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CORAL BLEACHING AND MORTALITY ASSOCIATED WITH THE 1997–98 EL NIÑO IN AN UPWELLING ENVIRONMENT IN THE EASTERN PACIFIC (GULF OF PAPAGAYO, COSTA RICA)

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ABSTRACT

Coincidental with the 1997–98 El Niño, overall coral bleaching (32.4% of all colonies) and mortality (5.7%) were observed on the Pacific coast of Costa Rica, in the seasonally cool waters of the Gulf of Papagayo and in the more thermally stable waters of Golfo Dulce. At a *Pavona clavus* reef (Culebra Bay, Gulf of Papagayo), mean seawater temperature at 7 m depth ranged from 0.2° to 3.9°C warmer than in previous years for nearly all months during 1997 and 1998. Water column temperature to 25–30 m depth was above 29°C for several days, which exceeded the long term average. Even though mortality was low for most coral species, it was severe (>90% decrease in live cover) in a small population of *Leptoseris papyracea* known only at Culebra Bay. *Pocillopora* spp. accounted for more than 60% and 80% of all bleached and dead colonies, respectively. Other coral species regained their normal pigmentation by the beginning of 1998 with little evidence of tissue mortality. The El Niño event of 1997–98 is considered the strongest on record by some measures, but coral mortality on the Pacific coast of Costa Rica was much less than in previous events, drawing attention to El Niño disturbance variability on local scales.

Increases in seawater temperature (SWT) associated with El Niño warming events cause high mortalities in many benthic organisms, especially reef-building (zooxanthellate) corals (Glynn, 1984; 1990; Robinson, 1985). At specific sites in the tropical eastern Pacific, unusually high SWT (≥30°C) can persist for weeks or months during a warming event (Podestá and Glynn, 1997), exceeding the physiological thermal tolerance limits of corals (Jokiel and Coles, 1977; Glynn and D'Croz, 1990). Coral mortalities of 50–100% were associated with the 1982–83 El Niño in the eastern Pacific (Glynn et al., 1988), interrupting 300 yrs of reef accretion (Colgan, 1990; Glynn and Colgan, 1992), and reducing populations of some coral species to near extinction (Glynn, 1997).

The impact of recent El Niño warming events has been studied at several localities in Costa Rica. Extensive coral bleaching and mortality were observed during the 1982–83 event (Cortés et al., 1984), resulting in about 50% mortality at Caño Island, off the south coast of Costa Rica (Guzmán et al., 1987), and up to 90% at offshore Cocos Island (Guzmán and Cortés, 1992). Coral bleaching associated with the 1991–92 El Niño was observed at Caño Island (30–80% of all colonies, Guzmán and Cortés, this issue) and at three localities off the central Pacific coast of Costa Rica (>50% of all colonies, Jiménez and Cortés, 2001).

The recent 1997–98 El Niño warming event, considered the strongest on record by some measures (Chavez et al., 1999; McPhaden, 1999a; Enfield, this issue), caused an estimated $33 billion in damage and 23,000 deaths worldwide (Kerr, 1999). This event modified oceanographic features such as sea level in the eastern Pacific (Nerem at al., 1999), current dynamics in the South China Sea (Yin et al., 1999), and day length (Dickey et al., 1999). The mass coral bleachings of 1997–98, coincident with the 1997–98 El Niño, are believed to be the most severe on record (ISRS, 1998). Coral reefs were severely affected in the Indian Ocean with shallow reef coral mortalities of up to 90%

(Wilkinson et al., 1999), and on the Australian Great Barrier Reef where the dominant acroporids suffered over 70% mortality at Orpheus Island (Baird and Marshall, 1998). In Costa Rica, the warming event affected corals as early as May 1997, peaked during August–October of that year and continued on a lesser scale until the first half of 1998.

This study documents coral bleaching and mortality associated with the 1997–98 El Niño at Culebra Bay and in the Murciélagos Islands (Fig. lA,B), areas known locally as Papagayo. This region, also known as the Gulf of Papagayo, experiences seasonal upwelling (Stumpf and Legeckis, 1977). Observations were also made at a small reef at Sándalo, Golfo Dulce, a nonupwelling site off the south coast of Costa Rica (Fig. lA).

MATERIALS AND METHODS

STUDY SITES.—The Murciélagos Islands (Fig. lA) support well developed coral communities (Cortés, 1996–1997). Twelve coral species are known from this area, with *Pocillopora* spp. and *Pavona* spp. being the most abundant taxa. Coral bleaching observations were restricted to the leeward side of San José, Cocineras, San Pedrito (hereafter *Pocillopora* spp. reef) and Golondrina Islands. (In this paper, coral reefs refer to structural reefs, i.e., to formations of living corals that accrete onto dead modern skeletal frameworks.) The small *Pocillopora* spp. patch reef (~0.3 ha) has low topographic relief, low diversity and high live coral cover (LCC) (47.5 to 95.2%; pocilloporid corals account for ~62% of the total live cover). Various coral communities formed of mixed assemblages of species are found in Culebra Bay, south of the Murciélagos Islands (Fig. 1). Twenty coral species have been reported from the Culebra Bay area (Jiménez, 2001a). Monitoring for bleaching was conducted in coral communities on basalt or sand substrates located around Palmitas, Viradores and Pelonas islands (Fig. lB, ~19–21% LCC mainly *Pocillopora* spp.) and on two patch reefs (Fig. lB), one constructed by *Pavona clavus* (hereafter *Pavona* reef; 0.8 ha, ~57% LCC) and the other by *Leptoseris papyracea* (hereafter *Leptoseris* reef 2.5 ha, ~58% LCC). Other coral species are present at both reefs, but their contribution to LCC is <30%. The patch reef at Golfo Dulce, Sándalo (hereafter Golfo Dulce, Fig. lA) has relatively low LCC (~29%), low topographic relief, moderate extension (4 ha), and is built mainly by *Porites lobata*, *Pocillopora damicornis* and *Pocillopora elegans* (Cortés, 1992; pers. obs.).

SUBSURFACE SEAWATER TEMPERATURE.—Four Hobo-Temp and Stow-Away (Onset Computer Inc.) underwater temperature data loggers (± 0.5°C accuracy) were used to monitor SWT at 7 m depth in Culebra Bay (Fig. 1). The thermistors were deployed on the *Pavona* reef from May 1997 to December 1998, and on the *Leptoseris* reef from August 1997 to December 1998. The data loggers were placed among coral colonies 10–20 cm above the bottom and set to record every 36 min. The units were replaced every month. Short-term temperature recordings (1–6 days) were also made at the Murciélagos Islands (7 and 12 m depth, *Pocillopora* spp. reef) and Golfo Dulce (5 m, *P. lobata*/*Pocillopora* spp. reef) during the bleaching event of 1997. In addition, SCUBA divers at Culebra Bay (May 1997 to March 1998) and at Murciélagos Islands (October 1997) recorded temperatures with a calibrated mercury thermometer (0.1ºC precision) to a depth of 20–30 m. The Bartlett and Hardy tests were used to evaluate the normality of data and the Cochran test the heterogeneity of variances (Underwood, 1981, 1997). When non-normality and heterogeneity of variances were significant ($P < 0.05$), the square root transformation was applied (Sokal and Rohlf, 1995). These results were compared with temperature data for the same localities and dates (Jiménez, 1998, 2001b) from previous years (1995–96), using Statistica ver. 5 analytical software. To identify the source of significant variation between months, a post hoc group analysis (Tukey HSD test) was utilized.

