

DISTRIBUTION OF CORAL REEFS IN THE PEARL ISLANDS (GULF OF PANAMÁ) IN RELATION TO THERMAL CONDITIONS¹

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ABSTRACT

The hypothesis that coral reefs are largely confined to the north and east sides of islands because of favorable thermal conditions was tested and confirmed in the Pearl Islands, Panamá.

The growth rate of *Pocillopora damicornis*, the chief reef-building species, declined markedly or ceased on shores exposed to temperatures in the range 20–21°C, when median growth rates dropped to below 1.0 mm month⁻¹ and a variety of alien benthic species invaded and overgrew the branch tips of corals. High rates of bedload sedimentation on exposed shores and a high organic matter content of sediments on reefs did not affect coral growth. Differences in coral growth preceding and following upwelling were correlated with seasonal variations in sky cover.

Other factors affecting coral growth and reef development include the ability of corals to feed and reproduce at low temperatures, the influence of turbulent conditions, the capacity of a reef structure to modify the surrounding thermal regime, and the effects of attrition due to corallivores.

Since the observations of Dana (1843), marine thermal conditions have been recognized to exert a strong influence on coral reef development and distribution. Geographically, this is evident in the general occurrence of major reef formations on the eastern sides of continents, in regions largely influenced by western boundary currents of high thermal character. Coral growth is markedly affected by temperature (e.g. Vaughan and Wells 1943; Shinn 1966; Clausen 1971). The generic diversity and age of scleractinian hermatypes also show a strong correlation with the global distribution of isotherm maxima (Stehli and Wells 1971).

Until recently (Glynn 1972; Glynn et al. 1972), it was generally believed that structural coral reefs were absent from the eastern Pacific coast of Central America (e.g. Darwin 1842; Crossland 1927). The reef formations described in Panamá reach maximum development under the relatively

high and stable thermal conditions in the Gulf of Chiriquí. We have now observed smaller reef structures in the Pearl Islands, more numerous on the eastern and northern sides of islands. We hypothesized that these positions would offer protection from upwelling currents, providing preferred sites for coral growth and reef development.

We wish to thank G. W. McLeod, A. Velarde and J. N. A. Bryan, Master of the RV *Tethys*, for assistance in the field. Aerial reconnaissance was made possible by Maj. D. S. Tracey, U.S. Army 352nd Aviation Detachment. The algae were identified by M. Díaz-Piferrer. We also acknowledge the help of C. Birkeland, J. B. Graham, I. Rubinoff, I. E. Wallen, and others who offered encouragement and advice.

METHODS

The distribution of coral reefs and reef coral communities was determined by aerial surveys made during low water and subsequently verified by direct underwater observation. The positions of reefs and coral patches were mapped from black and white vertical photographs (using a polaroid filter) superimposed on topographic charts; areal coverage was determined by

¹ This study was supported by the Smithsonian Tropical Research Institute and by the Office of Environmental Sciences, Smithsonian Institution.

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planimetry from enlarged aerial photographs. Color photography allowed identification of coral populations and coralline algal assemblages.

Bottom temperatures were monitored with thermographs (Peabody Ryan model F). All units were calibrated before and after use and had an accuracy of 2% for temperature and time, according to specifications. However, the instruments showed a 2–4 hr time lag in responding fully to temperature changes. Calibrated mercury thermometers, with an accuracy of 0.1°C, were also used.

Sedimentation rates were measured with opaque bottle traps (14–20-mm aperture) positioned upright in blocks buried flush with the bottom or wired to rods at various elevations above the bottom. Three to six replicate samples were collected at each station at about 30-day intervals and washed free of salts, allowing sufficient time between washings for the settlement of fine particles. All living macroscopic organisms were removed; we were also careful to exclude fouling organisms. Total dry mass was determined after drying to a constant weight (65°C initially then for a shorter time at 103°C), the inorganic fraction by ashing at 500°C for 4 hr, and organic matter estimated from the difference between the two.

Water clarity was determined routinely by estimating the distance of lateral visibility. Light penetration was measured synchronously at the surface and above the bottom with exposure meters calibrated in foot candles and converted to lux. All light data are based on the means of four readings made vertically up and down and horizontally to the north and south in May and June. Sky cover data, representing visual bihourly estimates, were obtained from the Meteorological and Hydrographic Branch of the Panama Canal Company.

Coral growth was measured by staining live animals with Alizarin Red S bone stain (Barnes 1971). At each site 3–5 whole colonies of the scleractinian hermatypic *Pocillopora damicornis* (Linnaeus) var. *bul-*

bosa Ehrenberg (c.f. *P. lacera* Verrill), 10–20 cm in diameter, were stained in situ in water-filled transparent plastic bags during midday for 5 hr. (Two coral specimens differing in growth form were deposited in the National Museum of Natural History, USNM Cat. No. 45681 and 45682.) After this treatment the corals were attached (by their dead basal branches with polyolefin insulated hookup wire) in normal growth position to construction blocks and placed on station. Colonies were reexamined after 24 to 53 days. The maximum growth of 10 branch tips in each colony was measured after cleaning with Clorox. Coral branches showing signs of cropping by corallivores were excluded. The corals used for the experiments all came from the sides of the islands showing structural reef development. Stained corals were usually placed on reefal shores first and subsequently on opposite sides of islands. To check the possibility of trauma during transportation, some corals were subjected to a trip around the island and then repositioned on the reefal side.

