GROWTH OF SEVEN SPECIES OF SCLERACTINIAN CORALS IN AN UPWELLING ENVIRONMENT OF THE EASTERN PACIFIC (GOLFO DE PAPAGAYO, COSTA RICA)

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ABSTRACT

Annual growth rates of seven coral species at the Islas Murciélagos and Bahía Culebra in the upwelling area of Golfo de Papagayo (Costa Rica) were measured during 1991–92 and 1995–97. Two methods were utilized: staining with alizarin red (*Pocillopora* spp., *Pavona clavus, Psammocora stellata*), and X-rays of cores and slabs of *P. clavus*. Growth increment rates during 1991–92 were significantly higher for *P. elegans, P. damicornis* and *P. stellata*. During 1995–97 *P. meandrina* and *P. clavus* had the highest growth rates and there were significant variations between the two study sites. Growth rates for *P. elegans, P. damicornis, P. clavus* and *P. stellata* in Golfo de Papagayo were the highest reported for these species in the eastern Pacific, and may be related to high nutrient input during upwellings. No core or slab of *P. clavus* was older than 1987 and we attribute this interruption to the 1987–88 El Niño event. A decrease in the growth rates during the 1990s can also be related to warming events and sedimentation from a road construction. Results suggest that upwelling environments are not completely restrictive to coral growth and therefore to reef construction in these seasonally fluctuating environments.

The study of seasonal density bands (Knutson et al., 1972; Highsmith, 1979) in the skeletons of corals is one of the most utilized methods in the study of growth histories and their major environmental controls (Buddemeier and Kinzie, 1976; Lough and Barnes, 2000). Since the 1930's, the effect of environmental fluctuations upon coral seasonal growth increments has been observed, though it was not until the 1960's that annual band deposition in coral skeletons was confirmed (Dunbar and Cole, 1993; Swart and Dodge, 1997). Some coral species clearly deposit two annual bands (high and low density), but others have shown complicated inter annual or even daily banding patterns (Brown et al., 1986; Risk and Pearce, 1992).

In the eastern Pacific, many studies have investigated the seasonal deposition of bands coincident with the rainy and dry season (Glynn and Steward, 1973; Glynn, 1977; Wellington, 1982; Glynn and Wellington, 1983; Wellington and Glynn, 1983; Guzmán and Cortés, 1989). Growth rates and stable isotopes in coral skeletons have facilitated environmental reconstruction during the last two centuries (Dunbar and Wellington, 1981; Glynn et al. 1983; Carriquirry et al., 1988; Carriquirry et al. 1994; Dunbar et al., 1994; Linsley et al. 1994; Wellington and Dunbar 1995, Linsley et al. 2000).

In this study, we examine the growth rate of seven eastern Pacific corals in the up-welling area of the Golfo de Papagayo, Costa Rica, and discuss the possible effect of natural and anthropogenic disturbances on one massive species, *Pavona clavus*.

MATERIAL AND METHODS

STUDY SITE.—The area known as Golfo de Papagayo, is under the influence of a seasonal up-welling (Stumpf and Legeckis 1977; Clarke 1988) during the dry season from December to April. Sea water temperature (SWT) can be 5–10 ±C below the annual mean for several days (Jiménez,
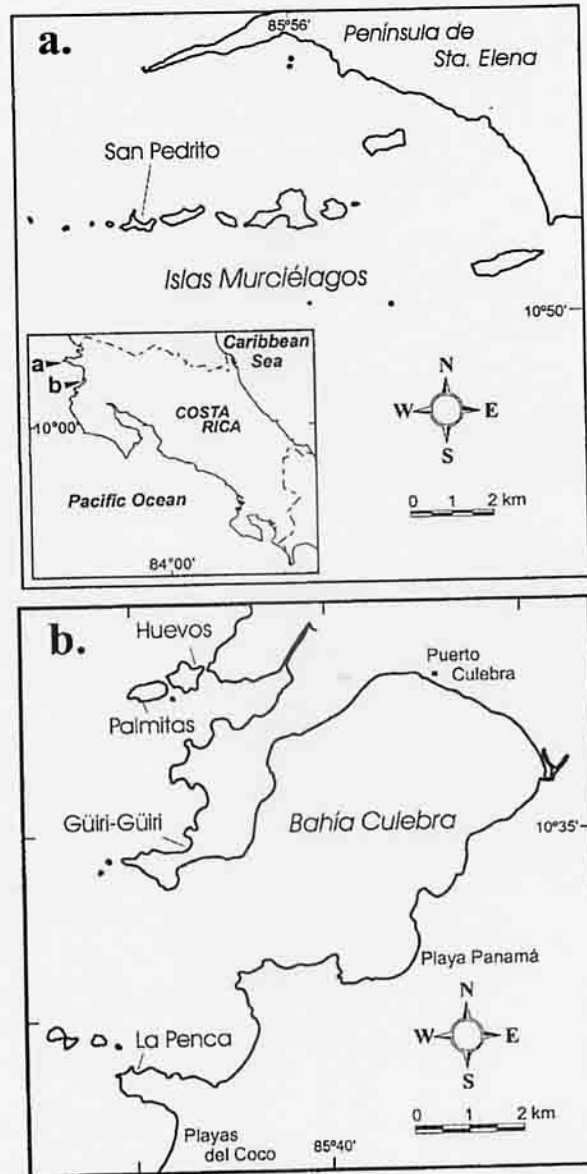
Figure 1. Location of the study sites at the northern Pacific coast of Costa Rica. a. Islas Murciélagos. b. Bahía Culebra.

