that r for each population is always positive.

Current measurements obtained during periods with a strong N component, presumably with a slight ability to augment the ambient current flow (as in the case of S winds), were observed on only 6 occasions in December. Although these data are limited, the interaction of wind and current did follow the expected result of a diminishing wind force moving from a NE to NNE direction. The tentative regression equations are

$$Q = 1.100\ V^{0.026}\ (\text{NE});\ Q = 0.5\ (\text{NNE}).$$

Hypothetical Relationship Between Wind and Current

It is seen that each equation has the form $Q = a(\log^{-1} V_w)^b$. The relationship between the exponent (b) of the regression curve and wind direction

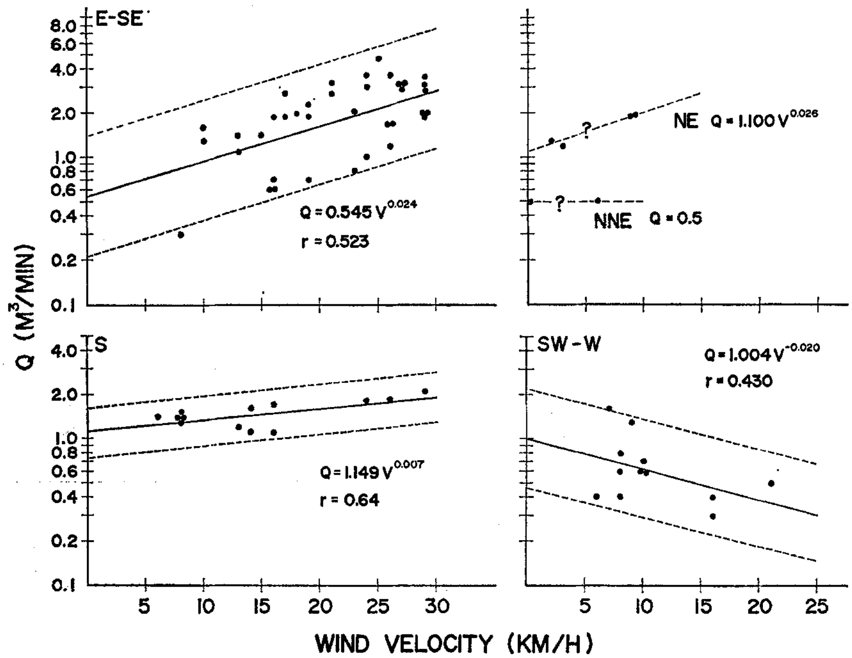

Fig. 13. Volume flow (Q) of water over Laurel Reef in relation to wind velocity and direction. Regression equations and curves are indicated in each plot; broken lines delimit 0.90 confidence limits. r: Correlation coefficient

reveals a sinusoidal function representing the rate effect of the wind direction on the current, i.e., the rate Q increases or decreases with increasing wind velocity (Fig. 14). This relationship is precisely what would be expected for a wind of varying direction on a constant current from the East. The intercept (a) of the regression curve is a more difficult term to define, in that it represents the ambient current flow during calm spells. It is suspected that the ambient current velocity changes throughout the year, as do the prevailing winds and tides in the area. The influence of tidal flow has not yet been determined. Moreover, it is likely that the ambient current velocity is affected by the prevailing wind direction. If this is found to be the case, (a) will then, to some extent, be under the influence of θ.

The general equation based on the above relations:

$$Q = 0.833\ (\log^{-1} V_w)^{0.025 \sin\theta},$$

where θ is the angle measured clockwise from N, lies within the 90% confidence limits of the E-SE and SW-W wind plots, and is a fair approximation for S winds. The exponents of these curves are, likewise, very well predicted by this equation. A poor correlation is apparent in the NE and NNE plots, perhaps in part due to insufficient data.