The growth rate of unstained corals was also determined from field photographic records. Five *Pocillopora* colonies, handled only briefly when being fitted into rubber tube supports, had a median growth rate of 1.98 mm month⁻¹ (1.42–2.83, 0.95 confidence limits). The median growth rate of a parallel group of corals treated with Alizarin bone stain was 1.84 mm month⁻¹ (1.75–2.04). The Mann-Whitney U-test indicated that the two techniques did not differ significantly ($p > 0.295$). (The non-parametric statistical tests used are from Siegel 1956. Significance level $\alpha = 0.05$ unless otherwise specified.) A greater precision was attained with the vital stain method, as evidenced by the comparatively narrow spread of the confidence limits.

STUDY AREA AND THE PHYSICAL ENVIRONMENT

The Pearl Islands Archipelago is on the isthmian shelf in the Gulf of Panamá, about 70 km SE of Panamá City (Fig. 1). The 20-m isobath lies close to most islands and

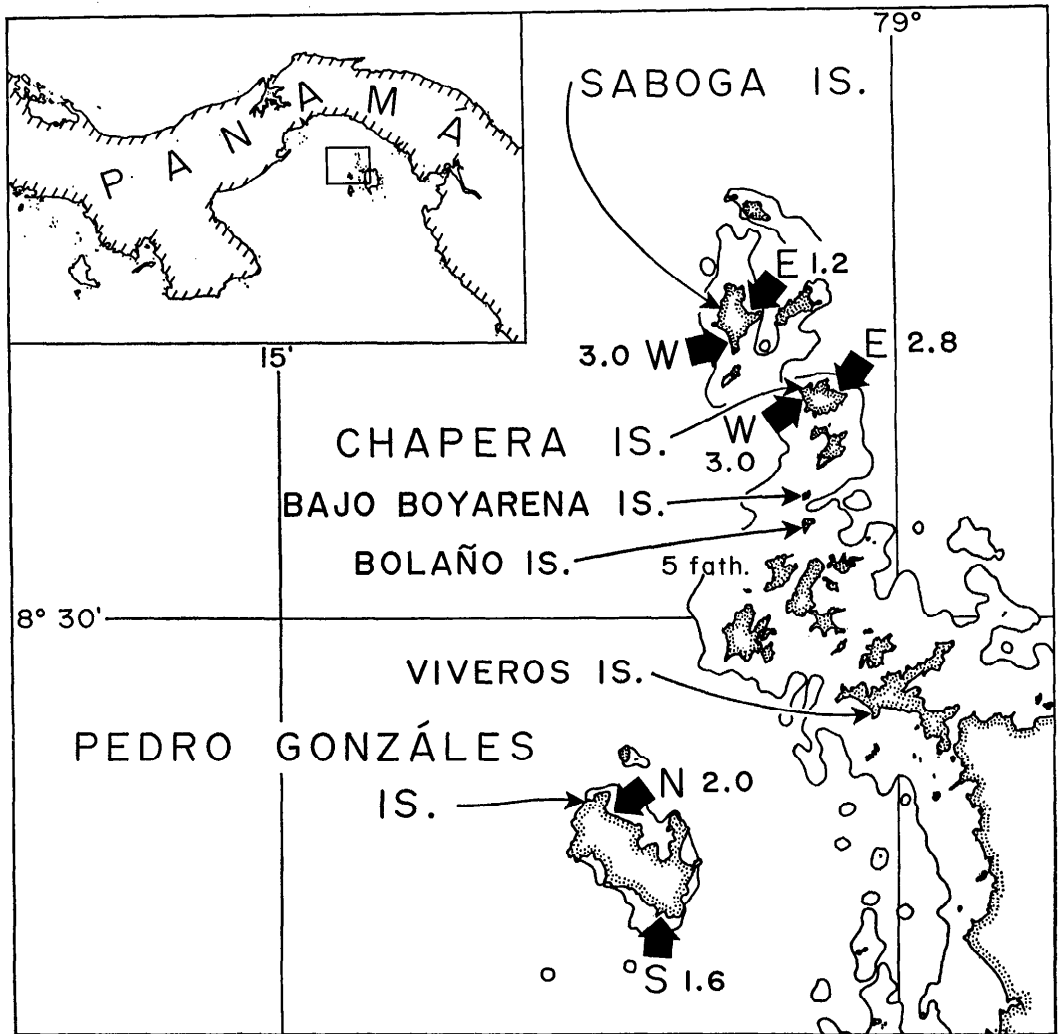


Fig. 1. Location of study sites in the Pearl Islands, Gulf of Panamá. Water depth at study sites relative to the MLLW datum is indicated.

the 50-m isobath approaches the western perimeter of the archipelago. A chief advantage offered by this island group for ecological study is the presence of a wide range of contrasting physical conditions. Seasonal variations in temperature commonly range over 10°C , comparable to a latitudinal spread of $20\text{--}30^{\circ}$ in thermally stable tropical seas.

From January through April, when the Intertropical Convergence Zone is at its most southerly position, northerly winds from the Trade Winds system predominate

over the Panamá Bight. Wind movement across the central sector of Panamá is relatively unobstructed due to the low relief. Climatically, this results in a dry season over the Gulf of Panamá (with decreased runoff) and accompanying increased incident radiation. The strong offshore winds produce a mass transport divergence which causes a lowering of sea level and upwelling of relatively cold water rich in micronutrients; mean primary production increases by a factor of two in the dry season (Forsberg 1969). Wind movement is of-