2001a). The Islas Murciélagos (Fig. 1A), the largest group of islands in the Golfo de Papagayo, support extensive coral communities to a depth of 20 m and one of the largest black coral populations off the coast of Costa Rica (Cortés, 1996–1997; Cortés and Jiménez, 2003). Twelve species are found in the islands, *Pocillopora* spp. and *Pavona* spp. being the most abundant. Reef frameworks built mainly by *Pocillopora* spp., *Gardineroseris planulata*, and *Pavona gigantea* are found in sheltered coves. In the present study, coral growth measurements were conducted at a small (<0.3 ha) *Pocillopora* spp. patch reefs located at Isla San Pedrito (hereafter San Pedrito; Fig. 1A).

Forty kilometers south from Islas Murciélagos, well developed coral communities and patch reefs can be found in Bahía Culebra (Jiménez, 1997; 2001b) (Fig. 1B). Twenty coral species have been reported with *Pocillopora* spp. and *Pavona clavus* being the most abundant taxa. Three small patch reefs built by *Pocillopora* spp. (~0.1 ha, hereafter Huevos), *Pavona clavus* (~0.8 ha, hereafter Güiri-Güiri), *Psammocora* spp. (~0.3 ha, hereafter La Penca) and one coral community established upon basalt (~0.1 ha, hereafter Palmitas) were selected for the study of coral growth (Fig. 1B).

SEA SURFACE TEMPERATURE (SST) AND METEOROLOGICAL DATA.—Environmental data were used to examine possible factors affecting coral growth during the studied time. SST ($1\pm \times 1\pm$ grid centered on $10.5\pm$N, $86.5\pm$W) and cloudiness ($2.5\pm \times 2.5\pm$ grid centered on $10.47\pm$N, $86.25\pm$W) data were extracted from Reynolds NCEP optimal interpolation analysis (Reynolds and Smith, 1994) and NCEP-NCAR reanalysis (Kalnay et al., 1996) data sets respectively, covering the period 1984-1997. Both data sets are a blend of in situ observations, ships, aircraft, and bias-corrected satellite data. Sun hours, rainfall and wind speed data from the nearest meteorological station to the study area (Llano Grande de Liberia, 10 ± 36N, 85 ± 32W), were provided by Costa Rica's Instituto Meteorológico Nacional. SST and the meteorological data were aggregated to annual averages to match the resolution of the coral growth increments. Annual anomalies of each variable were calculated as the difference from the 1984–1996 annual mean (1997 was not included because it was the onset of the very strong 1997–1998 El Niño).

CORAL GROWTH.—The growth rates of seven scleractinian corals were determined by staining branching (*Pocillopora damicornis*, *P. elegans*, *P. eydouxi*, *P. inflata*, *P. meandrina*), massive (*Pavona clavus*), and nodular (*Psammocora stellata*) species with Alizarin Red S (Lamberts, 1978) in 1991, 1995 and 1996 (Table 1), and then directly measuring the growth increments from the stain line to the tip of the branch, and also on X-rays of slabs of *P. clavus* cores and colonies (Knutson et al., 1972). The collected coral fragments (all from different colonies) and whole colonies were stained for 9–10 h in plastic boxes (110 L) with aerated seawater and re-located at the same place and depth of collection. *Pocillopora* spp. and *P. clavus* fragments were attached to iron rods with wire. *P. clavus* colonies were cemented to the bottom utilizing Portland II cement mix with plaster (3:2). *P.*

Table 1. Coral species utilized at the five studied sites. The method for measuring coral growth, the number (n) and year of staining/collection of samples are indicated.

Species	Method	Site	n	Year
Fragments (ca. 13 cm length, 3–5 m depth)				
Pocillopora elegans Dana 1856	Alizarin	Palmitas	20	1996
	Alizarin	San Pedrito	31	1996
	Alizarin	Huevos	16	1991
Pocillopora damicornis (Linnaeus 1748)	Alizarin	Palmitas	11	1996
	Alizarin	San Pedrito	20	1996
	Alizarin	Huevos	11	1991
Pocillopora meandrina Dana 1846	Alizarin	Palmitas	18	1996
	Alizarin	San Pedrito	13	1996
Pocillopora eydouxi Milne Edwards & Haime 1860	Alizarin	Palmitas	13	1996
Pocillopora inflata Glynn 1999	Alizarin	San Pedrito	13	1996
Colonies (9–25 cm diameter, 3–5 m depth)				
Psammocora stellata (Verrill 1860)	Alizarin	La Penca	11	1996
	Alizarin	Huevos	10	1991
Pavona clavus Dana 1856	Alizarin	San Pedrito	12	1996
	Alizarin	Güiri-Güiri	34	1995
	X-rays	Huevos	9	1991
Cores (25 cm length, 5 cm diameter, 4–5 m depth)				
Pavona clavus	X-rays	Güiri-Güiri	4	1995

stellata colonies were placed freely among other unattached *Psammocora* spp. colonies in a 1 × 1 m plot delimited by iron rods.

