CORAL BLEACHING AND MORTALITY IN PANAMA AND ECUADOR DURING THE 1997–1998 EL NIÑO–SOUTHERN OSCILLATION EVENT: SPATIAL/TEMPORAL PATTERNS AND COMPARISONS WITH THE 1982–1983 EVENT

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ABSTRACT

Bleaching and mortality of zooxanthellate corals during the 1997–98 El Niño–Southern Oscillation (ENSO) event are documented for eastern equatorial Pacific localities in Panama (Gulf of Chiriquí and Gulf of Panama) and Ecuador (Galápagos Islands and mainland coast). Overall, the very strong 1997–98 and 1982–83 ENSOs were similar in magnitude and duration, but varied spatially, resulting in different patterns of elevated sea temperature stress and coral responses during the two disturbance events. Two bleaching episodes occurred in the Gulf of Chiriquí, each coincident with high (≥30°C) in situ temperatures and warm water filaments visible in NOAA/NCEP SST fields. Coral mortality was significantly different among localities: Galápagos Islands (26.2%) > Gulf of Chiriquí (13.1%) > coastal Ecuador (7.0%) > Gulf of Panama (0%). Coral mortality was notably higher (52–97%) in the eastern equatorial Pacific in 1982–83 than in 1997–98. Coral mortality among most sites within localities was also significantly different. Highest coral mortalities occurred at offshore compared with nearshore sites in Panama, and at the Galápagos Islands compared with mainland Ecuador. Although species responses varied among localities, tissue death was especially high in *Millepora* spp., *Pavona* spp., *Pocillopora* spp., and *Porites* spp. Corals present in relatively deep (12–18 m), inter-reef habitats suffered lower rates of bleaching and mortality than similar and different species present in shallow (1–10 m) habitats. Bleached coral tissues in the Gulf of Chiriquí demonstrated a significant increase in zooxanthella density, but only a slight increase in chlorophyll *a* concentration over a 5 mo respite, from the end of the first bleaching event (October 1997) to the beginning of the second event (March 1998). The use of molecular DNA techniques to compare algal symbionts in bleached and healthy coral colonies revealed a strong correlation between bleaching severity and symbiont genotype, regardless of depth. In particular, one symbiont genotype (commonly found in the scleractinian genus *Pocillopora* in the Gulf of Chiriquí) was particularly resistant to bleaching, indicating that symbiont diversity can play an important role in explaining spatial and host systematic patterns of bleaching. Extreme reductions in abundance of some species populations in Panama have resulted in local extirpations. It is possible that *Millepora boschmai*, a Gulf of Chiriquí endemic hydrocoral, is now extinct. Remnant patches of *Gardineroseris planulata* that survived the 1982–83 ENSO in the Galápagos Islands have also disappeared following the 1997–98 event, causing local extinctions. Marked declines in external bioerosion and corallivore abundances in Panama before and after the 1997–98 ENSO should have less of an effect on surviving corals than in 1982–83 when such effects continued to degrade reefs long after the initial disturbance. Surviving corals in the Galápagos Islands are still subject to heavy grazing pressure by abundant echinoid populations. The response of eastern Pacific coral reefs to the 1997–98 El Niño cannot be fully understood without an appreciation of spatial/temporal variability and the historical stresses to which these reefs have been subject over the past 25+ yrs.

By several measures, the 1997–98 El Niño–Southern Oscillation (ENSO) has been judged to be the strongest event of the century (McPhaden, 1999; Chavez et al., 1999; but see Wolter and Timlin, 1998; Enfield, this issue). In the equatorial eastern Pacific, in the NIÑO 1+2 region (0–10°S, 80–90°W) off Ecuador and Peru, the 1997–98 ENSO exceeded the magnitude and duration of the sea surface temperature (SST) anomalies of the 1982–83 ENSO event (Enfield, this issue). However, the 1982–83 ENSO also was unusually strong, and at that time was claimed to have been the strongest documented ENSO ever (e.g., Gill and Rasmusson, 1983; Cane, 1986; Hansen, 1990). Both events have probably been enhanced by anthropogenic decadal warming during the 1980s and 1990s (Crowley, 2000; Karl et al., 2000; Stott et al., 2000). These extraordinary perturbations, causing elevated SSTs and other potentially stressful conditions to reef-building corals (e.g., increased solar insolation and penetration through the water column, river discharge, sedimentation, altered storm activity, increased incidence of pathogens), have been implicated in numerous coral reef bleaching and mortality events over the world's tropical seas during the past two decades (Brown, 1987; Coffroth et al., 1990; Williams and Bunkley-Williams, 1990; Glynn, 1993, 1996; Goreau and Hayes, 1994; Kushmaro et al., 1996). Since assessments of reef deterioration in the mid 1990s, which emphasized a dominant role for such direct anthropogenic stresses as nutrient pollution, sedimentation and over-exploitation (Smith and Buddemeier, 1992; Ginsburg, 1994), the recent heightened effects of sea warming have altered the opinion of several workers who now maintain that global climate change poses the greatest threat to coral reefs (Hoegh-Guldberg, 1999; Goreau et al., 2000; Wilkinson, 2000).

This contribution deals primarily with the effects of the 1997–98 ENSO event on eastern Pacific zooxanthellate corals in Panama and Ecuador. The occurrence and progression of SST anomalies in relation to zooxanthellate coral bleaching and mortality are examined. Quantitative comparisons are made of the various coral species affected in nonupwelling (Gulf of Chiriquí) and upwelling (Gulf of Panama) localities in Panama, the Galápagos Islands and the mainland coast of Ecuador. The responses of some small and threatened coral species populations are examined in detail. Observed variability in coral bleaching is examined in terms of the molecular identification of their dinoflagellate symbionts. The zooxanthellae found in scleractinian corals are a diverse assemblage of symbiotic dinoflagellates in the genus *Symbiodinium* (Rowan and Powers, 1991; Trench, 1997). Multiple symbiont taxa can often be found within single species (and colonies) of coral host (Rowan and Knowlton, 1995; Baker, 1999) and this information has been used to explain bleaching variability in Caribbean *Montastraea* (Rowan et al., 1997). We adopt a similar approach to test the generality of these findings and explore variation in bleaching response in the reef-building corals of the far eastern Pacific.

Finally, comparisons are made of the effects of the 1982–83 and 1997–98 ENSO disturbances on equatorial eastern Pacific coral communities. Since the moderately strong ENSOs of 1987 and 1990–95 (Trenberth and Hoar, 1996) caused only moderate to light coral bleaching in Panama and the Galápagos Islands (Podestá and Glynn, 1997), with no apparent lasting effects, they are not considered in this study. Corals adversely affected during the 1997–98 and earlier ENSO events in other parts of the eastern Pacific (Colombia, Costa Rica, Mexico) are considered elsewhere in this special issue. Recent ENSO disturbances to corals and coral reefs in other tropical regions worldwide are documented in Wilkinson (1998, 2000), Berkelmans and Oliver (1999), Hoegh-Guldberg (1999), Marshall and Baird (2000), McClanahan et al. (2000), and Souter et al. (2000).

STUDY SITES AND METHODS

STUDY SITES AND SAMPLING SCHEDULE.—This study embraces four localities (Gulf of Chiriquí and Gulf of Panama in Panama, the Galápagos Islands, and mainland Ecuador), each comprising several sampling sites (Fig. 1). The majority of the principal study sites have been monitored since the early 1970s in Panama and the mid-1970s in the Galápagos Islands (Glynn and Wellington, 1983; Glynn, 1990, 1994). Sampling sites in Panama are located in the nonupwelling Gulf of Chiriquí and the seasonally (mid-December to April) upwelling Gulf of Panama (Glynn and Stewart, 1973; Glynn, 1977) (Fig. 1A). These localities have been observed approximately annually during non-ENSO conditions and more frequently (two to four times per year) during ENSO activity. Beginning in 1997, quantitative surveys in Panama were conducted in March, September, October and November, in 1998 in March and April, and in 1999 in May. Sampling sites in the Galápagos Islands range from the southern and central archipelago to the northernmost islands (Fig. 1B). Field sampling also has been conducted approximately yearly in the Galápagos, except for the northern islands, which have been visited only every 3–4 yrs. Additionally, observations are noted from the central coastal area of mainland Ecuador, from La Plata and Islote Islands in the north to Ayangüe in the south (Fig. 1C). Coastal areas in Ecuador were surveyed on 31 January 1975, 19 August 1986, 7–9 March 1991, and 19–21 May 1998.

SEA WATER TEMPERATURE.—In situ sea temperatures were recorded at 2 m depth (relative to MLLW) at the Uva Island and Saboga Island coral reefs in Panama, and at 1.5–7 m at four sites in the Galápagos Islands, utilizing calibrated ($\pm 0.53°C$) Hobo, Stowaway and Tidbit temperature loggers (Onset Computer Corporation). Recording frequency varied from 36 min to 192 min, depending on the sensor memory capacity and the time the recorders were left in the field. In the Galápagos Islands, temperature recorders were maintained at (1) Xarifa Island, east end of Española Island, 2 m depth; (2) Devil's Crown, north side of Floreana Island, 1.5 m; (3) northeast anchorage of Santa Fe Island, 2 m; and (4) east side of Marchena Island, 7 m; Figure 1B. The temperature loggers were all located at sites with pre-1983 (Xarifa, Española, Santa Fe) or current (Marchena) abundant coral populations. To help plan site visits during the 1997–98 ENSO event, SSTs and SST anomalies (optimum interpolation analysis produced weekly on a one-degree grid) were also reviewed at the NOAA web site: www.cdc.noaa.gov/ENSO/. Weekly mean SST data off coastal Chiriquí (Panama), in the Gulf of Panama, Galápagos Islands and coastal Ecuador, from a $1 \times 1°$ grid, were obtained from Reynolds NCEP optimal interpolation (OI) analysis that combines ship reports, buoys and satellite measurements. The OI analysis uses in situ and satellite SSTs plus SSTs simulated by sea-ice cover. Before the analysis is computed, the satellite data are adjusted for biases (see Reynolds and Smith, 1994).

CORAL RESPONSES.—Coral condition was assessed for areas within single colonies displaying different health states. For example, the scoring of the condition of a patchily affected single colony might be 20% pale, 40% bleached, and 40% dead. Coral tissue pigmentation was scored as normal (N, full color characteristic of any given species in a healthy state), pale (P, evident loss of coloration), bleached (B, stark white with no obvious pigmentation), and dead (D). The dead category was further subdivided into recently dead, usually with filamentous algae invading the skeleton, and old dead, with macroalgae, coralline algae, bryozoans, barnacles, interalia, invading an often bioeroded skeleton. A flexible measuring tape calibrated in millimeters or a square wire mesh (2.5 cm $\times$ 2.5 cm) was used to measure colony surfaces. Monitoring results in Panama and the Galápagos indicated that recently dead coralla had succumbed over a period of a few to several weeks, whereas old dead coralla had been dead for several months to a few years. We suspect that bleaching in the Gulf of Chiriquí began at the end of July because all *Millepora intricata* Milne Edwards colonies were dead and covered with filamentous algae in September, 1997. Changes in live coral cover were determined by tracing the outlines of coral species in situ on gridded, water-resistant data sheets in permanently marked quadrats. Scanned coral images were imported into Sigma Scan Pro (SPSS) to obtain live surface areas. Sampling in the Galápagos Islands was performed 6 months after the first observed coral bleaching (10–20 May 1998). Coral condition in Panama was sampled
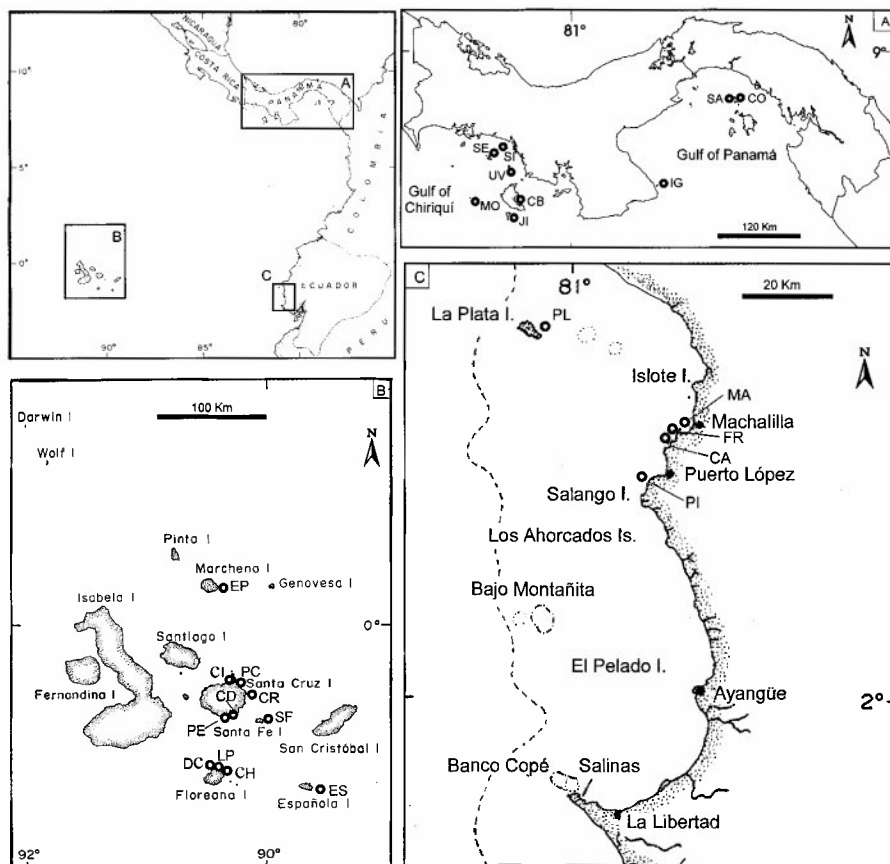
Figure 1. Equatorial eastern Pacific study localities in Panama (A), Galápagos Islands (B) and central mainland coast of Ecuador (C). See Figure 10 and Tables 1, 3, 4 and 5 for identity of 2-letter site codes. Panama - CO, Contadora 1; SA, Saboga 1; IG, Iguana 1; CB, Coiba 1. Galápagos 1s - Cl, Canal de Itabaca.