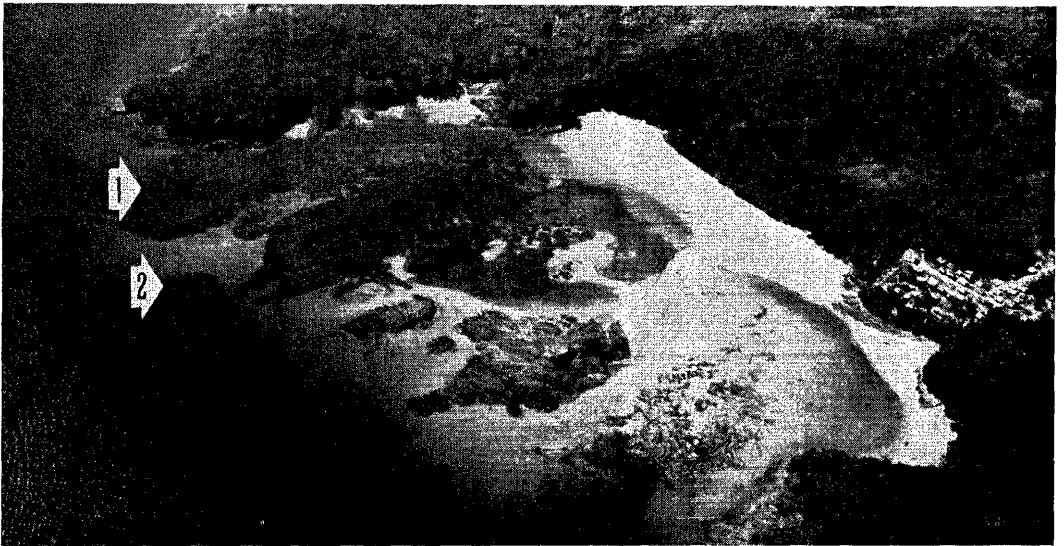


Fig. 2. Aerial view of *Pocillopora* reef (arrow 1) and algal biostrome (arrow 2), eastern shore of Saboga Island (elevation 1,200 m, tide ca. -0.2 m, 1 February 1972).

ten slight in the wet season, causing appreciable diel variations in sea surface temperature. Limited observations indicate that surface salinity varies between 33 and 30‰ in the dry season and thereafter until August and declines to around 28‰ by the end of the wet season. A fuller treatment of the physical environment was presented by Hubbs and Roden (1964), Smayda (1966), and Forsbergh (1969), with reference to the literature.

Although knowledge of the upwelling circulation system in the Gulf of Panamá is not detailed, present evidence does indicate that a major influx of cold water occurs to the west of the Pearl Islands along a submarine valley extending to the north (Smayda 1966). Some upwelling may also occur to the east of the Pearl Islands. We selected the three pairs of study sites (Fig. 1) largely on the differences expected in the thermal environment from the location of islands relative to the known patterns of upwelling circulation, with care to compare habitats on opposite sides of islands that were similar in depth, slope, substratum, and distance from possible effects of land drainage.

DISTRIBUTION OF CORAL REEFS

In this analysis coral reefs are defined as limestone formations, built principally by corals, that attain a minimum thickness of 1 m. The chief frame-building coral is *Pocillopora damicornis* with massive species of *Pavona* and *Porites* also commonly contributing to the reef structure. Reef development is shallow, largely from extreme low water to a depth of 4 m below MLLW. Maximum reef thickness is usually between 1 and 2 m, but occasionally approaches 3 m. Coralline algae, present as gravel and cobble-sized nodules, often occur as thin (biostromal) deposits at slightly greater depth. These two kinds of formations are illustrated in Fig. 2.

Figure 3 shows that coral reefs are more abundant and attain greater dimensions on the northern and eastern sides of islands, supporting the earlier impression noted by Glynn et al. (1972). Table 1 gives the percentage of areal coverage of coral reefs on the basis of their orientation; the small islands and shoals of Bajo Boyarena and Bolaño have also been included.