All corals were collected 10–12 mo after the staining and the tissue was removed with diluted (5 %) sodium hypochlorite for 12 h, rinsed in running fresh water and sun dried. For *Pocillopora* spp. and *P. stellata*, the growth increment was measured from the exposed staining line to the tip of the branch or branches (if more than one per fragment). Therefore, in some cases, the number of reported measurements is higher than the number of stained corals.

The mean growth rate in cores and slabs from *P. clavus* colonies (Table 1) was determined by density band widths from positives of X-ray films (Dodge, 1980). The cores and colonies were cut with a rock saw and the slabs (5–8 mm thick) X-rayed with a General Electric radiographic machine (0.3 s, 52 KV, 200 mA, 1 m distance). Annual coral growth increments were analyzed with a non-parametric test (Kruskal-Wallis, U Mann-Whitney).

RESULTS

The mean annual growth rates for branching corals were generally higher than for massive or nodular species (Table 2). The growth rate for pocilloporid corals was between 30.8 mm yr^{-1} (*P. eydouxi*) and 66.8 mm yr^{-1} (*P. damicornis*). *P. elegans* and *P. damicornis*, had the highest mean growth rates at all localities (>38.0 mm yr^{-1}), with the sole exception of San Pedrito, where *P. meandrina* growth rate was higher (~45.0 mm yr^{-1}). The lowest growth rate was of *P. inflata* (~31.0 mm yr^{-1}) in San Pedrito. The growth rate of the nodular and massive corals ranged from 9.5 to 20.6 mm yr^{-1} (Table 2). With the exception of *P. clavus*, the highest growth rates of all stained species occurred during 1991–1992 (Huevos).

The pooled mean growth rates as determined by Alizarin staining of four coral species (*P. elegans*, *P. damicornis*, *P. clavus* and *P. stellata*) are notably higher in the Golfo de Papagayo than at other localities in the eastern Pacific by 2–11 mm yr^{-1} (Table 3).

Pavona clavus cores and slabs showed interruptions which prevented a continuous growth record longer than 5–8 yrs. Invariably, the interruption was marked by a mortality line of different width where calcareous algae, bioeroders (*Lithophaga* spp.), and sediments were observed. The dead surface was later overgrown by peripheral tissue, starting from the perimeter of the interruption, as suggested by changes in the orientation of the growth axis. On the slabs growth was interrupted before 1991, and on the cores, in early 1987, 1989 and 1990.

The annual mean growth rate obtained by pooling all colonies and cores of *P. clavus* for the time period of 1987–1994, was 17.8 ± 3.2 mm yr^{-1} (range 13–26 mm yr^{-1}). There were significant annual differences in growth rates with a moderate decrease in recent years (Spearmann correlation r = –0.41, n = 47, P < 0.01; Table 2). During the time span studied in the *P. clavus* skeletons, El Niño warming events occurred in 1986–1987 and 1991–1994 (Kessler and McPhaden, 1995; Trenberth and Hoar, 1996, 1997; Goddard and Graham, 1997; but see Latif et al., 1997 for a different view). During these events, growth rates were lower than in non-El Niño years (17.0 ± 2.8 mm yr^{-1} vs 21.1 ± 3.0 mm yr^{-1}, respectively). The 1991–92 mean growth rate of *P. clavus* obtained from X-rays at Güiri-Güiri was higher (17.1 ± 2.9 mm yr^{-1}) than the rates determined by Alizarin staining at Huevos (12.7 ± 3.3 mm yr^{-1}) (P < 0.05).

A comparison of the pooled mean growth rates of *P. clavus* reported for four areas of the eastern Pacific under the influence of seasonal upwelling (Fig. 2), suggests that growth

Table 2. Growth (mm yr^{-1}) statistics of seven coral species in Golfo de Papagayo; n = number of measurements. Significant differences among sites/years *P < 0.05, **P < 0.001.

