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BLEACHING AND RECOVERY OF FIVE EASTERN PACIFIC CORALS IN AN EL NIÑO-RELATED TEMPERATURE EXPERIMENT

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ABSTRACT

Coral bleaching events have increased in frequency and severity, due mainly to elevated water temperature associated with El Niño-related warming and a general global warming trend. We experimentally tested the effects of El Niño-like sea temperature conditions on five reef-building corals in the Gulf of Panama. Branching species (*Pocillopora damicornis* and *Pocillopora elegans*) and massive species (*Porites lobata*, *Pavona clavus* and *Pavona gigantea*) were exposed to experimentally elevated seawater temperature, ~1–2°C above ambient. Differences in zooxanthellate coral responses to bleaching and ability to recover were compared and quantified. All corals exposed to high temperature treatment exhibited significant declines in zooxanthellae densities and chlorophyll *a* concentrations. Pocilloporid species were the most sensitive, being the first to bleach, and suffered the highest mortality (50% after 50 d exposure). Massive coral species demonstrated varying tolerances, but were generally less affected. *P. gigantea* exhibited the greatest resistance to bleaching, with no lethal effects observed. Maximum experimental recovery was observed in *P. lobata*. No signs of recovery occurred in *P. clavus*, as zooxanthellae densities and chlorophyll *a* concentrations continued to decline under ambient (control) conditions. Experimental coral responses from populations in an upwelling environment are contrasted with field responses observed in a nonupwelling area during the 1997–98 El Niño–Southern Oscillation event.

A variety of stressors can lead to coral bleaching, the whitening of coral tissue, a problem that threatens reefs worldwide. Some commonly observed conditions causing bleaching include tidal exposure, reduced salinities, lack of light, high irradiance, turbidity and starvation (Glynn, 1993, 1996; Shick et al., 1996; Brown, 1997a; Hoegh-Guldberg, 1999; Wilkinson, 2000). A major factor responsible for coral bleaching (the loss of symbiotic zooxanthellae and/or their pigments) is elevated sea water temperature. Numerous mass bleaching events have been correlated with elevated sea temperatures (Jokiel and Coles, 1990; Goreau et al., 1993; Goreau and Hayes, 1994; Glynn, 1996; Podestá and Glynn, this issue). Increases in sea surface temperature (SST) and coral bleaching are often associated with short-term events such as the El Niño phenomenon (Brown and Suharsono, 1990; Glynn, 1990, 1996; Podestá and Glynn, 1997), or possibly with long-term global warming trends (Williams and Bunkley-Williams, 1990; Glynn, 1990, 1991; Jokiel and Coles, 1990; Smith and Buddemeier, 1992; Chadwick-Furman, 1996; Wilkinson, 1996). Particularly strong warming events, such as the 1982–83 and 1997–98 El Niño events, not only result in coral mortality, but may begin a whole cycle of erosion and recolonization, including the restructuring of coral community composition (Eakin, 1990; Glynn, 1997).

Temperature thresholds of coral bleaching vary geographically (Coles et al., 1976; Brown, 1997b; D'Croz et al., this issue; Jiménez et al., this issue). Short-term warming events of 3–4°C above ambient or long-term warming of 1–2°C may lead to coral bleaching (Jokiel and Coles, 1990). Eastern Pacific corals bleach when SSTs exceed 30°C (Glynn and D'Croz, 1990; Glynn et al., 1992; Podestá and Glynn, 1997). The relative suscepti-

bilities of different coral species to these elevated temperatures are of special interest since ENSO events are associated with marked changes in reef community composition (Guzmán et al., 1987; Glynn et al., 1992).

Hoegh-Guldberg and Smith (1989a) offered evidence that the major reason for the coral tissue paling associated with elevated water temperature exposure is the increased expulsion of zooxanthellae. Also, exposure to elevated light can result in corals which pale or bleach as a result of reduced chlorophyll concentration per zooxanthella cell (Porter et al., 1984). Mass coral bleaching over the past 20 yrs, largely associated with episodes of elevated sea temperature, has now been shown to involve a loss of zooxanthellae due to chronic photoinhibition (Jones et al., 1998; Hoegh-Guldberg, 1999).