On six of the eight islands examined the NE quadrant contained over 50% of the

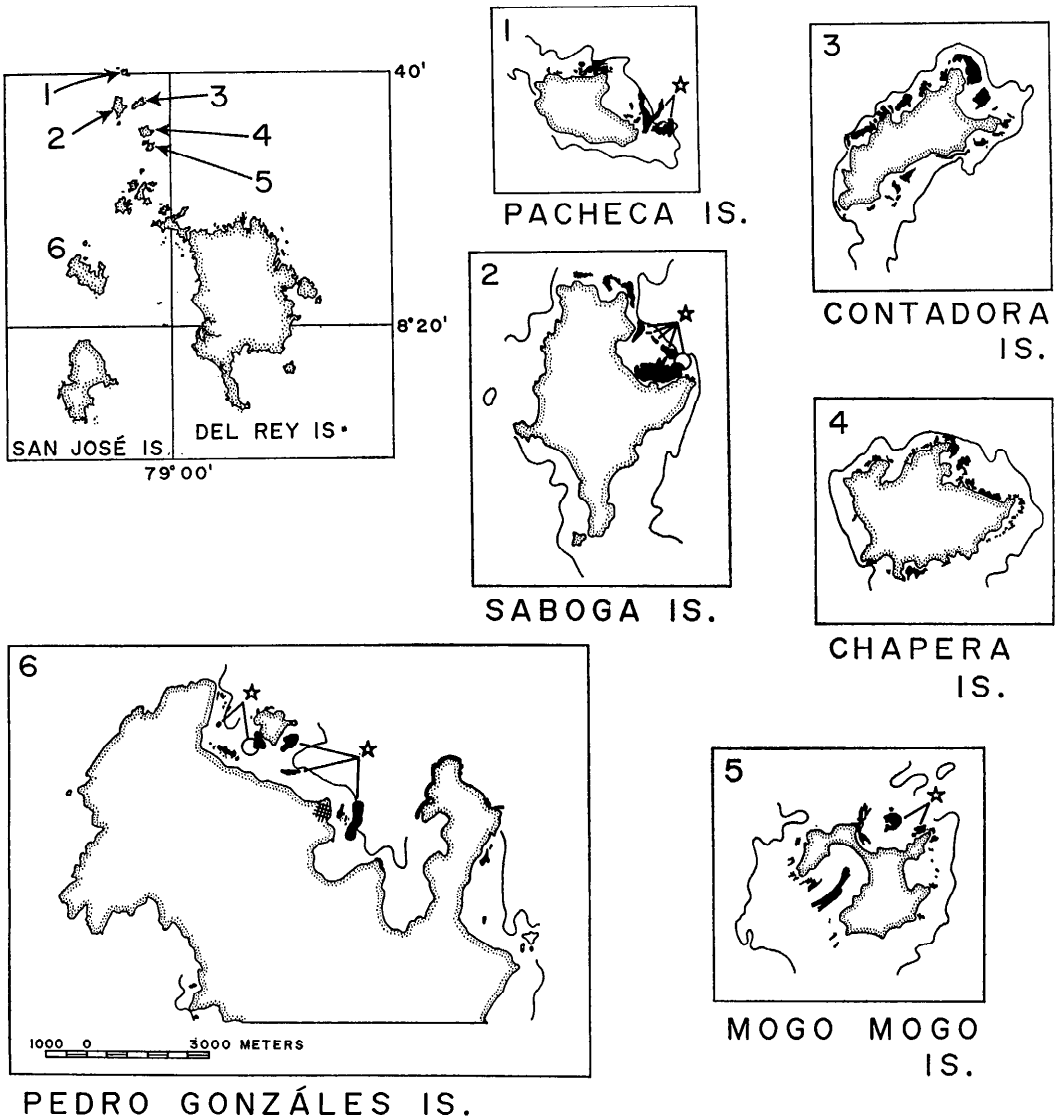


Fig. 3. Distribution of coral reefs and algal biostromes (denoted by stars) in the northernmost islands and at Pedro González Island, Pearl Islands Archipelago. Surveyed over period of study (November 1971-June 1972). The 3-fathom (5.4 m) contour is indicated.

total reef coverage. The relatively large area of bottom covered by reefs on Saboga and Contadora Islands, 14.3 and 11.7 ha, is due chiefly to two large formations. Mogo Mogo and Bolaño Islands showed greatest reef development on their northwest and southwest sides, respectively.

The distribution of reefs does not appear to be influenced by the area of available

shelf. Coral reefs are always developed shoreward of the 3-fathom (5.4 m) isobath. Extensive shelf areas in this depth range are without reefs, e.g. the south and south-east sides of Saboga Island. Moreover, the relatively narrow shelf on the north coast of Contadora contains many reefs, some close to 6-m depth.

The largest island surveyed, Pedro Gon-

Table 1. Areal coverage (ha) of coral reefs in relation to directional orientation on island shores. Total reef area per island, with respect to island size, is also indicated. Quadrants were delimited from coordinates drawn through the center of gravity of a two-dimensional cardboard model of each island

Islands and their respective areas*	Areal coverage†								Total reef area/100 ha island area
	NE		SE		SW		NW		
	area	%	area	%	area	%	area	%	
Pacheca (75.1 ha)	3.13	73.0	0.56	13.0	0	0	0.60	14.0	5.7
Saboga (297.0)	14.30	93.1	0	0	0	0	1.07	6.9	5.2
Contadora (138.8)	11.71	53.9	1.24	5.7	3.10	14.3	5.68	26.1	15.6
Chapera (186.2)	6.86	58.3	1.48	12.6	1.90	16.2	1.52	12.9	6.3
Mogo Mogo (98.0)	1.94	16.5	0.57	4.9	3.94	33.6	5.27	45.0	12.0
Bajo Boyarena, plus shoals (16.3)	0.54	100.0	0	0	0	0	0	0	3.3
Bolaño (21.2)	1.16	37.2	0	0	1.52	48.7	0.44	14.1	14.7
Pedro Gonzáles (1,485.0)	5.26	57.7	0	0	0	0	3.86	42.3	0.6
Mean	5.61	61.2	0.48	4.5	1.31	14.1	2.30	20.2	

*From U.S. Army topographic sheets 4341-1 and 4341-11, scale 1:50,000.

†Determined with planimeter from enlargements of vertical aerial photographs.

záles, has only 0.6 ha of coral reef per 100 ha of island area. Smaller islands showed a greater reef coverage, ranging from 3.3–15.6 ha per 100 ha of island area. The possibility that island size is a factor in reef development is discussed later.

Preliminary information on the rest of the Pearl Islands shows several coral reefs on the relatively broad shelf located off the northwest corner of Del Rey Island. One of these is at the northwest corner of Viveros Island. Reefs are sparse around Del Rey Island itself; those present are concentrated on the northeast shelf. Numerous dark patches (possibly communities of coralline algae) were observed off the south end of San José Island, but their identity has not yet been established.

RESULTS

Coral growth rate

The growth rate of *P. damicornis* was selected as a measure of the condition of coral and of its potential for proliferation on opposite island shores. Variations in coral growth are summarized for all study areas in Fig. 4; an evident general trend

was a decline in growth in February and March. On the south side of Pedro Gonzáles Island and the west sides of Chapera and Saboga Islands, median growth was below 0.5 mm month⁻¹. Before upwelling, median growth ranged between about 2 and 3 mm month⁻¹. Maximum growth, observed after upwelling, varied from about 4 mm month⁻¹ at Pedro Gonzáles to 5–6 at Chapera and Saboga Islands.