Species	Site	Year	Mean ± SD	n	Max	Min
Alizarin red staining						
Pocillopora elegans*	Palmitas	1996–97	41.2 ± 5.8	27	53	29
	San Pedrito	1996–97	43.8 ± 5.7	48	61	34
	Huevos	1991–92	52.1 ± 9.6	16	67.2	36
Pocillopora damicornis*	Palmitas	1996–97	53.1 ± 3.5	18	61	49
	San Pedrito	1996–97	38.0 ± 5.0	31	49	28
	Huevos	1991–92	66.8 ± 8.7	11	75.6	46.8
Pocillopora meandrina**	Palmitas	1996–97	34.2 ± 6.6	20	46	18
	San Pedrito	1996–97	44.6 ± 6.3	14	56	34
Pocillopora eydouxi	Palmitas	1996–97	30.8 ± 4.8	16	39	21
Pocillopora inflata	San Pedrito	1996–97	31.5 ± 8	16	44	20
Psammocora stellata**	La Penca	1996–97	9.5 ± 1.8	11	12	6
	Huevos	1991–92	18.7 ± 1.9	10	21.6	15.6
Pavona clavus**	San Pedrito	1996–97	15.8 ± 4.1	12	22	9
	Güiri-Güiri	1995–96	20.6 ± 4.1	34	28	11
	Huevos	1991–92	12.7 ± 3.3	9	17.2	8.5
Cores and slabs						
Pavona clavus*	Güiri-Güiri	1993–94	16.3 ± 1.1	9	21	13
		1992–93	16.3 ± 0.8	9	21	14
		1991–92	18.0 ± 0.9	9	22	14
		1990–91	17.1 ± 1	9	21	14
		1989–90	20.5 ± 0.2	4	21	20
		1988–89	20.7 ± 1.6	3	26	17
		1987–88	18.5 ± 0.2	2	19	18
		1986–87	23.0 ± 1.4	2	26	20

Table 3. Mean growth rates (mm yr^{-1}) of four scleractinian corals in Golfo de Papagayo and other localities in the eastern Pacific, determined by the Alizarin red staining method. Sources: 1. Wellington and Glynn (1983); 2. Guzmán and Cortés (1989); 3. Prahl and Vargas-Angel (1990); 4. Glynn (1994); 5. Feingold (1995); 6. Maté (1997) in aquarium.

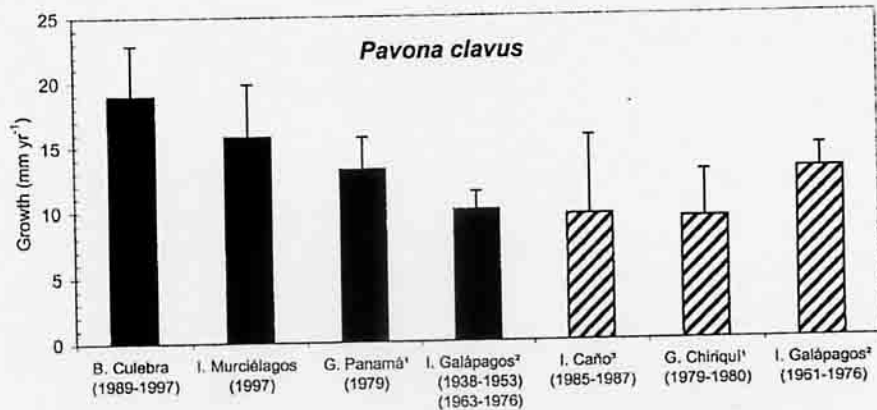| Species	Golfo de Papagayo	Other localities			
	Mean ± SD	Highest rate		Lowest rate	
Pocillopora elegans	44.5 ± 7.6	33.2	Galápagos[4]	17.5	Caño Is.[2]
Pocillopora damicornis	47.8 ± 12.4	39.6	Colombia[3]	12.7	Panama[6]
Pavona clavus	18.2 ± 5.2	13.2	Panama[1]	9.3	Panama[1]
Psammocora stellata	13.9 ± 5.0	11.2	Panama[6]	8.8	Galápagos[5]

Figure 2. Mean ± SD growth rates (mm yr^{-1}) of *Pavona clavus* (staining and X-ray methods) at eastern Pacific upwelling (black bars) and non-upwelling (dashed) localities. Time periods in parenthesis. Data from [1]Wellington and Glynn (1983); [2]Glynn and Wellington (1983), harmonic means of three islands under the effect of the Equatorial Undercurrent upwelling, and of four islands where upwelling is apparently absent; [3]Guzmán and Cortés (1989).

rates of *P. clavus* are higher (between 13 and 19 mm yr^{-1}) in upwelling areas, particularly at Bahía Culebra.

A comparison of the SST and meteorological data for the Golfo de Papagayo area during 1991–1992 and 1995–1996 demonstrates contrasting conditions (Fig. 3A–E). The study time period of 1991–1992 had higher SST, more sun hours, less cloud cover and rainfall, and stronger winds. In contrast, the highest rainfall and the weakest winds of the entire 1986–1997 record occurred in 1995–1996. No significant correlation was found between the annual growth rate of *P. clavus*, as determined in the cores, and the environmental data. Nevertheless, negative growth anomalies (Fig. 3F) coincided with the early 1991 launching of intense land removal activities for a road construction (~100 m distance from the study site) and the entry of heavy loads of sediments in the cove were the samples were collected.