The aim of this study is to compare the simultaneous responses of branching and massive eastern Pacific reef coral species to experimental sea warming, comparable to that occurring during El Niño events. Our primary hypothesis is based on the premise that branching and massive corals have differential environmental responses to elevated sea surface temperatures. Coral species with branching colony morphologies appear to be more susceptible to elevated SSTs than species with massive colonies (Jokiel and Coles, 1974; Glynn, 1990; Marshall and Baird, 2000; Glynn et al., this issue). Unlike previous experimental studies that have concentrated on only one or two species, here we compare the responses of two branching species (*Pocillopora* spp.) and three massive species (*Porites*, *Pavona* spp.).

Many studies have presented data concerning species-specific responses in the field and laboratory. The majority of these document the bleaching phenomenon after bleaching has already begun in reef environments. Here we follow the initiation, progression and initial recovery of the bleaching response. Experimental results are compared with previous field data (1982–83 El Niño) and bleaching responses during the 1997–98 El Niño. The exposure history of populations to elevated temperatures and irradiance as factors in the bleaching response are also considered.

Materials and Methods

Experimental conditions were adjusted in the laboratory to simulate as closely as possible sea surface temperature rise that is naturally experienced during El Niño events. Species differential responses were recorded and the recovery potential was assessed after exposure.

The five species selected for this work are all zooxanthellate scleractinian corals. They are among the most common and important reef-building corals in the Gulf of Panama (Glynn and Maté, 1997). Included were branching species, *Pocillopora damicornis* (Linnaeus), and *Pocillopora elegans* Dana, and the massive species, *Porites lobata* Dana, *Pavona clavus* Dana, and *Pavona gigantea* Verrill.

Collection and Pretreatment.—Corals were collected at Saboga and Contadora Islands, Pearl Islands, Gulf of Panama, Panama (Fig. 1). Sampling was performed on 17 March 1997 from about 4–6 m below mean low water (MLW) with hammer and chisel (Fig. 2). Fragments of approximately 100 cm^2 (length × width, live surface) were removed from 40 distinct colonies of each species and transported to Naos Island (about 60 km distance) in insulated coolers with running sea water. Corals were maintained during the acclimation period in outdoor tanks supplied with running sea water from Panama Bay at the Smithsonian Tropical Research Institute (STRI). Specimens were allowed to acclimate under ambient laboratory conditions for 37 d before the beginning of the exposure period on 23 April 1997. Only specimens that appeared normally pigmented at the beginning of the study were used.