Coral growth tended to be greater on the sides of islands showing greatest reef development, i.e. to the north and east. All but one pair of measurements (Saboga Island, April–May) disclosed significant differences (Mann-Whitney U-test). Overall, coral growth on the south side of Pedro Gonzáles Island was 65.9% of that on the north side, and growth on the west sides of Saboga and Chapera Islands was 76.3 and 85.1% of that on their eastern shores.

Thermal regime

Temperature declined markedly over the period February–March at all stations (Fig. 5). Low temperatures appeared suddenly in February, falling by as much as 6.4°C

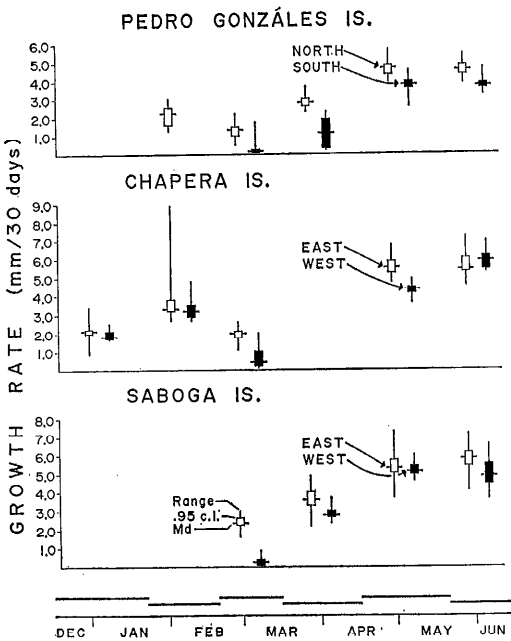


Fig. 4. Seasonal variations in the growth rate of *Pocillopora* on opposing island shores, November 1971–June 1972. Bold lines along time axis indicate sampling periods.

(from 25.0 to 18.6°C) in 2 days on the south shore of Pedro González Island. During a gradual warming trend after the upwelling season through June, the modal temperature classes changed from 19 and 21°C to 29°C. Stations on the south and west sides of islands invariably displayed lower thermal regimes; for example, Pedro González south and Saboga west had temperatures in the 19°C class (18.1–20.0°C) for over 50% of the time from 20 February to 15 March, although on the opposite sides of these islands temperatures were predominantly in the next higher thermal class (21°C). The similarity of temperatures between stations from May through June indicates that thermal conditions were approaching comparable levels with the coming wet season.

Daily variations in sea temperature were generally in phase at all stations. A close correspondence of the daily fluctuations with the predicted tide cycle is indicated in Fig. 6. This relationship is apparently

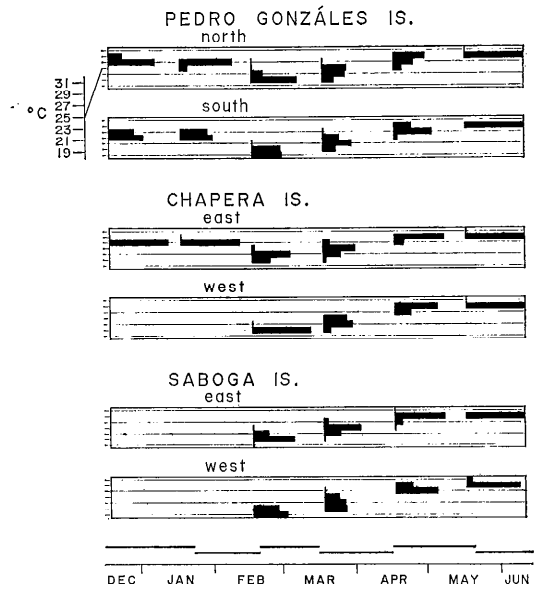


Fig. 5. Seasonal variations in the thermal regime on opposing island shores, December 1971–June 1972. Temperatures are the midpoint values of the 7 classes indicated. These were determined by planimetry from the actual curves.

due to surface warming of shoal water during ebb tide, followed by cooling as the tide floods and moves cooler, deeper water shoreward. On several occasions while SCUBA diving we encountered a cool water front along the bottom, which moved onto the reef with the flooding tide.

The predicted tidal curve and the temperature records are a few hours out of phase. Field observations of the state of the tide (time and height) demonstrated that it is very well predicted by the tide table (U.S. Dept. Com. 1971), so that this discrepancy presumably is due to the time lag noted during calibration.

Shores fringed with coral reefs display greater variations in temperature and have a higher mean temperature regime than nonreefal shores (Fig. 6). The usual temperature difference is not evident, however, at Pedro González for the particular period illustrated.

A large number of surface temperatures measured in the vicinity of the Pearl Islands were consistent with those in Fig. 6 in that