DISCUSSION

The growth rates reported here show the inherent variability among different species, morphologies, site location, and years. At Bahía Culebra, branching species (*Pocillopora* spp.) had the highest growth rates compared to massive and nodular corals. This has been reported at other reef localities of the eastern Pacific and partially explains the reason why these species are among the main reef builders in the region (e.g., Guzmán and Cortés, 1993; Glynn, 1997; Glynn and Maté, 1997). There are no published reports of the growth rates of *P. meandrina*, *P. eydouxi* and *P. inflata* in other parts of the eastern Pacific. These species have low abundance and restricted distributions in the reefs of the region (Glynn, 1997; 1999). At Bahía Culebra, however, *P. meandrina* and *P. eydouxi* can be found in moderate abundance in coral communities upon basalt (Jiménez, 1998, 2001b). *P. inflata* is a recently described rare species (Glynn, 1999) which has been found intermixed with other pocilloporid corals at the Galápagos Islands, Panama, Costa Rica and Mexico. In Costa Rica, *P. inflata* is found only in San Pedrito and during the 1997-98 El
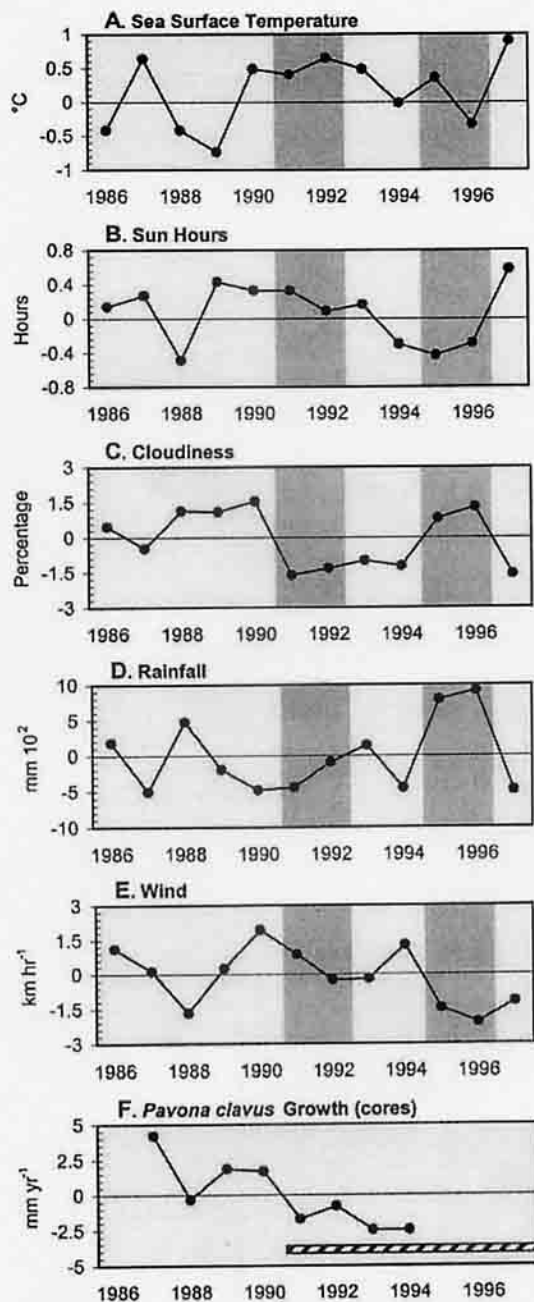
Figure 3. Annual mean anomalies of sea surface temperature (a), sun hours (b), cloudiness (c), rainfall (d), wind speed (e) and growth rate of *Pavona clavus* (cores) (f) at the Golfo de Papagayo area for 1986–1996. The vertical shading shows the study time period of coral staining. The horizontal stripped bar indicates the years of heavy sedimentation at the Güiri-Güiri study site.

Niño event, 75% of its colonies bleached, though no entire colony mortality was reported (Jiménez et al., 2001).

Comparing pocilloporid corals according to locality and study time (Table 2), *P. damicornis* had the highest mean growth rates (~50 mm yr^{-1}) while *P. eydouxi* had the lowest (~30 mm yr^{-1}). Growth rates in some corals are associated with structural characteristics of the skeleton, such as density, porosity, micro-architecture of skeletal components, and morphology of the colony (Highsmith, 1979, 1981; Hughes, 1987; Bucher et al., 1998). Though it is commonly thought that less dense skeletons are deposited by fast-growing species (references above), *P. damicornis* from Palmitas have a higher skeletal density than *P. eydouxi* (Jiménez, unpublished data). Consequently, it is necessary to further study other structural characteristics to explain the observed growth rate differences.

Given the environmental data for the study area, the following conclusions can be drawn. Weather conditions during 1991–92 seem to have been favorable for coral growth at Bahía Culebra until the second half of 1992 when an increase in sea water temperature produced bleaching and mortality of several coral species along the central and south Pacific coast of Costa Rica (Jiménez and Cortés, 2001). In comparison, during 1995–96, the seasonal mid year low in precipitation accompanied with extended doldrum-like weather, known as *Veranillo de San Juan* in Costa Rica (Ramírez, 1983), was nearly absent in 1996. This particularly prolonged rainy season (two months longer than usual), which produced devastating floods in the area (Waylen and Laporte, 1999), increased cloud cover with concurrent heavy surge (increasing resuspended sediments loads and coastal erosion), may have negatively impacted the corals growth during that period. Sediments dumped in the cove waters significantly changed the non-carbonate fraction of the bottom sediments in the reef (Jiménez, 1997, 1998). The surge completely eliminated a large meadow of the seagrass *Ruppia maritima* Loisel in the inner part of Bahía Culebra (Cortés, 2001), and killed one of the largest known populations in Costa Rica of the bivalve *Pinna rugosa* Sowerby that lived within the seagrass (Jiménez and Ruíz, unpublished data). None of these events was observed during 1991–92, when normal surge conditions prevailed for most of the time period. Additionally, in 1996, negative SWT anomalies at 7 m depth of 4±C and 3±C were recorded for several days during the seasonal upwelling (Jiménez, 2001a).

