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A dead Central American coral reef tract: Possible link with the Little Ice Age

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ABSTRACT

Radiocarbon analyses, stable isotopic measurements and extensive field observations were made of coral reefs off the Pacific coast of Costa Rica and Panama. These analyses showed that live coral reefs in the Gulf of Papagayo, Costa Rica, were severely depleted in number, size and variety of species, compared to reefs in the major upwelling zone of the Gulf of Panama. Coral growth in the Gulf of Papagayo consisted mainly of dead reefs that died from 150–300 years B.P. The $\delta^{18}O$ records revealed that most of the dead reefs were exposed to relatively cool water immediately preceding death. We propose that during the latter part of the Little Ice Age there was probably an equatorward shift of the Northern Trade Wind system, which caused an intensification of upwelling at lower latitudes. This increased upwelling was the likely cause of the demise of coral reefs in the Gulf of Papagayo.

1. Introduction

The adverse effects of cool water (15–20°C) on reef-building corals are well known (Wells, 1957; Stoddart, 1969; Clausen, 1971; Jokiel and Coles, 1977). Studies conducted over the past two decades have demonstrated the critical influence of upwelling (with attendant low temperatures and high nutrient input) in limiting coral reef development in a variety of areas (e.g., in Venezuela: Antonius, 1980; in Panama: Glynn and Stewart, 1973; Dana, 1975; Birkeland, 1977; in the Galapagos: Glynn and Wellington, 1983). In Panama, coral reef formations are present in the seasonally upwelling Gulf of Panama, but are notably limited in development compared with reefs in the nonupwelling Gulf of Chiriqui (Glynn *et al.*, 1972; Glynn and Stewart, 1973; Glynn, 1977). The chief motivation behind this study was to test the hypothesis that coral reefs in Costa Rica are well developed on the SE Pacific coast, a nonupwelling area in the lee of a high mountain range, and reef development is weak on the NW Pacific coast, an upwelling area bordering the Costa Rican–Nicaraguan isthmian gap (Fig. 1).

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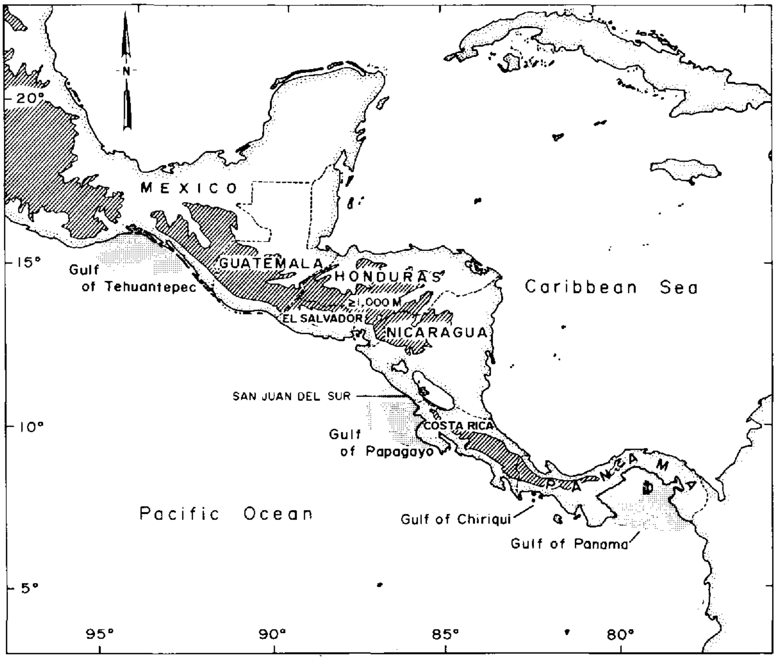

Figure 1. Location of major upwelling centers (stippling) on the Pacific coast of Middle America in relation to the central mountain ranges (cross hatching).

Several lines of evidence are presented in this study which indicate that the seasonally upwelling Papagayo area in NW Costa Rica is today less conducive to reef development than (a) the nonupwelling waters of SE Costa Rica and the Gulf of Chiriqui, Panama, and (b) the seasonally upwelling waters of the Gulf of Panama. Data examined here include reef size (area and thickness), live coral cover and diversity, maximum depth of framework construction, coral colony size distributions, growth rates, intensity of bioerosion, frequency of growth discontinuities, carbon-14 dating and stable isotope analyses of coral skeletons. Because the longevity of certain corals can also be influenced by predation (Connell, 1973), coral colony size was also examined in nonupwelling coral communities with and without the corallivorous sea star *Acanthaster*.

Results indicate that all of the coral reefs observed along the NW Costa Rican coast were dead. Radiocarbon measurements suggest that these coral reefs died between 1650–1800 A.D. Oxygen isotope analyses indicate that the corals composing the uppermost, accreting surfaces of the dead reefs were thermally stressed when they died. We propose that reef death in the Papagayo area resulted either from an intensification or an increase in duration of seasonal upwelling, which in turn was brought on by the migration of strong winds toward the equator during the height of the Little Ice Age (1675–1800 A.D.)

Several biological responses to Neoglaciation have been recognized in the northern hemisphere, e.g., shifts in tree line elevations and variations in tree ring records (LaMarche, 1972, 1974), changes in North Sea fisheries yields (Lamb, 1979), widespread crop failures (Kington, 1980), and human starvation (Lindgren and Neumann, 1981). Dunbar (1981) has inferred an increase in coastal upwelling along the southern California coast during the Little Ice Age from oxygen isotopic analysis of foraminifera from varved sediments of the Santa Barbara Basin. If the proposed causal connection between the Little Ice Age and coral reef death in Costa Rica is correct, this will represent a high latitude disturbance with a significant impact on a tropical marine ecosystem.

2. Methods

Coral formations were initially located by means of aerial surveys from a light, fixed-wing aircraft. Nearly vertical color photographs of each reef were obtained at 900 m to 1,200 m elevations, employing a polaroid filter to reduce glare. Overflights were made during periods of extreme low water when the shallow reefs were clearly visible (Glynn and Stewart, 1973). Coral formations along the NW Costa Rican (Guanacaste) coast were surveyed by aircraft in April 1973; coral formations present from the Gulf of Nicoya south to the Panama border were surveyed in February and April 1975. Of the 44 presently known coral formations on the Pacific Costa Rican coast, PWG observed 21 firsthand (numbers 2, 3, 8–15, 17, 35–44, Fig. 2) by surface and scuba diving during 18–23 April 1978 (Golfito and Guanacaste coast) and 12–16 December 1978 (Guanacaste coast). The general features of 23 of these formations were inferred from aerial reconnaissance and photography. Coral formations were classified as coral reefs or coral communities *sensu* Wainwright (1965).

Coral cover and diversity were estimated from chain transect sampling (Porter, 1972a,b). Each chain transect, 10 m in length and with 73 links per m, was laid out so as to conform with the bottom irregularities. Points in contact with each link were identified and numbered. Sampling sites were located by dropping the chain spool into a particular zone from the surface and then paying out the chain parallel to the depth contour.

Live massive corals, *Pavona gigantea* Verrill and *Porites lobata* Dana, were relatively uncommon between Samara and Cabo Santa Elena in the Papagayo area and were sampled by swimming over large areas (up to 200 and 300 m along the shore) until sufficient numbers were found (~20 colonies per 100 m^2). The heights and maximum diameters of all of these colonies were measured. All *Pavona* and *Porites* colonies first encountered in established study areas in the Pearl Islands (Contadora Island, 8°37′45″N, 79°02′25″W), and in the Contreras (7°48′40″N, 81°45′40″W) and Secas (7°57′50″N, 82°01′40″W) islands, Gulf of Chiriqui, were measured until adequate samples were obtained.

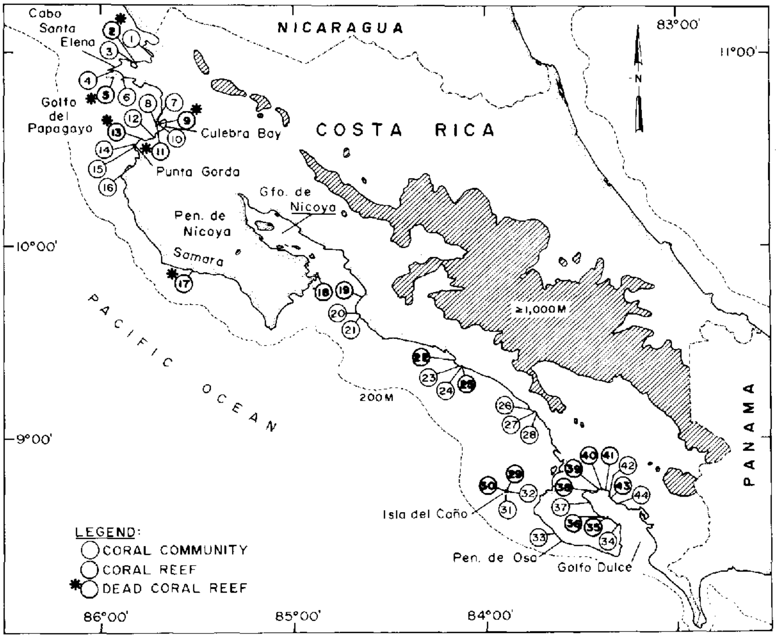

Figure 2. Distribution of coral communities and live and dead coral reefs along Pacific shores of Costa Rica. Central mountain range ≥1,000 m elevation denoted by cross hatching.

To assess the effect of *Acanthaster planci* (Linnaeus) on the distribution and size structure of a massive coral, feeding preference tests were carried out on the Uva study reef. These involved different individual *Acanthaster* and were initiated by placing two coral species, *Pocillopora damicornis* (Linnaeus) and *Pavona gigantea*, simultaneously and in contact at opposite sides of moving or resting sea stars. In the first two sets of observations (September 1981), the portions of coral colonies offered were broken from larger colonies and then transported about 200 m in large tubs to where the sea stars occurred naturally. Care was taken to include the normal complement of obligate crustacean symbionts in the *Pocillopora* colonies. The amounts of live coral offered were comparable: *P. gigantea* fragments were 6 to 8 cm wide and 10 to 15 cm long; *P. damicornis* fragments were 12 to 15 cm in maximum diameter. In the third set of observations (October 1981), whole, unbroken colonies were used. A blind design was utilized in both September experiments; coral emplacement was made by an experienced observer in the October experiment. Species choice was determined by noting the coral being eaten after 2–3 hours or the following day. Corals were offered again to sea stars that had moved away during the first 2–3 hours.