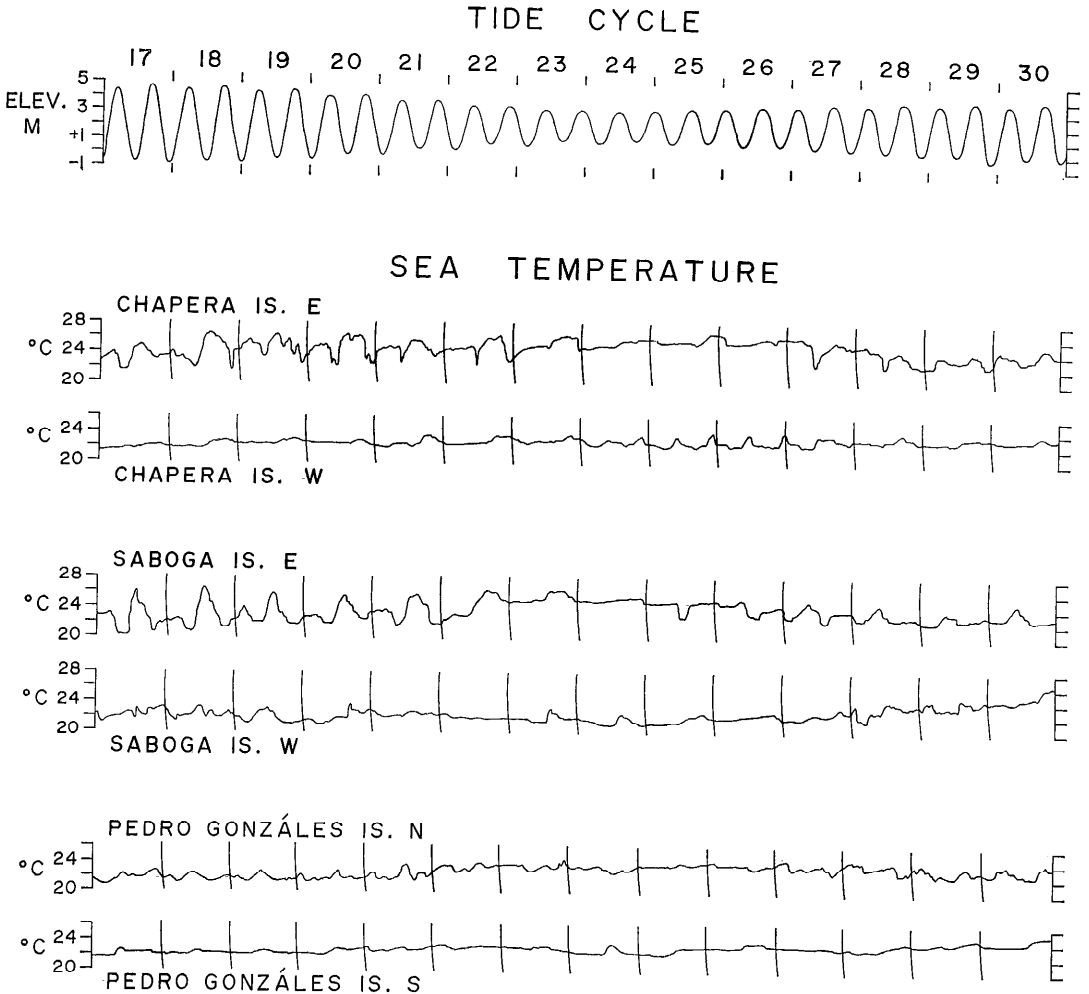


Fig. 6. Predicted tides (U.S. Dep. Com. 1971) and bottom sea temperatures recorded at Chapera, Saboga, and Pedro Gonzáles Islands from 17–30 March 1972.

they showed lower thermal conditions on the west and south sides of islands. The lowest temperature recorded, 18.6°C, was on station at Saboga west, 21 February 1972.

Comparison of our data with those obtained routinely by the Panama Canal Company at pier 18 in Balboa showed that surface temperatures began to decline nearly synchronously over a distance of 70 km. However, as expected, the low extreme temperatures recorded at Balboa were not as low as those observed offshore.

Sedimentation rate and organic matter content of sediments

It is clear from Fig. 7 that sedimentation rates were significantly greater on the south and west sides of islands. These differences approximated an order of magnitude at Pedro Gonzáles and Chapera Islands and reached two orders of magnitude at Saboga. Only at Chapera did the sedimentation rates of the east side (May–June) approach those to the west (December–February); the range of values was 50–70 mg cm⁻² day⁻¹. The data from some sta-

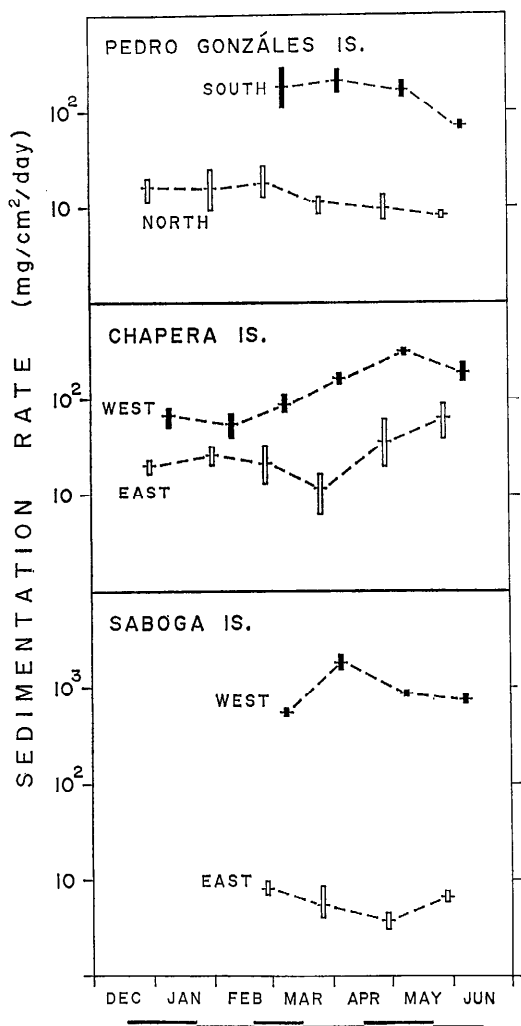


Fig. 7. Sedimentation rates observed at bedload level (≤ 20 cm above bottom) on opposing island shores. The range and mean values of inorganic accumulation are noted.

tions, e.g. Chapera west, suggest significant seasonal differences.

