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# Effects of the 1991-92 El Niño on scleractinian corals of the Costa Rican central Pacific coast

Carlos Jiménez [1-2] and Jorge Cortés [1]

[1]Centro de Investigación en Ciencias del Mar y Limnología (CIMAR), Universidad de Costa Rica, 2060 San José, Costa Rica. Fax (506) 207 3280. E-mail: jcortes@cariari.ucr.ac.cr

[2]Present address: Zentrum für Marine Tropenökologie (ZMT), Universität Bremen, Fahrenheitstrasse 6, D-28359 Bremen, Germany. Fax (049) 0421-2380-030. E-mail: carlos.jimenez@zmt.uni-bremen.de

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**Abstract:** Coral communities on the central Pacific coast of Costa Rica were affected during the 1991-92 El Niño warming event. More than 57% of all observed colonies at three localities (Parque Nacional Manuel Antonio, Punta Cambutal, and Parque Marino Ballena) were bleached. Mortality during this El Niño was much lower (∼9%) than in previous events. *Psammocora* spp. accounted for ∼66% of dead corals, while massive (*Porites lobata*, *Pavona* spp.) and branching (*Pocillopora* spp.) for ∼34%. Our results suggest that the observed bleaching in *P. lobata* was related to zooxanthellar densities and not to changes in pigment concentrations: only chlorophyll *a* varied between normally pigmented and bleached colonies at one locality (Ballena). Site differences in zooxanthellar densities or their pigment concentrations, may not be the result of the bleaching event itself, because a percentage of dead corals and zooxanthellar densities of bleached colonies seems to follow a trend with the exposure to tidal regimes and currents at each site. Local oceanographic conditions can be influencing the zooxanthellar densities and their response to the warming, together with intrinsic differences between colonies as well. The impact of this event can be considered serious given the short period of time that elapsed between El Niño related mortalities and the slow reefs recovery, the mode of reproduction of reef building species, and the anthropogenic-originated disturbances which affect the coral communities and reefs of the Costa Rican central Pacific coast.

**Key words:** El Niño, ENSO, bleaching, corals, Costa Rica, zooxanthella, eastern Pacific.

The 1990s are considered the warmest years on record (Vogel & Lawler 1998) and included the strongest El Niño event of the century (McPhaden 1999). This decade has also witnessed coral bleaching and mortality events worldwide at unprecedented scale (Anonymous 1998, Wilkinson *et al.* 1999). Whether this bleaching events are the result of a large scale global warming and/or a combination of physical and biological factors acting locally, coral reefs of the world are facing rapid deterioration (Bryant *et al.* 1998). Therefore, it is important to record all bleaching events regardless of their magnitude or extent, in order to find patterns, if any, and to relate this to the coral's health. As a baseline, a detailed account of bleaching events (such as the one described here) will assist in understanding the history and fate of coral communities and reefs of the Pacific coast of Costa Rica, which are under heavy pressure by anthropogenic and natural disturbances (Cortés & Jiménez in prep.).

The unusual period of extended warmth, observed in the tropical Pacific Ocean in the early 1990s, appears to be different from what was observed in previous decades (Goddard & Graham 1997, Zhang *et al*. 1998), and the nature of this warming has been of ample debate: Is it a forced global warming, expressed as a single 1990-95 El Niño event, or just decadal variability? (see Trenberth & Hoar 1996, 1997, Latif *et al.* 1997, Rajagopalan *et a*l. 1997). In any case, the 1991-92 warming event began in September 1991 with a dramatic relaxation of the easterly trade winds (Janowiak 1993), peaked in March-April 1992 , and returned to cold sea-surface temperature (SST) by August 1992 (Kousky 1993, Kessler & McPhaden 1995). However, it is considered to have lasted until 1993, with a briefer warming in March-April 1993 (Kessler & McPhaden 1995). It is suggested that, after the 1991 Pinatubo eruption, the 1991-92 warming seemed to have greatly increased (amplified) (Self *et al.* 1997).

The 1991-92 event reduced the primary productivity (Barber *et al.* 1996), the ocean-atmosphere $CO_2$ flux (Feely *et al.* 1995), and the carbon and nutrient concentrations (Wanninkhof *et al.* 1995) in the equatorial Pacific, and produced significant community changes on bottom macrobenthos at the central Peruvian Coast (Tarazona *et al.* 1995). Manifestations at mid-latitudes ranged from coherence with the north Atlantic Oscillation (Huang *et al.* 1998), to heavy rainfall in California (McPhaden *et al.* 1998), and to nutrients depletion and warming off the North American coast (McPhaden 1994, Chavez 1996).

Coincidental with the mature phase of this warming event, we recorded coral bleaching and mortality at the central Pacific coast of Costa Rica. Bleaching is the disruption of the symbiosis between the coral and photosynthetic zooxanthellae by stressors such as exposures to extremes in temperature, ultraviolet radiation, salinity, oxygen, pollutants and bacterial infections (Glynn & D'Croz 1990, Szmant & Gassman 1990, Gates *et al.* 1992, Kushmaro *et al.* 1996, Jones 1977a, Hoegh-Guldberg 1999), resulting in loss of zooxanthellae and/or its pigments and the subsequent paling or bleaching of the colony. Although it is not always possible to identify the source of stress (Brown 1987), this loss of coloration is present in other natural or experimentally stressed invertebrates (Jokiel 1980, Muscatine *et al.* 1991). There is evidence that, when the zooxanthellae photoinhibition sensitivity is impaired or lowered, coral bleaching is produced (Hoegh-Guldberg & Jones 1999), particularly under conditions of higher than normal temperatures. There are a number of cellular mechanisms, which reduce zooxanthellar densities in bleached corals. These are degeneration of cells *in situ*, and release of zooxanthellae from mesenterial filaments and within host cells (Gates *et al.* 1992, Brown *et al.* 1995). The zooxanthellae chlorophyll pigments allow light absorption, and corals or sections of colonies with higher concentration of pigments seem to be more efficient in capturing light (Muller-Parker & D'Elia 1997).

Here we present an account of the coral bleaching and mortality, zooxanthellae loss and pigment concentration at three localities of the Pacific coast of Costa Rica during and after the 1991-92 El Niño.