Estimates of Q can be computed from the general equation during periods of N and NW winds. For N and S winds, a constant Q value of 0.833 would be expected. For S winds this might be an accurate

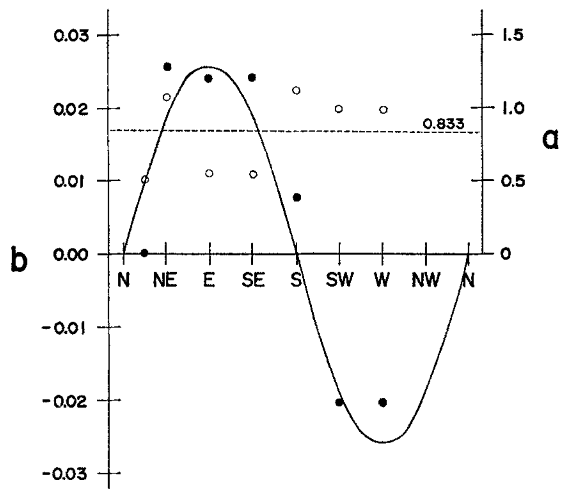

Fig. 14. Relationship between exponents (b, solid circles) and intercepts (a, open circles) of regression curves (for Q and V_w) and direction of wind movement. Curve is perfect sine wave of amplitude $b = 0.025$ ($b = 0.025 \sin\theta$), with 1 cycle traversing the full 4 quadrants of the compass. The near fit of field measurements (solid circles) to hypothetical curve is apparent

prediction at low wind-velocities; however, at moderate-to-high wind velocities, it probably underestimates actual volume flow. Winds from the NW, opposed to the prevailing SE current, would be expected to counter such water movement fairly effectively. The theoretical plot of V_w against Q gives a curve with a slightly steeper slope than that observed for SW-W winds. Q declines steadily from about 0.9 at 5 km/h to something less than 0.3 at 20 km/h.

Apart from an unknown effect of tide-induced current, it is suspected that improved measurements of the local winds would allow a more accurate expression of these observations. Although only a slight lag in the response of currents to winds was observed on reefs in this study and by Jones (1963) in Florida (USA), the current running at any particular time must be, to some extent, related to winds which prevailed several hours or perhaps even 1 to 2 days beforehand. For example, von Arx (1954) found that the velocity of the surface layer in Bikini lagoon corresponded most closely to the mean wind speed measured over a 12 h period. Moreover, a critical study of solitary waves should help to refine the analysis, and would be essential for understanding the actual mechanism of water transport.

Volume Flow

Aware of these limitations, estimates of volume transport over the reef were calculated and indicate a quite marked variation through the year (Table 5). As expected, the annual circulation pattern followed closely the mean wind-movement (Fig. 8). Maximum current flux occurred in May, June and July. Circulation was greatly reduced in March, and again in the fall season (October-December), at these times amounting to approximately 60% of the highest monthly value.

No obvious relationship between depth and Q was noted (e.g. a high Q was observed at MLW, Table 4, Observation No. 3). Observation showed that circulation ceased only at extreme low stands of the tide (15 cm below MLW or lower). Abatement of flow at these times, most prevalent in January and February, did not appreciably reduce the total monthly circulation.

Table 5. *Calculated monthly volume transport across a 1 m path, Laurel Reef flat. Computed from mean wind (Fig. 6) and tide data. Current flow greatly reduced or nil with tide at 15 cm level below mean low water or lower*

Month	% of total time current flow nil	Total volume transport (m^3/month)
Jan.	2.6	56,100
Feb.	3.4	52,500
March	0	39,900
April	1.4	50,200
May	1.6	64,000
June	1.2	68,700
July	0.1	62,800
Aug.	0	57,200
Sept.	0	52,500
Oct.	0	47,600
Nov.	0	43,100
Dec.	1.3	46,200

Discussion

The thermal conditions surrounding coral reefs in southern Florida and the Bahamas result in a markedly different climatic regimen from that characteristic of the Caribbean region. This fact is often not given due consideration when comparisons are made between relatively high latitude (marginal or subtropical) and tropical coral-reef environments. While the following discussion is necessarily confined to critical thermal conditions, it is not intended to dismiss the importance of other factors such as desiccation and actinic effects.

Long-term air-temperature records in Florida (e.g. Vaughan, 1918; Jones, 1963) disclosed greater seasonal variations in normal and extreme conditions than observed in Puerto Rico. Differences in extreme winter temperatures are most marked. Near Elliott Key, Florida, extreme minimum temperatures approached 0 °C in December and January, whereas at La Parguera, the lowest atmospheric temperature recorded over a 7 year period was 16 °C. Aside from possible deleterious effects upon corals and other reef populations inhabiting the intertidal zone, such extreme atmospheric thermal conditions also have a marked cooling effect on shallow marine waters.