For waters ~65 km from the study area, weekly mean sea surface temperatures (SST) during the 1982–83 and the 1997–98 El Niño events were compared utilizing Reynolds NCEP optimal interpolation analysis data sets (1×1 degree grid centered on 10.5ºN, 86.5ºW). These data are based on SST fields blended from buoys, ships and bias-corrected satellite data (Reynolds and Smith, 1994).

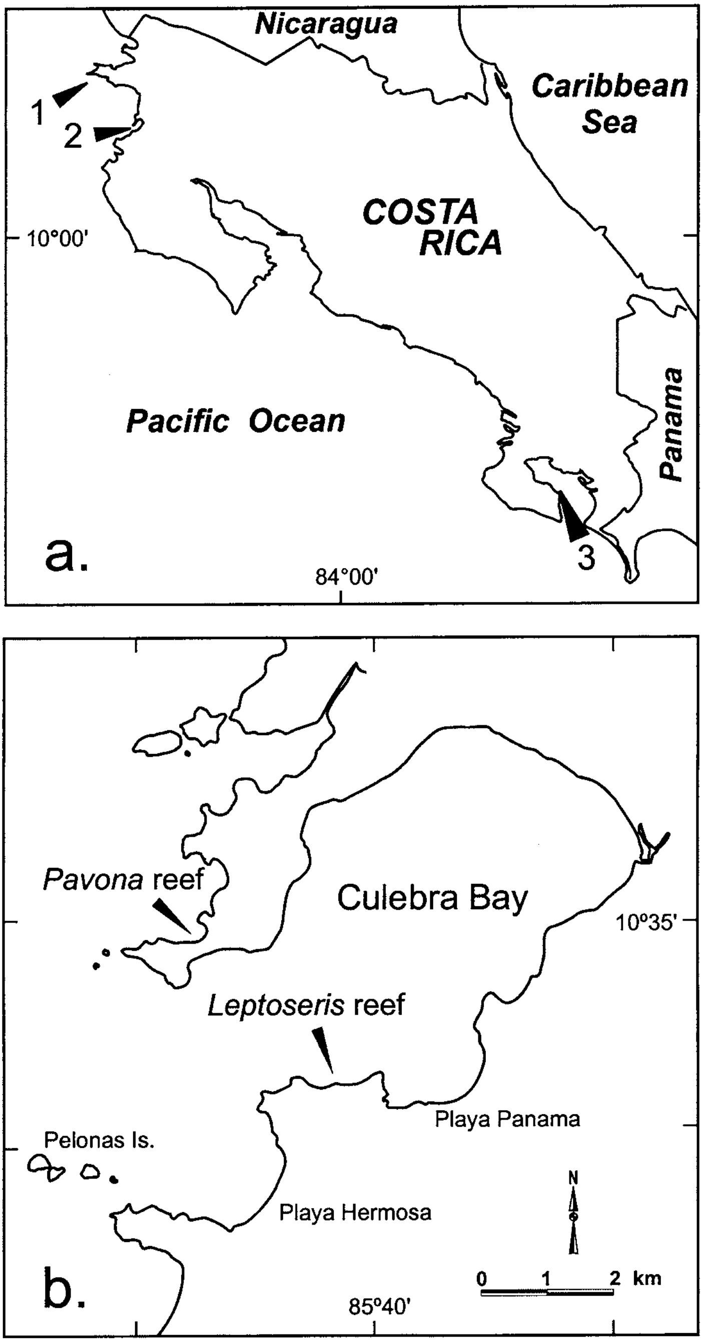

Figure 1. Locations of the coral bleaching study sites (a) on the Pacific coast of Costa Rica, and the in situ temperature recorders (b) at Culebra Bay. 1. Murciélagos Islands, 2. Culebra Bay, 3. Golfo Dulce (Sándalo).

CORAL BLEACHING OBSERVATIONS.—Coral communities were monitored for bleaching by diving at the study sites 3–4 d mo^{-1} from 1997 to 1998 (Culebra Bay), two d in July 1997 (Golfo Dulce), and six d in October 1997 (Murciélagos Islands). Bleaching was quantified at Culebra Bay (4–12 m depth) and in the Murciélagos Islands (4–8 m) by counting the number of colonies of all species in a 100 m-long × 4 m-wide transect positioned haphazardly across the study sites. At Golfo Dulce (3–6 m), coral communities were assessed in a 50 m × 2 m transect laid across the study site. A colony was scored as bleached if more than 5% of the colony surface area was white or pale, and dead if it was recently overgrown by algae. Changes in bleached surface areas in two massive *P. clavus* (2.5 and 10 m diameter approx.) and seven *Pavona gigantea* (0.25–0.60 m diameter) colonies were measured from nails marking the limits of bleaching from July to December 1997. At the *Leptoseris* reef in Culebra Bay, high mortality of this very small coral occurred during the onset of the El Niño warming event (May 1997). The percent of live and dead *L. papyracea* was recorded in April and May 1996, June 1997, and February 1998 with a 10 m long chain (1.1 cm link^{-1}) laid parallel to the shoreline and across the study site (15 m depth). Additionally, live cover loss was monitored with the aid of iron rods driven into the periphery of the assemblage in May 1996 (Jiménez, 1998). Percent coral cover was transformed (arcsine) before statistical testing.

RESULTS

SEAWATER TEMPERATURE.—Subsurface water temperatures at the *P. clavus* reef were significantly warmer for nearly all months during the study period (May 1997 to December 1998) when compared with the available temperature data from previous years (Table 1). Only April 1998 was not significantly different from April 1995 (Tukey, $P > 0.05$). Subsurface temperatures were colder in May 1996 and 1997 than in May 1995 and 1998 (Tukey, $P < 0.05$). Monthly mean temperatures were higher during the first two thirds of 1998, with differences in the range of 0.2° to 2.9°C, than in previous years. The largest temperature difference occurred in February 1996, usually the time of year with the lowest monthly average temperature (25.5° ± 1.8°C, Table 1). From December 1997 to April 1998 (upwelling months), water temperature was 1.0° to 2.9°C higher than in previous years.