## MATERIALS AND METHODS

**Study sites:** Coral communities were observed for bleaching at three localities of the central Pacific coast of Costa Rica (Fig. 1): in Parque Marino Ballena (Ballena) during four day field trips from May to November 1992, and Parque Nacional Manuel Antonio (Manuel Antonio) and Punta Cambutal (Cambutal) in June and November 1992. Patch reefs of *Porites lobata* Dana 1846 are common in protected coves and near sandy beaches of Manuel Antonio (Jiménez & Cortés in prep.). Dead *Pocillopora* frameworks are overgrown with live colonies of *Pocillopora elegans* Dana 1846, *Pocillopora damicornis* Linnaeus 1748, and *Psammocora* spp. Live coral coverage (LCC) is relatively high (33.7 ± 19.3%, range 9.2–81%) (Jiménez & Cortés in prep.). Coral communities upon basalt or sand of Punta Cambutal are located at a semi enclosed cove and have a LCC of 24.8 ± 11.6% (range 6.6-36.4%) dominated by *P. lobata*. Pacht reefs and coral communities of Ballena consist mainly of the massive species *P. lobata*, *Pavona gigantea* Verrill 1869 and scarce *Pocillopora* spp. (Jiménez & Cortés in prep.). LCC is low (7.6 ± 2.0 %, range 1.1-19%) but increases at the submerged banks and islets of the park.

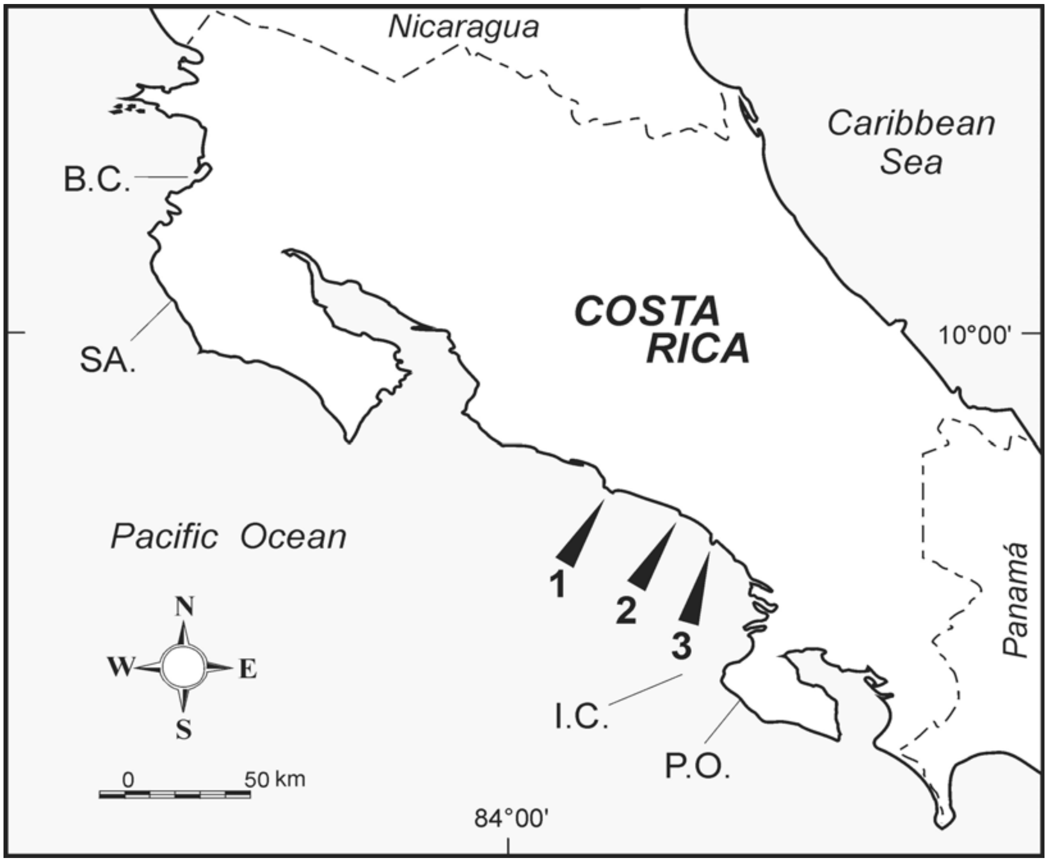

Fig 1. Study sites at the Costa Rican central Pacific coast. 1. Parque Nacional Manuel Antonio (Manuel Antonio in the text and other figures); 2. Punta Cambutal (Cambutal); 3. Parque Marino Ballena (Ballena). Other localities mentioned in the text: Bahía Culebra (B.C.), Sámara (SA.), Isla del Caño (I.C.) and Península de Osa (P.O.).

**Coral bleaching observations:** The occurrence of bleaching and mortality were determined by diving along four transects in Manuel Antonio (500 x 3 m long; 2-4 m depth), one at Cambutal (300 x 3 m; 2-4 m depth), and four at Ballena (600 x 2.5 m; 0.5-6 m). A colony was considered normal if it had no signs of bleaching; bleached if it showed more than 5% of the colony area white; dead if it was recently overgrown by algae. In order to monitor the condition of several large (1-1.5 m ø) colonies of a massive coral, *P. lobata*, tags were driven with steel nails into six colonies per study site (2-4 m depth, June 1992), recording the coral's appearance at the moment of tagging. Additionally, water column temperature was recorded several times during dives utilizing a calibrated bulb thermometer (0.05 °C accuracy). On subsequent visits during 1993 (April, May) and 1994 (June), only general observations on the state of the communities were made.