quantitatively on 11–15 March 1998, during the second bout of bleaching then about 14 mo later (19–21 May 1999). Coral condition at coastal sites in mainland Ecuador was assessed from 19–21 May 1998, an undetermined time after initial coral bleaching.

ZOOXANTHELLAE AND CHLOROPHYLL.—Zooxanthella densities and chlorophyll concentrations were determined in branching and massive coral species in normal, pale and bleached condition from Jicarón and Uva Islands (Gulf of Chiriquí, Panama) in October 1997 and March 1998 respectively (Fig. 1A). Samples were removed with hammer and chisel or pliers, wrapped in aluminum foil and frozen ($-20°C$) until processing. Coral tissues were separated from the skeleton with jets of distilled water from an air brush at low pressure (60 psi). Surface areas of corals were determined by the aluminum foil technique of Marsh (1970). The concentrations of chlorophyll a and c_2 were calculated according to Jeffrey and Haxo (1968).

ALGAL SYMBIONT TAXA.—Samples of 13 species of scleractinian corals were collected from Uva Island reef (Gulf of Chiriquí, Panama) under normal (non-bleached) conditions (12–17 July 1995; $n = 58$), and from the same site when El Niño bleaching was first documented (18 September 1997; $n = 61$). These samples were compared with a similar collection of healthy (non-bleached) corals from the Canal de Itabaca, Marchena and Española Islands (Galápagos Islands) made prior to El Niño bleaching (24–28 May 1997; $n = 18$). All samples were removed from colonies in situ by

SCUBA divers. Samples of pocilloporid corals [*Pocillopora damicornis* (Linnaeus), *Pocillopora elegans* Dana and *Pocillopora inflata* Glynn] were removed from the end termini (distal 2 cm) of outer branches. Samples from non-pocilloporid corals [*Psammocora stellata* (Verrill), *Psammocora superficialis* Gardiner, *Pavona clavus* Dana, *Pavona varians* Verrill, *Pavona* sp. a, *Pavona gigantea* Verrill, *Pavona frondifera* Lamarck, *Porites panamensis* Verrill, *Porites lobata* Dana, and *Gardineroseris planulata* (Dana)] were collected as small branch nubbins (*Psammocora* spp.) or shallow cores taken with a hollow steel punch (all other species). Samples were classified visually as N (normal), P (pale), B (bleached), and additionally M (mottled or patchy pigmentation). Colonies from Panama in 1997 that showed extreme variation in their bleaching were sampled once from a 'healthy' region and once from a 'bleached' region (see Fig. 2). All samples were preserved in liquid nitrogen (Uva Island) or saline DMSO buffer (Galápagos) at the surface within 1 h.

Tissue was removed from the skeleton of preserved samples by jetting with modified 'zooxanthella isolation buffer' (Rowan and Knowlton, 1995) using an airbrush, and DNA was extracted from the resulting tissue slurry using established methods (Rowan and Powers, 1991; Baker et al., 1997). Large subunit rRNA genes (lsrDNA) were PCR-amplified from the genomic DNA preparations using the primers 2415F4 (or 2415F1) and 2423R1. In some cases, mixtures of symbiont- and coral-derived PCR products were obtained; in these cases zooxanthella products were separated from the coral-derived products by gel purification and subsequently re-analyzed (Baker, 1999). Restriction Fragment Length Polymorphisms (RFLPs) in amplified dinoflagellate lsrDNA were obtained using the enzymes *TaqI* and *HhaI* (New England Biolabs) following established protocols (Baker and Rowan, 1997). Representative RFLP genotypes were cloned into the vector pGEM-T and their sequence obtained on an ABI 377 using primers that bordered the cloned insert (Baker, 1999) (see Fig. 3).

Results

In Situ Sea Temperatures and Coral Bleaching.—The development and propagation of SST anomalies (SSTA) along the equator and coastal areas of the eastern Pacific occurred from mid March 1997 to the end of June 1998. Of relevance to this study are the 3 to 4°C positive anomalies that extended unbroken from the Galápagos Islands to the mainland coast of Ecuador, and warm filaments, appearing during two periods (mid-1997, early to mid-1998), that moved from the equatorial warm pool in a northeasterly direction toward the Central American coast (Fig. 4). Positive SSTAs in the Panama Bight, present from the Colombian coast to the Gulf of Panama, were notably lower (~1°C) than surrounding anomalies to the south and west. In Panama (Gulf of Chiriquí), sea temperatures potentially stressful to corals ($\geq$30°C) first reached 30°C in March and April 1997, declined slightly to around 29°C, and then increased to 30–31°C from late July to October 1997. The latter period coincided with the first coral bleaching event, which was observed on 17 September 1997 (Fig. 5). All zooxanthellate corals showed some signs of bleaching, to their depth limits of 18–20 m. The most severely bleached (stark white) colonies still had extended polyps and no signs of algal overgrowth, suggesting the event occurred relatively recently. Since most shallow-occurring colonies of *M. intricata* were already dead and covered with a thin film of filamentous algae, it is probable that these zooxanthellate hydrocorals bleached as early as late July. Temperatures then fell slightly below 30°C in October, and began to rise gradually in December, and remained mostly between 29–31°C from March to the end of July 1998. This period marked the second coral bleaching episode (Fig. 5), which included corals that bleached earlier and recovered (i.e., regained their normal pigmentation in the intervening 4 mo) as well as corals that did not bleach earlier. Over the same 2 yr period, upwelling in the Gulf of Panama
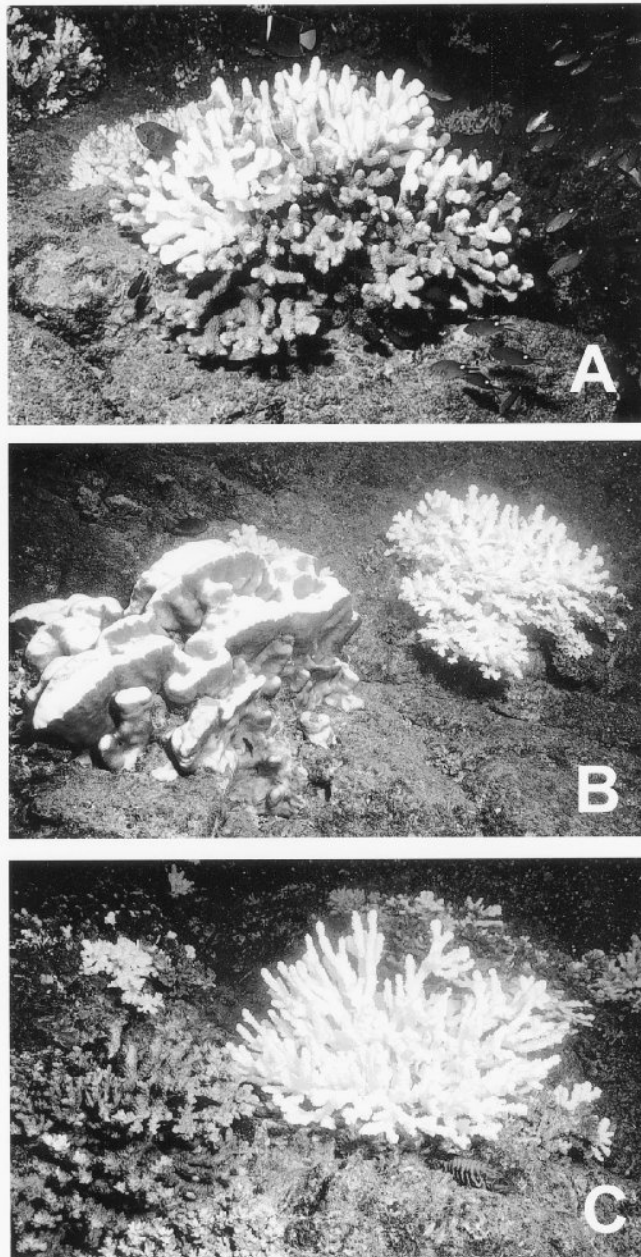
Figure 2. Bleaching variability in scleractinian corals at Uva Island, Gulf of Chiriquí, 15 October 1997. (A) (Apparent) single colony of *Pocillopora* showing distinct 'mottled' bleaching, with part of colony appearing severely bleached and remainder of colony unaffected. Bleaching severity appears independent of irradiance. (B) Colony of *Pavona clavus* (left) showing clear light-related patterns of bleaching, with top (brightly lit) surfaces significantly more bleached than side (dimly lit) surfaces. *Pocillopora* colony (right) completely bleached on all surfaces. (C) Two colonies of *Pocillopora* showing very different degrees of bleaching. Left-hand colony is apparently entirely unaffected; right-hand colony is severely bleached throughout.
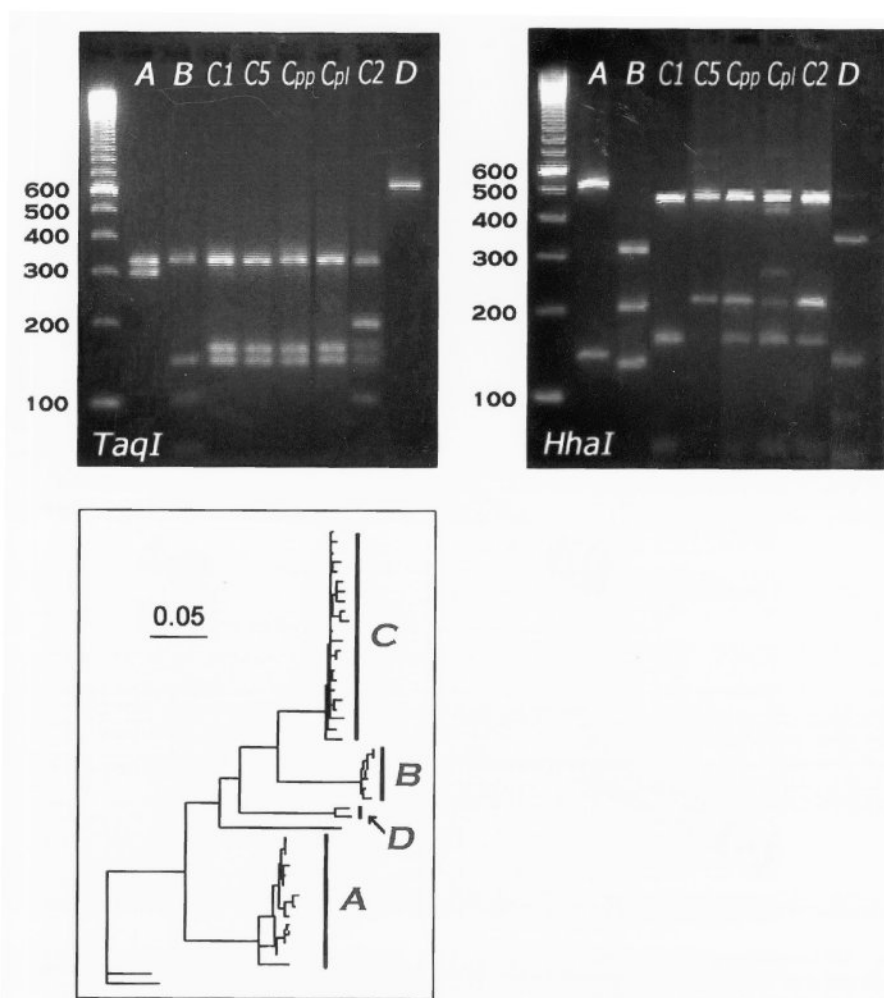
Figure 3. Diversity of symbiotic dinoflagellates in eastern Pacific coral reef cnidarians revealed by surveys of Restriction Fragment Length Polymorphisms (RFLPs) in symbiont large subunit ribosomal DNA. Two enzymes—*TaqI* (top left panel) and *HhaI* (right-hand panel)—distinguish eight distinct taxa within four clades of *Symbiodinium* (*A, B, C* and *D*) in these hosts. First lane of each gel is a molecular size marker with sizes (in bp) indicated. Nomenclature for RFLP genotypes in clade *C* uses numerals (1, 2, 5) or letters (pl, pp) to differentiate genotypes. Algal symbiont phylogeny (bottom left panel), inferred from partial large subunit rDNA sequences, reconstructs evolutionary relationships between these four clades. Scale bar indicates number of substitutions per nucleotide. See Baker (1999) for further details.