The last third of 1997 (September–December) was the warmest period with mean differences from 1998 in the range of 0.9° to 2.4°C. September and October of 1997 had the highest monthly mean temperatures (30.0° ± 0.5°C and 29.9° ± 0.1°C, respectively, Table 1), with the lowest mean temperature (May) 2°C higher than the lowest temperature in 1998 (December). The number of days with mean temperatures above 29°C for September and October in 1997 was 54 (Fig. 2), compared with 17 for the same period in 1998. Furthermore, water temperature was above 30°C for 32 consecutive days from 17 September to 20 October 1997. In general, 1997 had higher mean monthly temperatures (0.9–2.4°C) than in 1998 and, considering all shared months (May to December), it was a significantly warmer year (29.1° ± 1.0°C, $t = 28.26$, $P < 0.0001$, df=15,180) than 1998 (28.6° ± 1.6°C).

Monthly mean SWT at 7 m depth at the *P. clavus* and *L. papyracea* reefs was significantly warmer at the latter site during four months of the comparison period (Table 2). The greatest differences (0.30°–0.66°C) were observed in August, October and November of 1997. Although mean monthly temperatures at both reefs followed similar patterns, there were significant daily variations according to the tidal regime and exposure of the reefs to upwelling pulses.

Mean SWT at the Murciélagos Islands and Golfo Dulce, as measured by data loggers, was high during our visits in 1997. At the Murciélagos Islands, approximately 40 km

Table 1. Monthly temperature (ºC) means (standard deviation) at 7 m depth, *Pavona* reef, Culebra Bay. Square root transformations were performed before statistical testing. df, degrees of freedom; F and t, statistics; P, probability. Data for 1995 and 1996 from Jiménez (1998, 2001b).

Month	1995	1996	1997	1998	df	F	t	P
Jan	26.6 (0.2)	–	–	27.8 (0.8)	908	–	11.3	<0.0001
Feb	–	25.5 (1.8)	–	28.4 (1.2)	1,947	–	41.6	<0.0001
Mar	–	26.0 (2.5)	–	27.6 (2.3)	2,467	–	16.7	<0.0001
Apr	28.3 (0.7)	27.4 (2.6)	–	28.5 (1.6)	2	93.43		<0.0001
May	28.9 (0.7)	28.1 (1)	28.1 (0.8)	29.5 (0.8)	3	525.87	–	<0.0001
Jun	–	–	28.8 (2.1)	29.8 (0.4)	2,434	–	17.1	<0.0001
Jul	27.8 (1.3)	–	28.9 (0.6)	29.5 (0.4)	2	1,546.71	–	<0.0001
Aug	28.2 (0.6)	–	28.9 (0.6)	29.5 (0.5)	2	1,391.55		<0.0001
Sep	–	–	30.0 (0.5)	29.1 (0.7)	3,435	–	41.4	<0.0001
Oct		–	29.9 (1.1)	28.2 (0.6)	2,555	–	45.2	<0.0001
Nov	–	–	28.8 (0.3)	26.7 (1.2)	4,078	–	79.6	<0.0001
Dec	–		28.5 (0.4)	26.1 (1.6)	1,359	–	54.2	<0.0001

north of Culebra Bay (Fig.1), SWT was significantly warmer (29.2º ± 0.2ºC, t = 21.21, P < 0.0001, df = 827) at 7 m depth than at 12 m (28.9º ± 0.3ºC) during six days in October 1997. The lowest temperature (28.4ºC at 12 m) was recorded during the initiation of an off-season upwelling event. At Golfo Dulce (Fig. 1), water temperature at 7 m was 29.9º ± 0.3ºC (range 29.3–30.6ºC) during two d in July 1997. Culebra Bay was warmer (30.3º ± 0.5ºC, t = 36.6, P < 0.0001, df = 663) than the Murciélagos Islands area and slightly less warm (29.3º ± 0.4ºC, t = 17.73, P < 0.0001, df = 300) than Golfo Dulce for the corresponding periods of time.

Temperature readings made by divers at different localities around Culebra Bay, recorded values above 29°C to depths of 25–30 m from August to October 1997 (Table 3). In November 1997, water temperature was still around 28.8ºC at 21–25 m. Variation in SWT was slight (<0.5ºC) between 10–15 m depth, and below 21 m from September to November 1997. In January and February 1998, the variation in temperature was 0.7ºC, and in March it was 1.9ºC. In the Murciélagos Islands, water temperatures above 28ºC were recorded at relatively shallow depths (Table 3); SWT was 25.5–26.0ºC at 26–30 m depth. The difference between the mean temperatures at 10–15 m and deeper was 0.5ºC. In general, mean water column temperature at the Murciélagos Islands (27.6º ± 0.8ºC) was significantly lower than at Culebra Bay (29.8º ± 1.1ºC, t = 10.07, P < 0.0001, df = 43) in October 1997.

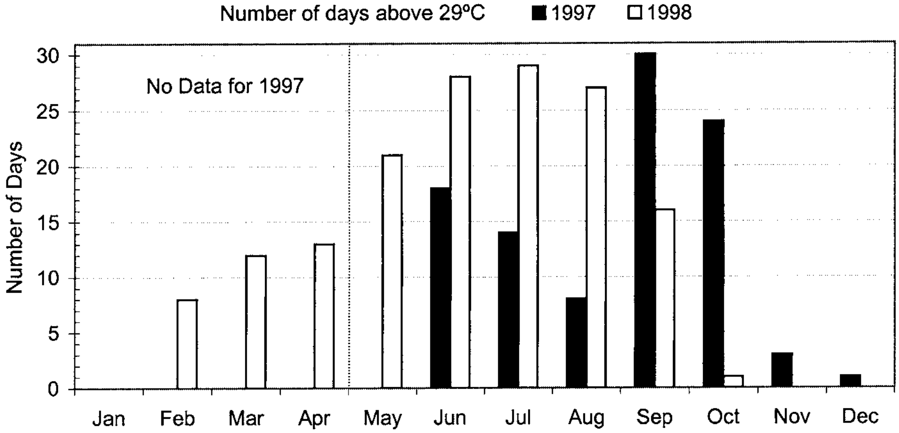

Figure 2. Number of days the daily mean seawater temperature (7 m depth) was above 29°C at the *Pavona* reef site, Bahía Culebra. Temperature recorders were installed in mid May 1997.

A comparison of weekly mean Reynolds SSTs in the Gulf of Papagayo during the 1982–83 and 1997–98 El Niño events reveals SSTs ≥29ºC for 33 consecutive wks in 1983, with 14 wks above 30ºC (Fig. 4A). In contrast, two prolonged warming periods occurred in 1997–98, the first over 28 consecutive wks in 1977 and the second for 26 wks (2 wks above 30ºC) the following year. In situ SWT at Culebra Bay (*Pavona* reef) during the 1997–98 El Niño showed marked deviations from the Reynolds SST data for the corresponding period (Fig. 4B). While both temperature records exhibited a roughly

Table 2. Differences in mean monthly temperature (ºC) at 7 m depth in *Pavona clavus* and *Leptoseris papyracea* reefs, Culebra Bay. Data were transformed utilizing the square root function. df, degrees of freedom; t, statistics; P, probability; N.D., no data due to unit failure.