**Zooxanthellar densities and chlorophyll concentrations**: On 13 June 1992, one fragment was sampled from eight normal and eight bleached colonies of *P. lobata* from Ballena (2-4 m depth) and Cambutal (3-4 m), and the following day from Manuel Antonio (2-4 m). All coral fragments were frozen and transported (5 hr) to the laboratory packed in ice. Within one month, tissues were removed from the skeletons utilizing an Airbrush (*sensu* Szmant & Gassman 1990). The zooxanthellar density was determined in the tissue homogenate from eight replicate grids per

TABLE 1

*In situ water temperature (℃) statistics at the three studied sites during the aftermath of the 1991-92 El Niño event*

| Date | Locality | Mean | Standard deviation | n | Max.°C | Min.°C | Depth Range (m) |
|---|---|---|---|---|---|---|---|
| 15-16.V.92 | Ballena | 31.2 | 0.4 | 13 | 32.0 | 31.0 | 0-5 |
| 12.VI.92 | Ballena | 29.8 | 0.3 | 12 | 30.5 | 29.5 | 0-5 |
| 13.VI.92 | Cambutal | 30.1 | 0.8 | 4 | 31.0 | 29.5 | 0-2 |
| 14.VI.92 | M. Antonio | 30.2 | 0.6 | 8 | 31.0 | 29.5 | 0-4 |
| 13-14.XI.92 | Ballena | 27.9 | 0.4 | 18 | 28.5 | 27.9 | 0-5 |
| 14.XI.92 | Cambutal | 27.7 | 0.3 | 6 | 28.0 | 27.5 | 0-2 |
| 15.XI.92 | M. Antonio | 28.0 | 0.8 | 8 | 29.0 | 27.0 | 0-3 |

Monthly mean SST (1971-1987) from April to January is 28.2 ± 0.45°C (Woodruff *et al.* 1987). n= number of temperature readings.

sample using a hemacytometer. Zooxanthellae were normalized to the homogenate volume and area of the coral fragment. For zooxanthellar chlorophyll (chl) *a* and *c* analysis, coral fragments were placed in 10 ml acetone 90% for 24 h at 5°C (Lorenzen & Jeffrey 1978). Samples (10 ml) were then centrifuged for 10 min at 3000 rpm, and the absorbances of the supernatant were read on a Schimadzu UV-160A spectrophotometer. The equations of Jeffrey & Humphrey (1975) were used to calculate chl-*a* and chl-*c* concentration which were normalized with the fragment's area and expressed as µg $cm^{-2}$. The Barlett and Hardy test was used to evaluate the normality of data and the Cochran test to evaluate the heterogeneity of variances (Underwood 1997), and the data were analyzed using Student's *t*-test and ANOVA to compare normal and bleached colonies and localities respectively.

## RESULTS

**Coral bleaching observations**: The first reports of bleaching along the central Pacific coast of Costa Rica during the 1991-92 El Niño event were in mid March 1992 from Manuel Antonio (B. Hedges, pers. com. 1992) and in April from Ballena (C. Gamboa, pers. com. 1992). Other bleaching reports in Costa Rica were in April at the southern Península de Osa (M. Nagy, pers. com. 1992), Isla del Caño (Guzmán & Cortés 2001), and Isla del Coco (M. Montoya, pers. com. 1992). In May 1992, coral bleaching was still wide spread in Ballena, and in June and November in Manuel Antonio and Cambutal. Although no new bleached corals were observed during the November survey (some bleached colonies indeed started to recover their pigments by then, see further down), some previously bleached corals died.

Seawater temperature (SWT), measured by the park rangers at 0-2 m depth in Ballena, was between 33 and 34°C during doldrum conditions which prevailed for several days in March-April 1992 (peak of the warming event). This corresponded to an increase in SWT of ~4-6°C from the COADS (Woodruff *et al.* 1987) monthly mean (28.5 ± 0.7°C, range 26.3-30.3°C) calculated for the zone (grid centered at 9°N 84°W) during the warm, dry season (December/March). During the aftermath of the 1991-92 El Niño event, mean SWT continued to be above 29°C at all three localities in June 1992 (Table 1), but in November it cooled below 28°C.

During our surveys, starting in May 1992, coral bleaching was recorded down to a depth of 8 m and it was not possible to observe a definite bleaching pattern in the affected colonies: massive colonies (*P. lobata*, *Pavona clavus* Dana 1846, *P. gigantea*) bleached indistinctly at the tops, flanks or sides in gradual or discrete patches; branching corals (*Pocillopora* spp.) and *Psammocora* spp. bleached whole or at certain branches which started to be colonized by filamentous algae. Pink pustules surrounding bleached sections of massive colonies were abundant at all localities and depths. It was also common to observe normally coloured or pigmented colonies interspersed with neighboring bleached or dead colonies.

The incidence of normal, bleached and dead colonies varied considerably among coral