Several recent studies have extended the earlier observations of Mayer (1914, 1916) and Vaughan (1916, 1918, 1919b) in relating the distribution of coral populations and reefs to lower temperature tolerance-limits in the Florida-Bahamas region. In the Bahamas, Busby and Dick (1964) recorded a surface-temperature difference of 5.8 C° between the sound and bank, and attributed this to the influence of a cold front. Shinn (1966) measured a minimum bottom temperature of 13.3 °C at Key Largo Island, Florida, in February, which resulted in the death of a transplanted colony of *Acropora cervicornis* (Lamarck). Further, Ginsburg (1964) noted a correlation between a higher thermal regime and the more northerly occurrence of coral reefs in the Bahamas. The extreme minimum temperature observed in Puerto Rico was 25 °C, but it is possible that shoal reef-flat waters may occasionally approach 20 C°. Thus, biological effects from low thermal conditions are expected to have a greater influence in the Florida-Bahamas region.

Temperature maxima at La Parguera commonly exceeded 30 °C, and ranged between 35° and 40 °C in bodies of standing water on the reef flat at low tide. Under similar conditions on the Galeta Point reef flat in Panamá, temperature maxima were observed to reach 38.5° and 39.0 °C (Meyer and Young, personal communication). Catastrophic mortalities often accompanied these periods. While such extreme periods of stress were largely restricted to a single season

(March-June) in Puerto Rico, they have been observed in Panamá throughout the wet season (ca. May-November) and even occasionally in the dry season (ca. December-April). Considering the apparent widespread occurrence of the high thermal characteristics of Caribbean reef flats (Glynn, 1968), it is highly probable that shoal-reef populations are affected more by upper temperature extremes than are those inhabiting comparable habitats at higher latitudes. It is hoped that this supposed regional difference will soon receive adequate analysis, thus providing quantitative data on the subject.

The immediate mechanical damage inflicted on shallow-reef zones by tropical storms has been well documented; however, some disagreement has arisen regarding the time necessary for recovery. Stoddart (1969b) cited evidence that recovery from cyclonic disturbances may require at least 10 to 20 years, whereas Shinn (1972) claimed significant re-growth in 1 year and complete restoration in 5 years. Whatever time scale is involved, evidence for mechanical alteration of *Porites furcata* on Puerto Rican reefs, either in the immediate or more distant past, is abundant. Examination of sedimentary deposits beneath the living reef frame, to 0.5 m depth, most often revealed accumulations of coral debris in disarray, similar to the deposits of broken coral produced by hurricane disturbances. In fact, these deposits were more abundant than subfossil coral colonies in normal growth position. Evidence for another storm-related influence, namely the enrichment of surface waters by nutrients (followed by an increase in plankton production), will be examined in the second part of this study.

Current velocities observed over coral reefs in the western Atlantic region are of the same order of magnitude as in Puerto Rico, indicating a generally high and similar rate of flow. Data reported in the literature usually represent current velocity (C, m/sec), and were obtained over a brief observation period.

Odum *et al.* (1959) reported current velocities over Puerto Rican reefs of ca. 0 to 0.15 m/sec, comparable with those observed in the present study. Current flow over deeper patch reefs (1 to 2 m depth) disclosed rates of 0.10 to 0.50 m/sec in Florida (Jones, 1963), 0.23 m/sec in the Bahamas (Storr, 1964) and 0.05 to 0.35 m/sec on reefs 5 to 18 m deep in the southwestern Caribbean Sea (Milliman, 1969).

Information available on the current velocity over coral reefs in the Pacific region also indicates a range of values similar to those reported above. Current flow over a Hawaiian fringing reef was 0.22 to 0.24 m/sec (Kohn and Helfrich, 1957). Independent measurements made over reefs in the Marshall Islands disclosed current velocities of 0.32 to 1.44 m/sec (Odum and Odum, 1955) and 0.10 to 0.40 m/sec (Marshall, 1965) at Eniwetok Atoll, 0.24 m/sec on Rongelap Atoll (Sargent and Austin, 1954) and 0.25 to 0.50 m/sec along the north shore of Bikini Atoll (von Arx, 1954).