High growth rates of *P. clavus* and *P. gigantea* (Glynn and Wellington, 1983), and *P. stellata* (Feingold, 1995) have been reported for some El Niño events at the Galápagos Islands probably due to a relaxation of the upwelling. A similar scenario may have occurred at Bahía Culebra during 1991–92, when weather conditions favored *Pocillopora* spp. and *Psammocora* growth. *P. clavus* is the only coral whose growth rates were lower during 1991–92 than in other years. It is possible that the wiring of fragments from massive species to iron rods had a negative effect, due to coral tissue damage by abrasion in several parts of the fragment. Although coral tissue eventually overgrew the wire and portions of the iron rod, modification of the growth pattern at the contact points was evident. That was not the case with the *Pocillopora* spp. fragments, which were attached to the rods only at the base, therefore limiting abrasion to that part. Although there were site-related differences in biotic and abiotic factors that may affect coral growth (e.g., turbulence, exposure to currents), *P. clavus* growth rates during 1991–92 were significantly higher at Güiri-Güiri (cores) than at Huevos (staining of fragments), suggesting that wiring the fragments to the rods had a negative effect on growth.

Growth increments during the eight years recorded in the cores and slabs of *P. clavus*, showed a drastic interruption before 1991 in five of the colonies, and only two reached 1987 despite a core length of 25 cm (~13 yrs of growth). A moderate to strong El Niño event occurred during 1987–88 (Quinn, 1993; Kessler and McPhaden, 1995), decreasing the growth rates of *Porites lobata* at Clipperton Atoll (Glynn et al., 1996). In Costa Rica, localized coral bleaching and mortality was observed during 1987–88 at the central Pacific coast of the country (Jiménez and Cortés, unpubl. data), but it is not known to what extent the corals in the Golfo de Papagayo were affected. It is possible that the observed mortality, coincidental with that time period, was the result of El Niño warming. Coral growth was re-established 1–3 yrs after.

After 1991, the growth rates of *P. clavus* tended to decrease below the 8 yr average. As mentioned above, 1991–94 was an anomalous warm period in the eastern Pacific, as a result of a long-lasting or several El Niño events. Also, during this time period, there was an intensification of road construction which likely facilitate terrestrial access to the small cove were Güiri-Güiri reef is located. Therefore, the combined effect of the warming and the increase in sedimentation in the cove starting in 1991 was probably responsible for the *P. clavus* growth rate decrease, as has been reported for other El Niño events (Wellington and Dunbar, 1995) and in near-shore reefs under the influence of terrigenous sediments (Cortés and Risk, 1985; Prahl and Vargas-Angel, 1990; Cortés, 1992). The same conclusions can be made with regard to *Pocillopora* spp., whose growth rates at Huevos and Palmitas decreased after 1991–92. These sites were not under the influence of sediment loads, as recorded for Güiri-Güiri, but they were vulnerable to any warming event, as observed for the 1997–1998 El Niño (Jiménez et al., 2001).

The higher growth rates of *P. clavus* in the upwelling areas of the eastern Pacific have been related to a higher nutrient availability during the upwelling season (Wellington and Glynn, 1983). This hypothesis is supported by the observation that at four upwelling localities in the gulfs of Papagayo and Panama, and during different time periods, *P. clavus* growth rates were consistently higher than in non-upwelling areas. However, the other corals studied show a high degree of variation in the eastern Pacific, preventing the identification of any general pattern associated with upwelling. The eastern Pacific system provides key elements for conducting further examinations on this topic: diverse areas with predictable seasonal upwelling in relative proximity to non-upwelling (control) localities, abundant coral reef communities in both environments, and coral species with a wide geographical distribution.

LITERATURE CITED

Brown, B., M. Le Tissier, L. Howard, M. Charuchinda, and J. Jackson. 1986. Asynchronous deposition of dense skeletal bands in *Porites lutea*. Mar. Biol. 93: 83–89.

Bucher, D., V. Harriott and L. Roberts. 1998. Skeletal micro-density, porosity and bulk density of acroporid corals. J. Exp. Mar. Biol. Ecol. 228: 117–136.

Buddemeier, R. and R. Kinzie. 1976. Coral growth. Oceangr. Mar. Biol. Ann. Rev. 14:183–225.

Carriquiry, J., M. Risk, and H. Schwartz. 1988. Timing and temperature record from stable isotopes of the 1982–1983 El Niño warming event in eastern Pacific corals. Palaios 3: 359–364.

_____, M. Risk and H. Schwarcz. 1994. Stable isotope geochemistry of corals from Costa Rica as proxy indicator of the El Niño/Southern Oscillation (ENSO). Geoch. Cosm. Acta 58: 335–351.