was pronounced in March and April 1997, with SSTs sometimes a full 10°C lower than in the Gulf of Chiriquí (Fig. 5). Also, after the upwelling season, during the two periods of coral bleaching in the Gulf of Chiriquí, Gulf of Panama SSTs reached only about 29°C and no evidence of bleaching was observed.

Reynolds SST data, centered at 7.5°N, 82.5°W, and the Uva reef in situ data were in good agreement during 1997–1998 (Figs. 5,6A). The peak SSTs of ~30°C and above, and their timing, are evident in both temperature records. The Reynolds SST record during the 1982–83 ENSO is also shown, revealing a generally lower warming trend
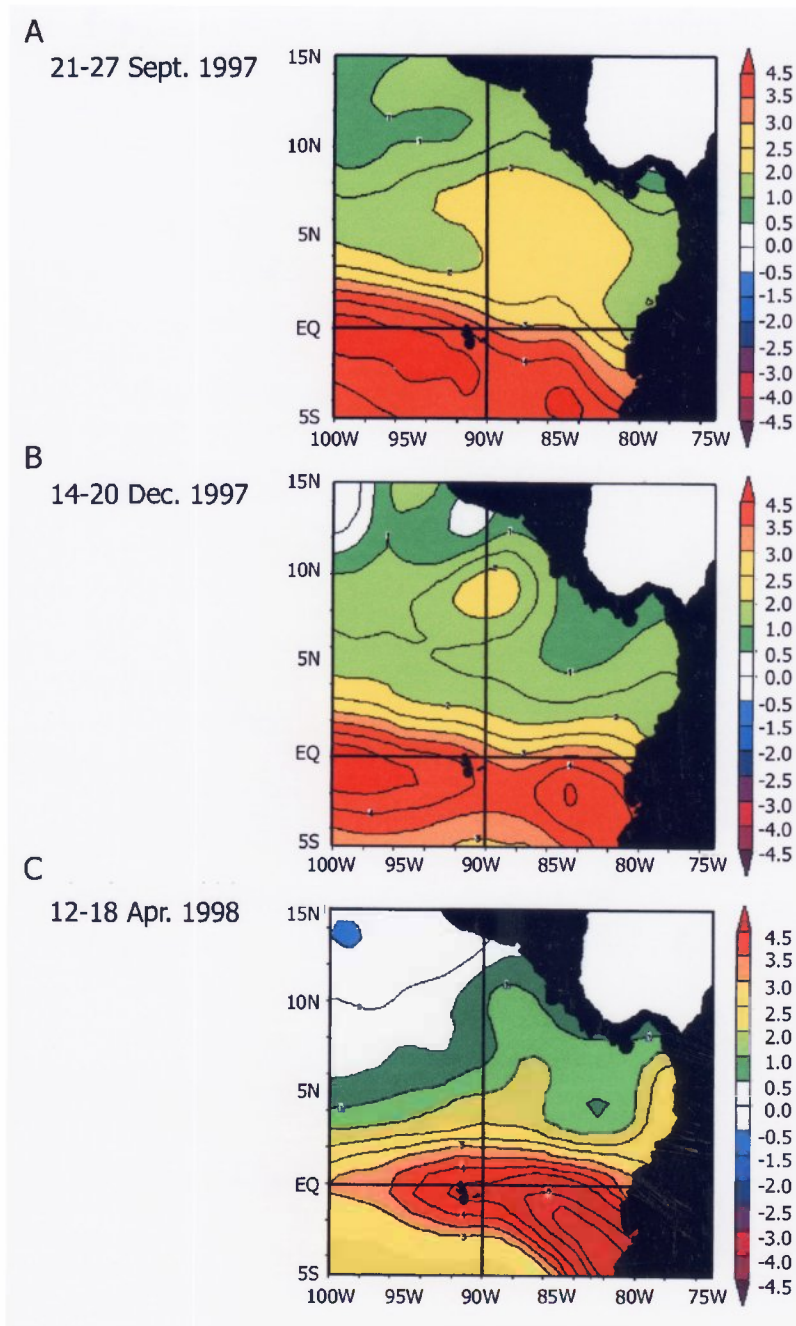
Figure 4. Sea surface temperature anomalies in the equatorial eastern Pacific for three periods during the 1997–98 El Niño: (a) 21–27 September 1997, (b) 14–20 December 1997, and (c) 12–18 April 1998. Data are NOAA/NCEP weekly SST fields (Reynolds and Smith, 1994), created by C. Mark Eakin using the NOAA-CIRES Climate Diagnostics Center, Boulder, Colorado, USA, from their Web site at http://www.cdc.noaa.gov/. Anomalies are relative to the base period of 1961–1990. Note the nonlinear color-coded temperature scale.
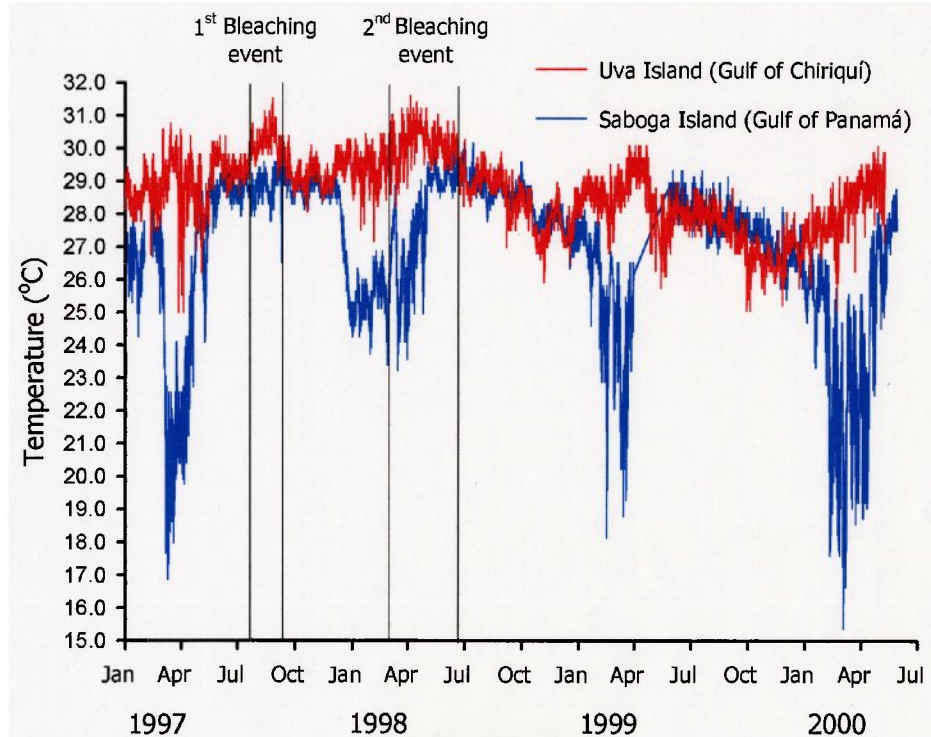
Figure 5. Sea temperature variability at Uva Island (red) and Saboga Island (blue) study reefs, January 1997–May 2000, 2 m depth. Coral bleaching events are denoted for Uva Island. Data are missing from the April–May 1999 period.

than during the more recent event. The mean weekly SST during the 1982–83 period was 28.9°C (SD = 0.64, n = 104) and 29.1°C (SD = 0.81, n = 105) during the 1997–98 period. The persistence of SSTs above 30°C, considered a bleaching threshold in the Gulf of Chiriquí, spanned 3 wks in April 1983 and 6 wks in April–May 1998. The single bleaching episode during the 1982–83 ENSO occurred only in 1983, near and over the interval of maximum SSTs. Gulf of Panama in situ SSTs were notably lower than Reynolds SSTs during upwelling, by −8.5°C in 1997 and −2.0°C in 1998 (Figs. 5,6B). Reynolds SSTs in the Gulf of Panama were also lower in 1982–83 than in 1997–98, especially during the first year (Fig. 6B). Coral bleaching in the Gulf of Panama in 1983 occurred when SSTs exceeded 29°C.

Galápagos Reynolds SSTs were nearly 2°C above (~28°C) the climatological seasonal cycle by April 1997, and maintained a high level (~27°C) from May to August, during the normally cool season in this area (Fig. 7A; Podestá and Glynn, this issue). Potentially stressful SSTs in the Galápagos are ≥28°C (Glynn et al., 1988; Podestá and Glynn, 1997). By late December 1997, temperatures recorded at 2 m depth at Xarifa Island (Fig. 1B, east end of Española Island) began to increase sharply and fluctuated between 29 to 31°C until the first of June, a period of about 4.5 mo (Fig. 8). The first report of coral bleaching by Eric Eisenhardt, issued over the internet (ftp://coral.aoml.gov/pub/champ/bleach/B980106.dat), occurred during 18–30 December 1997. At this time, SSTs were nearly 28°C and SSTAs of 3.5–4.5°C had persisted in the area for about 3 mo (Figs. 4,7A).
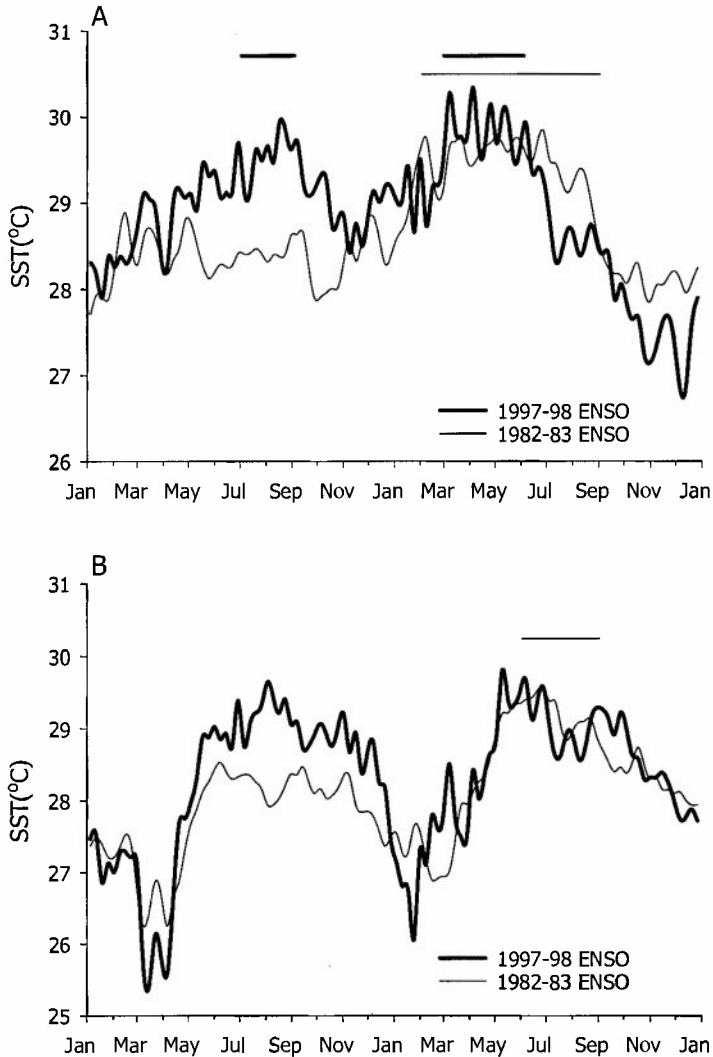
Figure 6. (A) weekly mean SSTs (Reynolds NCEP optimal interpolation analysis) in the Gulf of Chiriquí, Panama (07°N, 82°W), 1982–1983 and 1997–1998, and (B) Gulf of Panama (08°N, 79°W). Coral bleaching periods in A and B are denoted by thin (1982–83) and thick (1997–98) lines at the tops of the temperature plots.