Month	*Pavona*	*Leptoseris*	Difference	df	t	P
1997						
Aug	28.82	29.48	–0.66	291	10.41	<0.0001
Sep	30.00	29.95	0.05	3,418	3.07	0.0021
Oct	29.87	29.51	0.36	1,708	10.92	<0.0001
Nov	28.78	29.08	–0.30	3,404	33.34	<0.0001
Dec	28.55	28.43	0.12	2,691	8.81	<0.0001
1998						
Jan	27.84	27.71	0.13	1,698	3.24	0.0012
Feb	28.38	28.40	–0.02	2,255	0.44	0.6585
Mar	27.63	27.61	0.02	2,457	0.13	0.8978
Apr	28.52	28.58	–0.06	2,397	0.90	0.3663
May	29.48	29.40	0.08	2,333	2.33	0.0200
Jun	29.85	N.D.	–	–	–	–
Jul	29.52	29.55	–0.03	2,392	2.36	0.0183
Aug	29.53	29.59	–0.06	2,478	3.68	0.0002
Sep	29.10	28.96	0.14	2,353	4.54	<0.0001
Oct	28.24	28.08	0.16	2,364	5.15	<0.0001
Nov	26.73	26.70	0.03	2,368	0.63	0.5335
Dec	26.05	26.15	–0.10	2,381	1.46	0.1442

Table 3. Subsurface water temperature (ºC) ±1 SD measured by divers at Culebra Bay and Murciélagos Islands. n = number of measurements.

Location Month	10–15 m	16–20 m	21–25 m	26–30 m
Culebra Bay				
1997				
May	26.9 ± 1.9 n = 16	26.2 ± 1.6 n = 4	26.0 ± 1.6 n = 8	25.7 ± 1.5 n = 3
Jun	24.7 ± 2.9 n = 17	24.6 ± 3.9 n = 7	25.7 ± 3.6 n = 6	22.1 ± 3.8 n = 6
Jul	28.6 ± 1.1 n = 21	25.6 ± 1.2 n = 3	25.0 ± 0.9 n = 3	–
Aug	30.9 ± 0.9 n = 19	28.8 ± 1.0 n = 3	28.8 n = 1	–
Sep	30.3 ± 1.3 n = 17	30.2 ± 1.2 n = 5	30.6 ± 0.9 n = 12	–
Oct	30.0 ± 1.4 n = 16	29.4 ± 0.6 n = 11	30.0 ± 0.1 n = 3	30.0 n = 1
Nov	29.0 ± 0.6 n = 25	28.7 ± 0.2 n = 4	28.8 ± 0.2 n = 2	
Dec	28.7 ± 0.5 n = 26	27.5 ± 0.1 n = 4	–	–
1998				
Jan	27.6 ± 0.4 n = 18	26.9 ± 0.2 n = 7	–	–
Feb	27.0 ± 1.0 n = 26	26.2 ± 0.6 n = 7	26.3 ± 0.3 n = 3	–
Mar	28.1 ± 1.3 n = 17	26.7 ± 0.5 n = 9	26.2 ± 0.3 n = 2	–
Murciélagos Is.				
1997				
Oct	28.0 ± 0.4 n = 16	27.6 ± 0.6 n = 9	27.2 ± 0.5 n = 16	25.7 ± 0.3 n = 4

similar trend, Reynolds SSTs were more uniform, not showing the abrupt thermal swings and extremes that occurred at 7 m depth on the reef.

CORAL BLEACHING.—The first signs of bleaching and mortality at the *Leptoseris* reef in Culebra Bay (Fig. 1) were documented during the first visit of the year in mid May 1997. Dead and bleached colonies of *L. papyracea* were observed at 15 m depth and bleached *Fungia* (*Cycloseris*) *curvata* individuals at 12 m. However, it was not until June 1997 that severe bleaching and mortality were observed in *L. papyracea*, and six other coral species, at several reefs and coral communities to a depth of 15 m (Table 4). In general, affected pocilloporid species showed almost complete bleaching along the bathymetric range at which they occur in Culebra Bay (1–10 m). Bleached massive corals had discolored or white patches on both their upper surfaces and shaded bases, covering more than two-thirds of each colony. No additional bleaching was observed in *P. clavus* and *P. gigantea* colonies marked with nails in July 1997, or in any other colonies. By August, the bleached

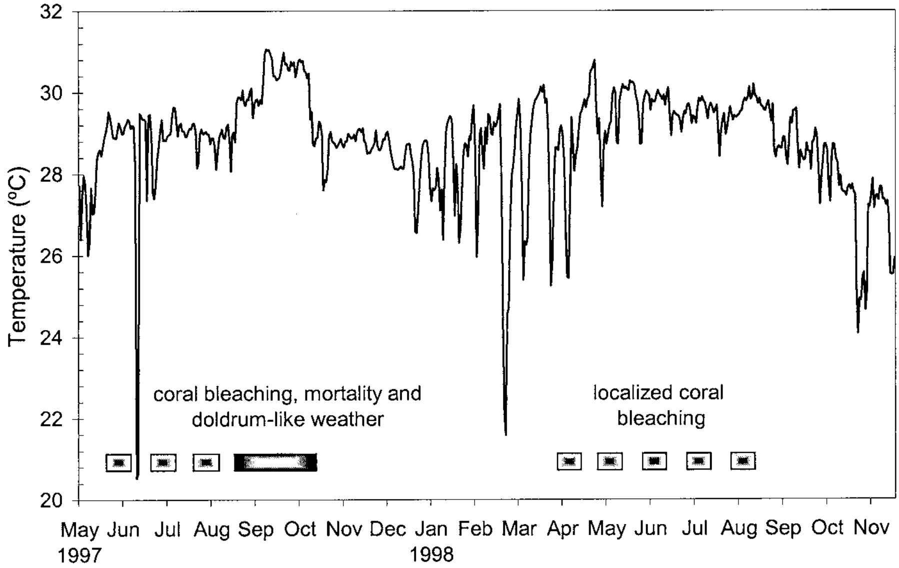

Figure 3. Daily mean seawater temperature at the *Pavona* reef (7 m depth), Bahía Culebra, from 15 May 1997 to 31 December 1998. Horizontal shaded blocks denote periods of coral bleaching and mortality.

patches and nails were covered with filamentous algae. However, in September 1997 the living coral tissue started to advance, overgrowing the sediment-coated, dead areas completely by January 1998. These bleached colonies were interspersed among normal appearing colonies of smaller dimensions, which did not bleach during the bleaching episode or in subsequent months.