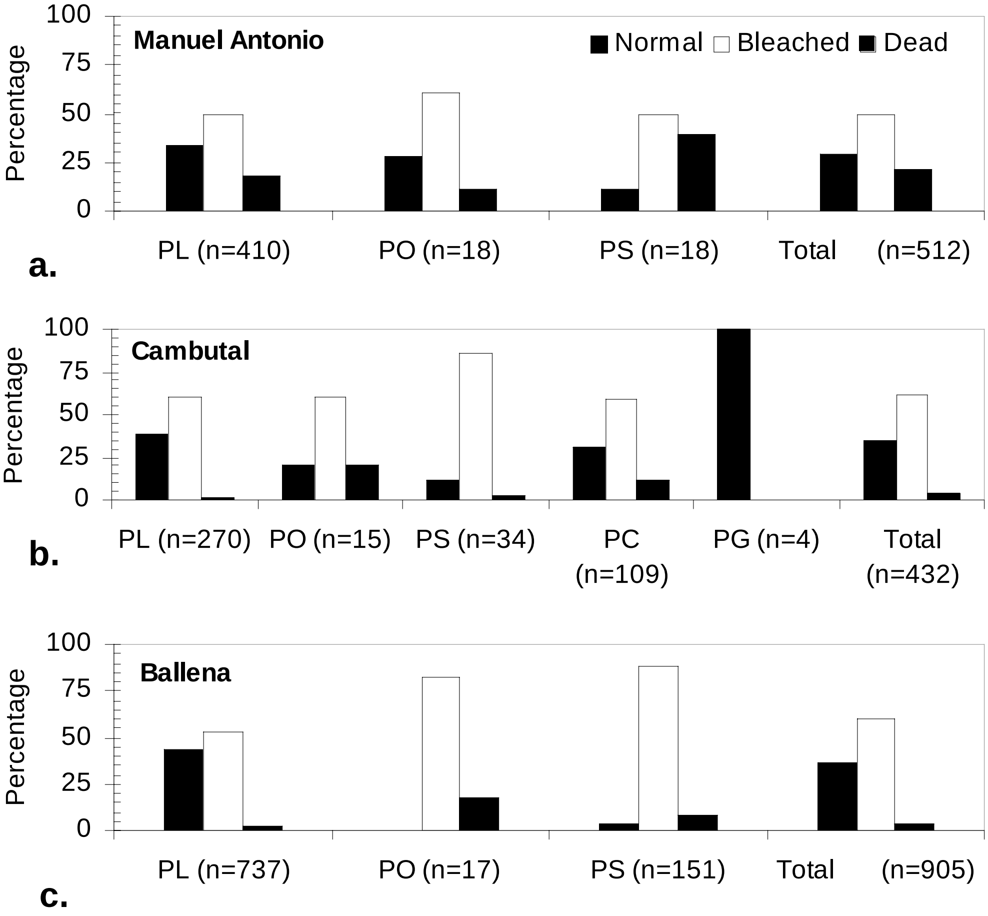

Fig. 2. Percentage of normal (black bars), bleached (white) and dead (stripped) coral colonies at the three studied sites during May, June and November 1992. PL= *P. lobata*, PO= *Pocillopora* spp., PC= *P. clavus*, PG= *P. gigantea*, PS= *Psammocora* spp. n= number of colonies.

species and locality (Fig. 2). At Manuel Antonio, *Psammocora* spp. was the most affected coral with ~40% of all colonies dead, while more than 60% of all *Pocillopora* spp. colonies were bleached (Fig. 2a). At Cambutal, 38 km south of Manuel Antonio (Fig. 1), the situation was inverse: *Pocillopora* spp. had the highest percentage of dead colonies (20%), and *Psammocora* spp. of bleached colonies (>80%) (Fig. 2b). Interestingly, colonies of *P. gigantea* at this locality remained pigmented and showed no signs of any discoloration or dead portion in the tissue. At Ballena, approx. 50 km south from Manuel Antonio (Fig. 1), *Pocillopora* and *Psammocora* were again the most affected species, with the highest percentage of dead (~18%) and bleached (88%) colonies respectively (Fig. 2c). *P. lobata* was another species which showed differences among localities, having in Manuel Antonio and at Cambutal the highest percentage of dead and bleached colonies respectively (Fig. 2).

Grouping all coral species per study site ("Total" in Fig. 2), it is easier to identify Manuel Antonio as the most affected locality during the 1991-92 El Niño event: the percentages of bleached (~60%) and dead (~4%) colonies were similar at Cambutal and Ballena respectively, whilst Manuel Antonio had the highest percentage of dead corals (~21%).

Considering all coral species from the three localities, ~57% of all observed colonies (n= 1849) bleached during the 1991-92 El Niño event, and mortality was ~9%. *Psammocora* spp. accounted for ~66% of dead corals, and massive and branching corals for ~33%. Comparing these results with the impact of the 1997-98 El Niño on corals of the northern Pacific coast of Costa Rica (Jiménez *et al.* 2001), bleaching and mortality were lower in 1997-98 (~32 and ~6% respectively). *Pocillopora* spp. accounted for ~84% of the total mortality, and massive corals and *Psammocora* spp. for ~16%.

The tagging in June 1992 of large colonies of *P. lobata* (six at each locality), helped to notice changes (if any) in the condition of individual colonies that occurred until our last survey in November 1992 (Table 2). The six fully pigmented colonies ("normal") showed no change, including the one with the pink pustules. From 12 colonies which had bleached either at their tops, flanks or all over, four remained bleached and had tissue partial mortality (TPM), six changed to a pale tan coloration with TPM (except for colony 17), and two acquired a dark brown or mustard coloration (considered normal) with TPM (one had also purple pustules).

By November 1992, as mentioned earlier, no further noticeable bleaching was observed. The remaining bleached colonies were the ones observed before (June), and mortality (mostly TPM in massive corals) was still recorded. Small stands of *Psammocora* spp. were completely overgrown by a mat of brown algae in Manuel Antonio and Cambutal. At Ballena, in several medium sized *P. lobata* colonies, territorial damselfish were observed with expanded algal mats over the corals' TPM areas colonized by algae. At all localities, mortality of whole colonies was noticed to have been more common in *Pocillopora* spp., *Psammora* spp. and small (<20 cm ø) *P. lobata*, particularly at 1 to 3 m depth.

The sites were visited twice in 1993 and once in 1994. Some of the corals previously bleached had overgrown the TPM sections which were formerly invaded by filamentous algae. More commonly, sponges, coraline algae, barnacles and polychaetes thrived at the spots were the TPM was observed. No large *P. lobata* colonies were found dead, and some of the former bleached corals had overgrown the TPM and the tags, preventing further individual identification.

**Zooxanthellar densities and chlorophyll concentrations**: When comparing zooxanthellar densities between localities (Fig. 3a), normal pigmented colonies of *P. lobata* had no significant differences (p»0.05, df=2, F=

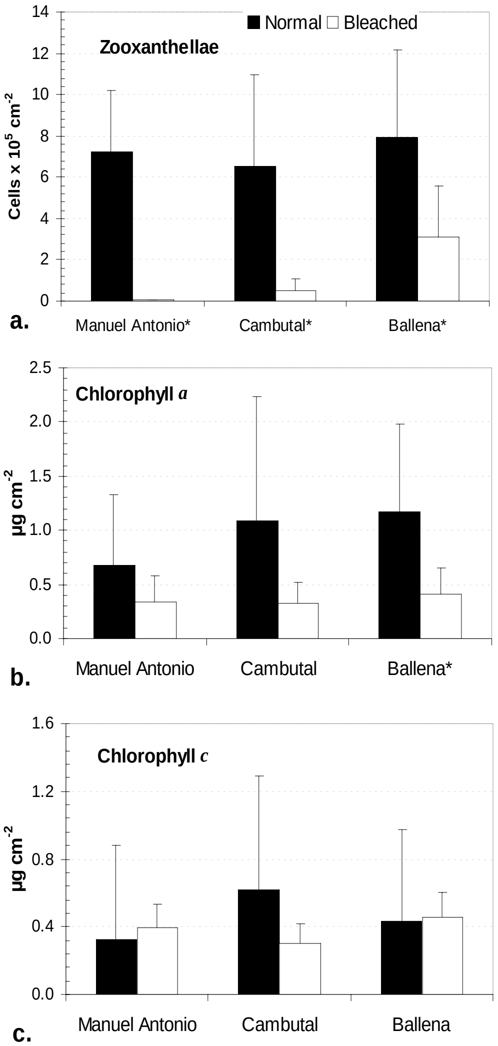

Fig. 3. Mean (bars) ± standard deviation of (a.) zooxanthellar density; (b.) Chlorophyll-*a*, and (c.) Chlorophyll-*c* in normal (black bars) and bleached (white) *P. lobata* colonies (8 per locality), sampled in June 1992 at the three studied sites. *Differences between normal and bleached colonies are significant (p<0.05).