Clarke, A. 1988. Inertial wind path and sea surface temperature patterns near the Gulf of Tehuantepec and Gulf of Papagayo. J. Geophys. Res. 93: 15491–15501.

Cortés, J. 1992. Los arrecifes de Golfo Dulce, Costa Rica: aspectos ecológicos. Rev. Biol. Trop. 40: 19–26.

_____. 1996–1997. Comunidades coralinas y arrecifes del Área de conservación Guanacaste, Costa Rica. Rev. Biol. Trop. 44/45: 623–625.

_____. 2001. Requiem for eastern Pacific seagrass bed. Rev. Biol. Trop. 49 (Suppl. 2): 273–278.

_____. and C. Jiménez. 2003. Corals and Coral Reefs of the Pacific of Costa Rica: history, research and status. Pages 361–385 *in* J. Cortés (ed.): Latin American Coral Reefs. Elsevier, Amsterdam.

_____. and M. Risk. 1985. A reef under siltation stress: Cahuita, Costa Rica. Bull. Mar. Sci. 36: 339–356.

Dodge, R. 1980. Preparation of coral skeletons for growth studies. Pages 615–618 *in* D. Rhoads and R. Lutz eds. Skeletal growth of aquatic organisms. Plenum, London.

Dunbar, R. and G. Wellington. 1981. Stable isotopes in a branching coral monitor seasonal temperature variation. Nature 293: 453–455.

_____ and J. Cole. 1993. Coral records of ocean-atmosphere variability. NOAA Climate and global change program special report 10. 38 p.

_____ G. Wellingon, M. Colgan and P. Glynn. 1994. Eastern Pacific climate variability since 1600 A.D.: stable isotopes in Galápagos corals. Paleoceanography 9: 291–315.

Feingold, J. 1995. Effects of elevated water temperature on coral bleaching and survival during El Niño disturbance events. Ph.D. Diss., University of Miami, Miami. 235 p.

Glynn, P. W. 1977. Coral growth in upwelling and nonupwelling areas off the Pacific coast of Panamá. J. Mer. Res. 35: 567–585.

_____. 1994. State of coral reefs in the Galápagos Islands: natural vs anthropogenic impacts. Mar. Poll. Bull. 29: 131–140.

_____. 1997. Eastern Pacific coral reef biogeography and faunal flux: Durham's dilemma revisited. Proc. 8ᵗʰ Int'l. Coral Reef Symp., Panama 1: 371–378.

_____. 1999. *Pocillopora inflata*, a new species of scleractinian coral (Cnidaria, Anthozoa) from the tropical eastern Pacific. Pac. Sci. 53: 168–180.

_____ and J. Maté. 1997. Field guide to the Pacific coral reefs of Panama. Proc. 8ᵗʰ Int'l. Coral Reef Symp., Panama 1: 145–166.

_____ and R. Steward. 1973. Distribution of coral reefs in the Pearl Islands (Gulf of Panama) in relation to thermal conditions. Limnol. Oceanogr. 18: 367–379.

_____ and G. Wellington. 1983. Corals and coral reefs of the Galápagos Islands. (With annotated list of the scleractinian corals of the Galápagos by J. W. Wells). Univ. Californis Press, Berkeley. 330 p.

_____, E. Druffel and R. Dunbar. 1983. A dead Central American coral reef tract: possible link with the Little Ice Age. J. Mar. Res. 41: 605–637.

_____, J. Veron, and G. Wellington. 1996. Clipperton Atoll (eastern Pacific): oceanography, geomorphology, reef-building coral ecology and biogeography. Coral Reefs 15: 71–100.

Goddard, L. and N. Graham. 1997. El Niño in the 1990s. J. Geophys. Res. 102: 10,423–10,436.

Guzmán, H. and J. Cortés. 1989. Growth rates of eight species of scleractinian corals in the eastern Pacific (Costa Rica). Bull. Mar. Sci. 44: 1186–1194.

_____ and J. Cortés. 1993. Arrecifes coralinos del Pacífico oriental tropical: revisión y perspectivas. Rev. Biol. Trop. 41: 535–557.

Highsmith, R. 1979. Coral growth rates and environmental control of density banding. J. Exp. Mar. Biol. Ecol. 37: 105–125.

_____. 1981. Coral bioerosion: damage relative to skeletal density. Am. Nat. 117: 193–198.

Hughes, T. 1987. Skeletal density and growth form of corals. Mar. Ecol. Prog. Ser. 35: 259–266.

Jiménez, C. 1997. Corals and coral reefs of Culebra Bay, Pacific coast of Costa Rica: anarchy in the reef. Proc. 8th Int'l. Coral Reef Symp., Panama 1: 329–334.

_____. 1998. Arrecifes y comunidades coralinas de Bahía Culebra, Pacífico norte de Costa Rica (Golfo de Papagayo). M.Sc. Thesis, Universidad de Costa Rica, San Pedro, Costa Rica. 218 p.