The high values reported at Eniwetok, over a depth of 0.5 to 1.5 m, suggest that volume flow on this atoll may be exceptionally high. In the Caroline Islands, Tracey *et al.* (1961) observed a volume flow (Q) of 2.1 m^3/min on Ifaluk Atoll, equivalent to 3000 m^3/day. This is nearly two times the mean volume flow over Laurel Reef, Puerto Rico. The Pacific data were obtained in the summer season; more vigorous circulation would be expected in the winter when the NE trade winds prevail. If some of these apparent differences are substantiated through further study, it would be of interest to investigate the extent to which such contrasting current regimes influence the character of shoal-reef communities.

Summary

1. The present study is concerned with certain abiotic factors (temperature, precipitation, cyclonic effects, salinity, tidal characteristics and variations in sea level) that can influence shoal-reef populations, and with the physical conditions (wind, tide and seasonal variations in sea level) that control the volume flow of water over the reef. Integration of results is the object of a forthcoming paper that will relate water transport to the supply of plankton and offer evidence for its utilization by the suspension-feeding component of the reef-flat benthos.

2. Laurel Reef, located on the insular shelf off SW Puerto Rico, approximately 3.5 km SSW of La Parguera, was selected as the principal study site. Observations were largely confined to the reef flat, characterized by shallow deposits of bioclastic rubble and, along its leeward margin, a flourishing population of the hermatypic coral *Porites furcata* Lamarck. Differences in zonation are described; however, *P. furcata* is the dominant framebuilding element, present as continuous patches 3 to 50 m in width at 1 to 1.5 m depth.

3. Marked seasonal variations in air temperature, rainfall and wind conditions were noted. Monthly mean temperatures ranged between 25° and 31 °C annually, and were highest from May through October. Precipitation was relatively low, 500 to 1200 mm annually, and greatest from May through November; during cyclonic disturbances, daily records may exceed 200 mm. The wind field has its strongest components from the E (10 to 15 km/h, 30 to 50% of total time) and SE (15 to 25 km/h, 30 to 40% of total time) quadrants; velocity from these quarters reaches a maximum from May through July, steadily diminishing through December. Hurricanes have a strong influence on coral survival, and also play an important role in modifying emergent and shoal-reef structures.

4. Seasonal variation in mean sea-water temperature followed closely that of the atmosphere,

ranging between 25° and 30 °C, and reaching a maximum in August-October. Increased wind movement in the spring appeared to be causally related to a slight decline in the surface thermal structure. Mean salinity values ranged between 34 and 37‰, with maxima observed in the dry season (April-June). New data confirmed an earlier observation of a higher mean elevation of sea level in the late summer and fall. For the first time, a daily time progression of approximately 50 min was observed during periods of spring low-water tides. A comparatively low stand of mean sea level prior to 1960, coupled with adverse conditions accompanying periods of extreme low-water exposure, are implicated in a widespread mortality of *P. furcata* ($\leq$ 10 cm below MLW).

5. Westerly moving, inshore, surface currents produce a vigorous, predominantly unidirectional flow over the reef flat. The general equation

$$Q = 0.833\ (\log^{-1} V_w)^{0.025 \sin\theta}$$

derived from measurements of depth, wind direction and velocity, was found to describe adequately the volume flow of water. Total volume flow across the reef was greatest from May through July, exceeding $6 \times 10^4\ m^3$/month; water movement in March and November was about 40% less.

6. Differences in the marine thermal climate of shoal coral-reef environments in subtropical (Florida and Bahamas) and tropical (Caribbean) areas were compared. The contrasting regimes substantiate a greater influence of low and high temperature extremes, respectively, in high versus low latitudinal regions.

7. The texture of subsurface sedimentary deposits on the reef flat was found to provide evidence of past fragmentation and death of *P. furcata* (similar to that caused by hurricane disturbances) despite subsequent reef recovery.

8. A review of current-velocity measurements over coral reefs indicates values either similar to those observed in Puerto Rico or greater by a factor of about two. In particular, certain atolls in the western Pacific Ocean experience vigorous circulation and, presumably, greater volume transport over the reef-flat biotope.

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