Annual linear skeletal growth in *P. gigantea* was estimated from the thickness of density bands measured with calipers and rule directly on X-ray negative film

(Buddemeier, 1978). *P. gigantea* was selected for this analysis because of the distinctness of the density bands in this species. Two to three 5 mm-thick slabs were cut along the main growth axis of each coral and these were X-rayed in cardboard holders (0.7 sec., 46 KVP, 200 ma) with a GE 600 three-phase generator unit. Medial colony growth was determined by measuring about 10 band couplets per colony although the number of measurements varied from about 5 to 25 depending on the size of the slab and condition of the skeleton. Median coral growth for particular sites was determined from the median colony measurements. Growth discontinuities were inferred from continuous horizontal hiatuses, internal corrosion surfaces or laminae of crustose coralline algae that were visible in the X-ray negatives. Numbers of bore holes were also enumerated from X-rays; a bore hole was counted if it was ≥ 1 mm in diameter and if it completely penetrated the skeletal slab.

Reef framework thickness was estimated by probing with iron pipe, as described by Glynn and Macintyre (1977), and by measuring (through surface inspection) the vertical distance between the reef crest and base bordering the talus slope. Maximum reef thickness values obtained from the probe-hole method are based on the longest sections of continuous coral framework recovered from the pipe (12.7 mm ID) probes.

Corals collected from the dead reefs for isotopic analyses were excavated from the reef flat by breaking and exposing 20–35 cm fresh vertical sections of the reef frame. All of the reef flats examined were in normal growth position at about 30 cm below the MLWS datum. The coral samples were air dried initially, then cleaned by scraping to assure complete removal of calcareous boring and encrusting organisms, as well as calcareous cement, and then oven-dried at 100°C to a constant weight. The corals were soaked in a solution of sodium hypochlorite (5% for the radiocarbon analysis and 0.2% for the stable isotopic analysis) for 24 hours, and then rinsed and dried.

Radiocarbon was measured using gas proportional counting techniques at both the Woods Hole Oceanographic Institution and the University of California, San Diego by one of the authors (EMD). Each sample was converted to carbon dioxide by acid digestion, and then to acetylene gas, via lithium carbide. The gas was counted for two days each in two of four quartz gas proportional beta counters (volumes of 0.75, 1.5, 2.0 and 2.2 liters). The $\delta^{13}C$ value was determined for reburned acetylene and the net count rate for each sample was corrected for isotope fractionation to a standard $\delta^{13}C$ value of $-25.0‰$ (PDB). Known-aged samples were corrected for decay since the time of formation to A.D. 1950. The results are reported in terms of $\Delta^{14}C$ (Broecker and Olson, 1961) which is the per mil (‰) deviation from the activity of nineteenth century wood. The activities were converted to radiocarbon ages, using the Libby half-life for radiocarbon of 5568 years, and reported as years B.P. (before A.D. 1950). The error reported is ± one sigma based on counting statistics. The ages since death of the individual coral samples were determined by subtracting a correction for the apparent radiocarbon age with respect to atmospheric CO_2 of the dissolved inorganic carbon

(DIC) in the surface ocean water in the Costa Rican region. This correction is determined from the average of several radiocarbon analyses of a pre-A.D. 1931 *Gardineroseris planulata* (Dana) from Panama.

Terminal branches from pocilloporid corals, dominantly *Pocillopora damicornis*, were selected for stable isotopic analysis and ultrasonically cleaned in distilled water. The branches were then cut in half along their axes of growth with a low-speed stainless steel Dremel-tool$^{(R)}$ saw. In cross section, branch lengths varied from 60 to 175 mm. Using dental drill bits, small ($<$1 mm in diameter) holes were drilled every 2 to 3 mm along recognizable trends of polyp growth. Care was taken to avoid parts of the coral skeleton that had been altered by boring organisms. As these corals grow radially as well as longitudinally, no samples were drilled near the surface of the branches. The powder resulting from drilling was collected and about 2 mg retained for roasting and isotopic analysis. X-ray diffraction of these samples indicated that the fossil corals were still 100% aragonite and that calcite did not form during low-speed cutting and drilling. After drilling, pieces of the branch cross-sections were polished and mounted for Scanning Electron Microscopy (SEM) to determine the magnitude of any overgrowth by inorganically precipitating aragonite in the interiors of the branches.

The samples were roasted in a vacuum at 250°C for one hour to remove organic matter. The results of a calibration study in the Gulf of Panama (Dunbar and Wellington, 1981), and treatment experiments with both recent and fossil specimens, indicate that treatment with sodium hypochlorite, if followed by vacuum roasting, has no effect on isotopic composition. The roasted powder was converted to CO_2 by reaction in 100% phosphoric acid at 50°C. Isotope analyses were made with an "on line" V.G. Micromass 602C mass spectrometer. Results are reported in the standard δ (‰) notation relative to the Chicago PDB standard. Precision for isotopic measurement of these samples was better than 0.10‰ for both $\delta^{18}O$ and $\delta^{13}C$.

3. Study areas

a. Upwelling and nonupwelling environments. Three major upwelling centers have been identified on the Pacific coast of Middle America, namely the gulfs of Tehuantepec, Papagayo, and Panama (Schaefer *et al.*, 1958; Roden, 1961; Renner, 1963; Hubbs and Roden, 1964; Blackburn, 1966; Forsbergh, 1969). The seasonal movements of winds from the Gulf of Mexico and Caribbean Sea (mainly from November to April) across the mountain gaps of southern Mexico, southern Nicaragua/northern Costa Rica and central Panama (Fig. 1), affect the Pacific Ocean surface by causing an upward entrainment of subsurface waters and mixing. Such winds are especially strong when a continental anticyclone extends far southward into the Gulf of Mexico or when the Azores high is located far to the southwest (Hubbs and Roden, 1964). During these times, the Gulf of Panama, which borders the central isthmian mountain gap, experiences upwelling, whereas the Gulf of Chiriqui, in the lee of the Talamanca and Central mountain ranges, remains a nonupwelling environment (Glynn *et al.*, 1972; Glynn, 1977; Dana, 1975). Some of the differences between these environments, with regard to coral reefs in the nonupwelling Gulf of Chiriqui, are: (a) a greater number of coral reefs per unit area; (b) larger reef dimensions (both horizontally and vertically); (c) greater age of reefs; (d) higher rates of coral growth; and (e) a greater number of reef-building and reef-associated species (Glynn *et al.*, 1972; Rosenblatt *et al.*, 1972; Glynn, 1977; Glynn and Macintyre, 1977; Dana, 1975).

The SE sector of the Pacific coast of Costa Rica (including Golfo Dulce and the Osa Peninsula) is also in the lee of the Talamanca and Central mountains (Fig. 2), and thus its waters are not subject to upwelling. On the other hand, high mountains are absent from southern Nicaragua and NW Costa Rica (including San Juan del Sur, Cabo Santa Elena, and the Gulf of Papagayo) which allows seasonal winds (derived from the NE Caribbean trade winds) to induce a strong upwelling system in the Gulf of Papagayo and surrounding areas.

b. Strength and duration of upwelling in Costa Rica and Panama. Sea surface temperature (SST) data from the upwelling centers in Costa Rica and Panama (summarized by Hubbs and Roden, 1964) suggest that upwelling today is more intense and prolonged in Costa Rica than in Panama. Mean minimum temperatures recorded in San Juan del Sur, Nicaragua (about 80 km NW on Culebra Bay) were below 20°C (18.2°–19.6°C) for 3 months (January–March). Mean minimum temperatures recorded over the same period at Naos Island, Panama, did not fall below 21.6°C. Moreover, the mean minimum SSTs in Nicaragua were lower than in Panama for every month of the year, ranging from 0.9°C below the Panama SST in April to 5.3°C below the Panama SST in May. The length of the season during which the mean minimum SST was equal to or below 22°C in Costa Rica extended from December to June (6 months), whereas in Panama it lasted only from February to May (3 months).

The most reliable and extensive daily SST data available for the upwelling centers in Nicaragua/Costa Rica and Panama (National Ocean Survey, 1970) also indicate a more pronounced upwelling regime in the high latitude areas (Fig. 3). On four occasions in 1950 and 1951, SSTs in Nicaragua fell below 18°C, temperatures that have been found to retard coral growth in Panama (Glynn and Stewart, 1973). Unfortunately, no dry season sea temperature data are available from the dead coral reef areas in NW Costa Rica. The two plots of minimum monthly SSTs (showing a slight warming trend in Nicaragua) are significantly different ($p \ll 0.001$, Wilcoxon matched-pairs signed-ranks test) and support the local differences in mean minimum temperatures noted above.

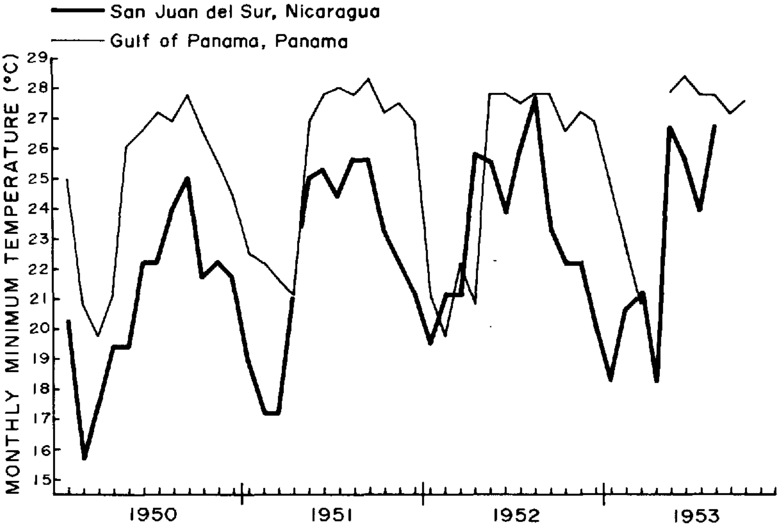

Figure 3. Monthly minimum sea surface temperatures recorded in the upwelling areas in the Gulf of Papagayo (San Juan del Sur), Costa Rica, and the Gulf of Panama, Panama (1950–1953) (National Ocean Survey, 1970).