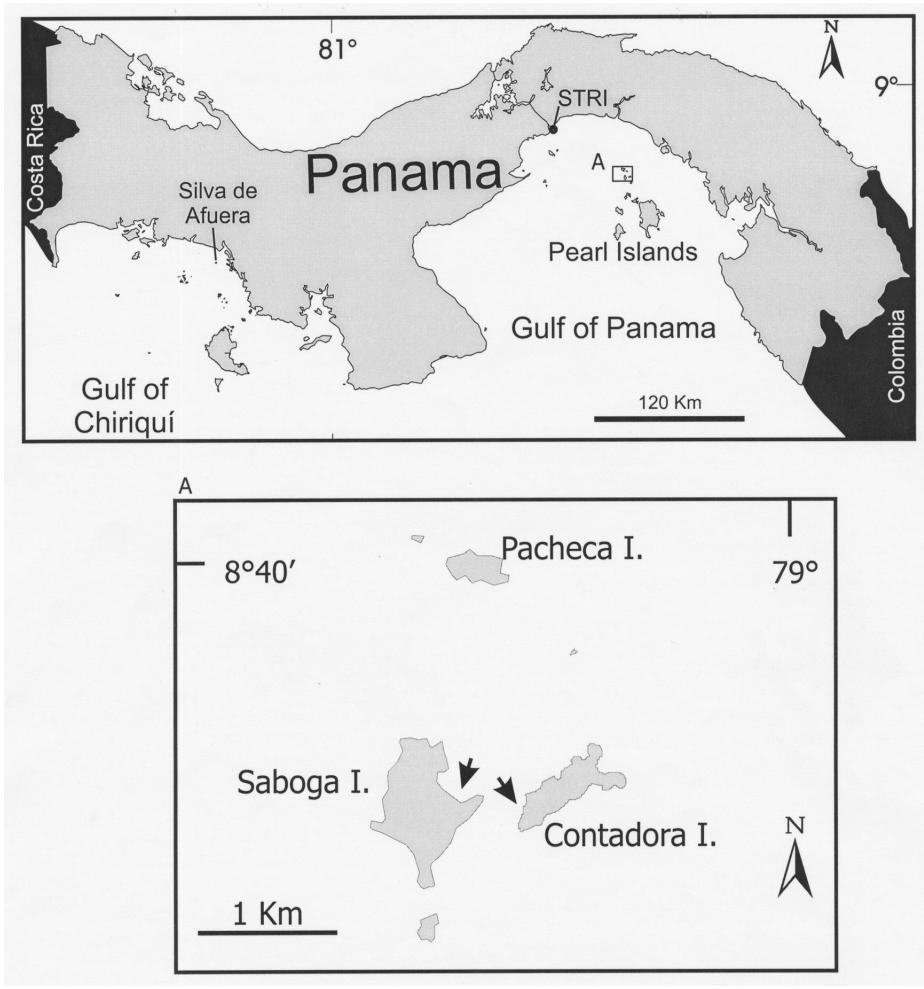

Figure 1. Location of collection and survey sites, Panama.

Experimental Design.—Coral bleaching generally begins at about 1°C above mean maximum seasonal temperatures (Glynn et al., 1988). Coral responses to El Niño events in the field have suggested that 30–31°C is a critical temperature for bleaching in Panama (Glynn et al., 1988). Therefore, the temperature range of 30–31°C was selected for our study.

About 10 d before commencement of the heat treatment exposure, two smaller fragments were cut from each of 30 of the sampled colony pieces acclimating in the outdoor tanks (Fig. 2). Tips about 2–3 cm in length were taken from branching species, and fragments of massive species included about 4 cm^2 of tissue surface area. These fragments were allowed to recover for 5 d and were then stained with Alizarin-Red S (Lamberts, 1978) for growth rate estimates at the end of the study (Fig. 2).

The two fragments from the same parent colony were randomly assigned to the high temperature treatment and to the ambient control. One of these clonal fragments from each species (five total) was placed in a 3.8-L jar which was used as the experimental unit. The complementary clonal fragment of each of these five pairs comprised the control jar. Therefore, one of each of 30 jars in the heated treatment was genetically identical to one of each of the 30 jars held at ambient condi-