Generally, the samples contained a large amount of calcareous bioclastic material. On nonreefal shores this component was composed largely of cirriped skeletal elements; on reefs it contained chiefly coral fragments.

Our study of sedimentation rates was directed primarily to the bedload component since this was suspected to have an

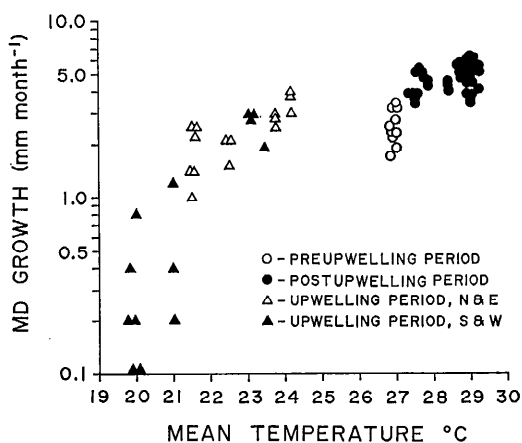


Fig. 8. Relationship between mean water temperature and the median growth rate of *Pocillopora damicornis* ($r = 0.751$, $N = 78$).

influence on coral growth. The curve based on sedimentation rate versus distance above the bottom was characterized by an inflection point at 20 to 30 cm. Above this height, suspended sediments probably contribute more to the inorganic particulate load in the water column.

Sediment collected higher in the water column (between 49–122 cm) at Chapera Island from December to June showed median rates of accumulation of 3.5 mg cm⁻² day⁻¹ (1.8–6.7, 0.95 confidence limits) for $n = 9$ on the east side and 7.7 (4.4–30.3) for $n = 12$ on the west side. These differences are not significant.

The organic matter content of sediments was significantly higher in the coral reef communities on the north and east sides of islands (Table 2). The median percent differences were least at Chapera Island (H_0 barely unacceptable) which has a small reef patch on the west side. A relatively constant percentage of organic matter was observed through the seasons at all stations except Chapera east, where a peak value of 12.2% was found in February–March.

Water turbidity and sky cover

Estimates of water clarity at depth and measurements of the visible light intensity

Table 2. Percent organic matter content of bedload sediments (≤ 30 cm) collected from sediment traps in study areas

Sampling statistics	Study areas					
	Pedro Gonzáles		Chapera		Saboga	
	N	S	E	W	E	W
Md	9.1	7.2	6.1	5.1	11.5	1.7
0.95 confidence limits	8.2-10.5	5.5-8.3	4.7-9.7	4.3-5.6	10.0-13.1	1.4-1.9
N	26	15	25	21	15	16
U*	353		339		0	
z†	4.26		1.71		-	
P	<< 0.00003		0.0436		<< 0.001	

* Mann-Whitney statistic.

† Standardized normal deviate, $\mu = 0, \sigma = 1$.

at the surface and bottom indicated marked variations in turbidity at all sites throughout the study. Lateral visibility ranged from ~ 10 m at Pedro Gonzáles south (December) and ~ 12 m at Saboga west (February and March) to ~ 1 m at Pedro Gonzáles south and Chapera east (March). Absolute light intensities at depth fluctuated widely, depending on time of day, state of tide, sky cover, sea surface conditions, and other factors. Minimum values at midday under clear skies were $< 20,000$ lux and the maximum level observed $\sim 100,000$ lux. Relative light intensities on the bottom varied only slightly at all stations with a range of 54-66% of the surface values. The mean extinction coefficient for all stations following upwelling (May and June) was 0.18 m^{-1} ; this is

slightly higher than the mean value reported by Roy and Smith (1971) for clear water ($\epsilon = 0.13 \text{ m}^{-1}$) in Fanning Lagoon but lower than in the turbid water areas ($\epsilon = 0.28 \text{ m}^{-1}$). Reflection of light from the bottom was considerable—usually comparable to readings made horizontally.

High turbidity was due largely to dense patches of phytoplankton that appeared in the upwelling season. Saboga Island was the only study area where the presence of plankton caused notable differences in turbidity on opposite shores; the water at Saboga west was exceptionally clear (10-12 m) during upwelling.

Sky cover at Balboa had a mean value of 68% for the 2-month period preceding upwelling. From 24 January to 15 March, sky cover was 45% and increased steadily

Table 3. Correlation of coral growth with seawater temperature, sedimentation rate, and organic matter content of sediment

Environmental variables	Statistics				
	N	τ^*	z	p	H ₀
Mean temperature	78	0.751	9.75	<< 0.00003	reject
Bedload sedimentation rate	86	-0.078	-1.05	0.1469	accept
Organic matter content of bedload	83	-0.056	-0.75	0.2266	accept

*Kendall rank correlation coefficient.

thereafter as the wet season progressed; by 21 May to 13 June, it had reached 90%. These seasonal differences follow the general pattern characteristic of the region and are presumably representative of conditions over the Gulf of Panamá.

Physical correlates of coral growth

Temperature and coral growth showed a highly significant positive correlation with $r = 0.751$ (Table 3). The growth rate declined rapidly at and below 21°C on the south and west sides of islands (Fig. 8).

Neither bedload sedimentation rates nor the organic content of sediments showed significant correlation with coral growth (Table 3).

These data do not allow a rigorous interpretation of the effects of light on coral growth. Two factors affected light levels: turbidity and sky cover. During upwelling clear skies would be expected to increase coral growth (Goreau and Goreau 1959) and plankton blooms, through turbidity, to decrease it. The relatively high cluster of points around 24°C in Fig. 8 may have been influenced by the low sky cover at this time, and the relatively low growth rates near 27°C before upwelling by more overcast conditions. The critical influence of temperature was shown most clearly at Saboga west: coral growth nearly ceased during upwelling, when water transparency was the greatest we observed anywhere.