The occurrence of bleached colonies at Culebra Bay peaked during August–October 1997 when mean daily SWT (7 m depth) was above 29°C. This period coincided with doldrum-like weather conditions and sparse cloud cover. Such conditions prevailed for almost 40 days, until the end of October (Fig. 3). The most commonly bleached corals (>50% of colonies) were *Pavona varians*, *P. lobata* and the azooxanthellate coral *Tubastraea coccinea* (Table 4). Mortality was observed in eight species and ranged between 0.7 to 11% (Table 4). *L. papyracea* (not shown in Table 4 because its colonies were not counted, but instead measured by the chain transect method) suffered the highest mortality at Culebra Bay, with a decrease of 94.7% in live cover relative to a previous survey in April 1996 (Jiménez, 1997; Fig. 5). Mortality in *Leptoseris* continued until June 1997. In February 1998, the percentage of live coral cover was similar to that recorded in June 1997 ($t = 0.492$, $P = 0.6400$, $df = 8$), indicating, as previously suggested, that further significant mortality did not occur. In February 1998, the average distance between the reef periphery in May 1996 and the remaining live *Leptoseris* colonies was 1.0 ± 0.15 m (range 0.73–1.25 m, n = 11), showing the extent of contraction of this assemblage.

By February and March 1998, almost all of the coral colonies at Culebra Bay had recovered their normal coloration and further bleaching was not observed. However, in April 1998 a small patch (10 m^2) of *Pocillopora* spp., located on the peninsula in front of the Pelonas Islands (Fig. 1B), bleached and remained in this condition for five consecu-

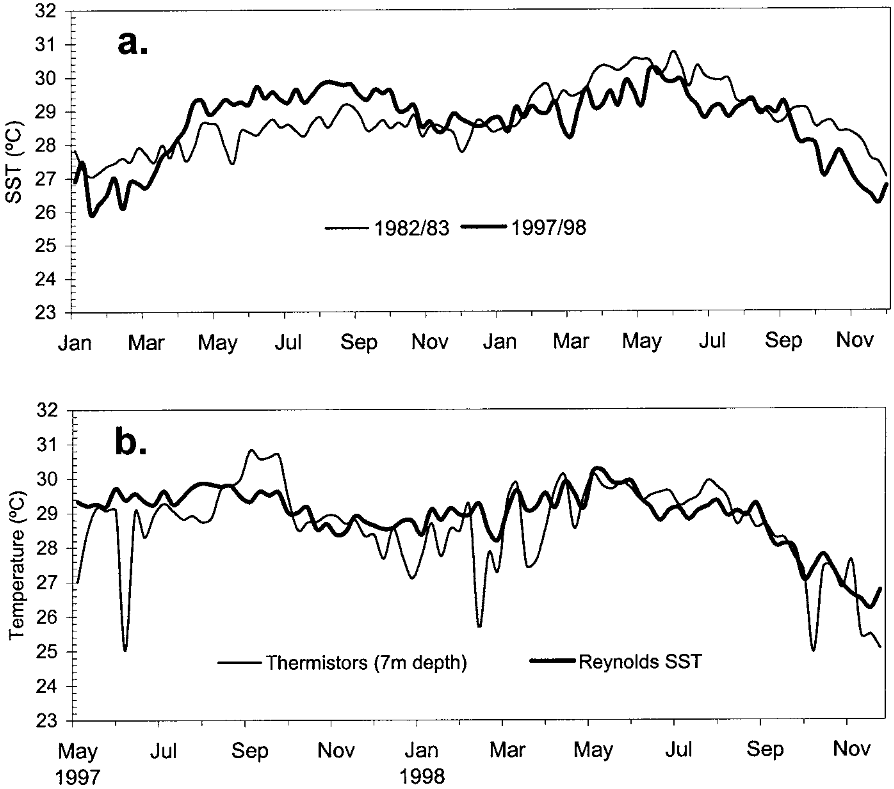

Figure 4. Comparison of weekly mean sea surface temperature (SST) (Reynolds NCEP optimal interpolation analysis) ~65 km offshore of the study area during the 1982–83 and 1997–98 El Niño events (a). In situ *Pavona* study reef temperature records at 7 m compared with Reynolds SSTs, 1997–98 (b).

tive months. This patch regained its normal appearance by September 1998 with no partial or total mortality of colonies evident.

Coral bleaching and mortality at the Murciélagos Islands were observed in October 1997, particularly in shallow sections (4–8 m) of one *Pocillopora* spp. reef (San Pedrito Island). Totally bleached corals were surrounded by normally-pigmented colonies, as was observed in Culebra Bay. Seventy-five percent of the colonies of *P. inflata,* a recently described species (Glynn, 1999) with a limited distribution in the eastern Pacific, were bleached (Table 4). Mortality of *P. inflata* was not observed at the time of the survey. Other affected species with more than 20% of bleached colonies were *P. damicornis*, *P. lobata* and *Pocillopora eydouxi* (Table 4). Coral mortality in the Murciélagos Islands was less than in Culebra Bay and occurred only in *P. elegans* (~3%), *P. damicornis* (~2%) and *P. gigantea* (~1%) (Table 4). One massive colony of *Gardineroseris planulata* (~1.5 m in diameter) had discolored or bleached patches colonized by filamentous algae alternating with normally pigmented areas (the same mortality pattern observed in two massive *P. clavus* colonies at Culebra Bay, see above).

At Golfo Dulce, more than 300 km south of Culebra Bay (Fig. 1), coral bleaching was observed in five coral taxa (Table 4). The most affected were *Psammocora* spp. (~75%), *P. elegans* (~63%) and *P. damicornis* (~61%). Only *P. damicornis* and *P. elegans* experi-

Table 4. Percentage of affected coral colonies (number of colonies) by species at the three sites examined in 1997. N = normal, B = bleached, D = dead.

Species	Culebra Bay 4–12 m, June–October			Murciélagos Islands 4–12 m, October			Golfo Dulce 3–6 m, July		
	N	B	D	N	B	D	N	B	D
Pocillopora elegans Dana 1846	61.3 (449)	31.5 (231)	7.2 (53)	84.3 (91)	13.0 (14)	2.8 (3)	32.6 (14)	62.8 (27)	4.7 (2)
Pocillopora damicornis (Linnaeus 1748)	54.0 (881)	35.0 (570)	11.0 (179)	70.8 (276)	27.2 (106)	2.1 (8)	26.7 (27)	61.4 (62)	11.9 (12)
Pocillopora eydouxi Milne Edwards & Haime 1860	74.8 (77)	25.2 (26)	0	79.3 (23)	20.7 (6)	0	–	–	–
Pocillopora meandrina Dana 1846	50 (24)	47.9 (23)	2.1 (1)	–	–	–	–		
Pocillopora inflata Glynn 1999	–	–	–	25 (6)	75 (18)	0	–		
Pavona clavus Dana 1846	58.7 (254)	37.4 (162)	3.9 (17)	88.4 (107)	11.6 (14)	0	75 (9)	25 (3)	0
Pavona gigantea Verrill l869	59.8 (55)	33.7 (31)	6.5 (6)	86.1 (192)	13 (29)	0.9 (2)	–		
Pavona varians Verrill l864	41.4 (12)	58.6 (17)	0	100 (13)	0	0	–		
Psammocora spp.	60.2 (350)	36.3 (211)	3.4 (20)	80.4 (86)	19.6 (21)	0	24.2 (8)	75.8 (25)	0
Porites lobata Dana 1846	50 (23)	50 (23)	0	76.2 (16)	23.8 (5)	0	68.6 (24)	31.4 (11)	0
Porites panamensis Verrill 1870	58.1 (81)	40.1 (55)	0.7 (1)	87.3 (62)	12.7 (9)	0	–	–	–
Gardineroseris planulata (Dana 1846)	100 (2)	0	0	96.7 (87)	3.3 (3)	0	–	–	–
Fungia (*Cycloseris*) *curvata* (Hoeksema 1989)	46.1 (18)	43.6 (17)	10.3 (4)	–	–	–	–	–	–
Tubastraea coccinea Lesson 1829	45 (18)	55 (22)	0	85.3 (64)	14.7 (11)	0	–	–	