4. Results

a. Nature and distribution of coral formations. The coral communities and coral reefs observed in Costa Rica were relatively small (a few hectares at most in planar view), present at shallow depths (5–15 m), and contained few corals (3–9 species), a situation similar to that in Panama (Glynn *et al.*, 1972; Glynn and Macintyre, 1977; Porter, 1972a; Dana, 1975). The chief reef-building corals in Costa Rica were *Pocillopora damicornis, Pocillopora elegans* Dana, and *Porites lobata.* Five dead coral reefs examined directly in the Papagayo area and at Samara (2, 9, 11, 13, and 17, Fig. 2; Fig. 4A) were built dominantly by pocilloporid corals with *P. damicornis* the principal species. A live algal turf and live crustose coralline algae coated the dead coral framework. Massive colonies of *P. lobata* were the principal framebuilding corals present in the live reefs (35, 36, 38–41, Fig. 2) examined in Golfo Dulce. Hermatypic scleractinian species present as minor members of coral reefs, or present in coral communities, were the following: *Pavona clavus* Dana, *Pavona gigantea, Pavona varians* Verrill, *Pocillopora eydouxi* Milne Edwards and Haime, *Pocillopora meandrina* Dana, and *Psammocora* (*Stephanaria*) *stellata* Verrill.

Coral communities and coral reefs were present along most sectors of the Costa Rican Pacific coast from the Cabo Santa Elena area, bordering Nicaragua, southeast to the Golfo Dulce embayment (Fig. 2). Structural reef development was confined largely to sites protected from direct wave assault (Dana, 1975; Glynn and Macintyre, 1977).

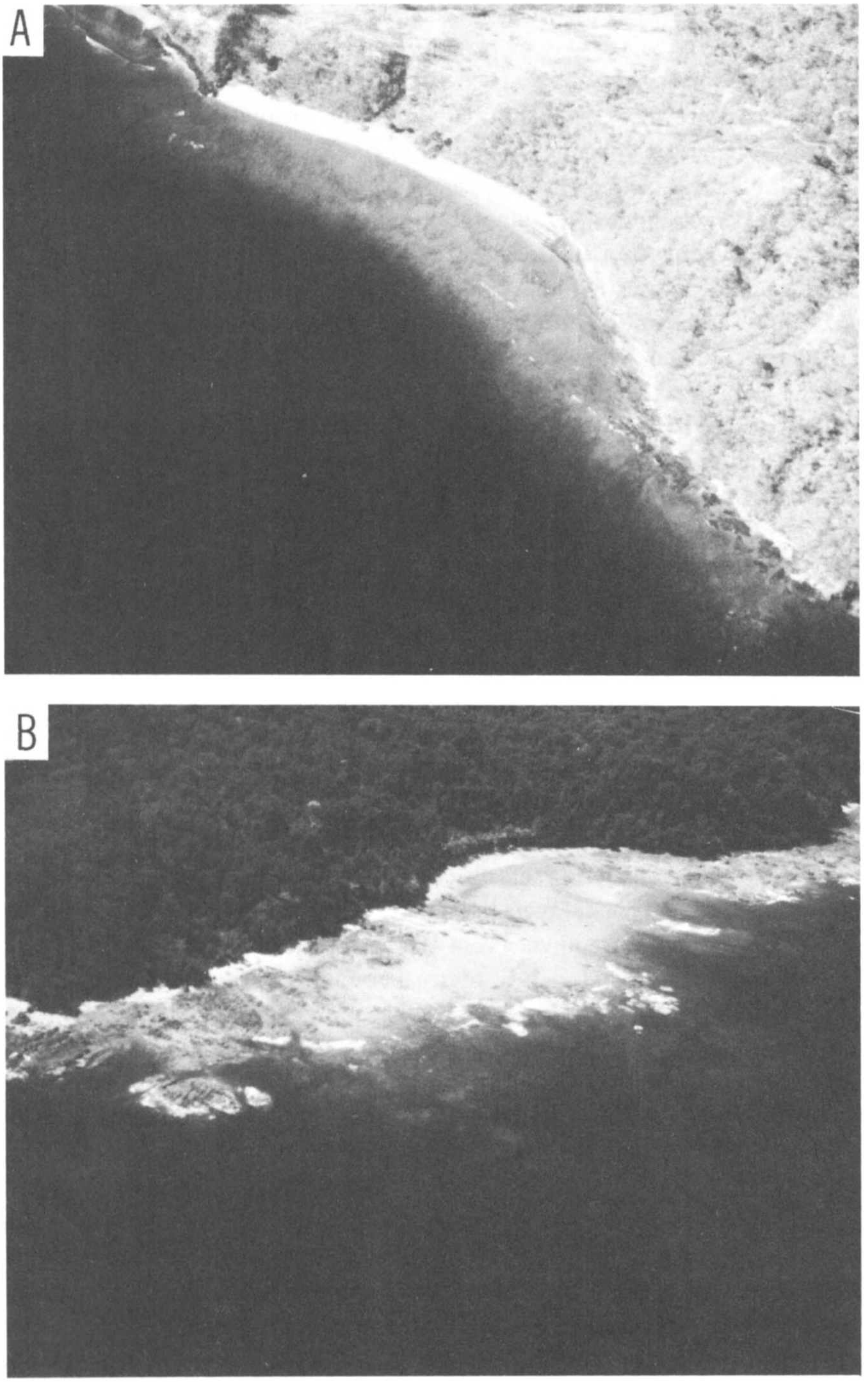

Figure 4. Oblique aerial views of (a) the dead Punta Gorda fringing reef (17 April 1973) and (b) a portion of the living, north shore Isla del Cano fringing reef (28 February 1975). Both reefs photographed at low water and at approximately 1,000 m elevation.

Direct inspection with scuba showed that five of the six coral reefs found in the Papagayo area were dead. The subtidal formation located between two of the Bat Islands was observed only during the aerial reconnaissance and is assumed to be a dead coral reef similar to the others in this area. Typically the pocilloporid framework of the dead reefs was erect and largely intact, but no corals comprising the reef proper were alive. The only living corals associated with the dead reefs were small and highly dispersed colonies encrusting the old reef framework. These dead reefs appeared uniformly greyish red or dull brown during the aerial reconnaissance. Live pocilloporid coral reefs appeared golden brown from the air in Panama.

All coral formations viewed from the air from the Gulf of Nicoya to Isla del Cano (Fig. 4B) appeared to be alive. The poritid reefs in Golfo Dulce were variegated grey in appearance and proved to be alive when inspected *in situ*. Six of the seven coral reefs examined in Golfo Dulce (35, 36, 38–41, Fig. 2) were virtually monospecific and composed of *Porites lobata*. The larger of these reefs (38–41), near the Esquinas River drainage, were several hectares in planar area. The reef fronts were often steep (≥45°) and the poritid framework occasionally extended to 12–15 m depth. Colonies composing the reef crest and upper reef front (to ca. 5 m) were truncated (microatolls) or hemispherical, and colonies in deeper water (>5 m) tended to form horizontal, platelike extensions. Underhangs, recesses and caves were common in the deep forereef zone, and most corals at this depth were dead and coated with live crustose coralline algae. Small pocilloporid formations (42–44, Fig. 2) were also observed in Golfo Dulce. The corals on one of these (43), a small patch reef, were mostly dead. According to local divers this reef was alive in 1976; the reason for its death is unknown.

In summary, all pocilloporid reefs observed *in situ* in the Papagayo area were dead, and all pocilloporid and poritid reefs but one (a small pocilloporid patch reef) observed *in situ* in Golfo Dulce were alive. From the aerial surveys and first-hand reports of workers in this area (D. Dexter, J. E. McCosker and R. Richmond, pers. comm.), it is highly probable that few, if any, dead reefs are present from Golfo de Nicoya to the Peninsula de Osa.

b. Reef framework thickness. Probe holes were excavated on three dead pocilloporid reefs in the Papagayo area (Table 1). These revealed mean reef framework thicknesses ranging from 1.0 to 2.2 m. Surface inspection indicated that the dead Samara pocilloporid reef was about 2 m in thickness. The only reef examined outside of the upwelling Papagayo area, in terms of thickness, was the live Mogos poritid reef (41, Fig. 2) in Golfo Dulce. This reef had an apparent mean-maximum thickness of 10 m, and it is probable that reefs 38–40 (Fig. 2) had similar maximum vertical buildups.

Five pocilloporid reefs probed in the Gulf of Panama disclosed mean-maximum thicknesses ranging from 3.0 to 4.8 m (Glynn and Macintyre, 1977); one of these cored reefs (Saboga Island) showed a maximum vertical buildup of 5.6 m (Table 1). A statistical comparison of median reef thicknesses (probe hole data) in the upwelling areas of Papagayo ($\mathrm{Md} = 1.8$, $n = 14$) and Panama ($\mathrm{Md} = 4.0$, $n = 15$), shows that

Table 1. Coral reef framework thicknesses (M), Costa Rica and Panama compared.

Locality	Probe holes	Core holes	Surf. inspec.	Mean
	COSTA RICA			
Papagayo reef tract (upwelling region)				
Santa Elena Bay	1.8 2.1 2.4 2.4			2.2
Culebra Bay	0.6 1.8 3.0			1.8
Point Gorda	0.6 0.6 1.2 1.2 1.5			1.0
Samara			2.0 2.5	2
Golfito (nonupwelling region)				
Los Mogos *Porites* reef			9 11	10
	PANAMA			
Gulf of Panama (upwelling region)				
Pedro Gonzalez Is.	3.4 3.7 4.0 4.3			3.8
Contadora Is.	1.8 2.1 3.4 4.6			3.0
Saboga Is.	3.0 4.0 5.2 5.5	5.6		4.7
Canas Is.	4.3 4.9 4.9			4.7
Iguana Is.	3.4 4.9 6.1			4.8
Gulf of Chiriqui (nonupwelling region)				
Canales de Tierra Is.	5.8 7.9 10.4			8.0
Ensenada de Muertos	7.6 7.9			7.8
Coiba Is.	4.3 7.6 9.4			7.1
Secas study reef	13.4	10.8 12.0		12.1
Cavada Is.	8.2 9.2			8.7
Uva Is.		2.4 4.2 6.2 11.0		6.0

framework accumulation was significantly greater in Panama than in Costa Rica ($P < 0.001$, Mann-Whitney U-test). The relatively high values from the Iguana Island reef (3.4–6.1 m), which is located almost outside of the Gulf of Panama, were excluded from this analysis.