TABLE 2

*Condition of the tagged* Porites lobata *colonies at the three study sites during the 1991-92 El Niño aftermath*

| Locality | Colony | June 1992 | November 1992 |
|---|---|---|---|
| Manuel Antonio | 1 | Bleach at top and flanks | Normal with purple dots, TPM |
| | 2 | Bleach mostly at the top | Pale tan coloured |
| | 3 | Normal | Normal |
| | 4 | Normal | Normal |
| | 5 | Normal | Normal |
| | 6 | Bleach all over | Bleach, TPM |
| Cambutal | 7 | Normal | Normal |
| | 8 | Bleach at top and flanks | Pale tan coloured, TPM |
| | 9 | Bleach all over | Bleach, TPM |
| | 10 | Bleach at top and flanks | Normal, TPM |
| | 11 | Bleach mostly at the top | Pale tan, TPM |
| | 12 | Bleach mostly at the top | Bleach at the top, TM |
| Ballena | 13 | Bleach mostly at flanks | Pale tan coloured, TPM |
| | 14 | Bleach all over | Pale tan coloured, TPM |
| | 15 | Normal with purple dots | Normal with purple dots |
| | 16 | Normal | Normal |
| | 17 | Bleach at top and flanks | Pale tan coloured |
| | 18 | Bleach all over | Bleach, TPM |

Bleach= more than 5% of colony area white coloured. TPM= tissue partial mortality with overgrowing algae.

0.23, ANOVA) and ranged from 6.5 to 7.9 cells $10^5$ $cm^{-2}$. On the other hand, zooxanthellar densities in bleached colonies varied significantly ($p<0.01$, df=2, F= 10) according to locality, being the lowest in Manuel Antonio (0.04 ± 0.04 cells $10^5$ $cm^{-2}$) and the highest at Ballena (3.1 ± 2.5 cells $10^5$ $cm^{-2}$) (Fig. 3a). Normally pigmented colonies had significantly higher zooxanthellar densities (Student's *t*-test, df=7) than bleached colonies at all localities (Manuel Antonio $p<0.01$, t=2.36; Cambutal $p<0.01$, t=2.36; Ballena $p<0.05$, t=2.2). For example, at Manuel Antonio, mean zooxanthellar density was more than 150 times higher in normal than in bleached colonies, while at Cambutal and at Ballena was 12.7 and 2.5 times respectively.

Pigments' concentration (chl-*a*, chl-*c*, Fig. 3b, c) had no significant differences (p»0.05) among localities in either normal or bleached colonies. Additionally, only at Ballena the concentration of one of the pigments, chl-*a*, was significantly higher ($p<0.05$, df=8, t= 2.54) in normal (1.1 ± 0.8 µg $cm^{-2}$) than in bleached (0.4 ± 0.2 µg $cm^{-2}$) colonies.

## DISCUSSION

A vast majority of mass coral bleaching (on a geographical scale) have been associated with warmer than normal SWT (Glynn 1993, 1996, Hoegh-Guldberg 1999). In 1991, a mass bleaching event occurred in almost all coral reef regions of the world (Goreau & Hayes 1994) and it was coincidental with the onset and development of the 1991-92 El Niño (Glynn 1996). It was not until May of 1992 that extended bleaching occurred in the eastern Pacific, specifically at the central Pacific coast of Costa Rica. During May 1992, a small and localized bleaching event was also reported in the Caribbean Sea (Winter *et al.* 1998). Subsequent bleaching events were reported in 1994 and 1995, non-ENSO years (Glynn 1996).

The 1991-92 El Niño effects in Costa Rica were restricted to the central and southern coast. Other localities were visited in the north of the country, Bahía Culebra (27-28.IV.1992) and Sámara (24-26.IV and 17.VII.1992) (Fig. 1), but no evidence of coral bleaching or recent mortality that could be attributed to the on-going warming event was observed. In contrast, the 1982-83 warming event affected corals at widely separated localities along the Pacific coast: Bahía Culebra, Sámara, Isla del Caño, Manuel Antonio and several areas around Ballena (Cortés *et al*. 1984, Guzmán *et* *al*. 1987). At Manuel Antonio, no live corals were seen in November 1983, and at Ballena, bleached corals were noticed, though no evidence of massive mortalities was found during the short survey. At those localities, branching corals (*Pocillopora* spp.) and *Psammocora* spp. were more affected than massive species (Cortés *et al*. 1984), as we noted during the 1991-92 El Niño. At Isla del Caño, live coral cover was reduced by approximately 40% during the 1982-83 El Niño (Guzmán *et al*. 1987). Live coral cover was unaffected by the 1991-92 event, and reduced by 5% after the 1997-98 El Niño (Guzmán & Cortés 2001).

Although on a regional scale the 1991-92 El Niño was not as severe as the 1982-83 event (less than 9% coral mortality in 1991-92 vs. 50-90% in 1982-83), its impact was far from negligible because the coral communities affected were recuperating from previous events. For example, in 1987-88, coral bleaching and mortality were observed by divers at Manuel Antonio (J. Cruz, pers. com. 1992) and at Cambutal (H. Sánchez, pers. com. 1992), coincidental with a "strong" El Niño event (Kessler & McPhaden 1995). The impact of both events could explain the abundance of large, dead massive colonies of *P. lobata* and *P. clavus*, and stands of *Pocillopora* spp. and *Psammocora* spp. in Manuel Antonio, Cambutal and Ballena.