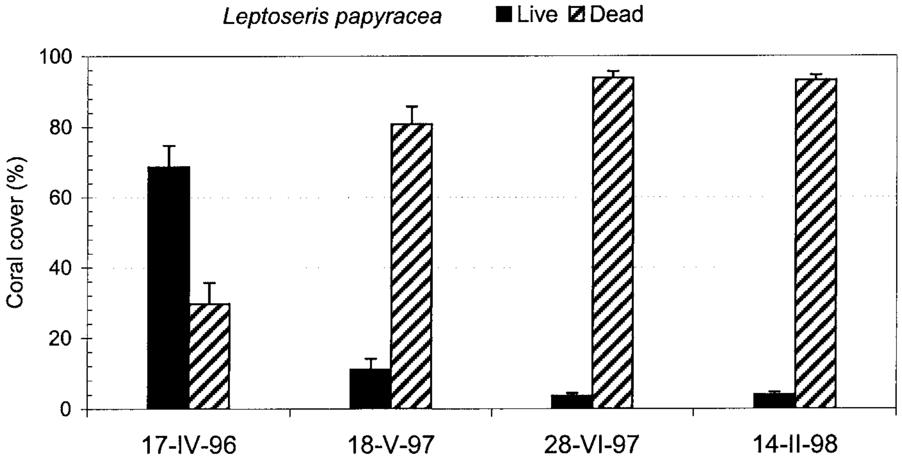

Figure 5. *Leptoseris papyracea* percent cover (chain transect method) at 15 m depth, Culebra Bay.

enced mortality (~12% and ~5% respectively) at the time of the survey in July 1997. Branching colonies bleached in a pattern similar to that observed in Culebra Bay and the Murciélagos Islands. Almost all sampled colonies of massive species (*P. clavus* and *P. lobata*) showed complete tissue bleaching.

Branching corals (*Pocillopora* spp.) had the highest percentage of bleached colonies in Golfo Dulce and the lowest in the Murciélagos Islands (Fig. 6A). Massive species (*P. clavus, P. gigantea*, *P. lobata*, *G. planulata*) were more affected in Culebra Bay than in the Murciélagos Islands, and although bleaching was high in Golfo Dulce (~30%), no mortality was observed (Fig. 6B). For crustose (*P. varians*, *P. panamensis*), nodular (*Psammocora* spp.), free-living (*F. curvata*) and cryptic (*T. coccinea*) coral species pooled (Fig. 6C), bleaching was highest in Golfo Dulce (~76%). In general, the highest mortality occurred in branching corals, while bleaching was prevalent in crustose, nodular, free-living, cryptic, and branching colonies. Bleaching and mortality were relatively low in most massive species (Fig. 6D).

Considering all coral species (excluding *L. papyracea,* which was quantified using the chain transect method) from the three study localities, only 32.4% of all colonies (n = 5409) bleached during the 1997–98 ENSO event, and overall mortality was 5.7% (Fig. 7A). Branching species comprised more than 80% of the dead corals. They formerly contributed 40 to 90% of the total live coral cover (Jiménez, 2001a). Comparing these results with the impact of the 1991–92 ENSO event (Fig. 7B) on corals along the central Pacific coast of Costa Rica (Jiménez and Cortés, 2001), it is evident that bleaching and mortality were higher during the earlier disturbance (57.3% and 8.8%, respectively). The abundant massive corals *(P. lobata*, *P. clavus)* and the nodular *Psammocora* spp. accounted for 28.8% and 66.3% of the total mortality, while the less common *Pocillopora* spp. suffered only 4.9% mortality (Fig. 7B).

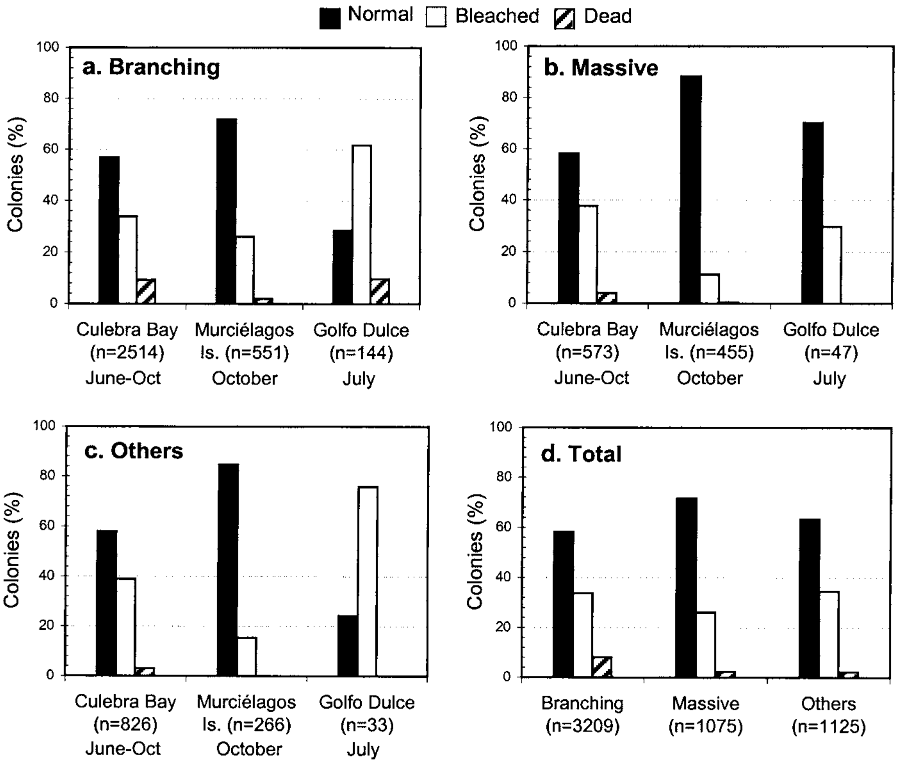

Figure 6. Percentage normal (black bars), bleached (open) and dead (striped) coral colonies at three study sites. Branching colonies = *Pocillopora* spp.; massive colonies = *P. clavus*, *P. gigantea*, *P. lobata* and *G. planulata*; other colony morphologies = *P. varians*, *P. panamensis*, *Psammocora* spp., *F. curvata* and *T. coccinea*.