Bleaching was observed in the southern (Española) and central (Santa Fe, Santa Cruz and Bartolomé) Galápagos Islands, and involved the upper surfaces (~20%) of about 80% of the colonies of ?*Porites lobata* (species identity questionable). In all likelihood *P. lobata* was the species affected according to the brief description noted. Surveys conducted from 25 January to 7 February 1998 at Floreana Island, Santa Cruz Island, and two western island sites (Isabela and Fernandina Islands), documented high levels of community-wide bleaching (R. H. Bustamante, P. Martínez and F. Rivera, pers. comm.). Overall, between 70 to 90% of all corals were bleached, including species in the genera *Pocillopora, Porites, Pavona, Psammocora, Diaseris* and *Cycloseris*. Additionally, some colonies of
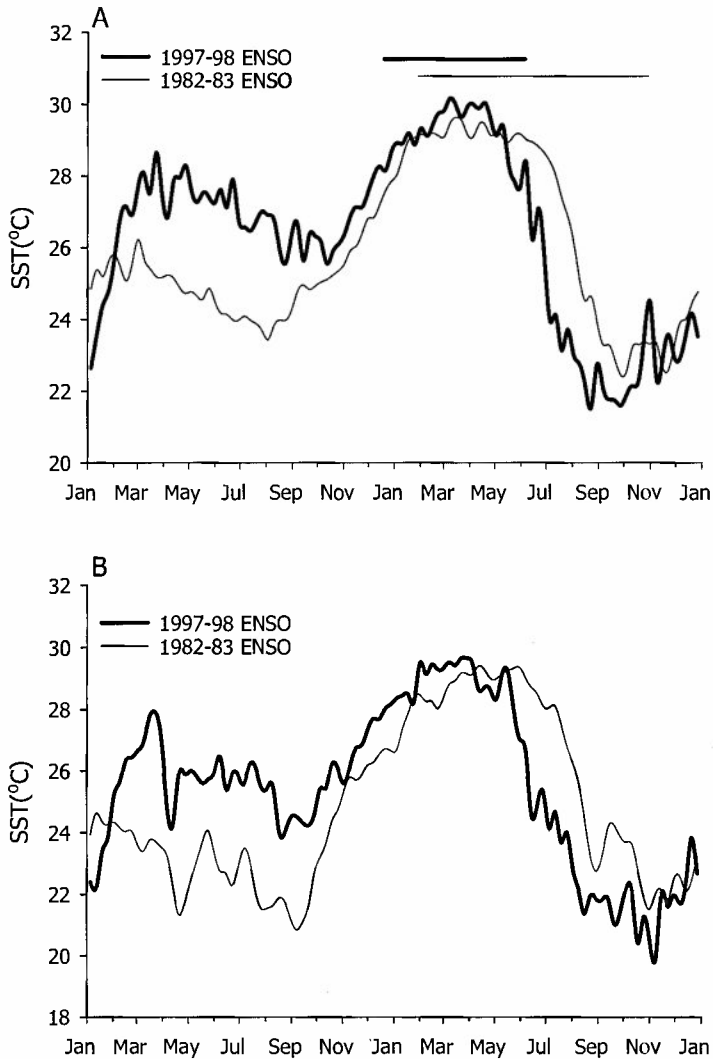
Figure 7. (A) Weekly mean SSTs (Reynolds NCEP optimal interpolation analysis) in the Galápagos Islands (00°, 90°W), 1982–83 and 1997–98, and (B) off the central Ecuadorean coast (02°S, 82°W). Coral bleaching periods in A are denoted by thin (1982–83) and thick (1997–98) lines at the top of the temperature plots.

the azooxanthellate coral *Tubastraea coccinea* Lesson appeared to lose their normal pigmentation, numerous barnacles died, and black corals and gorgonians experienced tissue loss and invasion by filamentous algae. Coral bleaching began in mid January 1983, affecting all species, but at slightly lower Reynolds SSTs than in 1998 (Fig. 7A).

In terms of timing, the in situ 1997–98 temperatures at Xarifa Island were similar to those recorded at Santa Fe, Devil's Crown and Marchena Islands. A correlation analysis (Pearson product moment correlation) of the temperatures at these four sites, comparing only identical time intervals (Santa Fe omitted due to three missing months), revealed highly significant ($P < 0.0001$) correlation coefficients, ranging from 0.909 to 0.987.

Table 1. Statistical comparison of temperature differences among sites in Galápagos Islands. Dunn's a posteriori multiple comparisons testing indicated significant mean differences (P < 0.05) among all sites.

Site	Code	n	Mean	Median	H	P
Marchena Island	EP	1687	26.5	27.1		
Xarifa Island	ES	1687	25.7	26.1	210.06	<0.001
Devil's Crown Island	DC	1687	25.9	26.6		

However, statistical testing indicated significant temperature differences among sites (P < 0.001, Kruskal-Wallis anova on ranks). A multiple comparison procedure (Dunn's method, P < 0.05) demonstrated that the highest median (Md) temperature at Marchena (Md = 27.10°C, mean = 26.52°C) was statistically higher than those at Xarifa (Md = 26.10°C, mean = 25.72°C) or Devil's Crown (Md = 26.60°C, mean = 25.97°C). The median temperature at Devil's Crown was also significantly higher than at Xarifa (Table 1).

A comparison of Xarifa temperatures at 2 m depth with Reynolds SSTs from coastal Ecuador (centered at 1.5°S, 81.5°W) during the 1997–98 event indicates that near-shore sea warming was not so pronounced as in the Galápagos Islands (Figs. 7B,8). Sea temperatures at Xarifa and coastal Ecuador demonstrated similar excursions in 1997, showing sudden increases to about 28°C by April and then marked fluctuations of 3–4°C soon after. However, in early to mid-1998, Xarifa temperatures climbed to and remained at 30°C for about 3 mo whereas off mainland Ecuador SSTs never quite reached 30°C over the same period. A comparison of 1982 with 1997 shows the latter period to be 2–3°C higher on several occasions (Fig. 7B). However, 1998 and 1983 demonstrated similar high temperatures, both with weekly means near 30°C, with the recent ENSO maximum SSTs occurring 1–1.5 mo earlier in the year. The mean weekly SST during 1982–83 was 25.3°C (SD = 2.47, n = 104) and 25.9°C (SD = 2.30, n = 105) during 1997–98. Notably high SSTs of ≥29°C persisted for 11 wks during May–July 1983 and for 10 wks during March–May 1998 (Fig. 7B). The timing of mainland bleaching episodes is not known.
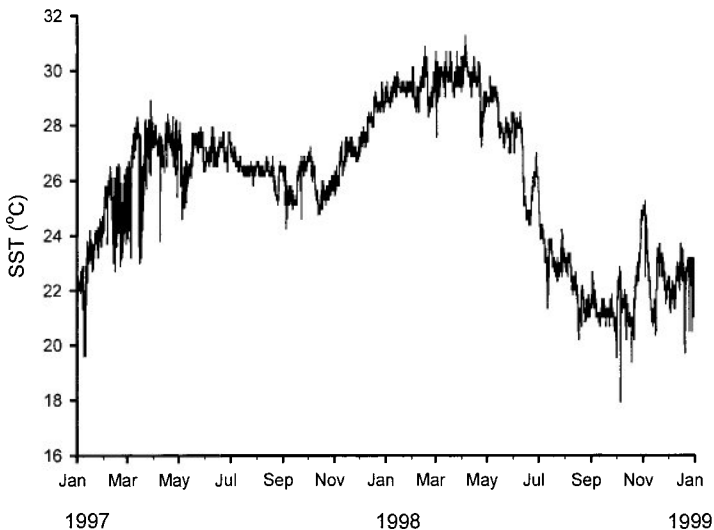

Figure 8. Approximately hourly sea water temperatures at Xarifa Island (2 m depth), eastern end of Española Island, Galápagos Islands, 1997–1998.
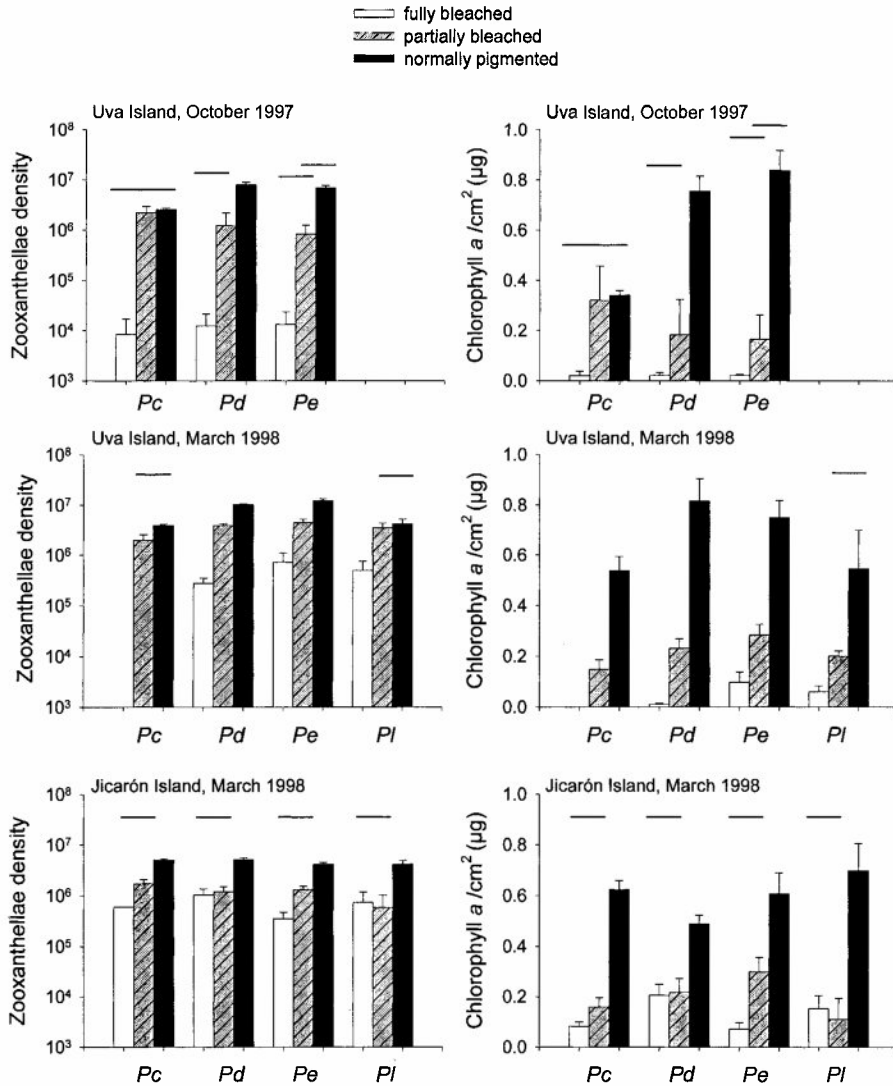
Figure 9. Zooxanthella densities (cm^{-2}) and chlorophyll a concentrations in corals at Uva Island, October 1997 and March 1998, and at Jicarón Island, March 1998, Gulf of Chiriquí, Panama. Pc - *Pavona clavus, Pd - Pocillopora damicornis, Pe - Pocillopora elegans, Pl - Porites lobata.*

TISSUE BIOMASS ATTRIBUTES.—At the end of the first bleaching event (October 1997) in the Gulf of Chiriquí (Panama), normally pigmented tissues in *P. clavus, P. damicornis* and *P. elegans* contained between 10^6 to 10^7 zooxanthellae cm^{-2}, and partially bleached tissues around 10^6 zooxanthellae cm^{-2} or slightly less (Fig. 9). Mean zooxanthella densities in bleached tissues were around 10^4 cells cm^{-2}. Chlorophyll a concentrations were more variable, demonstrating highest levels (0.8 µg cm^{-2}) in normally pigmented *Pocillopora* species to values of less than one-half of the former in *P. clavus*. Photosynthetic pigments in partially bleached tissues ranged from about 0.2 to 0.3 µg cm^{-2}, and were barely detectable (~ 0.03 µg cm^{-2}) in bleached tissues. Zooxanthella densities exhib-

Table 2. Statistical comparison of percent coral mortality among localities.