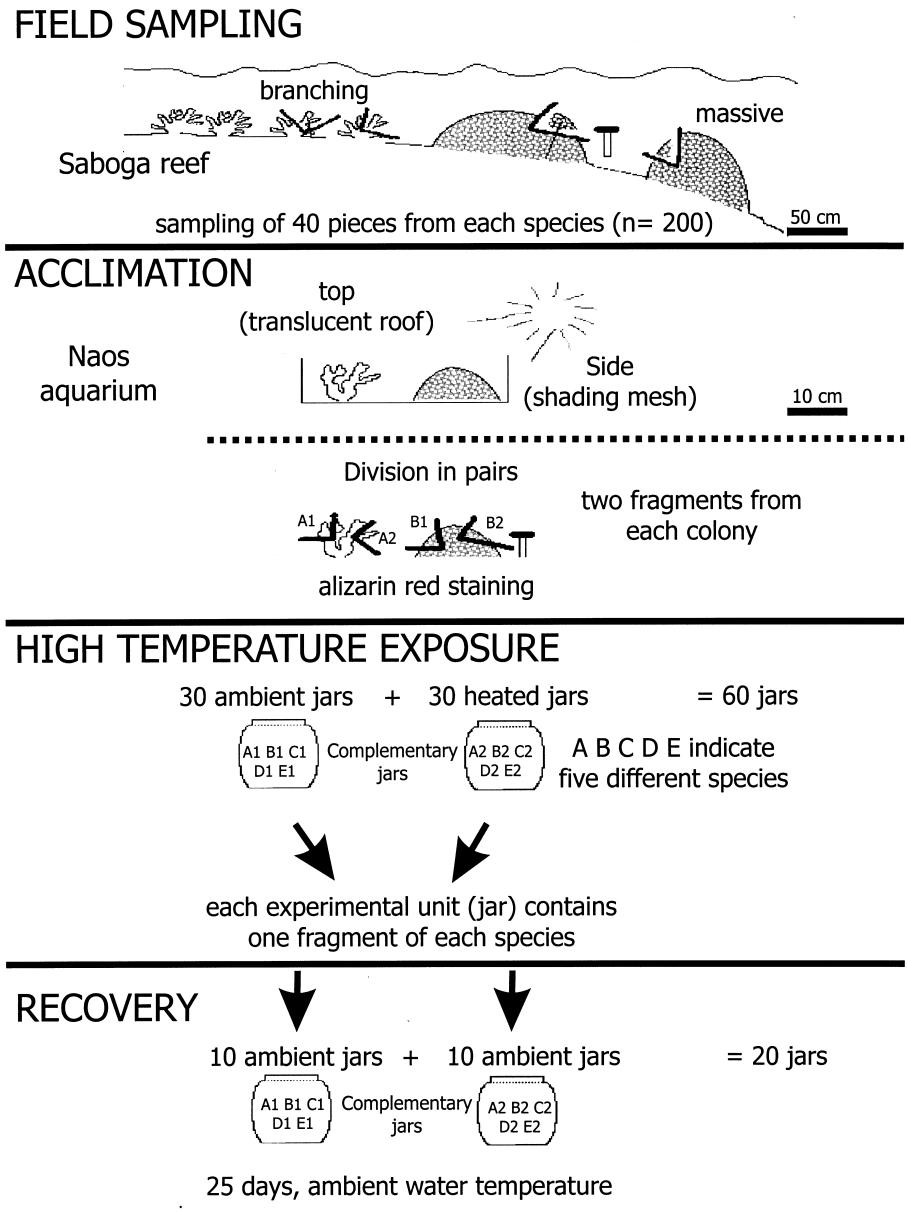

Figure 2. Protocol of sampling and experimental design. Broken line within acclimation panel represents time at which 10 samples of each species ($5 \times 10 = 50$ total) were harvested for initial sampling. Coral fragments (20 total of each species) were randomly selected by jar at days 25, 50 and 75. Ten of these jars were heated and 10 were at ambient temperature. Recovery period represents 10 heated and 10 ambient jars also included in the high temperature exposure panel.

tions. This design allowed for pair-wise comparisons to be made with genetically identical fragments. A preliminary pilot experiment was run comparing jar units containing fragments of five different species and units containing five fragments of only one species. No differences or evidence of negative interactions (visual comparisons) were found.

All jars were independently supplied with aerated flowing seawater through individual tubes from either elevated or control temperature reservoirs. The flow to each jar was approximately 11 L h^{-1}, and complete volume exchange occurred 2.5 time h^{-1}. Water exited the tube at the bottom of the jar such that extended polyps were well agitated. Even under this moderate flow regime our results could have been influenced by this parameter since some workers have reported that flow rates may affect bleaching responses under field conditions (Hoegh-Guldberg and Smith, 1989a). Two heated reservoirs in series were employed in order to keep experimental temperatures stable. Water temperature was monitored in the jars three times a day with a calibrated Digi-Thermo© digital thermometer (0.1°C accuracy).

The entire system was supplied with filtered (1 μm Strainrite polyester felt filter) sea water in a flow-through system. The jars were randomly arranged on dry holding tables with drain holes to allow for jar overflow. Coral fragments were placed on PVC rings to ensure an upright orientation and to avoid direct tissue contact with the bottom and sides of jars.

Translucent fibreglass roofing panels covered the outdoor aquarium facility at Naos to prevent changes in salinity during rainstorms. Additionally, the drain tables were shaded by one layer of black neutral density screen to prevent possible bleaching from direct sunlight. This design, including the glass jars, shielded the corals from UVR radiation. Therefore, we assume that the coral bleaching effects were due only to temperature and not to high PAR or UVR.