DISCUSSION

During the onset of the 1997–98 El Niño warming event, coral bleaching and mortality were observed as early as May 1997, when large stands of *L. papyracea* bleached at 15 m in Culebra Bay. But it was not until June 1997 that other coral species started to bleach, showing partial or total mortality to a depth of 12 m. The extent of *L. papyracea* bleaching and mortality in May, and the thick carpet of algae and sponges growing over the dead colonies, suggest that mortality occurred 1–2 mo before our survey. Suspected mortality of *L. papyracea* in March–April is coincident with the arrival in the eastern Pacific of the first set of ENSO-generated Kelvin waves in December 1996/January 1997 (Chavez et al., 1998; McPhaden and Yu, 1999), which reached the Central American coast by February (Yu and Rienecker, 1998). The bleaching and mortality response may have occurred sometime after the initial temperature rise, as has been observed in experimentally heated corals (Berkelmans and Willis, 1999) and under natural conditions (Winter et al., 1998). Differences in monthly sea temperatures between the *Leptoseris* and *Pavona* reefs indicate that these areas are subjected to different microscale oceanographic conditions, and that one site can be warmer than the other during the same period. Therefore, it is possible that the warming at the *Leptoseris* reef was greater or occurred earlier than at the other reefs in Culebra Bay, which had experienced no coral bleaching as of May 1997.

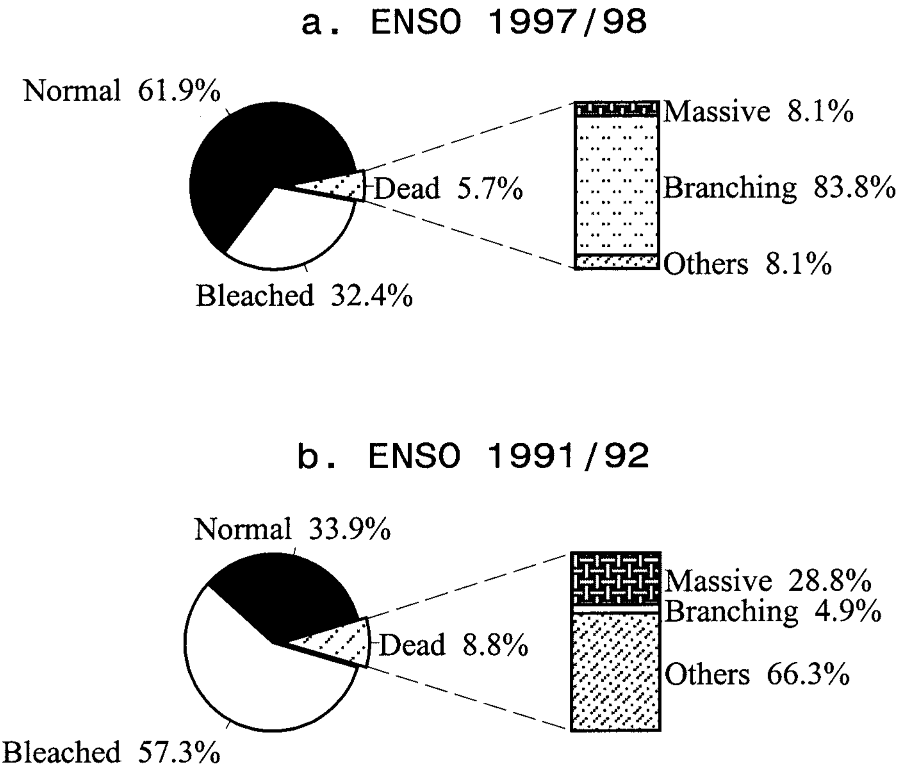

Figure 7. Percentage normal (black), bleached (white) and dead (striped) coral colonies observed during the 1997–98 (a) and 1991–92 (b) El Niño events at the Pacific coast of Costa Rica. Coral species colony morphologies as in Fig. 6.

The warming in Culebra Bay started during the Papagayo upwelling season (December–April), when corals at 12 m are normally exposed to temperatures as low as 12°C for a few hours and to 20°C for several days (Jiménez, 2001b). It is possible that corals such as *L. papyracea*, typically found in deep and cool waters (Dinesen, 1980), are seasonally acclimatized to lower temperatures during the upwelling season. A limited, possibly seasonal, thermal acclimatization has been observed in other coral species (Coles and Jokiel, 1978; Brown, 1997; Berkelmans and Willis, 1999). It may be the case that *Leptoseris* has a bleaching threshold that is lower during the upwelling season than that present in other coral species inhabiting shallow areas, which are not exposed to such low temperatures. Additionally, *L. papyracea* was shown to be very sensitive to temperature changes in all attempts to repopulate dead *Leptoseris* reefs at Culebra Bay (Jiménez, 1998).

For other coral species, bleaching and mortality were observed at Culebra Bay during 6 mo beginning in June 1997, and peaked after a rapid temperature increase, when SWT at 7 m depth exceeded 29°C for 97 d. During this period El Niño developed rapidly, setting record high temperatures in the eastern equatorial Pacific (McPhaden, 1999b). Doldrum-like weather conditions lasted for more than 50 consecutive days and were coincidental with the peak months (September–October) of coral bleaching and mortality. Water column temperature was above 30°C to a depth of 25–30 m for several days. An unusual continuation of the mid-year (usually June) decrease in precipitation and doldrum-like weather, known as ‘Veranillo de San Juan’ in Costa Rica, also occurred during the 1982–83 El Niño event (Ramírez, 1983). Doldrum-like weather, when coastal waters are clear and calm, facilitate light penetration, increasing the irradiance levels reaching corals. In 1997, water visibility (>25 m) and light penetration increased during the doldrum-like weather conditions over Culebra Bay, while the year 1998 had very few days with clear waters (less than 10 m visibility, see below). Bleaching has been observed when high water temperatures, and the likely synergistic effect of increased irradiance (Goreau and Hayes, 1994; Glynn, 1996), increase the sensitivity of zooxanthellae to photoinhibition (Hoegh-Guldberg and Jones, 1999). Bleaching also has been observed after sudden temperature increases during the normally warmest months of the year (Winter et al., 1998). Calm weather conditions preceded and accompanied the progression of the bleaching event at Culebra Bay, as has been observed on the Australian Great Barrier Reef (Harriot, 1985), in the Florida Keys (Causey, 1988), French Polynesia (Drollet et al., 1994), and the Caribbean coast of Costa Rica (Cortés et al., 1984; Jiménez, 2001c). Despite this, calm spells have not accompanied other bleaching events, such as the 1993 episode in the US Virgin Islands (Quinn and Kojis, 1999). Worthy of note, the two bleaching episodes in Culebra Bay (from August to October 1997, and from April to August 1998, Fig. 3) also occurred in the Gulf of Chiriquí, Panama (Glynn et al., this issue) and at Gorgona Island, Colombia (Vargas-Ángel et al., this issue). Although the timing of bleaching was not identical at these widely separated localities (3–11° N), the height of each bleaching episode corresponded closely with the local maximum sustained sea temperatures.