_____. 2001a. Seawater temperature measured at the surface and at two depths (7 and 14 m) in one coral reef at Culebra Bay, Gulf of Papagayo, Costa Rica. Rev. Biol. Trop. 49 (Suppl. 2): 153–161.

_____. 2001b. Arrecifes y ambientes coralinos de Bahía Culebra, Pacífico de Costa Rica: aspectos biológicos, económico-recreativos y de manejo. Rev. Biol. Trop. 49 (Suppl. 2): 215–231.

_____ and J. Cortés. 2001. Effects of the 1991–92 El Niño on scleractinian corals of the Costa Rican central Pacific coast. Rev. Biol. Trop. 49 (Suppl. 2): 239–250.

_____, J. Cortés, A. León and E. Ruíz. 2001. Coral bleaching and mortality associated with the 1997–98 El Niño in an upwelling environment in the eastern Pacific (Gulf of Papagayo, Costa Rica). Bull. Mar. Sci. 68: 151–169.

Kalnay, E., M. Kanamitsu, R. Kistler, W. Collins, D. Deaven, L. Gandin, M. Iredell, S. Saha, G. White, J. Woollen, Y. Zhu, M. Chelliah, W. Ebisuzaki, W. Higgins, J. Janowiak, K. C. Mo, C. Ropelewski, J. Wang, A. Leetmaa, R. Reynolds, R. Jenne, and D. Joseph, 1996: The NMC/NCAR 40-Year Reanalysis Project. Bull. Amer. Meteor. Soc. 77: 437–471.

Kessler, W. and M. McPhaden. 1995. The 1991–1993 El Niño in the central Pacific. Deep-Sea Res. II 42: 295–333.

Knutson, D., R. Buddemeier, and S. Smith. 1972. Coral chronometers: seasonal growth bands in reef corals. Science 177: 270–272.

Lamberts, A. 1978. Coral growth: alizarin method. Pages 523–527 in D. Stoddart and R. Johannes, eds. Coral reefs: research methods. UNESCO, Paris.

Latif, M., R. Kleeman and C. Eckert. 1997. Greenhouse warming, decadal variability, or El Niño? an attempt to understand the anomalous 1990s. J. Climate 10: 2221–2239.

Linsley, B., R. Dunbar, G. Wellington and D. Mucciarone. 1994. A coral-based reconstruction of Intertropical Convergence Zone variability over Central America since 1707. J. Geophys. Res. 99: 9977–9974.

_____, Lei Ren, R. Dunbar and S. Howe. 2000. El Niño Southern Oscillation (ENSO) and decadal-scale climate variability at 10 N in the eastern Pacific from 1893 to 1994: a coral-based reconstruction from Clipperton Atoll. Paleoceanography 15: 322–335.

Lough, J. and D. Barnes. 2000. Environmental controls on growth of the massive coral Porites. J. Exp. Mar. Biol. Ecol. 245: 225–243.

Maté, J. 1997. Experimental responses of Panamanian reef corals to high temperature and nutrients. Proc. 8th Int'l. Coral Reef Symp., Panama 1: 515–520.

Prahl, H. von and B. Vargas-Angel. 1990. Tasa de crecimiento del coral Pocillopora damicornis en un arrecife costero del Pacífico Colombiano. Rev. Cienc. Univ. del Valle 2: 37–44.

Quinn, W. 1993. The large-scale ENSO event, the El Niño and other important regional features. Bull d'Institut Francais d'Etudes Andines 22:13–34.

Ramírez, P. 1983. Estudio meteorológico de los Veranillos en Costa Rica. Nota de Investigación No. 15, Instituto Meteorológico Nacional, San José, Costa Rica. 24 p.

Risk, M. and T. Pearce. 1992. Interference imaging of daily growth bands in massive corals. Nature 358: 572–573.

Reynolds, R. and T. Smith. 1994. Improved global sea surface temperature analyses. J. Clim. 7: 929–948.

Stumpf, H. and R. Legeckis. 1977. Satellite observations of mesoscale eddy dynamics in the eastern equatorial Pacific. J. Phys. Oceanogr. 7: 648–658.

Swart, P. and R. Dodge. 1997. Climate records in coral sekeletons. Proc. 8th Int'l. Coral Reef Symp., Panama 2: 1695–1696.

Trenberth, K. and T. Hoar. 1996. The 1990–1995 El Niño–Southern Oscillation event: longest on record. Geophys. Res. Lttrs. 23: 57–60.

_____ and T. Hoar. 1997. El Niño and climate change. Geophys. Res. Lttrs. 24: 3057–3060.

Waylen, P. and M. Laporte. 1999. Flooding and the El Niño–Southern Oscillation phenomenon along the Pacific coast of Costa Rica. Hydrol. Process 13: 2623–2638.

Wellington, G. 1982. An experimental analysis of the effects of light and zooplankton on coral zonation. Oecologia 52: 311–320.

_____ and R. Dunbar. 1995. Stable isotopic signature of El Niño–Southern Oscillation events in eastern tropical Pacific reef corals. Coral Reefs 14: 5–25.

_____ and P. Glynn. 1983. Environmental influences on skeletal banding in eastern Pacific (Panamá) corals. Coral Reefs 1: 215–222.

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