Coral fragments were exposed to the heated treatment (~30–31°C) for 50 d (23 April–11 June 1997). Just prior to this exposure (day 0), the remaining 10 unfragmented samples of each species of coral not represented in jar units were wrapped in aluminum foil and frozen (−20°C) until later processing for zooxanthellae density and chlorophyll concentrations. These 10 samples (colonies), plus the 30 represented in the experimental or control jars, comprised the 40 samples per species originally collected in the field. After the exposure phase, all jars were supplied with ambient sea water (~27–29°C) for 25 d (12 June–6 July 1997, recovery period). During the study period, 10 heat treatment corals were harvested randomly (by number assignment) along with their genetically identical controls at (1) 25 d exposure; (2) at the end of the exposure period (50 d); and (3) at the end of the recovery period (day 75). Harvested fragments were wrapped in aluminum foil and treated as stated above for later processing.

Assessment of Bleaching.—The condition of 10 heat treatment fragments of each species harvested for processing was visually categorized as normal, pale to fully bleached ('bleached') and dead. Ten fragments each were assessed at days 25, 50 and 75. The following parameters were measured to estimate the effects of elevated temperature on the coral/zooxanthella symbiosis and coral tissues: coral bleaching and mortality, zooxanthellae densities, chlorophyll *a* and c_2 concentrations, and skeletal growth. Bleaching (paling or completely white coenosarc/polyp tissue) and mortality (no polyps or coenosarc visible for more than 5 d) were determined visually and confirmed by microscopic examination.

To determine the coral fragment surface area, an improved version of the paraffin method of Glynn and D'Croz (1990) was used. Clean skeleton was used instead of aluminium foil to measure surface area. Also, five different species-specific regression curves describing the area/weight relationship were created.

Zooxanthellae density counts are a common method for stress assessments in corals and are useful in quantifying bleaching responses (e.g., Jones, 1997). An airbrush was used to remove the tissue from each frozen coral fragment. Tissue slurries were mixed with a battery operated tissue homogenizer. The zooxanthellae from this tissue homogenate were then counted immediately (3 replicates) in a haemocytometer (Neubauer chamber) employing a compound light microscope at 40×.

For the quantitative extraction of selected algal pigments (chlorophyll *a* and c_2), the homogenate was centrifuged (460 g) for 10 min and the clear supernatant discarded. The pellet was then immersed in 10 ml methanol (100%), stirred vigorously for 3 min and placed in darkness under refrigeration (4°C) for 24 h. Methanol was selected for pigment extraction because it is among the most efficient solvents for symbiotic dinoflagellates (Chalker and Dunlap, 1981; Jaubert, 1981). Chlorophyll concentration was measured spectrophotometrically according to the method of Jeffrey and Haxo (1968). The chlorophyll *a* concentrations reported here also include their breakdown products (i.e., phaeophytin *a* and pyrophaeophytin *a*). At the end of the study, each of 10 Alizarin-stained fragments of each species was measured at four positions along the linear growth axis to calculate mean skeletal growth.

Statistical Analyses.—The use of paired clonal fragments (for intraspecific comparison) in the experimental design allowed a more sensitive statistical test to be employed (paired t-test) for detecting differences in bleaching sensitivity. Interspecific differences in zooxanthellae densities and chlorophyll concentrations were calculated employing one-way ANOVA, and for a posteriori testing the Fisher-test. All fragments that died during the experiment were excluded from these data, however, their genetically identical ambient controls were not. Before parametric statistical analysis, data were tested for normality by the KST method.