Except for *L. papyracea,* coral mortality during 1997–98 was generally low at the three study localities and was concentrated mostly in Culebra Bay (>90% of the total mortality). We consider this mortality pattern valid, despite the different observation times at the three localities in 1997 (>30 d at Culebra Bay, 6 d at Murciélagos Islands, and 2 d at Golfo Dulce). Additional coral mortality was not observed at the Murciélagos Islands in February, April, or from June to October 1998 (G. Bassey, pers. comm. 1999), nor during a visit to this site in May 1999. This suggests that most mortality at the Murciélagos Islands occurred during the few months before our visit in October 1997, and decreased thereafter. Similarly, coral mortality was observed mainly before November 1997 in Culebra Bay, but not afterwards. Although our surveys at Golfo Dulce were conducted during July 1997, additional coral mortality was not observed in subsequent visits in 1998 (E. Ruíz, pers. observ.).

The relatively high percentage of coral mortality at Culebra Bay could be attributed to local oceanographic conditions, which can change the rate of warming. For example, the 1997 off-season occurrence of upwelling in June (Culebra Bay, Fig. 3) and October/November (Murciélagos Islands), due to an unusual intensification of Trade Wind strength at that time of year (IMN, 1998), may have interrupted sea warming, thus lowering the impact of high temperature stress on corals. Intensification of the Trade Winds over the northern Costa Rican Pacific coast has been observed during other El Niño warming events (Fernández and Ramírez, 1991; Amador and Alfaro, 1996), and this occurs in the second half of years during ENSO events. Mean SWT at 7 m and throughout the water column was significantly lower (0.8° and 2.2°C, respectively) at the Murciélagos Islands area than in Culebra Bay during October 1997. The former area is more exposed to oceanic conditions and Papagayo upwelling than the latter (A. Gutiérrez, pers. comm. 1997), thus lessening the impact of the warming event there. In addition, upwelling was absent at Culebra Bay during the doldrum-like weather, which occurred after June 1997.

Although coral colonies recovering from mass coral reef bleaching events elsewhere have suffered moderate to heavy mortality (Williams and Bunkley-Williams, 1990), the majority of colonies at Culebra Bay recovered their normal pigmentation by the beginning of 1998 with only slight tissue mortality. Tissues in large *P. clavus* and medium-sized *P. gigantea* colonies completely overgrew the dead areas in 7 mo. Even though bleaching strongly compromises tissue damage repair (Mascarelli and Bunkley-Williams, 1999), it has been suggested that large colonies have more energy available for regeneration (Loya, 1976; Bak, 1983). That large colonies often have sizeable areas of healthy tissue (with apparently normal densities of symbiotic zooxanthellae) directly surrounding bleached patches, tissue regeneration may be accelerated by the translocation of energy (Mascarelli and Bunkley-Williams, 1999). This would lead to a more rapid recovery of damaged areas (Meesters et al., 1997). It is also important to consider that partial bleaching may result from physiological and/or genetic variation in different parts of the same host colony (Brown, 1997) or differences in the environmental tolerances of zooxanthella strains within a colony (Muller-Parker and D'Elia, 1997; Rowan et al., 1997; Glynn et al., this issue). These same factors may also contribute to differential responses among and within coral colonies.

We cannot rule out the possible selective effects of the 1982–83 and 1991–92 El Niño events on the survivorship of more tolerant colonies or clones to elevated temperature stress, together with a limited ability of corals to acclimatize. Branching corals, severely impacted during the 1982–83 El Niño event in the eastern Pacific (Glynn, 1984, 1990; Guzmán et al. 1987; Guzmán and Cortés, 1993), with mortalities greater than 80%, fared quite well during the 1997–98 event, with only 8% mortality at the three sites investigated here. Similar conclusions can be drawn when comparing coral mortality in the Gulf of Panama, another upwelling area in the eastern Pacific. Total coral mortality was ~85% during the 1982–83 warming event, and this was associated with the normally lower, more variable temperatures in the Gulf of Panama (Glynn et al., 1988). We report here less than 6% overall coral mortality on the Pacific coast of Costa Rica coincident with the 1997–98 El Niño event, despite sustained temperatures ≥ 30ºC that resulted in 51% overall coral mortality at Caño Island, Costa Rica in 1983 (Glynn et al., 1988). However, the fact that some coral reefs have bleached repeatedly during every major ENSO event suggests that there have been no major shifts in reef community structure in favor of heat tolerant taxa (Hoegh-Guldberg, 1999). This possibility needs to be investigated at local scales or on specific reefs where coral responses to warming stressors demonstrate varied patterns.

It is particularly surprising that the 1982–83 El Niño was more detrimental to eastern Pacific coral reefs than the 1997–98 event because the latter event appears to have been as strong as (or stronger than) the former (Chavez et al., 1999; McPhaden, 1999a; Enfield, this issue). While the intense phase of the 1982–83 ENSO was fairly short (4 mo), peaking in April–May 1983 (Hansen, 1990), the intense phase of the 1997–98 El Niño was much longer, from spring 1997 to spring 1998 (Chavez et al., 1999; McPhaden, 1999a,b; Enfield, this issue; Podestá and Glynn, this issue). This suggests that physical factors alone may not determine the bleaching response of coral reefs to thermal stress (Williams and Bunkley-Williams, 1990; Brown et al., 1994; Glynn, 1996; Hoegh-Guldberg, 1999). This conclusion is supported by the observation (documented in reports to NOAA's Coral

Health and Monitoring Program) that reefs in the far eastern Pacific showed significant variation in their affected species, degree of bleaching and eventual mortality. Local differences in oceanographic conditions that affect the length and rate of warming (Glynn et al., 1988; Glynn, 1993, 1996; Fong and Glynn, this issue) are likely to play a role in explaining the incidence and severity of bleaching at particular sites. The differences between nearshore SWTs at Culebra Bay and the more exposed Murciélagos Islands (both measured in situ on the study reefs) validate this notion. Similarly, warming events may act very differently at local scales depending on the population structure of the reefs concerned. Historical patterns of thermal stress, combined with genetic variation within and between different species of coral host (Edmunds, 1994; Knowlton and Jackson, 1994; Brown, 1997) and/or algal symbionts (Buddemeier and Fautin, 1993; Rowan et al., 1997; Glynn et al., this issue) will contribute to bleaching variability. Taken together, these observations indicate that bleaching thresholds are most likely site and time dependent (Winter et al., 1998). This perspective cautions against predictions of bleaching incidence and severity over larger spatial and temporal scales without an appreciation of the physical and biological factors that interact during bleaching episodes.

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