Our results indicates that *P. lobata* response to the 1991-92 El Niño related bleaching was mainly the expulsion of zooxanthellae without a significant change in pigment concentration. Bleached colonies had reduced zooxanthellar densities compared to full pigmented colonies, and in all sites but one (Ballena, chl-*a*), they did not have a generalized decrease in the zooxanthellar specific pigments, as noted in other bleached corals (e.g. Hoegh-Guldberg & Smith 1989, Le Tissier & Brown 1996, Jones 1997b). Although a lowering of chlorophyll's concentration in bleached corals have been reported (Kleppel *et al*. 1989, Brown *et al*. 2000), there are no reports of bleaching exclusively due to pigments loss (Hoegh-Guldberg 1999), and the reasons for that remains unclear (Jones 1997b). Additionally, given also the presence of chl-*a* in the endolithic green algae hosted in the coral skeleton (Kleppel *et al*. 1989), we can not rule out their potential interference with our analysis. In general, chlorophyll concentrations are known to vary considerably depending on the species, the depth of collection, light exposure, and degree of photosynthetically active radiation and ultraviolet light (Dustan 1979, Titlyanov 1981, Kinzie *et al*. 1984, Hoegh-Guldberg & Smith 1989, Brown *et al*. 2000). Furthermore, it has been found that concentration of a particular pigment can be higher or lower than another (e.g. Titlyanov 1981, Kinzie *et al*. 1984), and this calls for caution when searching for a pattern between pigmented and bleached colonies. Whether the concentrations reported here for the normal pigmented colonies are typical for *P. lobata*, is a topic that needs to be studied in more detail.

Zooxanthellar densities reported here varied from 6.5 to 7.9 cells $10^5$ $cm^{-2}$, which are in the range documented for other scleractinian corals: between 5 and 200 cells $10^5$ $cm^{-2}$ (Hoegh-Guldberg & Smith 1989, Brown *et al*. 1995, 2000). These broad variations can be related to seasonal changes in population densities of zooxanthellae (Fagoonee *et al*. 1999) and inherent differences between colonies and species (Jones 1997a), which can make the sampling of similar symbionts densities difficult when comparing colonies in space and time. Although these changes may account for the small observed variations in normal corals, the zooxanthellar densities in bleached colonies appear to follow a geographical gradient according to exposure level to tidal regimes and currents of the study site. Surveyed coral communities at Manuel Antonio, showed the lowest zooxanthellar densities and they are located in more enclosed and protected coves than in the other two sites. The enclosure nature of Manuel Antonio probably facilitates the entanglement of water by eddies formation reducing water exchange with open waters, which in its turn may amplify the thermal stress due to the warming event. In a lesser extent, Cambutal is a semi enclosed cove but with much more water exchange during tidal fluctuations than at Manuel Antonio. Although eddies and entanglement of phytoplankton blooms have been observed in Ballena (Cortés & Jiménez in prep.), corals are more exposed to surge and open waters than at the other study sites.

If *P. lobata* loses its symbionts, but pigment concentration do not change significantly, the coral metabolic functions may not be impaired, and they may probably continue at a lower level. The latter has been related to the lowering of growth rates, healing and shedding of sediments capacities, and the higher susceptibility to diseases of bleached *vs.* pigmented corals (Goreau & MacFarlane 1990, Glynn 1993, Meesters & Bak 1993, Mascarelli & Bunkley-Williams 1999). The implications are important as many new epizootic diseases have been observed to be concurrent with bleaching related damage (Goreau *et al.* 1998).

At a local scale, during the 1991-92 warming event, corals were commonly observed to differ in their tendency to bleach and to exhibit a gradation of discoloration intensity, as reported by many authors (Hoegh-Guldberg 1999 and references therein). This was also observed in Costa Rica during one bleaching event coincidental with the 1997-98 El Niño (Jiménez *et al.* 2001). Several factors can be responsible for such a variability: light intensity reaching the corals, genotypes of the zooxanthellae and the corals, zooxanthellar cell size, and micro-scale environments (Edmunds 1994, Glynn 1996, Rowan *et al.* 1997, Jones 1997a, Hoegh-Guldberg 1999). Additionally, there is apparently a threshold limit for some corals which defines the level of zooxanthellae loss required for the colonies to discolor. For example, *Acropora formosa* Dana 1846 begin to discolor when they have lost more than 50% of the algal standing stock (Jones 1997b). It is not known if there is any such threshold for *P. lobata*. Studies focused on the zooxanthellae dynamics and responses to periodic El Niño related warmings are needed, particularly concentrating on the main reef building corals in the eastern Pacific.

To summarize, the 1991-92 El Niño related coral mortality in the coral communities of the central Pacific coast of Costa Rica, was less severe than the 1982-83 event, but it affected coral communities that were still recovering. This is a serious problem because they show slow recovery rates from impacts due to the combination of factors such as the main mode of reproduction (asexual), low recruitment, high rates of bioerosion, anthropogenic-generated coastal sedimentation, and phytoplankton blooms (Glynn 1990, Guzmán 1991, Cortés & Jiménez, in prep.). Nevertheless, given appropriate conditions (e.g. absence of catastrophic El Niño events, massive coral mortalities, and management of marine and terrestrial areas), recovery of Costa Rican coral reefs and communities is feasible in the long term (10-14 yr.), as observed in the protected reefs of the national park Isla del Caño (Guzmán 1999, pers. obs.).

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## RESUMEN

El Niño 1991-92 afectó las comunidades coralinas del Pacífico de Costa Rica. Se blanquearon más del 50% de todas las colonias de coral observadas en tres lugares (Parque Nacional Manuel Antonio, Punta Cambutal y Parque Marino Ballena). La mortalidad asociada al calentamiento 1991-92 fue menor (~9%) que en eventos anteriores de El Niño. Cerca del 66% de los corales muertos eran *Psammocora* spp.; el resto especies masivas (*Porites lobata*, *Pavona* spp.) y ramificadas (*Pocillopora* spp.). Los resultados sugieren que el blanqueamiento en *P. lobata* fue producido por cambios en la densidad de las zooxantelas y no por cambios en la concentración de pigmentos. Las condiciones oceanográficas particulares de cada localidad, junto con las diferencias intrínsecas de las colonias de coral, puede que afecten la densidad de zooxantelas y la concentración de los pigmentos. El impacto de El Niño 1991-92 en las comunidades coralinas del Pacífico de

Costa Rica puede considerarse serio debido a: 1- el poco tiempo entre eventos de calentamiento, 2- la recuperación lenta de las comunidades a los calentamientos, 3- la forma de reproducción predominante (asexual) de las especies constructoras de arrecife, y 4- el impacto de disturbios antropogénicos.