Probing and coring in the Gulf of Chiriqui revealed that live pocilloporid reefs in Panama had a median framework thickness of 7.9 m ($n = 17$); this is comparable to the live poritid reefs in Golfo Dulce (Table 1). The extent of surface coverage (inferred from aerial reconnaissance) of the presumed live pocilloporid reefs at Cano Island, and along the outer mainland coast between the Osa Peninsula and the Gulf of Nicoya, was also comparable to reefs present in the Gulf of Chiriqui.

c. Coral cover, diversity and reef framework depths. Live coral cover veneering the three dead pocilloporid reefs sampled in the Papagayo area was appreciably lower than on comparable living pocilloporid reefs in Panama (Table 2). The highest value

Table 2. Live coral cover and coral species present on dead reefs in Costa Rica and on living reefs in Panama.

Locality	Live coral cover (%)	Coral species[1]	Depth (m)	Reef zone
		COSTA RICA		
Punta Gorda	0[2]	O	4	Seaward base
reef no. 13	0	O	3	Reef flat
12 December 1978	0.1	A	2	Reef flat
	2.7	A	4	Seaward base
Culebra Bay	0.7	A	2	Reef flat
reef no. 11	1.2	A	2	Reef flat
13 December 1978	0.1	A	3	Seaward base
Santa Elena Bay	1.1	A	3	Seaward slope
reef no. 2	0	O	4	Seaward base
15 December 1978	0	O	2	Reef flat
		PANAMA		
Uva Island[3]	7.5	BC	5	Seaward base
Gulf of Chiriqui	29.0	BCDA	4	Seaward base
	12.4	BCDEF[4]	1	Reef flat
	42.3		2	Reef flat
Secas study reef[5]	18.5	CAD	3	Reef flat
Gulf of Chiriqui	13.1	CA	3	Reef flat
	11.3	CD	3	Reef flat
	77.4	C	2	Reef crest
	35.9	CA	4	Seaward slope
	71.0	C	5	Seaward slope
	66.9	C	6	Seaward slope
	13.0	BCGH	8	Seaward base
	6.9	BCGFAHI	11	Seaward base
Saboga Island[6]	10.9	C	1	Inner reef flat
Gulf of Panama	27.3	CDA	3	Outer reef flat
Md	10.2	CAD	1–3	Inner & outer reef flat

1. A, *Psammocora stellata;* B, *Pocillopora elegans;* C, *Pocillopora damicornis;* D, *Porites panamensis;* E, *Pavona gigantea;* F, *Pavona varians;* G, *Gardineroseris planulata;* H, *Millepora intricata;* I, *Pavona clavus.* Listed in rank order of abundance.
2. Predominantly dead pocilloporid reef frame.
3. Seaward base transects were obtained on 13 January 1980; reef flat transects are from Porter (1972c).
4. Coral species probably present although not listed in Porter (1972a); not necessarily in rank order of abundance.
5. Sampled 17 June 1974; see Glynn (1976) Figure 4.
6. All transects obtained after low water tidal exposures with mortality (Glynn, 1976); Md signifies median values for 8 transects.

observed in Costa Rica, along the seaward base of the Punta Gorda fringing reef, was only about 3% live coral. In the Gulf of Chiriqui, Panama, coral cover ranged from 7% in the seaward base zone to 77% on the reef crest. Live coral cover was also relatively high in the Gulf of Panama, ranging from 11% to 27% in inner and outer reef flat zones respectively, even after significant mortality following extreme low water exposures (Table 2).

Although *Psammocora stellata* was the only live coral found in the Costa Rican transects (Table 2), other live coral species were present but not encountered in the sampling. One to seven live coral species (including *Millepora intricata* Milne Edwards, a hermatypic hydrocoral) were sampled per transect in Panama (Table 2). Pocilloporid corals were the predominant species in Panamanian reefs; *Psammocora stellata* was usually a minor species and did not rank first in abundance in any of the 21 transects examined.

The median depths of reef framework in the seaward base zone in Costa Rica (Md = 4 m, $n = 4$) and Panama (Md = 6.5 m, $n = 4$) were significantly different ($P < 0.05$, Mann-Whitney U-test); coral framework was present only at relatively shallow depths on dead Costa Rican reefs.

d. Coral colony sizes and Acanthaster feeding preferences. The size structure of populations of live massive corals (two species) was assessed in the Papagayo area and in upwelling (Gulf of Panama) and nonupwelling (Gulf of Chiriqui) areas in Panama. *Porites lobata* colonies in the Gulf of Papagayo were small; the median linear growth axis was only 10 cm ($n = 24$ colonies), compared with median growth axes of 47 cm ($n = 34$) and 101 cm ($n = 41$) respectively for this species in the Gulfs of Panama and Chiriqui (Fig. 5). A second population of *P. lobata* was sampled at Uva Island (where *Acanthaster planci*, a corallivore, is present), Gulf of Chiriqui; this population had a median linear growth axis of 28 cm ($n = 44$). Colony size differed significantly at the four localities ($P \ll 0.001$, Kruskal-Wallis test). Dunn's multiple-comparison procedure (DMCP) indicates that coral colony size differed significantly ($\alpha = 0.20$) between all sites except for populations in the Gulf of Panama and at Uva Island (Gulf of Chiriqui).

Population size structures of *Pavona gigantea* (Fig. 6) also showed pronounced differences between sites ($P \ll 0.001$, Kruskal-Wallis test). Corals sampled in the Gulf of Papagayo were significantly smaller (Md = 16 cm, $n = 42$) than in the Gulf of Panama (Md = 65 cm, $n = 28$) or in the Gulf of Chiriqui (Md = 44 cm, $n = 52$) (DMCP, $\alpha = 0.20$), at a site from which *Acanthaster* is presumably absent. The only corals that were similar in size to those sampled in the Gulf of Papagayo (Md = 16 cm) were those in the Gulf of Chiriqui (Md = 14 cm, $n = 35$) where *Acanthaster* has been present since at least 1970 (Glynn, 1974).

Prey-choice field tests indicated how predation can affect coral longevity. In 2 of 3 sets of observations, *Pavona gigantea* was preferred over *Pocillopora damicornis*

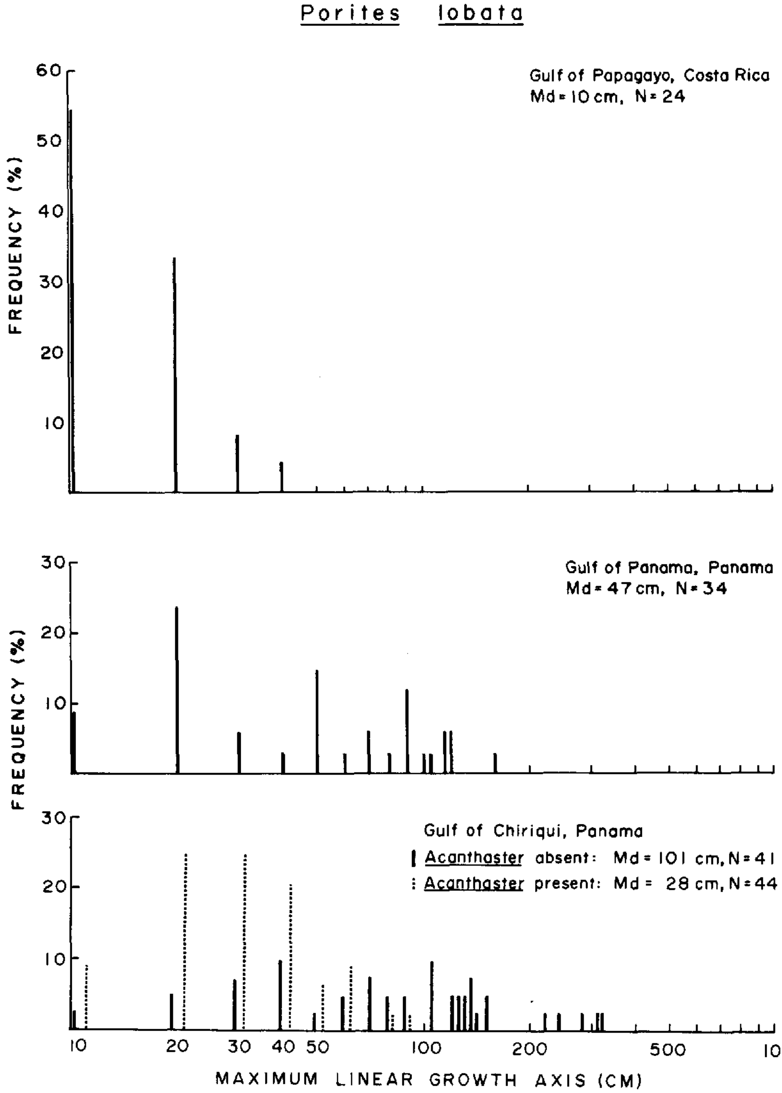

Figure 5. Sizes of colonies of *Porites lobata* from population samples in the Gulf of Papagayo (12 December 1978), the Gulf of Panama (7 January 1979) and the Gulf of Chiriqui (5 February 1979). N refers to number of coral colonies sampled.