Site	n (colonies)	n (species)	mean mortality (%)	H	P
Panama (Gulf of Chiriquí)	3,552	12	13.1	428.14	<0.001
Galápagos Islands	1,163	13	26.2		
Ecuador (mainland coast)	917	9	7.0		

ited a marked increase in the bleached tissues of *Pocillopora* spp. after the first bleaching event (by March 1998), with between 10^5 to nearly 10^6 cells cm^{-2}. *P. lobata* demonstrated similar zooxanthella densities as *Pocillopora* spp. at this time. Chlorophyll *a* concentration did not show any consistent change over the 5 mo period, but was lower (<0.2 µg cm^{-2}) in partially bleached colonies of *P. clavus* than after the first bleaching event. *P. elegans* exhibited an increase in chlorophyll *a* in bleached tissues, to a mean concentration of 0.1 µg cm^{-2} after 5 mo. Tissue biomass parameters sampled at Jicarón Island in March 1998, also in the Gulf of Chiriquí (Fig. 1A), generally demonstrated similar values to those reported at Uva Island.

COMPARISON OF AREAS.—Differences in coral condition were examined in relation to localities, sites within localities, and species within sites. The condition of all zooxanthellate scleractinian corals, ranging from nine to 13 species per locality, was compared among three localities: Panama (Gulf of Chiriquí), the Galápagos Islands, and mainland Ecuador. Since corals in the Gulf of Panama (Panama) showed no signs of bleaching or mortality at three sites (Iguana Island, Saboga Island, Contadora Island) during the 1997–98 warming period, this upwelling locality was omitted from the statistical treatment. Mean coral mortality was highly significantly different among localities (P < 0.001, Kruskal-Wallis anova on ranks). Corals in the Galápagos Islands suffered the highest mortalities (26.2%), followed by Panama (13.1%), then coastal Ecuador (7.0%). A posteriori testing indicated that all of these mean mortality values were significantly different (Table 2). Mean instead of median values are reported due to the high numbers of colonies showing no (zero) mortality.

Coral mortalities among four sites in Panama were significantly higher at the offshore islands of Montuosa (54.8%) and Jicarón/Jicarita (11.9%) than mortalities of less than 4% at the inshore islands of Uva and Silva de Afuera (Table 3). Of the 10 island sites examined in the Galápagos Islands, Española and Santa Fe islands demonstrated the highest coral mortalities, 75.5% and 49.1% respectively, which were not statistically dissimilar (Table 4). A second group of relatively high mortalities occurred in Academy Bay, Santa Cruz Island, off the Charles Darwin Research Station (45.6%) and at Punta Estrada (29.0%), at the entrance of Academy Bay. Mortality values declined steadily at three sites on or near Floreana Island, from 23.3% at Devil's Crown to 19.7% at Playa La Picona. The

Table 3. Statistical comparison of percent coral mortality among sites in Panama (Gulf of Chiriquí). Dunn's a posteriori multiple comparisons testing indicated significant mean differences (P < 0.05) among all sites except for Silva de Afuera Island and Uva Island.

Site	Code	n (species)	n (colonies)	mean mortality (%)	H	P
Montuosa Island	MO	2	90	54.8	391.06	<0.001
Jicarón/Jicarita Islands	JI	10	1,071	11.9		
Uva Island	UV	10	636	3.2		
Silva de Afuera Island	SI	6	245	3.8		

Table 4. Statistical comparison of percent coral mortality among sites in the Galápagos Islands (Ecuador). *a,b* identify mean values that are not significantly different (Dunn's method, P < 0.05).

Site	Code	n (species)	n (colonies)	mean mortality (%)	H	P
Española Island	ES	5	105	75.5^a		
Santa Fe Island	SF	3	49	49.1^a		
Charles Darwin Research Station	CD	6	123	45.6^b		
Pta. Estrada (Santa Cruz Island)	PE	5	81	29.0^b		
Devil's Crown (Floreana Island)	DC	6	181	23.3		
Champion Island	CH	2	51	22.3	344.78	<0.001
Playa La Picona (Floreana Island)	LP	6	51	19.7		
Pta. Carrión (Santa Cruz Island)	PC	3	49	11.6		
Pta. Espejo (Marchena Island)	EP	3	447	11.6		
Caleta Robinson (Santa Cruz Island)	CR	4	24	10.4		

lowest mortalities (10.4–11.6%) occurred at two sites on the northeast corner of Santa Cruz Island, and at Marchena Island, the northernmost island sampled in the Galápagos in 1998. Only one of five sites surveyed along the mainland coast of Ecuador, namely Los Frailes, revealed exceptionally high coral mortality with 75.6% of the surface area affected (Table 5). This high value occurred in *P. damicornis*, a particularly sensitive species which was the only one present at this site. Mortality was relatively low at the remaining four sites, ranging from 1.4% at Cabuya to 6.8% at Machalilla.

COMPARISON OF SPECIES.—The condition of five abundant and widely distributed eastern Pacific coral species contributing most to reef building is summarized in Figure 10 for all sites surveyed in the principal study localities. Two pocilloporid species, *P. damicornis* and *P. elegans*, suffered moderate to high incidences of bleaching and high mortalities at several sites, particularly in the Galápagos Islands. *P. elegans* appears to have suffered less bleaching than *P. damicornis* in the Galápagos. *P. damicornis* was heavily affected at Los Frailes in mainland Ecuador. The massive species, *P. clavus*, experienced frequent bleaching and relatively high mortality, especially in the Galápagos Islands. Extensive bleaching, but relatively lower levels of mortality, also occurred in *P. gigantea* and *P. lobata*.

ENDANGERED SPECIES.—Three hydrocoral species (*Millepora platyphylla, Millepora boschmai, M. intricata*) and three scleractinian species (*Pavona* sp. a, *P. panamensis, G. planulata*) that experienced presumed extinctions, local extirpations or severe reductions

Table 5. Statistical comparison of percent coral mortality among sites at mainland Ecuador. *a* identifies mean values that are not significantly different (Dunn's method, P < 0.05).

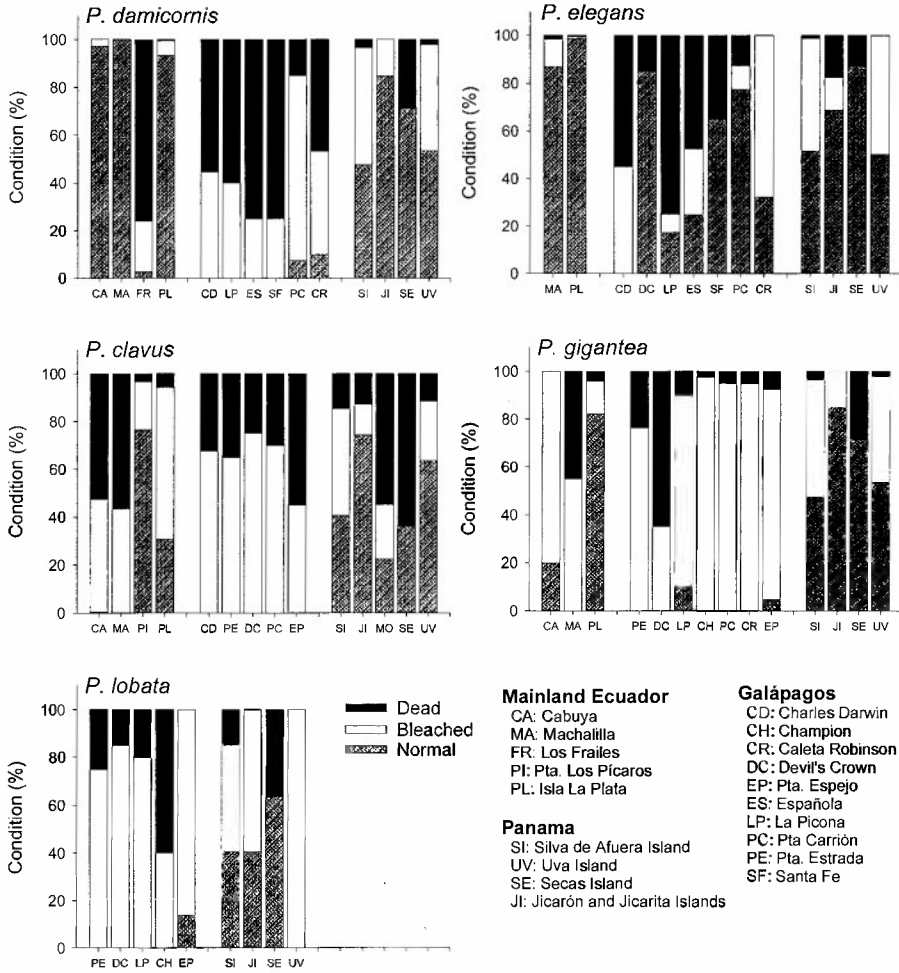| Site	Code	n (species)	n (colonies)	mean mortality (%)	H	P
La Plata Island	PL	9	570	4.8		
Pta. Los Pícaros	PI	1	93	3.3		
Los Frailes	FR	1	34	75.6	263.68	<0.001
Machalilla	MA	5	183	6.8^a		
Cabuya	CA	3	155	1.4^a		

Figure 10. Coral colony condition in five zooxanthellate species sampled at several sites in Panama (Gulf of Chiriquí), 10–15 March 1998; the Galápagos Islands,10–20 May 1998; and the mainland coast of Ecuador, 19–21 May 1998. The dead, bleached and normal categories refer to the mean condition of numerous colonies surveyed at each site. Colony sample sizes are noted in Tables 4–6.

in abundances following recent very strong ENSOs (Glynn, 1997) are considered here. Due to the difficulty of establishing the population status of coral species over their ranges, these corals are tentatively regarded as endangered, i.e., they would seem to face "... a very high risk of extinction in the wild in the near future" (IUCN, 1994). Since *M. boschmai*, *Pavona* sp. a and *P. panamensis* are likely eastern Pacific endemics, these species would appear to be the greatest at risk.

No live colonies of the zooxanthellate hydrocoral *M. platyphylla* Hemprich and Ehrenberg have been seen in the Gulf of Chiriquí since 1983. The five live colonies of *M. boschmai* discovered at Uva Island (Lazarus Cove) in 1992, the first since the 1982–83 ENSO disturbance (Glynn and Feingold, 1992), were all dead on 13 March 1998. These were last observed alive on 29 January 1997. Lazarus Cove was again searched on 19

Table 6. *Millepora intricata* patch sizes, numbers of colonies and maximum colony dimensions in a 1 ha area at the north/northwest sector of Uva reef, 23–29 January 1997, 4–8 m depth.