## REFERENCES

Anonymous. 1998. Statement on Global Coral Reef Bleaching in 1997-98. International Society for Reef Studies. Reef Encounter 24: 19-20.

Barber, R., M. Sanderson, S. Lindley, F. Chai, J. Newton, C. Trees, D. Foley & F. Chavez. 1996. Primary productivity and its regulation in the equatorial Pacific during and following the 1991-1992 El Niño. Deep-Sea Res. II 43: 933-969.

Brown, B. 1987. Worldwide death of corals: natural cyclical events or man made pollution?. Mar. Poll. Bull. 18: 9-13.

Brown, B., M. Le Tissier & J. Bythell. 1995. Mechanisms of bleaching deduced from histological studies of reef corals sampled during a natural bleaching event. Mar. Biol. 122: 655-663.

Brown, B., R. Dunne, M. Goodson & A. Douglas. 2000. Bleaching patterns in reef corals. Nature 404: 142-143.

Bryant, D., L. Burke, J. McManus & M. Spalding. 1998. Reefs at risk: a map-based indicator of threats to the world's coral reefs. World Resources Institute, Washington DC. 60 p.

Chavez, F. 1996. Forcing and biological impact of onset of the 1992 El Niño in central California. Geophys. Res. Letr. 23: 265-268.

Cortés, J., M. Murillo, H. Guzmán & J. Acuña. 1984. Pérdida de zooxantelas y muerte de corales y otros organismos arrecifales en el Caribe y Pacífico de Costa Rica. Rev. Biol. Trop. 32: 227-231.

Dustan, P. 1979. Distribution of zooxanthellae and photosynthetic chloroplast pigments of the reef-building coral *Montastrea annularis* Ellis & Solander in relation to depth on a West Indian coral reef. Bull. Mar. Sci. 29: 79-95.

Edmunds, P. 1994. Evidence that reef-wide patterns of coral bleaching may be the result of the distribution of bleaching-susceptible clones. Mar. Biol. 121:137-142.

Feely, R. R. Wanninkhof, C. Cosca, P. Murphy, M. Lamb & M. Steckley. 1995. $CO_2$ distributions in the equatorial Pacific during the 1991-1992 ENSO event. Deep-Sea Res. II 42: 365-386.

Fagoonee, I., H. Wilson, M. Hassel & J. Turner. 1999. The dynamics of zooxanthellae populations: a long-term study in the field. Science 283: 843-845.

Gates, R., G. Baghdasarian & L. Muscatine. 1992. Temperature stress causes host cell detachment in symbiotic cnidarians: implications for coral bleaching. Biol. Bull. 182: 324-332.

Glynn, P. W. 1990. Coral mortality and disturbance to the coral reefs of the tropical eastern Pacific, p. 55-126. *In* P. W. Glynn (ed.), Global Ecological Consequences of the 1982-83 El Niño-Southern Oscillation. Elsevier, Amsterdam.

Glynn, P. W. 1993. Coral reef bleaching: ecological perspectives. Coral Reefs 12: 1-17.

Glynn, P. W. 1996. Coral reef bleaching: facts, hypotheses and implications. Global Change Biol. 2: 495-509.

Glynn, P. W. & L. D'Croz. 1990. Experimental evidence for high temperature stress as the cause of El Niño-coincident coral mortality. Coral Reefs 8: 181-191.

Goddard, L. & N. Graham. 1997. El Niño in the 1990s. J. Geophys. Res. 102: 10423-10436.

Goreau, T. & R. Hayes. 1994. Coral bleaching and ocean "hot spots". Ambio 23: 176-180.

Goreau, T. & A. MacFarlane. 1990. Reduced growth rate of *Montastrea annularis* following the 1987-88 coral-bleaching event. Coral Reefs 8: 211-215.

Goreau, T., J. Cervino, M. Goreau, R. Hayes, M. Hayes, L. Richardson, G. Smith, K. DeMeyer, I. Nagelkerken, J. Garzon-Ferrera, D. Gil, G. Garrison, E. Williams, L. Bunkley-Williams, C. Quirolo, K. Patterson, J. Porter & K. Porter. 1998. Rapid spread of disease in Caribbean coral reefs. Rev. Biol. Trop. 46 (Suppl. 5): 157-171.

Guzmán, H. 1991. Restoration of coral reefs in Pacific Costa Rica. Conserv. Biol. 5: 189-195.

Guzmán, H. 1999. Large-scale restoration of eastern Pacific reefs: the need for understanding regional biological processes. p. 97. *In* Program and abstracts. International Conference on Scientific Aspects of Coral Reef Assessment, Monitoring, and Restoration. National Coral Reef Institute, Nova Southeastern University, Florida, USA.

Guzmán, H., J. Cortés, R. Richmond & P. W. Glynn. 1987. Efectos de El Niño-Oscilación Sureña 1982/83 en los arrecifes coralinos de la Isla del Caño, Costa Rica. Rev. Biol. Trop. 35: 325-332.

Guzmán, H. & J. Cortés. 2001. Changes in reef community structure after fifteen years of natural disturbances in the eastern Pacific (Costa Rica). Bull. Mar. Sci. 69(1): 133-149.

Hoegh-Guldberg, O. 1999. Climate change, coral bleaching and the future of the world's coral reefs. Aust. J. Mar. Freshwater Res. 50: 839–866.

Hoegh-Guldberg, O. & R. Jones. 1999. Photoinhibition and photoprotection in symbiotic dinoflagellates from reef-building corals. Mar. Ecol. Prog. Ser. 183: 73-86.

Hoegh-Guldberg, O. & G. Smith. 1989. The effects of sudden changes in light, temperature and salinity on the population density and export of zooxanthellae from the reef corals *Seriatopora hystrix* and *Stylophora pistillata*. J. Exp. Mar. Biol. Ecol. 129: 279-303.

Huang, J., K. Higuchi & A. Shabbar. 1998. The relationship between the North Atlantic Oscillation and El Niño-Southern Oscillation. Geophys. Res. Lett. 25: 2707-2710.

Janowiak, J. 1993. The global climate for September-November 1991: Warm (ENSO) episode conditions strengthen. J. Climate 6:1616-1638.