Results

Temperature and Light.—During the 50-d exposure period, the mean heat treatment temperature was 30.7 ± 0.33 (1 SD)°C, compared with 28.7 ± 0.55°C for the ambient controls (Fig. 3). Minimum and maximum temperatures in the heat treatment were 29.7°C and 31.6°C, respectively. Ambient minimum and maximum temperatures were 25.9°C and 29.7°C, respectively. The daily mean temperatures of the ambient and heat treatment were significantly different during the exposure period (t-test, $H_0 \geq 0$, $n = 50$, $P < 0.0001$). Ambient tank variation in temperature was due predominantly to the natural variation of

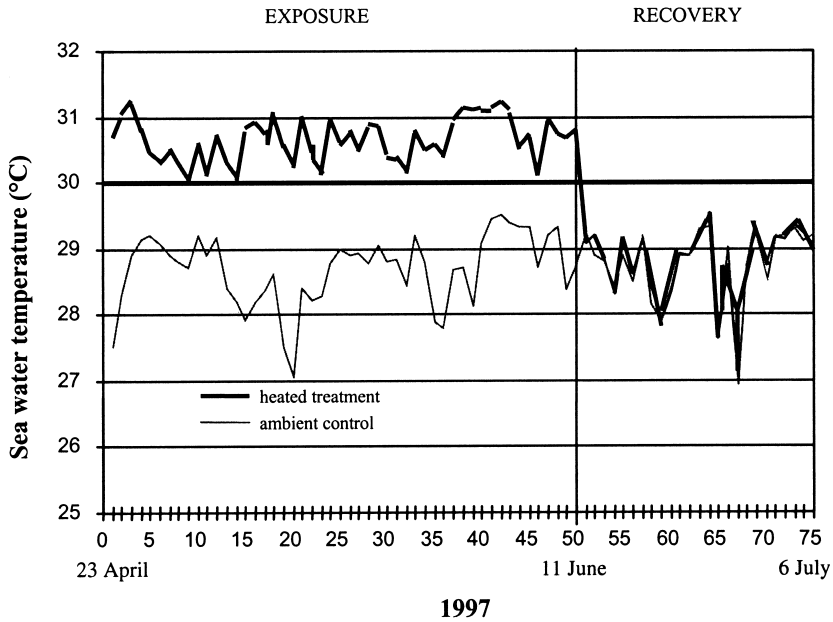

Figure 3. Daily mean sea water temperatures (n = 3 daily readings) during the experimental period.

SST in Panama Bay. Variations of nearly 4°C can occur over 24-h periods and 2–3°C in a few hours. See Glynn et al. (fig. 5, this issue) for in situ variations in temperature at the Saboga Island reef, Pearl Islands. No significant difference was found between mean daily temperatures in the experimental and ambient jars during the recovery period (Fig. 3).

Experimental irradiance values (Table 1) compared with field values (this study, below; D'Croz and Robertson, 1997) indicated that experimental corals were at an equivalent depth of approximately 14 m. Experimental illumination was, therefore, above the minimum field depth for photosynthesis. This determination was made by comparison with a PAR profile conducted in this study at the Pearl Islands at 4–10 m depth. This was further corroborated from light attenuation profiles in Panama Bay during the wet season (D'Croz and Robertson, 1997).

Experimental irradiance values were probably underestimated because a flat sensor was employed. The translucent roof scattered the sunlight and caused much light to enter from the sides. Additional indirect light entered through the black mesh in front of the drain tables. A spherical sensor may have been more suitable in this design.

Bleaching and Mortality.—The progression of coral condition over the 75-d experimental study period is shown in Figure 4. During the first 25 d, some level of bleaching was evident in the heat treatment in all species except *P. gigantea.* No lethal effects were observed during this time. Between 25 and 50 d, mortality occurred in *P. damicornis* and *P. elegans* in the heat treatment: 5 of 10 fragments (50%) in each of these species. Bleaching had progressed in the massive species, but no mortality had occurred over the same period. Slight recovery was evident in *P. damicornis* and *P. clavus* during the 25-d recovery period. However, during the first few days of recovery, 3 of 10 fragments of *P. lobata* and 2 of 10 fragments of *P. clavus* succumbed. These fragments were already severely bleached during the warming treatment. It is possible that the temperature shock from the heat treatment to ambient conditions caused this additional mortality. The highest overall mortality rates (50%) occurred in *P. damicornis* and *P. elegans.* No *P. gigantea* fragments died during the treatment or recovery phase of the experiment.