DISCUSSION

When upwelling was most pronounced, corals on the south and west sides of islands had some branches showing no growth at all. At such times soft parts were seen to slough off the branch tips of both stained and undisturbed colonies, and these portions of affected colonies were subsequently overgrown by a variety of benthic organisms. The first to appear were diatoms and filamentous algae (Table 4). Foraminifers, hydroids, cheilostome bryozoans, and cirripeds also settled and grew on the corals. We do not know whether the invading species established themselves on weak-

Table 4. Marine plants found growing on Pocillopora on the south and west sides of study islands during the upwelling season

Bacillariophyceae	<u>Licmophora flabellata</u> (Carm.) Agardh (<u>Exilaria flabellata</u> Greville)
Cyanophyceae	<u>Calothrix crustacea</u> Thuret
Chlorophyceae	<u>Enteromorpha prolifera</u> (Muller) J. Agardh
Phaeophyceae	<u>Giffordia mitchellae</u> (Harvey) Hamel <u>Giffordia rallsiae</u> (Vickers) Taylor
Rhodophyceae	<u>Goniotrichum alsidii</u> (Zanardini) Howe <u>Herposiphonia secunda</u> (C. Agardh) Ambronn

ened and necrotic tissues or on bare skeletal areas. In any case, the end result was rapid proliferation and overgrowth of coral branches by alien species.

These results indicate that temperature may control the distribution of coral reefs in the Pearl Islands by lowering the ability of corals to compete with other benthic species. Since sparse populations of all coral species do occur on nonreefal shores, their distribution does not seem to be limited through the effects of minimum temperatures on reproduction, a possibility suggested by Yonge (1940) and extended recently to the Indian Ocean (Rosen 1971).

Mayor (1916) and Edmondson (1928) showed that low temperature affects the capacity of corals to feed. In our observations during periods of extreme cool water, most of the polyps of *Pocillopora* were retracted. Corals can grow in the absence of zooplankton (Franzisket 1969; Johannes et al. 1970), but whether reduced feeding at lowered temperatures or low temperature itself influenced the observed growth rates is not known.

The degree of exposure to seas of nonreefal shores was rejected as a factor preventing reef development on the basis of observations in the Gulf of Chiriquí. In the Secas Island group, fringing reefs composed largely of *Pocillopora* have formed on the south and northwestern sides of is-

lands commonly exposed to highly turbulent conditions (Glynn et al. 1972).

We did not find that higher sedimentation rates on exposed shores affected coral growth, in agreement with Marshall and Orr (1931) that *Pocillopora* was resistant to large quantities of sediment. However, these results apply only to adult colonies.

Variations in salinity at the Pearl Islands are greatly influenced by the northerly movement of a salinity front located off Colombia (Forsbergh 1969). Considering the known range in salinity and the high tolerance of the planulae of *Pocillopora* to freshwater dilution (Edmondson 1946), this factor cannot be regarded as critical.

An island size effect is perhaps responsible for the absence of reefs on the west side of Del Rey Island; the large drainage area of this island may lead to unfavorable conditions of salinity and sedimentation along its western shores. An explanation for the scarcity of reefs at Pedro Gonzáles, the largest island that we studied in detail, is not readily apparent.

The maximum annual growth of *Pocillopora*, adjusting for seasonal differences, ranged from 32–52 mm yr⁻¹. This exceeds the mean growth reported for species of *Pocillopora* in Hawaii (Edmondson 1929) and Samoa (Mayor 1924), 15 and 24 mm yr⁻¹, respectively. Although part of this discrepancy is attributable to differences in computation—slow growing and even dead portions of colonies (Mayor) were included in the calculations of the earlier workers—our values are still comparable to those in other tropical areas.

The minimum critical temperatures that we found to have a debilitating effect on corals, in the range 20–21°C, are close to the lower limits set by Vaughan (1919) and agree with the results of Clausen (1971). However, we found the highest growth rates around 29°C, in contrast to the optimum skeletogenesis at 25°C observed by Clausen for *P. damicornis* under laboratory conditions.

The greater variations in temperature

found on reefs than on nonreefal shores show the effect of a reef structure in modifying its own hydrographic surroundings and raise the question of how coral growth is affected by a widely fluctuating thermal regimen. Further, Fig. 6 shows that the low ambient temperatures of the upwelling period were not observed on reefs at neap tide.

A biotic factor affecting coral growth was the activity of corallivores. The removal of known coral-eating crustaceans and molluscs and the placement of corals a short distance away from the main reef formation reduced this source of error. However, fishes were not excluded and the branch tips of some colonies were cropped by them. This was most noticeable on shores with sparse coral growth. Such losses should be evaluated and included in calculations of gross coral growth.

In addition to the possible application of our findings to other coastal areas experiencing upwelling, it is likely that upwelling in equatorial waters far removed from the coast may affect open ocean reefs. For example, in the Pacific, zones of divergences occur along the Equator and northward of the Equatorial Countercurrent; these cause upwelling in the Galápagos Islands area west to about the 180° meridian (Smith 1968). Ranson (1952) and Ladd (1971) suggested that upwelling in this region may be responsible for the relatively poor development of coral reefs in the Marquesas Islands.

A related problem is the influence of thermal conditions on the vertical distribution of corals and on reef framework construction. The movement of the thermocline across deep coral communities may have an important effect. The assumed invariant nature of this parameter at the lower limits of reef formation (Stoddart 1969) still needs study.

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Submitted: 27 September 1972

Accepted: 16 January 1973