Patch area (m²)	Number of colonies	Maximum linear growth axis (cm)	Coral mortality (%)
1	3	26, 35	100
2	3	80, 86, 112	100
4	26	56	100
20	63	21, 36	100
288	76	54, 55, 75	100

May 2000 (7 man-h) and 18 February 2001 (1 man-h), but no live colonies were found. In the May 2000 and February 2001 surveys, 58 and 35 dead colonies were found respectively, and none contained live tissue. Three live colonies of *M. boschmai* were also present at the north end of Coiba Island (Fig. 1A) in the early 1990s (Anonymous, 1993). Only a single dead colony was found in this area after 8 sites were searched with SCUBA for 25.5 man-h on 26–27 May 2000. Following the nearly total elimination of *M. intricata* in 1983 (Glynn and Weerdt, 1991), the Uva reef population demonstrated moderate recovery, through sexual and asexual recruitment, by January 1997 (Fig. 11A). Most of the recruitment occurred at the north/northwest sector of the reef, chiefly in five patches comprising from three to 76 colonies each (Table 6). By 13 October 1997, 90% of the hydrocoral surface cover was dead with the remaining 10% bleached, a result of the first bleaching episode in late July–September 1997 (Fig. 5). By 25 May 1999, only a single 2 cm branch tip was alive in the 288 m² patch. Several 8–12 cm diameter colonies survived both bleaching episodes intact in deeper water: 9 colonies at 10–13 m off the Uva reef (23 May 2000); 10 colonies at 18 m off the Secas reef (16 May 2000); 2 colonies at 12 m off Isla Ranchería (26 May 2000). One of the colonies at Ranchería measured 30 cm in diameter. More recent and extensive surveys at the Secas reef (20 and 21 February 2001), from 12 to 20 m depth, have revealed hundreds of live colonies of *M. intricata*.

Scleractinian coral mortality in the Gulf of Chiriquí fell heaviest on *Pavona* sp. a (Fig. 11B, Table 7) and *P. panamensis* (Table 8). The following quantitative measurements are from the Uva Island reef and surroundings, but are generally representative of several areas surveyed in the Gulf of Chiriquí. *Pavona* sp. a suffered high losses of live tissue, with six colonies revealing losses ranging from 47.3 to 99.4% 1 yr after the bleaching event (Table 7). However, colony regeneration by the lateral growth of surviving patches was rapid, with five colonies showing increases of 37.9 to 548.3% by May 2000. One colony showed a small decrease in live surface cover of 14.8%. *P. panamensis* demonstrated a severe reduction in colony densities that ranged from pre-disturbance densities of three to 52 colonies per m² to 0 to 1 colony per m² by May 2000 (Table 8). Live tissue losses ranged from 96.4 to 100% in four monitored plots. *G. planulata* demonstrated widespread bleaching in the Gulf of Chiriquí, especially on upper colony surfaces, but mainly experienced only patchy mortality (Fig. 11C). The single known living colony of *G. planulata* in the southern and central Galápagos Islands (present at Punta Estrada, Academy Bay, Santa Cruz Island, see fig. 2 in Glynn, 1994), with a combined total of ~550 cm² live tissue, was totally bleached on 11 May 1998. This colony could not be found in May, 1999; it was buried beneath a pile of boulders that apparently resulted from a natural rock slide (J. Feingold, pers. comm.).
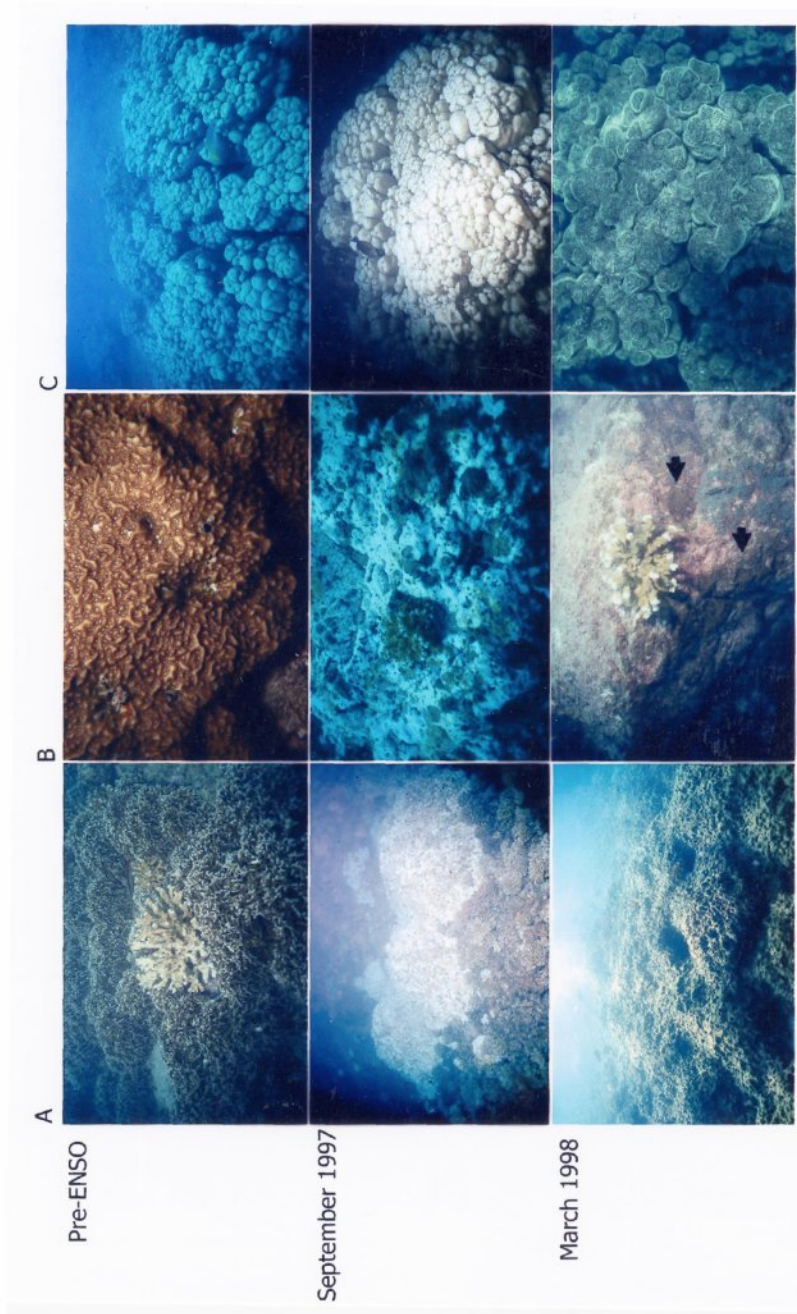
Figure 11. Coral colony condition before and during the 1997–98 ENSO at Uva Island, Gulf of Chiriquí, Panama. A, *Millepora intricata,* 8–9 m, February 1994 (pre-ENSO); B, *Pavona* sp. a, 3 m, May 1997 (pre-ENSO); C, *Gardineroseris planulata,* 2–3 m, May 1997 (pre-ENSO). Bottom panels: A, a 2×4 m field of dead *M. intricata*; B, ~10–20 cm diameter patches of live *Pavona* sp. a (arrows), remainder of substrate surrounding *Pocillopora elegans* with dead *Pavona* sp. a overgrown by mostly turf algae; C, top of ~3 m diameter colony of *G. planulata* with numerous dead lobes rimmed with live tissue.

Table 7. Pre- and post-1997–98 ENSO *Pavona* sp. a live coral tissue area (Uva Island, Panama).

Colony	Pre 1997–98 ENSO live coral size (m²)	Live coral size May 1999 (m²)	Coral mortality (%)	Live coral size May 2000 (m²)	Live tissue increase from 1999–2000 (%)
1	2.574	0.660	74.36	0.562	−14.85
2	0.549	0.169	69.21	0.233	37.86
3	0.132	0.028	78.79	0.057	103.57
4	0.150	0.077	47.33	0.147	90.99
5	0.385	0.042	89.09	0.077	83.33
6	10.150	0.058	99.43	0.376	548.28

DISTRIBUTION OF SYMBIONT GENOTYPES IN BLEACHED AND HEALTHY CORALS.—Six distinct algal symbiont taxa were found in the scleractinian coral communities sampled from the far eastern Pacific (Fig. 3). Based on analysis of large subunit ribosomal DNA sequences (Genbank accession nos. AF170129, AF170142, AF170143, AF170145-170150, AF170152-170155) and/or comparison with RFLP standards (Baker, 1999), five of the RFLP genotypes are members of *Symbiodinium* clade *C* and one is a member of clade *D* (sensu Baker, 1999).

At Uva Island, *Pocillopora* hosts a mixed community of algal symbionts that includes *Symbiodinium* RFLP genotypes *C1, C2, C5* and *D*. Additionally, two RFLP genotypes, C_{pp} and C_{pl}, are found in the non-pocilloporid species *P. panamensis* and *P. lobata*, respectively (Baker, 1999). All other coral hosts contain only *Symbiodinium C1* (although a single colony of *P. lobata* sampled in 1995 contained a mixture of *Symbiodinium C2* and *D*). In the Galápagos, *Pocillopora* (*P. damicornis, P. elegans* and *P. inflata*) contained *Symbiodinium C1* (n = 4) or *C2* (n = 11), while *P. varians* (n = 2) and *Pavona* sp. a (n = 1) contained only *C1*. The distribution of *Symbiodinium* clades *C* and *D* in relation to coral host, location and time of sampling is shown in Figure 12. *Symbiodinium A* and *B*, although absent from the scleractinian corals surveyed here (Baker and Rowan, 1997), are found in other cnidarians at Uva reef: examples are the hydrocoral *M. intricata* (which was the first zooxanthellate coral to bleach at this site, where it contains the unusual *Symbiodinium A*), and the anemone *Aiptasia* sp. (*Symbiodinium B*) (Baker and Rowan, 1997).

Bleaching at Uva Island was characterized by extreme variability among the affected coral hosts (Figs. 2 and 10 show normal/bleached/dead data for each site). Some species (e.g., *Millepora* spp.) were highly sensitive to the bleaching event, while others (e.g., *Psammocora* spp.) appeared highly resistant. Most scleractinian species (e.g., *P. lobata, P. gigantea*) showed patchy bleaching, with upper (high irradiance) surfaces more bleached

Table 8. Reduction in *Porites panamensis* colony density and live surface cover, Uva Island reef.