Zooxanthellae Densities.—Intraspecific variations in mean zooxanthellae densities over the 75-d experiment are shown in Figure 5. At the beginning of the experiment, the five coral species exhibited initial values of mean zooxanthella densities of approximately 9×10^6–19×10^6 cells cm^{-2}. The highest initial mean values were found in *P. elegans* (18

Table 1. Irradiance measurements on overcast and clear days conducted adjacent to coral fragments inside experimental jars. Measurements were taken randomly on different days. For each of three different time periods n = 20 d during the course of the experiment. Mean ± 1 SD, ranges in parentheses.

	PAR (watts m^{-2})	UVA (watts m^{-2})
Morning (0700–0830)	3.4 ± 1.28	0.17 ± 0.09
	(1.31–5.17)	(0.04–0.44)
Noon (1200–1330)	4.6 ± 5.01	0.27 ± 0.14
	(1.07–7.64)	(0.10–0.69)
Afternoon (1600–1730)	1.6 ± 1.05	0.10 ± 0.06
	(0.20–4.10)	(0.05–0.24)
Daily mean	3.2	0.18
	(0.2–7.64)	(0.04–0.69)

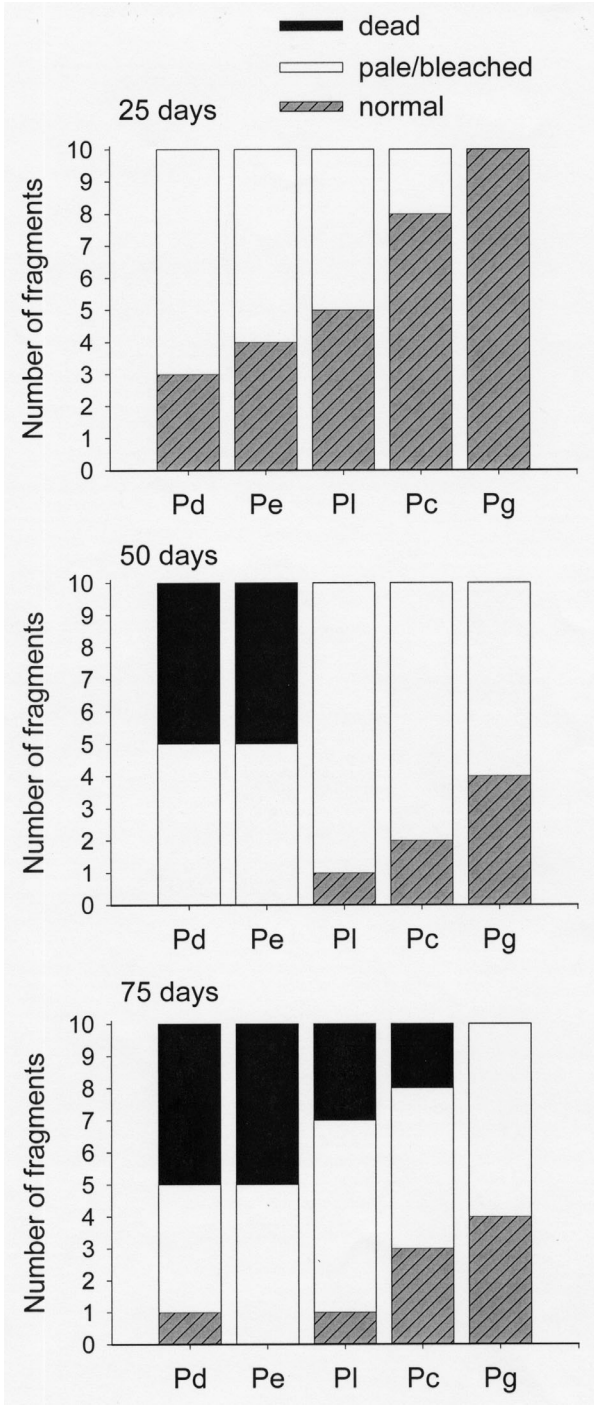

Figure 4. Coral condition in the heat treatment throughout the duration of experiment. Number of fragments normally pigmented, pale/bleached or dead for each sampling period of 25, 50 and 75 d. Heat treated fragments (n = 10) for each species for each sampling. Pd, *Pocillopora damicornis*; Pe, *Pocillopora elegans*; Pl, *Porites lobata*; Pc, *Pavona clavus*; Pg, *Pavona gigantea*.