($P < 0.02$, binomial probability test) (Table 3). No species preference was indicated in observations from the Secas Islands (Table 3, 23–24 September). However, twice when *Acanthaster* attempted to mount and feed on *P. gigantea,* something (boring sponges?) associated with the broken skeletal surface irritated the sea stars, producing rapid arm withdrawal and causing them to move off and to feed on *P. damicornis.* On three occasions, crab (*Trapezia*) symbionts of *Pocillopora* repulsed sea stars that

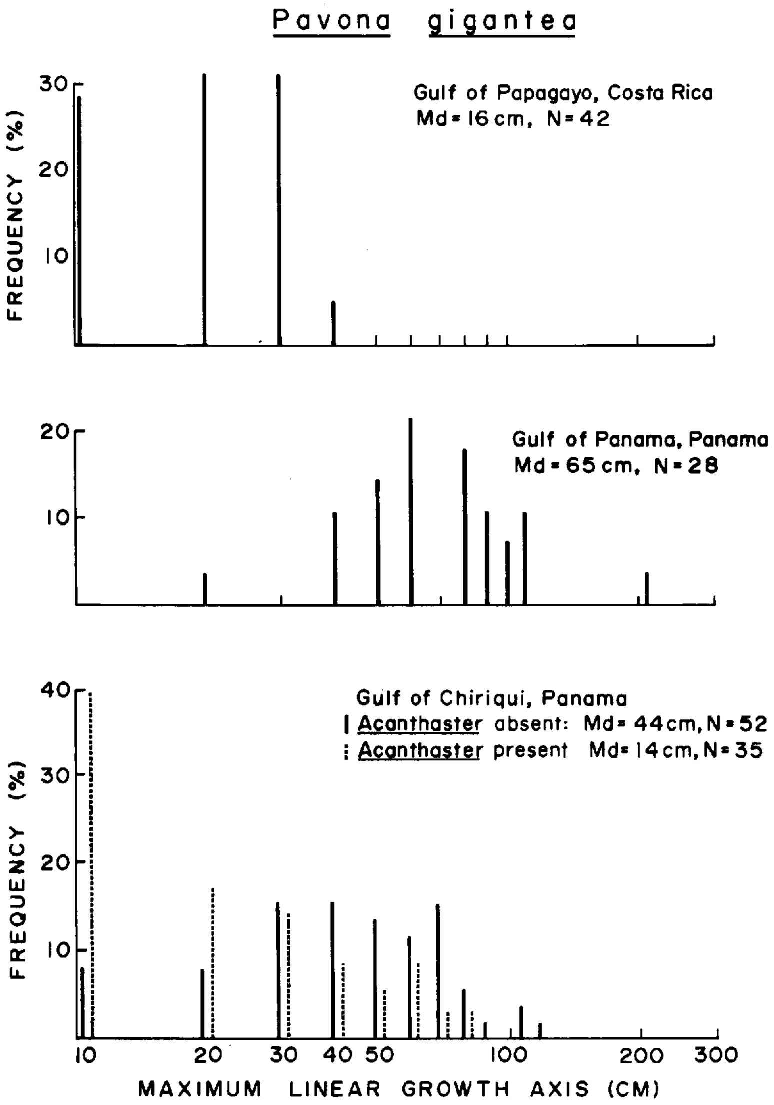

Figure 6. Sizes of colonies of *Pavona gigantea* from populations sampled in the Gulf of Papagayo at Punta Gorda, Playa de Ocotal, Cabo Santa Elena (12–14 December 1978), the Gulf of Panama at Contadora Island, Pearl Islands (13 December 1980), and the Gulf of Chiriqui (12–14 December 1980). Sampling in Chiriqui was performed at Uva Island and a reef in the Secas Islands where *Acanthaster* is present, and on the south, exposed coast of a Secas island without *Acanthaster*. N refers to number of coral colonies sampled.

Table 3. Prey choice by *Acanthaster* offered two coral species simultaneously, Gulf of Chiriqui, Panama.

Locality	Number corals eaten *Pavona gigantea*	 *Pocillopora damicornis*	Binomial probability p = 0.5	Number failures to feed	Total number trials
Uva Island, Uva reef and adjacent shores, 21–22 September 1981[1]	8	1	0.018	6	15
Secas Islands, Pampano reef 23–24 September 1981[1]	4	4	0.269	6	14
Uva Island, Uva reef and adjacent shores, 7–8 October 1981[2]	9	1[3]	0.018	12	22
Totals	21	6	0.002[4]	24	51

1. Blind design; coral species offered to sea stars by naive observer MD.
2. Whole, unbroken colonies offered to sea stars by author PWG.
3. *P. gigantea* eaten first and then about 50% of *P. damicornis* colony killed.
4. Binomial probability for pooled results ($n = 27$).

assumed a feeding posture. The pooled results showed an overall preference by *Acanthaster* for *P. gigantea* ($P \sim 0.002$, $n = 27$), very similar to earlier laboratory results ($P \sim 0.006$, $n = 17$) (Glynn, 1976).

e. Coral growth, bioerosion and skeletal discontinuities. Analysis of annual linear growth rates in living colonies of *Pavona gigantea*, based on skeletal density banding, indicates that coral growth differed significantly between sites ($P < 0.001$, Kruskal-Wallis test). Median annual skeletal growth in the Gulf of Papagayo was only 7.0 mm/yr, whereas in Panama medial growth ranged from 9.0 to 9.9 mm/yr at three sites (Fig. 7). Linear skeletal growth was significantly lower in the Gulf of Papagayo than at the three sites sampled in Panama ($\alpha = 0.20$, DMCP); the three Panama sites did not differ significantly among themselves.

Colonies of *P. gigantea* (the 5-mm-thick slabs used in the growth analysis above) were also examined for (a) intensity of bioerosion, and (b) frequency of discontinuities and/or hiatuses along skeletal growth axes. The major bioeroders at all sites were, in order of decreasing effect (judged from the size and abundance of bore holes), lithophagine gastropods, hapalocarcinid crabs, clionid sponges, and worms (chiefly polychaetous annelids).

Bore holes were most abundant in coral samples in the Papagayo area with a median incidence of 7 holes per 100 cm^2 (Table 4). Bore hole frequencies in corals form the Uva/Cavada Islands area and from the Secas-SW site (both in the Gulf of Chiriqui) were 4 and 3 per 100 cm^2, respectively (Table 4). Boring activity was not equal at the

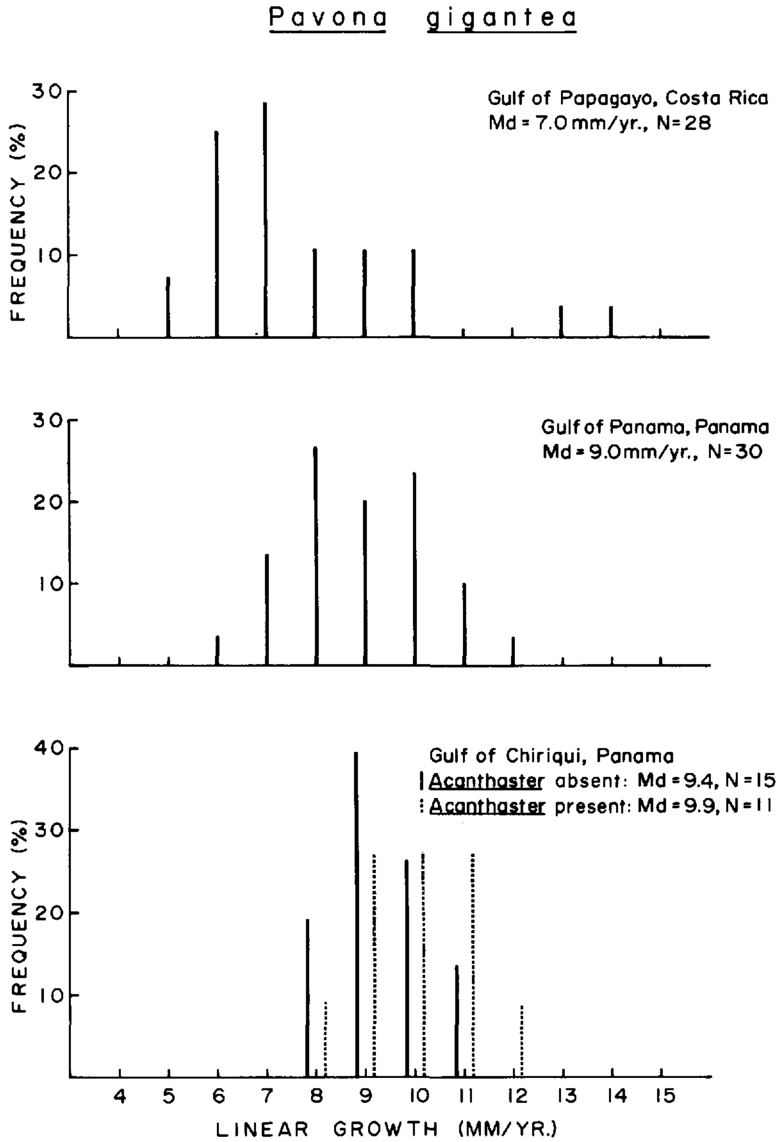

Figure 7. Annual linear growth rates (mm/yr) of *Pavona gigantea* sampled in Costa Rica and Panama. See Figure 6 for sampling information for the gulfs of Papagayo and Panama; Chiriqui collections were made at Cavada Island (*Acanthaster* present), and Secas-W (*Acanthaster* absent), 20 July 1981. N refers to number of coral colonies sampled.

Table 4. Numbers of bore holes (per 100 cm^2) in skeletal slabs of *Pavona gigantea* at four localities.

	Papagayo area	Pearl Islands	Uva/Cavada Islands	Secas SW
Median	7	6.5	4	3
DMCP[1]	———	———		
		———	———	
			———	———
.95 conf. lim.[2]	6–10	5–9	2–7	1–8
Range	0–38	1–28	0–15	0–17
Number colonies sampled	28	30	20	15

1. Dunn's multiple comparisons procedure ($\alpha = 0.20$); lines connect median values that were not significantly different.
2. Confidence limits of median calculated as $K = 0.5 (n + 1) - (n)^{1/2}$ of the range, where K is the number of units from each end of the distribution toward the median.

four sites ($P < 0.01$, Kruskal-Wallis test). The Dunn's multiple-comparison procedure indicates that bioerosion was equally high in NW Costa Rica and the Gulf of Panama, and that corals in the Gulf of Chiriqui had significantly lower levels of skeletal excavation than in NW Costa Rica (Table 4).

The Fisher exact test indicates that the incidence of skeletal discontinuities was significantly higher ($P < 0.0007$) in the Papagayo area than in Panama (data from the three Panama localities were pooled, Table 5). At least one interruption in skeletal growth (one colony had two interruptions) was observed in 36% of the corals examined from NW Costa Rica; in Panama the frequency of skeletal discontinuities ranged from 3% in the Pearl Islands to 10% in the Uva/Cavada areas (Table 5).

f. Isotope analyses

Radiocarbon dating. Samples of dead coral reefs from four localities in the Gulf of Papagayo and Samara, Costa Rica were radiocarbon dated (Table 6). Three samples that contained visible quantities of cemented $CaCO_3$ and boring organisms were also analyzed and, as expected, the results yielded post-bomb ^{14}C dates (>A.D. 1950).

Table 5. Numbers of growth discontinuities in skeletal slabs of *Pavona gigantea* from four localities.