Jeffrey, S. & G. Humphrey. 1975. New spectrophotometric equations for determining chlorophylls *a*, *b*, *c*1 and *c*2, in higher plants, algae and natural phytoplankton. Biochem. Physiol. Pilanzen. 167: 191-194.

Jiménez, C., J. Cortés, A. León & E. Ruíz. 2001. Coral bleaching and mortality associated with the 1997/98 El Niño event in an upwelling environment at the eastern Pacific (Gulf of Papagayo, Costa Rica). Bull. Mar. Sci. 49(1): 151-169.

Jokiel, P. 1980. Solar ultraviolet rediation and coral reef epifauna. Science 207: 1069-1071.

Jones, R. 1997a. Zooxanthellae loss as a bioassay for assessing stress in corals. Mar. Ecol. Prog. Ser. 149: 163-171.

Jones, R. 1997b. Changes in zooxanthellar densities and chlorophyll concentrations in corals during and after a bleaching event. Mar. Ecol. Prog. Ser. 158: 51-59.

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

Kinzie, R. III, P. Jokiel & R. York. 1984. Effects of light of altered spectral composition on coral zooxanthellae associations and on zooxanthellae *in vitro*. Mar. Biol. 78: 239-248.

Kleppel, G., R. Dodge & C. Reese. 1989. Changes in pigmentation associated with the bleaching of stony corals. Limnol. Oceanogr. 34: 1331-1335.

Kushmaro, A., Y. Loya, M. Fine & E. Rosemberg. 1996. Bacterial infection and coral bleaching. Nature 380: 396.

Kousky, V. 1993. The global climate of December 1991-February 1992: Mature-phase warm (ENSO) episode conditions develop. J. Climate 6: 1639-1655.

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

Le Tissier, M. & B. Brown. 1996. Dynamics of solar bleaching in the intertidal reef coral *Goniastrea aspera* at Ko Phuket, Thailand. Mar. Ecol. Prog. Ser. 136: 235-244.

Lorenzen, C. & C. Jeffrey. 1978. Determination of chlorophyll in seawater. UNESCO Technical Papers in Marine Science 35: 1-20.

McPhaden, M. 1994. The eleven-year El Niño?. Nature 370: 326-327.

McPhaden, M. 1999. Genesis and evolution of the 1997-98 El Niño. Science 283: 950-954.

McPhaden, M., A. Busalacchi, R. Cheney, J. Donguy, K. Gage, D. Halpern, M. Ji, P. Julian, G. Meyers, G. Mitchum, P. Niiler, J. Picaut, R. Reynolds, N. Smith & K. Takeuchi. 1998. The tropical Ocean-Global atmosphere observing system: a decade of progress. J. Geophys. Res. 103: 14169-14240.

Mascarelli, P. & L. Bunkley-Williams. 1999. An experimental field evaluation of healing in damaged, unbleached and artificially bleached star coral, *Montastraea annularis*. Bull. Mar. Sci. 65: 577-586.

Meesters, E & R. Bak. 1993. Effects of coral bleaching on tissue regeneration potential and colony survival. Mar. Ecol. Prog. Ser. 96: 189-198.

Muller-Parker, G. & C. D'Elia. 1997. Interactions between corals and their symbiotic algae. p. 96-113. *In* Birkeland, C. (ed.). Life and death of coral reefs. Chapman. New York.

Muscatine, L., D. Grossman & J. Doino. 1991. Release of symbiotic algae by tropical sea anemones and corals after cold shock. Mar. Ecol. Prog. Ser. 77: 233-243.

Rajagopalan, B., U. Lall & M. Cane. 1997. Anomalous ENSO occurrences: an alternative view. J. Climate 10: 2351-2357.

Rowan, R., N. Knowlton, A. Baker & J. Jara. 1997. Landscape ecology of algal symbionts creates variation in episodes of coral bleaching. Nature 388: 265-269.

Self, S. M. Rampiro, J. Zhao & M. Katz. 1997. Volcanic aerosol perturbations and strong El Niño events: no general correlation. Geophys. Res. Lett. 24: 1247-1250.

Szmant, A. & N. Gassman. 1990. The effects of prolonged "bleaching" on the tissue biomass and reproduction on the reef coral *Montastrea annularis*. Coral Reefs 8: 217-224.

Tarazona, J., W. Arntz & E. Canahuire. 1995. Impact of two El Niño events of different intensity on the hypoxic soft bottom macrobenthos off the central Peruvian coast. Mar. Ecol. 17: 425-446.

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

Trenberth, K. & T. Hoar. 1997. El Niño and climate change. Geophys. Res. Lett. 24: 3057-3060.

Titlyanov, E. 1981. Adaptation of reef-building corals to low light intensity. Proc. 4th Int. Coral Reef Symp., Manila 2: 39-43.

Underwood, A. 1997. Experiments in ecology: their logical design and interpretation using analysis of variance. University of Cambridge. 504 p.

Vogel, G. & A. Lawler. 1998. Hot year, but cool response in congress. Science 280: 1684.

Wanninkhof, R., R. Feely, D. Atwood, G. Berberian, D. Wilson, P. Murphy & M. Lamb. 1995. Seasonal and lateral variations in carbon chemistry of surface water in the eastern equatorial Pacific during 1992. Deep-Sea Res. II 42: 387-409.

Wilkinson, C., O. Lindén, H. Cesar, G. Hodgson, J. Rubens & A. Strong. 1999. Ecological and socioeconomic impacts of 1998 coral mortality in the Indian Ocean: an ENSO impact and a warming of future change?. Ambio 28: 188-196.

Winter, A., R. Appeldoorn, A. Bruckner, E. Williams & C. Goenaga. 1998. Sea surface temperatures and coral reef bleaching off La Parguera, Puerto Rico (northeastern Caribbean Sea). Coral Reefs 17: 377-382.

Woodruff, S., R. Slutz, R. Jenne & P. Steurer. 1987. A comprehensive ocean atmosphere data set. Bull. Am. Meteorol. Soc. 68: 1239-1250.

Zhang, R., L. Rothstein & A. Busalacchi. 1998. Origin of upper-ocean warming and El Niño change on decadal scales in the tropical Pacific Ocean. Nature 391: 879-883.