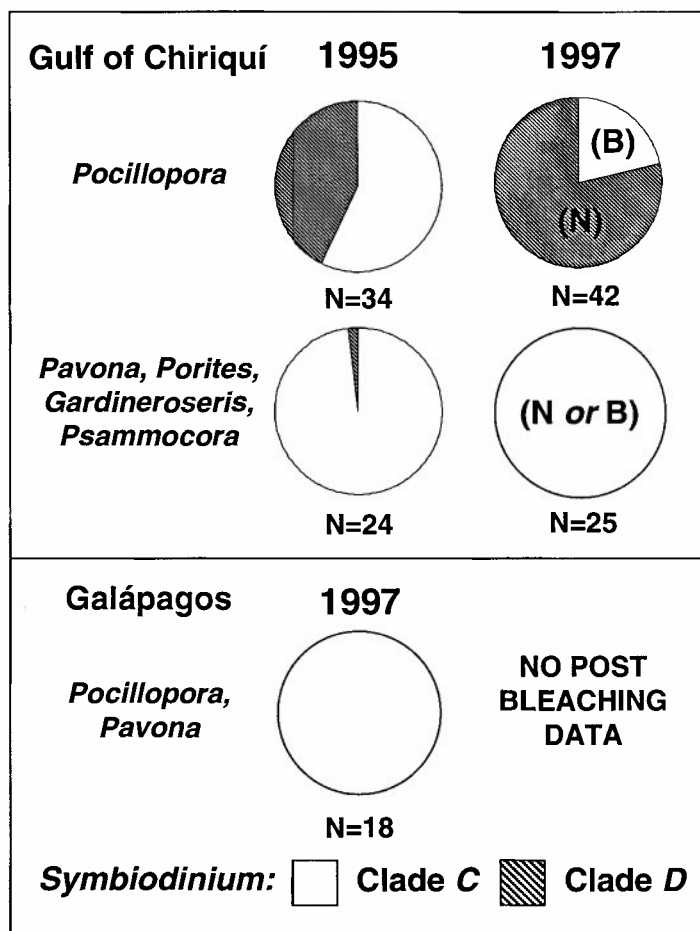| Plot area (m²)	Colony density (No./m²)		Live tissue (cm²)		Loss (%)
	Jan. 1997	May 2000	Pre-ENSO	Post-ENSO	
20	4.2	0.05	2,035	74	96.4
1	3	0	128	0	100
1	49	0	559	0	100
1	52	0	489	0	100
1	37	1	377	10	97.4
1	20	0	211	0	100

Figure 12. Distribution of symbiont RFLP genotypes in reef-building scleractinian corals of the far eastern Pacific as a function of host species, location and time of sampling. For clarity, RFLP genotypes are pooled by clade (*C1, C2, C5, C_{pp}* and C_{pl} = *Symbiodinium* clade *C*). Samples from Uva Island (Gulf of Chiriquí, Panama) are compared from 1995 (prior to El Niño, all samples classified as N - 'normal') and 1997 (after onset of El Niño, samples classified as either N or B - 'bleached'). Uva Island samples are further divided into corals in the genus *Pocillopora*, and corals in all other genera (*Porites, Pavona, Gardineroseris, Psammocora*). Samples from the Galápagos are from May 1997 only (prior to El Niño bleaching, all samples classified as N). Pie charts represent proportion of colonies sampled containing *Symbiodinium* RFLP genotypes in clades *C* and *D*. Pie chart bleaching classifications in parentheses (N, B, N or B) represent bleaching status of each pie slice.

than lower surfaces or colony sides. In general, at Uva Island, conspecific corals at similar depths showed similar bleaching incidence and severity. However, corals in the genus *Pocillopora* were unusual in two respects: (1) conspecific colonies at similar depths showed dramatic differences in bleaching severity, with some colonies appearing entirely unaffected while neighboring colonies were severely bleached; (2) there was little or no evidence of upper surfaces being more severely bleached—instead, some colonies showed distinct 'mottled' or 'patchy' bleaching (Fig. 2).

Identification of *Symbiodinium* communities in *Pocillopora* revealed that colonies (or parts of colonies) classified as N ('normal') contained only *Symbiodinium D* (n = 33). *Pocillopora* colonies (or parts of colonies) classified as B ('bleached') contained either *Symbiodinium C1* or *Symbiodinium C2+D* (n = 9). See Fig. 12 top right hand panel. In contrast, non-pocilloporid colonies contained *Symbiodinium* RFLP taxa in clade *C* regardless of bleaching status (Fig. 12, center right hand panel). In the Galápagos, all coral samples collected prior to bleaching contained *Symbiodinium* RFLP genotypes in clade *C* only (Fig. 12, lower left hand panel).

DISCUSSION

PATTERNS ACROSS LOCALITIES AND SITES.—It is difficult to report definitive overall community mortality effects for particular sites or localities. Obvious confounding factors are variable species specific responses and differences in species relative abundances among sites (Marshall and Baird, 2000). In addition, different coral species demonstrate varying response times to elevated temperature stress. For example, *M. intricata* is one of the first corals to bleach and die, usually 2 mo before bleaching is apparent in other zooxanthellate species. And bleaching and mortality are markedly delayed in *P. panamensis*, occurring 2 to 3 mo or more after other species have died. These different response times have been observed in the eastern equatorial Pacific during both very strong ENSOs (1982–83, 1997–98). Moreover, coral tissue loss does not end with the demise of an ENSO event and the moderation of sea temperatures. In the Caribbean, damage to corals was reported for more than a year beyond the first documentation of sea warming and bleaching in 1987 (Bunkley-Williams et al., 1991). Numerous delayed effects, such as predator concentration (Glynn, 1985a, 1990), increased bioerosion (Glynn, 1988; Eakin, 1996, this issue; Reaka-Kudla et al., 1996), susceptibility to disease by parasites and pathogens (Santavy and Peters, 1997), and a decreased capacity for wound healing (Mascarelli and Bunkley-Williams, 1999) continue to take a toll long after the initial bleaching responses. In spite of these complications, the several sites and large numbers of colonies assessed near the end of the 1997–98 ENSO event, increases confidence in the reality of the trend observed, namely increasing bleaching-related mortality from the Gulf of Panama, Panama (0% mortality), to coastal Ecuador (7.0%), the Gulf of Chiriquí, Panama (13.1%), and the Galápagos Islands (26.2%).

The two coral bleaching episodes observed in the Gulf of Chiriquí also occurred in Costa Rica (Jiménez et al., this issue) and Colombia (Vargas Ángel et al., this issue), overlapping temporally but of varying duration at the different localities. The longest bleaching intervals occurred in Costa Rica (June–October 1997, April–August 1998) and the shortest in Colombia (July–August 1997, April–May 1998). Corals began to regain their normal pigmentation at all localities during the 5 mo respite (November 1997–March 1998) between the two bleaching events. Each bleaching episode corresponded with peak in situ SSTs and SSTAs portrayed in the NOAA/NCEP weekly plots (Fig. 4).

Highest coral mortalities in Panama and Ecuador tended to occur at offshore or oceanic sites compared with nearshore areas. For example, in the Gulf of Chiriquí, overall coral mortality was significantly higher at Montuosa (55%) and Jicarón (12%) islands than at Uva (3%) and Silva (4%) islands, which are located relatively close to the mainland. In Ecuador, all 10 Galápagos sites revealed over 10% coral mortality each whereas four of

five mainland sites experienced less than 7% mortality. Los Frailes, an exceptional main-
land site, experienced 76% mortality. This high value is based on only 34 colonies of *P.
damicornis*, a particularly vulnerable species to high temperature stress. We propose that
the offshore-to-inshore decline in mortality is a result of higher stressful SSTs that are
prevalent in more oceanic settings during ENSO activity. Additionally, water clarity would
be higher offshore, thus allowing for greater light penetration and irradiance stress. This
hypothesis is supported by the occurrence of the largest accumulations of coral reef frame-
works in near-shore eastern Pacific areas that are partly or completely sheltered from El
Niño warming events and cool upwelling conditions (Macintyre et al., 1993).

COMPARISON OF 1982–83 AND 1997–98 ENSOs.—On the Uva Island reef (Gulf of
Chiriquí), temperatures at 2 m depth were 30°C or slightly higher during 2 mo in 1997
and for 3 mo in 1998. It appears that the potential for high temperature stress during
1997–98 was comparable, if not slightly greater, than during the 1982–83 ENSO. For
example, Reynolds mean weekly SSTs (center of sampling grid about 80 km from Uva
Island) were, on several occasions, 0.5 to 1.0°C higher in 1997–98 than in 1982–83. Also,
the 2 yr mean weekly SST in 1997–98 was 29.1°C compared with 28.9°C during 1982–
83. Finally, the rate of warming, calculated as the slope of Reynold's SSTAs, was 0.306
from April to August 1997 (Fong and Glynn, this issue). The slope of sea warming in
1982–83 was 0.161, from June 1982 to March 1983 (Glynn et al., 1988). The in situ daily
SSTs recorded in the Gulf of Panama and the Galápagos Islands since the early 1970s
also offer an opportunity to contrast the two very strong ENSO events at these localities
(Podestá and Glynn, this issue). Bivariate plots of a degree days index—the number of
days of heating stress, i.e., the time above a site-specific bleaching threshold (see Gleeson
and Strong, 1995)—and the annual maximum monthly mean SST demonstrated signifi-
cantly lower thermal stress in the Gulf of Panama in 1998 compared with 1983. The
Galápagos comparison indicated that the 1982–83 and 1997–98 values were very similar
at nearly 700 degree days with maximum monthly mean yearly SSTs of ~28.5°C.

Unlike the high overall coral mortality of 85% observed in the Gulf of Panama during
the 1982–83 ENSO, no detectable ENSO-related bleaching or mortality occurred there
during the 1997–98 ENSO event. The reason for this, we propose, is because of the sea-
sonal upwelling in 1997 and 1998, which occurred on schedule and suppressed local
SSTs. Reynolds upwelling SSTs were about 1°C lower in 1997–98 compared with 1982–
83. Upwelling was minimal in 1983, resulting in 9 mo of positive SSTAs, which reached
3°C in March (Glynn et al., 1988; Glynn, 1990). Not only were SSTs markedly lower in
1997–98 compared with 1982–83, but the rate of temperature rise in 1997–98, measured
by the slope of the longest run of positive anomalies, was 0.077 compared with 0.201 in
1982–83 (Fong and Glynn, this issue). Relatively low SSTs occurred throughout the
Panama Bight in 1997 and 1998, thus also alleviating high temperature stress along the
Colombian coast and at Malpelo Island (Vargas-Ángel et al., this issue).

The relatively low coral mortality observed along the central Ecuadorean coast was
unexpected considering the location of this area within NIÑO zones 1+2, which are usu-
ally characterized by the highest SSTs and SSTAs during ENSO events. Although the
coral reefs in this area were not examined after the 1982–83 ENSO until 1986, the dead
and heavily eroded pocilloporid frameworks were in a similar state to those damaged by
the 1982–83 ENSO in the Galápagos Islands and Panama (Glynn, in press a). Thus, it is
likely that the 1982–83 ENSO warming event had a severe effect in this area. A small
proportion of the 7% coral mortality observed in 1998 consisted of branching and mas-

sive species that had recruited onto damaged reef frameworks. The low coral mortality at La Plata Island (4.8%) also involved mostly isolated, non-framework colonies.

Overall coral mortality attributed to the 1982–83 ENSO in the Gulf of Chiriquí amounted to 75%, compared with only about 13% in 1997–98. Reef frame coral cover has not been seriously affected in the more recent event. Perhaps the greatest effect has occurred among coral species with small population sizes (see below). The reversal of mortality values in the two Panamanian gulfs (Chiriquí and Panama), coincident with the 1982–83 and 1997–98 ENSOs, is believed a result of the dampening of upwelling during the earlier event and normal upwelling conditions in 1997 and 1998.

As in 1982–83, in 1997–98 the Galápagos Islands experienced the highest coral mortality of all surveyed localities in the eastern equatorial Pacific. However, the more recent 26% mortality was considerably less than the 97–99% mortality caused by the earlier ENSO disturbance. While entire structural coral reefs bleached and died in 1983, the highest site mortalities occurring in 1998, 76% at Española Island and 49% at Santa Fe Island, affected mostly scattered or highly dispersed colonies. The dead coral reef frameworks remaining after 1983 have been subject to extensive bioerosion, and have been totally eliminated from several sites (Glynn, 1988, 1994; Reaka-Kudla et al., 1996). Only rarely have the dead coral frameworks been recolonized by coral recruits, which occur more commonly on basaltic substrates. Another similar response that occurred during the two very strong ENSO events was the bleaching of fungiid (*Diaseris*, *Cycloseris*) and siderastreid (*Psammocora*) corals in relatively deep water (14–25 m) east of Devil's Crown (Fig. 1B), but without mortality (Robinson, 1985; Feingold, 1996). The survival of this coral community is probably related to the lower temperatures and reduced light levels in this habitat. Continuously monitored temperatures at 2 m and 15 m during the 1990–95 ENSO demonstrated that temperatures in the deep coral community were between 0.5–1.0°C lower during the peak warming period (Feingold, 1995). See Feingold (this issue) for temperature data from 1997–98 that further support this relationship.

ZOOXANTHELLA SYMBIONT DISTRIBUTIONS.—The molecular data presented here indicate that *Pocillopora* is unusual in its ability to host *Symbiodinium D* with some frequency in the Gulf of Chiriquí. *Pocillopora* was also unusual in its highly variable bleaching response in this region. Taken together with the significant absence of clade *C Symbiodinium* in healthy *Pocillopora* ($\chi^2 = 42.0$, df = 1, P < 0.001), these observations strongly support the conclusion that *Symbiodinium D* was highly resistant to the El Niño bleaching recorded in the far eastern Pacific in 1997–98. This supports earlier findings from Caribbean reef corals that different symbiont taxa vary in their response to bleaching (Rowan et al., 1997).