	Papagayo area	Pearl Islands	Uva/Cavada Islands	Secas SW
Number colonies with discontinuities	10	1	2	1
% colonies with at least 1 discontinuity	35.7	3.3	10.0	6.7
Range of number of discontinuities per colony	0–2	0–1	0–1	0–1
Number colonies sampled	28	30	20	15

These dates were eliminated from the present survey due to contamination with modern carbon.

It has been shown by numerous investigators that dissolved inorganic carbon and calcareous skeletons of living organisms in the surface ocean are depleted in radiocarbon with respect to that in the atmosphere (Bien *et al.*, 1960; Nozaki *et al.*, 1978; Druffel and Linick, 1978). Therefore, in order to determine the time since death of the Costa Rican corals, the apparent radiocarbon age of the surface ocean must be subtracted from the radiocarbon age of the individual samples. The age of the surface seawater was determined from 4 samples of coral density bands that grew from A.D. 1923–31 in the Gulf of Chiriqui. This coral (*Gardineroseris planulata*) was collected live in 1980. Upon X-ray of a thin slab, the coral displayed well-defined high and low density band pairs, similar to the annual band pairs reported by numerous authors (Knutson *et al.*, 1972; Macintyre and Smith, 1974; Hudson *et al.*, 1976). The coral was sectioned in the manner described by Druffel (1981). Results of this calibration revealed an average $\Delta^{14}C$ value of −56 ± 3‰, which corresponds to an apparent radiocarbon age of 465 ± 25 years B.P. for surface waters in the Panama area. The apparent age for upwelling waters at the Costa Rica location is the same (±25 years) as that in the nonupwelling Panama area. This assumption is based on a study of preanthropogenic surface corals from the Galapagos Islands (1S, 90W) where Druffel (1981) found no significant difference (±3‰ or 25 years) between the radiocarbon content in upwelling waters versus that in warm, nonupwelling waters during El Nino, which have their origin in the Panama Bight and the western equatorial Pacific. In any case, the fact remains that there are no surface water locations in the temperate or tropical oceans with ^{14}C ages as low as those found for the dead Costa Rican corals. Peru Current water is the oldest, with a value of 520 years (−69‰) (Druffel and Suess, 1983).

The ages of the Costa Rican corals, corrected for an apparent 465 year age of the surface ocean, are listed in Table 6. These results show that coral framework structures

Table 6. Radiocarbon dates of dead Costa Rican coral reef framework and live coral colonies in Panama.

Locality	Material sampled	I.D. No.	$\delta^{13}C$ (‰)	$\Delta^{14}C$ (‰)	^{14}C age in years B.P.	^{14}C age minus[3] 465 years
Santa Elena Bay	*Pocillopora* frame, 25 cm below reef flat surface	S8 LJ-4818[1]	−2.6	−78 ± 4	654 ± 32	179 ± 41
Culebra Bay	*Pocillopora* frame, 35 cm below reef flat surface	C4 LJ-4714	−2.0	−76 ± 3	633 ± 32	168 ± 41

Table 6. Continued.

Locality	Material sampled	I.D. No.	$\delta^{13}C$ (‰)	$\Delta^{14}C$ (‰)	^{14}C age in years B.P.	^{14}C age minus[3] 465 years
	Pocillopora frame, do.	C5 LJ-4814	−3.2	−75 ± 3	619 ± 30	154 ± 39
	Pocillopora frame, do.	C6 LJ-4816	−2.6	−79 ± 3	664 ± 30	199 ± 39
Point Gorda	*Pocillopora* frame, 35 cm below reef flat surface	P1 LJ-4715	−2.0	−90 ± 5	757 ± 47	292 ± 53
	Pocillopora frame, do.	P2 LJ-4717	−2.0	−86 ± 3	725 ± 31	240 ± 40
	Pocillopora frame, do.	P3 LJ-4819	−2.7	−79 ± 3	661 ± 32	196 ± 41
Samara	*Pocillopora* frame, 20 cm below reef flat surface	S10 LJ-4817	−3.2	−82 ± 4	686 ± 35	221 ± 43
	Porites lobata, 1 m diam. colony comprising reef flat frame	S11 LJ-4744	−0.6	−86 ± 5	723 ± 45	258 ± 51
For calibration:						
Gulf of Chiriqui	*Gardineroseris*, coll. live, Uva Is., 1923–1924	LJ-5207	−0.8	−61 ± 4	*501 ± 35	
	Gardineroseris, coll. live, Uva Is., 1925–1926	LJ-5208	−0.8	−55 ± 4	*456 ± 35	
	Gardineroseris, coll. live, Uva Is., 1929	WH-0030[2]	−0.9	−55 ± 4	*454 ± 52	
	Gardineroseris, coll. live, Uva Is., 1930–1931	WH-0031	−2.0	−54 ± 4	*446 ± 35	

1 University of California, San Diego, La Jolla Radiocarbon Laboratory.

2 Woods Hole Oceanographic Institution Radiocarbon Laboratory.

3 465 ± 25 years subtracted from age of each ^{14}C date, to correct for age of surface ocean water bicarbonate relative to nineteenth century atmospheric CO_2.

*The depletion of ^{14}C in years B.P. of coral that grew at Uva Island during the period 1923 to 1931. ^{14}C age for these samples only reflects that at the time of ring formation, not at A.D. 1950.

extending from Santa Elena to Samara stopped growing over the time period from 155 years (C5) to 290 years (P1) B.P. It is most unlikely that the calculated ages of corals represent instead a depletion of ^{14}C due to the addition of ^{14}C-free fossil fuel CO_2 (Suess effect) to the surface water DIOC. The Suess effect in the ocean ranged from only 50 ± 20 years B.P. in the Peru Current (Druffel, 1981) to 90 ± 20 years B.P. in the Gulf Stream (Druffel and Linick, 1978; Druffel, 1980). Thus, it appears that all of the NW Costa Rican coral reefs observed in this study died between A.D. 1660–1795.

$^{18}O/^{16}O$ and $^{13}C/^{12}C$ analyses. Three specimens of *P. damicornis* from the dead reef tract at Culebra Bay and one specimen from the dead reef tract at Santa Elena Bay were analyzed for $\delta^{18}O$ and $\delta^{13}C$. In addition, a specimen collected live from the surface of the Culebra Bay reef in 1978 was analyzed. The $\delta^{18}O$ stratigraphies are presented in Figure 8a. The dead corals from Culebra Bay (C4, C5, and C6) and Santa Elena Bay (S8) are enriched in ^{18}O by 1.2‰ and 1.5‰ respectively, relative to the recent specimen (CR).

An enrichment in ^{18}O in the dead corals due to inorganic overgrowth of aragonite ($\delta^{18}O \sim -2‰$) is not likely. Although the surface of the dead corals shows signs of weathering, the interiors of the branches appeared unaltered. Examination by SEM reveals the presence of a 2 to 10 μm thick layer of inorganic precipitated aragonite needles in some polyp cavities of one of the dead corals (C4). If we assume that a 10 μm thick inorganic layer occurred in all polyp cavities of the dead corals, then the mass contribution of inorganic aragonite to the total coralline aragonite would be about 3%. As such a contribution of inorganic aragonite would alter the oxygen isotopic compositions of the dead corals by less than 0.1‰, we believe the net effect of post-mortem inorganic precipitation on our results is negligible. Additional evidence supporting this conclusion is provided by the $^{13}C/^{12}C$ ratios of the recent and dead specimens (Fig. 8b).

Pocillopora damicornis precipitates aragonite out of carbon isotopic equilibrium with seawater. The magnitude of the ^{13}C disequilibrium is nearly twice that of the ^{18}O disequilibrium (Fig. 9 and caption). If inorganic precipitation of aragonite were more important than environmental variations in determining the isotopic composition of the dead corals, the difference in $\delta^{13}C$ between the recent and dead specimens would be large. Figure 8b shows, however, that the differences in $\delta^{13}C$ between the recent and dead corals are smaller than the differences between $\delta^{18}O$ levels.

The live *Pocillopora* sampled in Culebra Bay (CR) exhibited a variation in oxygen isotopic composition from −5.6 to −6.9‰ mostly due to seasonal temperature variation. In the Gulf of Panama, seasonal upwelling is accompanied by a marked decline in rainfall, causing a large annual range (up to 8‰) in salinity (Hubbs and Roden, 1964; Forsbergh, 1979; Glynn, 1972). Consequently, the surface water is enriched in ^{18}O during the upwelling (dry) season and depleted in ^{18}O at the end of the

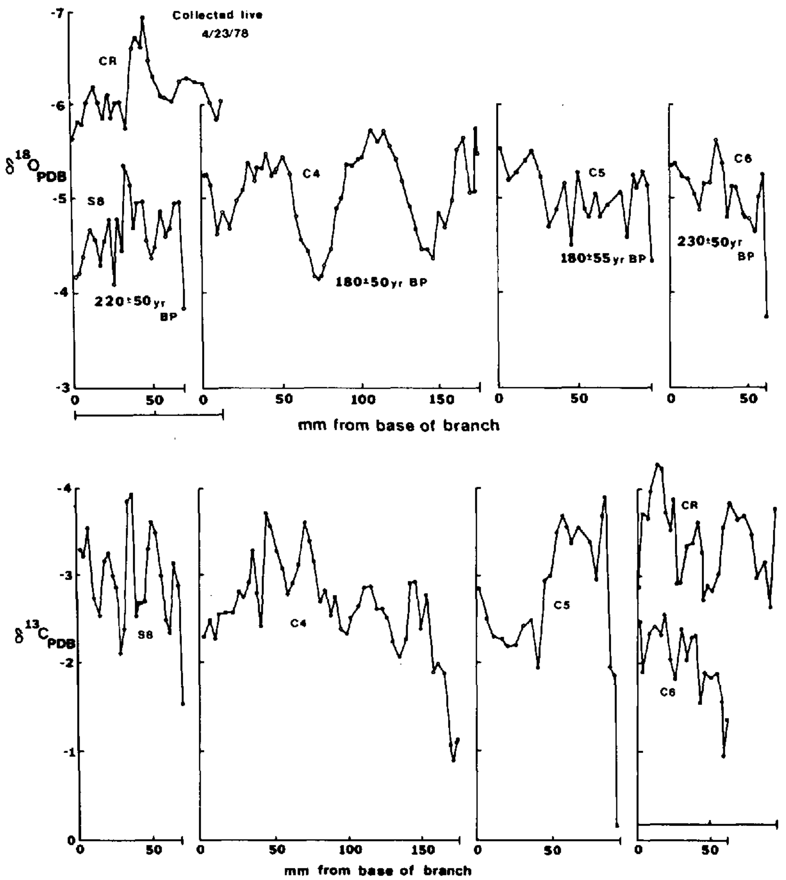

Figure 8. (a) Oxygen isotopic composition ($\delta^{18}O$ relative to the Chicago PDB standard) of four dead specimens of *Pocillopora damicornis* from Santa Elena Bay (S8) and Culebra Bay (C4, C5, and C6) and one specimen collected live from Culebra Bay in 1978 (CR). $\delta^{18}O$ is plotted versus the distance from the base of the branches; the forward termination of each stratigraphy represents a sample from within 1 mm of the branch tip. (b) Carbon isotopic composition ($\delta^{13}C$). Sample identity relative to ^{14}C analysis: C4 (LJ-4714); C5 (LJ-4814); C6 (LJ-4816); S8 (LJ-4818).

wet season. The magnitude of this effect, based on analysis of water samples from the Gulf of Panama, is $d\delta/dS(‰) = 0.12$ (Dunbar *et al.*, 1980; Dunbar and Wellington, 1981).

In the Gulf of Papagayo, however, the seasonal variation in salinity is much less, ranging between 34‰ and 35‰ (Hubbs and Roden, 1964). Based on the Gulf of Panama data, the surface seawater $\delta^{18}O$ in the Gulf of Papagayo is expected to average about -0.30‰ relative to SMOW, with a seasonal range of less than 0.20‰.

From the empirical relation between $\delta^{18}O$ and temperature in the Gulf of Panama

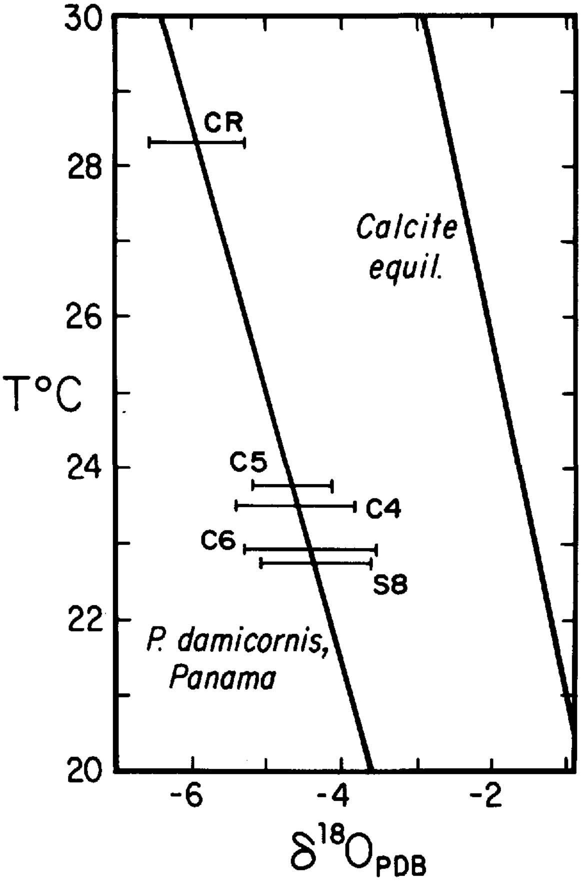

Figure 9. T-^{18}O curve from calibration study on Contadora Island, Gulf of Panama (Dunbar and Wellington, 1981) and equilibrium calcite curve from Epstein *et al.* (1953). *P. damicornis* precipitates carbonate out of calcite (and aragonite) equilibrium with seawater. The curves are calculated based on a seawater $\delta^{18}O$ value of 0.0‰ relative to SMOW. Also shown are the isotopic ranges of the recent coral (CR) and four dead corals (C4, C5, C6, and S8) from the Gulf of Papagayo, corrected for a $\delta^{18}O$ value of Gulf of Papagayo surface water of −0.30‰. The coral $\delta^{18}O$ ranges are plotted on the calibration curve according to the median point of the range. Assuming a surface seawater ΣCO_2 $\delta^{13}C$ of 2‰ the calculated equilibrium $\delta^{13}C$ of aragonite precipitating at 25°C is 4.7‰ (Rubinson and Clayton, 1969). As for ^{18}O, these corals are precipitating carbonate out of carbon isotopic equilibrium, by about 7‰ (Fig. 8b).

(Fig. 9), corrected for changes in seawater isotopic composition, we estimate that the oxygen isotopic variation in the recent coral from Culebra Bay represents growth in water between 25°C and 30°C. Comparing the isotopic data with the temperature record, the recent coral (CR) has recorded summer temperatures in the correct range, but appears isotopically depleted in that portion of the branch presumably secreted during the upwelling season.

Assuming little variation in Gulf of Papagayo seawater $\delta^{18}O$, the isotopic composition of the dead corals indicates growth between 20° and 26°C (Fig. 9), an average of 4° to 6°C cooler relative to the isotopic temperature indicated by the recent specimen. Three of the four fossil corals (S8, C5, and C6) were notably enriched in ^{18}O near the tips of the branches, most likely indicating terminal growth in cooler water immediately preceding death.

The $\delta^{13}C$ of the fossil corals ranged from -4.0 to $-1.0‰$ relative to PDB. All fossil corals were enriched in ^{13}C at their tips. While the terminal growth in three of the corals was enriched in both ^{18}O and ^{13}C, the ratio of $^{18}O/^{13}C$ enrichment varied. In addition, the enrichment in ^{13}C is evident several mm in advance of the enrichment in ^{18}O near the branch tips.

5. Discussion

While available information suggests that upwelling is presently more intense in the Papagayo area than in the Gulf of Panama, only a vague impression of the magnitude of this difference is evident due to the paucity of coastal temperature data in this region. We are still ignorant of the patterns and centers of upwelling and the seasonal persistence of surface cooling. Perhaps the greatest question, with relevance to reef building, concerns the extent to which the cool conditions observed in southern Nicaragua are felt in NW Costa Rica. The presence of reef-building corals and the absence of contemporary coral reefs in the Papagayo area is strong evidence that upwelling is more pronounced in Costa Rica than in Panama.

a. Death of the Costa Rican reefs—isotopic evidence. We have previously suggested (Dunbar *et al.*, 1980; Dunbar and Wellington, 1981) that $^{18}O/^{16}O$ profiles in branches of fossil specimens of *Pocillopora damicornis* permit climatic inferences to be made for discrete time slices in the past, covering periods of up to several years. Based on our calibration data (Fig. 9), we believe that the isotopic enrichment of ^{18}O in the dead corals from the Gulf of Papagayo indicates growth in cool water relative to modern conditions. As an independent check, we measured the isotopic composition of a recent coral from Culebra Bay and found that it has grown in warmer water than the dead corals. It is unlikely that the $\delta^{18}O$ enrichment observed in the dead corals reflects a large shift in seawater $\delta^{18}O$. During the past several hundred years, global sea level and ice volume variations have been negligible and only local changes in the intensity of evaporation, precipitation, and the rate of upwelling could affect the average isotopic composition of seawater in the Gulf of Papagayo.

Increased local precipitation has the effect of depleting the surface water in ^{18}O and results in corals becoming isotopically depleted, not enriched. Variations in the magnitude of upwelling, which could cause a large change in the average annual temperature, should have little effect on seawater isotopic composition in the Gulf of Papagayo. Due to the relatively small change in the isotopic composition of seawater with depth in this region (Epstein and Mayeda, 1953), we expect the magnitude of upwelling-related variation in the $\delta^{18}O$ of seawater to be less than 0.2‰. An evaporation excess (resulting from decreased rainfall) can only cause large changes in salinity and $^{18}O/^{16}O$ ratios in areas with restricted circulation. The dead pocilloporid reefs in Culebra Bay and Santa Elena Bay occur as small fringing reefs exposed to the open ocean. Of the overall differences in $\delta^{18}O$ between the recent and dead corals (~1.5‰), at least 1‰ may therefore be ascribed to temperature change, hence our estimate of a temperature difference of 4° to 6°C (Fig. 9).

Three of the four corals (S8, C5, and C6) become very enriched in ^{18}O near the tips of the branches, possibly indicating that terminal growth in relatively cool water immediately preceded coral death. In experiments with *P. damicornis* in Hawaii, Jokiel and Coles (1977) found that at temperatures of 18°C or lower, coral death occurs in less than two weeks. At 15°C, "cold death" occurs in less than 24 hours (Clausen, 1971). Porter *et al.* (1983) reported that 96% of the shallow-water reef corals in a Dry Tortugas (Florida) study area died during a mid-January intrusion of 14°C water in the winter of 1976–1977. Our data, while indicating a relationship between cooler temperatures and cessation of coral growth, do not necessarily imply that coral death was synchronous in all colony branches.

Comparing the isotopic data with the temperature record, the recent coral (CR) has recorded summer temperatures in the correct range, but appears isotopically light in that portion of the branch presumably secreted during the upwelling season. It is possible that water temperatures dropped rapidly to a level where coral growth nearly ceased. Glynn and Stewart (1973) found that between 20°C and 21°C, the growth rate of *P. damicornis* in the Gulf of Panama changed rapidly and dropped below 1 mm month^{-1}. Maximum growth rate (3.5 to 6.0 mm month^{-1}) was observed immediately following upwelling. If relatively cool temperatures are maintained for the duration of the upwelling season in Culebra Bay, it is likely that isotopic sampling on the order of 2 to 3 mm (with 1 mm drill holes) would lack the resolution necessary to detect these conditions.

The poor development of the dead reefs in Culebra Bay and the small amount of recolonization by certain coral species implies thermally stressful conditions. While recent temperature records from the Culebra Bay region are needed to understand fully the relation between temperature and isotopic seasonality in this specimen, we believe that low growth rates related to strong upwelling prevent very low temperatures (<20°C) from being recorded.

b. Alternative causes of reef death. Other possible causes of reef death in the Papagayo area besides low sea temperatures must also be considered. It is highly improbable that the relative positions of the reefs with respect to sea level were a factor. The reefs have drying reef flats that are exposed only at extreme low tides, as in Panama (Glynn, 1976), and show no signs of tectonic movement. Tectonic elevation of a pocilloporid reef in the Galapagos, of the order of 0.5 m in 1–2 years, caused coral death only on the top (~30 cm stratum) of the reef flat (Glynn and Wellington, 1983). All corals composing the old Papagayo reef frames, to a depth of 4 m, were dead.