Here we propose a bleaching model, consistent with the symbiont distributions and bleaching data presented in this study, in which mixed communities of *Symbiodinium C* and *D* in *Pocillopora* were differentially affected by bleaching. Under this model, clade *C Symbiodinium* was almost entirely lost from pocilloporid hosts during the 1997–98 bleaching event. Consequently, colonies containing only members of *Symbiodinium C* were severely affected by the ENSO warming, and were left with only remnant (but still detectable by PCR) populations of this genotype after bleaching. Colonies dominated by members of *Symbiodinium C* but with a low abundance of *Symbiodinium D* were also severely affected by bleaching, and were left with their (original) *Symbiodinium D* populations together with the remainder of the (expelled) *Symbiodinium C*. Colonies domi-

nated by *Symbiodinium D* showed no visible bleaching and contained only this genotype after the bleaching event.

In contrast, nonpocilloporid corals at Uva Island typically host only clade *C Symbiodinium*. Unlike *Pocillopora*, these species do not appear to frequently host more than one symbiont genotype (one exceptional colony of *P. lobata* contained *C2* and *D*). The symbionts of these hosts (predominantly *Symbiodinium* RFLP genotypes *C1*, C_{pp} and C_{pl}) appear to have been most severely affected when high temperature was combined with irradiance stress, resulting in more severe bleaching on the tops of corals compared to sides or edges. While symbiont identity may contribute to determining differences in bleaching resistance between different species of host (e.g., a relatively resistant *Symbiodinium C1* in *Psammocora* vs relatively sensitive *Symbiodinium* C_{pl} or C_{pp} in *Porites*) there is no evidence to suggest any of the clade *C* genotypes were as resistant to bleaching as *Symbiodinium D* in *Pocillopora*.

These data, and the model proposed here, demonstrate how symbiont distributions can explain the highly variable bleaching response of *Pocillopora* at one site in the Gulf of Chiriquí, Panama. *Pocillopora* is the dominant framework builder of many eastern Pacific coral reefs and its unusually variable bleaching response is worthy of investigation in this context. Similarly, the high degree of bleaching and mortality in Galápagos *Pocillopora* may be explicable in the context of its symbiotic associations. In surveys undertaken prior to bleaching in 1997 no *Pocillopora* colonies (of 15 sampled) contained *Symbiodinium D* (Fig. 12). Under the bleaching model proposed above, all of these colonies would have been severely affected by thermal stress similar to that encountered in the Gulf of Chiriquí. Taken together, these conclusions support the notion that it is the particular combination of coral host, algal symbiont and environmental stress (both current and historical) that determines bleaching response.

ENDANGERED SPECIES.—The three species of zooxanthellate hydrocorals known only from the Gulf of Chiriquí (in the eastern Pacific region) have demonstrated a high sensitivity to anomalous warming events. *M. intricata* suffered 100% mortality in shallow reef zones (1–10 m) during the two very strong ENSO events, but demonstrated a capacity of moderate-to-strong recovery a few years after 1983, most likely from surviving populations in deeper water. Judging from the large number of live colonies observed in deep water (12–18 m) after 1998, we predict that *M. intricata* will begin to colonize shallow reef habitats within a few years. The absence of living *M. platyphylla* in Panama since 1983 strongly suggests the regional extirpation of this species resulting from ENSO 1982–83 elevated SSTs. Since no living colonies of *M. boschmai* could be found for several years after 1983, it was presumed that the 1982–83 ENSO caused the global extinction of this Gulf of Chiriquí endemic (Glynn and Weerdt, 1991; Weerdt and Glynn, 1991). Subsequently, however, a total of eight live colonies, five at Uva Island (Glynn and Feingold, 1992) and three at the north end of Coiba Island (Anonymous, 1993), were found in the early 1990s. Surveys of these sites during and following the 1997–98 ENSO (to February 2001) have failed to reveal any live colonies. Therefore, this species may now be extinct, owing its demise to a second ENSO warming event. If true, this is the first documented extinction of a coral reef species, although on theoretical grounds around 1000 reef species could have become extinct recently due largely to anthropogenic disturbances (Carlton et al., 1999). Two other site specific zooxanthellate corals that have not been seen since the early 1980s are *Acropora valida* at Gorgona Island, Colombia (Glynn, 1997) and *Porites rus* off the Nicoya Peninsula (Cortés and Guzmán, 1998). These disappearances,

which followed (and may have been causally linked to) the 1982–83 ENSO, could also be classified as regional eastern Pacific extinctions if the species are not found again. In addition to the examples above, several other endangered or threatened zooxanthellate corals were enumerated by Glynn (1997) and Glynn and Ault (2000). These vulnerable corals include 12 species that are rare or have experienced extreme population reductions at particular sites. The local population sizes of nine of these species in the mid 1990s were <100 colonies per site.

CORAL COMMUNITY-LEVEL DISTURBANCES.—Because several reef-associated azooxanthellate species were affected during the 1982–83 warming event, it is of interest to examine the responses of such species in 1997–98 and to compare their effects with the earlier disturbance. Azooxanthellate cnidarians, such as *T. coccinea* Lesson, retained their normal bright orange pigmentation in Panama and on the Ecuadorean coast during the height of bleaching in 1998 (March–May). However, at some sites in the Galápagos Islands (e.g., Champion Island, Fig. 1B), a few colonies of *T. coccinea* were pale-olive with white tips in late January 1998. Black corals [*Antipathes panamensis* Verrill and *Antipathes galapaganus* Deichmann] and gorgonians also were stressed in late January in the Galápagos Islands, with tissue sloughing and some moribund colonies covered with filamentous algae. Many black corals and gorgonians were dead a few weeks later (February). Barnacles and crustose coralline algae also were seriously affected in early 1998. Both taxa experienced high mortalities in the southern and middle Galápagos Islands. Non-shaded coralline algal patches typically bleached and were then invaded by green and red filamentous algae (Galápagos observations courtesy of F. Rivera). Robinson's (1985) observations of the responses of invertebrates to the 1982–83 ENSO warming event were very similar to those noted above for cnidarians (antipatharians and gorgonians) and barnacles. *T. coccinea* was not seriously affected, but *Tubastrea tagusensis* Wells died and then disappeared from Tagus Cove, where it was formerly abundant (Glynn and Wellington, 1983). The status of this species is presently unknown.

Secondary effects such as predation and bioerosion continued to degrade coral communities in the aftermath of the 1982–83 ENSO. When *Acanthaster planci* (Linnaeus) densities fluctuated around 10–12 ind ha^{-1} after 1983 (Glynn, 1990), their concentration on preferred remnant coral prey had an important effect, further reducing the relative abundances of certain encrusting and massive species at Uva Island (Glynn, 1985a). Also, the large-scale mortality of pocilloporid corals eliminated protective barriers, thus allowing *Acanthaster* access to coral prey that was formerly sheltered by pocilloporids and their crustacean guards. A steady decline in *Acanthaster* abundance since 1988 (Fong and Glynn, 1998), and their virtual absence from the Uva reef more recently (as of February 2001, and see Fong and Glynn, this issue), has negated the importance of this corallivore in recent years. Besides, crustacean guard mortalities were less severe in 1997–98 and few protective barriers had formed since 1983. Another potentially significant corallivore, the ovulid gastropod *Jenneria pustulata* Lightfoot, has also been uncommon on Panamanian reefs in recent years. This corallivore was abundant on the Uva reef in 1982 with 15–28 ind m^{-2} (Glynn, 1985b). Post-1998 sampling has disclosed low densities of 0–4 ind m^{-2}, comparable with the low densities reported from 1984 to 1988 (Glynn, 1985b, 1990). Finally, pufferfish and hermit crabs that crop the branch tips of pocilloporid corals have recently maintained stable to low population abundances respectively.

High densities of *Diadema mexicanum* A. Agassiz have caused considerable erosion of dead coral frameworks on reefs in the Gulf of Chiriquí and the Gulf of Panama following the 1982–83 ENSO (Glynn, 1988; Eakin, 1996, this issue). Population densities before 1982–83 were <10 ind m^{-2} and increased to 50–80 ind m^{-2} 2–3 yrs following the ENSO event, maintaining these high levels for several years. Large sections of pocilloporid reef frames killed during the 1982–83 ENSO were subsequently eroded as a result of intense echinoid grazing. A marked decline in *D. mexicanum* began in 1998, and mean densities following the recent ENSO were around 0.05 ind m^{-2} (Eakin, this issue; Glynn, in press b). Thus, external bioerosion by echinoids would seem not to be important in post-1998 coral recruitment and reef recovery. In summary, the low abundances of corallivores and external bioeroders in Panama following the 1997–98 warming event would seem not to subject surviving corals to high levels of secondary disturbances, a condition that continued to degrade coral reefs long after the initial sea warming coral mortalities of the 1982–83 ENSO event. Following the nearly total mortality of framework building corals in the Galápagos Islands during the 1982–83 ENSO, the grazing activities of *Eucidaris galapagensis* Döderlein resulted in the wholesale destruction and elimination of coral formations in the southern and middle islands of the archipelago (Glynn and Colgan, 1992; Glynn, 1994; Reaka-Kudla et al., 1996). This was due chiefly to an increase in the population densities of the echinoid (through redistribution), from about 5 ind m^{-2} before the event to 30 ind m^{-2} afterwards. Currently (as of May 2000), since few reef frame structures remain, *Eucidaris* populations are more dispersed with densities of about 10 ind m^{-2} in shallow (1–5 m) habitats. The echinoids are now grazing predominantly on algae on coarse sand and basaltic rock substrates, but also continue to prey on live pocilloporids when these are encountered.

Compared with coral reefs in other regions, mainland eastern Pacific reefs are only infrequently subject to storm damage. Tropical cyclones usually form between 10–20°N and move in a NW direction off the Mexican coast (Glynn and Maté, 1997). The only known storm damage to corals in 1982–83 was observed at Champion Island and Devil's Crown, Floreana Island (Galápagos), when heavy swells, moving in a contrary direction, dislodged massive corals and pocilloporid blocks, which were then deposited along the shoreline (Robinson, 1985). This did not occur in 1997–98. However, storm tracts were altered in 1997–98, resulting in three storms that caused relatively minor damage to coral reefs along the southern Mexican coast (Glynn et al., 1998; Lirman et al., this issue). The main damage was patchy, causing the dislodgment of reef frame blocks and branch tip fragmentation. Hurricanes did not affect Mexican coral reefs in 1982–83. Unlike the significant delayed effects following storm damage in Jamaica, which involved the invasion of algae on reef substrates cleared of corals (Hughes, 1989); and high mortality of storm-generated coral fragments due to sedimentation, predation and disease (Knowlton et al., 1981), such disturbances have not been observed in the eastern Pacific. Echinoid and fish grazing generally limit benthic algal colonization on eastern Pacific reefs (Glynn, 1988; Eakin, 1996, this issue; Reaka-Kudla et al., 1996). And one study of the fate of storm-generated coral fragments in southern México demonstrated high survivorship by fusion with reef frameworks that remained intact (Lirman and Glynn, this issue).

In conclusion, it is evident that over the past 25 yrs a concatenation of multiple disturbances have affected equatorial eastern Pacific coral reefs. The responses of coral communities to the 1997–98 ENSO must be considered against the backdrop of the 1982–83 ENSO event. Coral bleaching in 1982–83 resulted in differential coral mortality (and the

potential for changes in symbiont communities following bleaching), increased preda-
tion, bioerosion and the eventual loss of carbonate substrates. Midday, extreme low tidal
exposures (Eakin, this issue) and plankton blooms (Guzmán and Cortés, this issue) have
also contributed to coral mortality. An appreciation of the rich history of varied distur-
bances is a necessary step toward the understanding of eastern Pacific coral community
structure and dynamics. This has been emphasized by Hughes and Connell (1999) for
coral reefs in Australia and Jamaica, and is equally true for those of the far eastern Pacific.
However, the potential role of stress history in increasing the resilience of coral reef
ecosystems should not be ignored.

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