Increased rainfall and runoff (causing an increase in water turbidity and sedimentation) that might have occurred 150–300 years ago could also be implicated in widespread reef death. We have found no evidence for a pluvial period in the normally semi-arid Papagayo area during this time.

West (1964) listed five extinct or dormant volcanoes that are present in the Guanacaste highlands, and which range from 35 to 100 km from Culebra Bay. It is possible that eruptive events (lava flows, heating, ash fallout) could have caused significant reef death, but the last two volcanic eruptions in this area were between A.D. 800 to 1200 (Moreau, 1978), long before the death of the Papagayo reefs (A.D. 1650–1800).

Since hermatypic corals in the Papagayo area today are living so close to their lower thermal tolerance limits, only a slight intensification of upwelling could induce mortality. By analogy with the last major glacial advance (approximately 18,000 years B.P.), we propose that during the Little Ice Age (A.D. 1600–1900), there was an equatorward shift of the northern hemispheric high-pressure systems and the polar frontal systems (CLIMAP, 1976). This resulted in a stronger trade wind system, which in turn caused prolonged, more intense upwelling at lower latitudes (Lamb, 1979). Molina-Cruz (1977) demonstrated that the wind velocity of the Southern Hemisphere trades intensified during cool climatic stages. If this interpretation is correct, the major Pleistocene ice ages would have had a truly marked, if not disastrous, effect on reef-building corals throughout the eastern Pacific region (Hubbs, 1952; Hubbs and Rosenblatt, 1961).

c. Coral growth in upwelling regimes of the Western Hemisphere. Small pocilloporid fringing and patch reefs, generally situated in areas protected from direct wave assault, were the predominant reef types in both upwelling and nonupwelling environments. Reefs of this kind are prevalent throughout the eastern Pacific region (Glynn and Macintyre, 1977; Glynn *et al.*, 1983; Glynn and Wellington, 1983). Some reefs were built by *Porites lobata* in nonupwelling Golfo Dulce, but no particular reef type or location was characteristic of upwelling or nonupwelling areas. Possibly the only other region outside of the eastern Pacific having monogeneric pocilloporid reefs is the Marquesas Islands, French Polynesia (Chevalier, 1978). It has been suggested that the meager development of reefs in the Marquesas is due to upwelling (Ranson, 1952; Ladd, 1971), but this notion has been contested by Sournia (1976) and Brousse *et al.* (1978). Brousse *et al.* (1978) suggested that high nutrient levels give a competitive advantage to nonreef builders, an idea proposed by Birkeland (1977) to account for community development in the Gulf of Panama.

According to the reef profiles of Chevalier (1978), fringing reefs in the Marquesas are only 2–3 m thick. This indicates that the vertical dimensions of Marquesan reefs are perhaps intermediate to eastern Pacific reefs in severe (Papagayo, median dead reef thickness = 1.8 m) and moderate (Gulf of Panama, median live reef thickness = 4.0 m) upwelling regimes. Small patch and fringing coral formations are present in an upwelling center in eastern Venezuela (Antonius, 1980), but development of a framework there is even less than in Panama or the Marquesas.

The ages of the dead Papagayo pocilloporid reefs can be estimated from reef accumulation rates reported in the Gulf of Panama (Glynn and Macintyre, 1977). By applying the Panama mean rate of 1.3 m/1,000 years, and assuming equal rates of buildup during the favorable periods in the two upwelling areas, the 1.0-m-thick Punta Gorda reef could have formed in 800 years and the 2.2-m-thick Santa Elena reef in 1,700 years. The live Mogos *Porites* reef in nonupwelling Golfo Dulce cannot be compared directly with the growth rates of ramose pocilloporid reefs because it is composed chiefly of massive coral colonies. Accumulation rates vary greatly for reefs made up dominantly of massive corals. Values reported for forereef zones in the Caribbean range from 1–3 m/1,000 years to 5–8 m/1,000 years (Macintyre *et al.*, 1982). A 10 m section of the Mogo reef, whose environment seems most similar to the conditions of reef growth for the lower and most frequently reported rates, could have formed in 3,000–10,000 years. These first order approximations suggest that some of the oldest coral reefs in Golfo Dulce have formed over periods roughly five times as long as the oldest reefs in the Papagayo area.

The small amount of live coral cover (0–2.7% of the reef bottom), of a nonframe-building species (*Psammocora stellata*), on the dead Papagayo reefs is puzzling. If conditions for coral growth improved after the Little Ice Age, from the early 19th century onward (La Marche, 1974; Rasool and Hogan, 1969), then there has been a period of over 100 years for recolonization of old reef surfaces. Two factors, acting alone or in combination, could slow the initiation of reef growth: (1) an insufficient source of propagules, and (2) generally harsher conditions in the Papagayo area compared with the Gulf of Panama. The recovery of coral communities following local but severe perturbations can occur relatively rapidly, on the order of 10 to 50 years (Colgan, 1982; Endean, 1976; Grigg and Maragos, 1974). Such perturbations, however, have occurred in areas adjacent to large coral stocks and under favorable physical conditions. Another factor that may slow recolonization in NW Costa Rica is the low rate of recruitment of *Pocillopora* by planula larvae, a condition observed over many years in Panama (Glynn, pers. obs.; Wellington, 1981).

It is remarkable that only one coral species is needed for reef building. In the upwelling areas *Pocillopora* is the chief reef builder, and *P. damicornis* is the most important species. A single coral hermatype may also be sufficient to form reefs in the Marquesas (Chevalier, 1978), but in eastern Venezuela, where 22 hermatypic scleractinian and hydrocorals are present, reef construction is virtually nonexistent. Antonius (1980) suggested that reefs have not formed in this area due to the absence or rarity of *Acropora* spp. and *Montastrea annularis* (Ellis and Solander), corals important in reef building elsewhere in the Caribbean.

The limited depth range of reef framework construction observed in upwelling areas was not unexpected. The lower depth limit of reefs in the upwelling Gulf of Panama, 3 to 5 m, was similar to that in Papagayo. In nonupwelling Golfo Dulce and Chiriqui, where the thermocline (≤25°C) normally fluctuates between 30–40 m (wet season) and 20–30 m (dry season) in depth (Dana, 1975), reef building occurred at 10–15 m depth. Depth of coral growth is also dependent on light penetration (Roy and Smith, 1971) and where this is great in nonupwelling areas, reef formation can occur at relatively deep levels, e.g. at 15–20 m in the Galapagos Islands (Glynn and Wellington, 1983).

The small sizes and hence generally youthful age structures of massive corals in the harsh and recently perturbed Papagayo environment are not surprising results. The relationship between coral colony size and intensity of upwelling is not clear cut, however. For example, while *Porites lobata* populations sampled in Papagayo and at one site in nonupwelling Chiriqui contained the smallest and largest colonies respectively reported in this study, colony sizes at a second Chiriqui site (Uva Island) were equal to those sampled in the upwelling Gulf of Panama. Although *Acanthaster* is moderately abundant (20–25 ind./hectare) on the Uva Island reef where *P. lobata* colonies are small, poritid corals are not often eaten by *A. planci* when the sea stars are present at low densities (Barnes *et al.*, 1970; Branham *et al.*, 1971; Goreau *et al.*, 1972; Laxton, 1974; Ormond *et al.*, 1976; Glynn, pers. obs.). Therefore, it is likely that other factors besides upwelling and predation are limiting the development of longevous colonies of *P. lobata* at Uva Island.

The small sizes of *Pavona gigantea* in the Gulf of Papagayo were comparable to those sampled at Uva Island, Gulf of Chiriqui. The low proportion of longevous colonies in these two areas could be due to upwelling in Papagayo and to chronic predation by *Acanthaster* on the Uva reef. Three lines of evidence are consistent with the high proportion of youthful colonies at Uva: (1) *P. gigantea* is a highly preferred prey species (Glynn, 1976 and present study), (2) *P. gigantea* is present on the Uva reef only where *Acanthaster* is absent (e.g. along the leeward reef flanks and in patches of coral rubble surrounded by live *Pocillopora* spp.), (3) *P. gigantea* at Uva Island, at a second site in Chiriqui and in the Pearl Islands showed equal rates of skeletal growth (Fig. 7), suggesting that physical conditions related to coral growth are similar in the three areas. A high relative abundance of *P. gigantea*, and other massive corals preferred by *Acanthaster*, has been observed in three areas (Gorgona Island, Malpelo Island, Galapagos Islands) elsewhere in the eastern Pacific from which *Acanthaster* is absent (Glynn *et al.*, 1983).

Because the numbers of filter-feeding bioeroders show a strong correlation with plankton productivity (Highsmith, 1980), it is possible to assess the general fertility of an area from the intensity of coral bioerosion. Bioerosion due to lithophagine bivalves was equally high in *P. gigantea* in upwelling Papagayo (Md = 5.1 ind./100 cm^2). Boring bivalves were also most abundant in *P. gigantea* (Md = 2.8 ind./100 cm^2) at Urvina Bay, Galapagos, where the cool Equatorial Undercurrent is most strongly felt (Glynn and Wellington, 1983). The three upwelling areas in Costa Rica, Panama and the Galapagos were similar in terms of boring bivalve activities ($0.10 > P > 0.05$, Kruskal-Wallis test).

Discontinuities or hiatuses perpendicular to the skeletal growth axes of corals are assumed to represent records of unfavorable growth conditions in the physical environment (Glynn and Wellington, 1983). Portions of the colony surface die, are temporarily invaded by algae, and then resume vertical growth after the dead suface is overgrown by live coral from surrounding areas. The killing of large surface areas by *Acanthaster* could also cause such breaks, but this source of disturbance did not seem important in the present study. On the basis of this criterion, conditions unfavorable for *Pavona gigantea* growth were experienced most frequently in Papagayo. A similar analysis among a variety of thermal regimes in the Galapagos showed that growth discontinuities were also most frequent in the strongest upwelling area. For example, on the west side of Isabela Island (Urvina Bay), where upwelling is strong, 54% ($n = 13$) of the colonies of *P. gigantea* contained at least one growth discontinuity. In Papagayo, the harshest Pacific mainland area presently known, 36% ($n = 28$) of the colonies of *P. gigantea* had at least one growth discontinuity. The Papagayo and Urvina Bay corals did not differ in terms of frequency of skeletal hiatuses ($P > 0.10$, Mann-Whitney U-test).

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