$\times 10^6 \pm 4.5$ cells cm^{-2}) and *P. lobata* ($16 \times 10^6 \pm 6.0$ cells cm^{-2}), whereas the lowest densities occurred in *P. damicornis* ($8 \times 10^6 \pm 1.5$ cells cm^{-2}). Ambient control densities varied only slightly during the course of the experiment (Fig. 5). During exposure to the heat treatment, all species showed a significant decline in zooxanthella numbers after 25 d and a more severe loss by 50 d. After 75 d, some recovery of zooxanthellae was observed in all species except *P. clavus*. Recovery of zooxanthellae in *P. lobata* increased to above its 25-d exposure densities, with an increase in this species' ambient values as well. However, the relatively high mean density of zooxanthellae in the heat treatment, attained during recovery, is not significantly different from the mean values at days 25 ($P > 0.60$, t-test) or 50 ($0.10 > P > 0.05$, t-test).

An interspecific comparison showed that heat treatment corals contained from 20% to greater than 50% less zooxanthellae than ambient controls by day 25 of exposure (Fig. 6). The severity of the loss increased as time progressed, from 50% to more than 95% at day 50. After 25 d of exposure, there were no significant differences in loss between the five species, whereas after 50 d *P. damicornis* was the most severely affected followed by *P. elegans* and then *P. lobata*. Recovery ranged from more than 10% of ambient values (*P. lobata*) to no recovery at all (*P. clavus*). Values of *P. clavus* at the end of the recovery period were even lower than after the 50-d exposure. However, at the end of the recovery phase (day 75), *P. damicornis* still had the lowest percentage of ambient zooxanthellae values, followed by *P. elegans*. At the end of the exposure (day 50) and recovery period (day 75) branching corals were significantly more affected by high temperature than massive species. *P. gigantea* was clearly the most resistant species examined, although recovery was slow.

Chlorophyll Concentrations.—Variations in mean chlorophyll concentration were similar to the trends exhibited by zooxanthellae densities, also demonstrating species-specific differences (Fig. 5). The lowest initial mean pigment concentration was found in *P. damicornis* (10 µg chlorophyll *a* cm^{-2}) and the highest value occurred in *P. gigantea* (25 µg chlorophyll *a* cm^{-2}). Declines in chlorophyll content during the heat treatment were statistically significant in all five species by 25 d and 50 d (Fig. 5).

Notable recovery of chlorophyll *a* concentration occurred in all species except for *P. damicornis* and *P. clavus* (Fig. 5). An increase in chlorophyll *a* concentration occurred in *P. lobata* on day 75, above the level on day 25. *P. lobata* ambient values on day 75 were even greater than initial values by almost 50%.

A progressive loss of chlorophyll *a* was observed in all corals by day 50 (Figs. 5,7). In contrast to zooxanthella losses, chlorophyll *a* concentration was already significantly different between species after 25 d of heat stress. Chlorophyll reduction ranged from 10–40% by day 25 and from 60–95% by day 50 (Fig. 7).

After 50 d of high temperature exposure and 25 d of recovery, a difference between the two coral growth forms was particularly evident. By day 50 (end of exposure) and 75 (end of recovery), the chlorophyll *a* concentrations of branching corals were notably affected (Fig. 7), whereas the massive corals showed less severe effects (Fisher test, $P < 0.05$). Again, *P. damicornis* (branching) was the most and *P. gigantea* (massive) the least affected species. Chlorophyll pigments in *P. clavus* continued to decline through day 75.

Mean chlorophyll c_2 concentration trends were similar to those of chlorophyll *a* and zooxanthella densities over the course of the experiment. Initial individual colony values of chlorophyll c_2 were slightly lower (7–17 µg cm^{-2}, depending on the species) than the chlorophyll *a* values (10–25 µg cm^{-2}). These pigment concentrations resulted in nearly

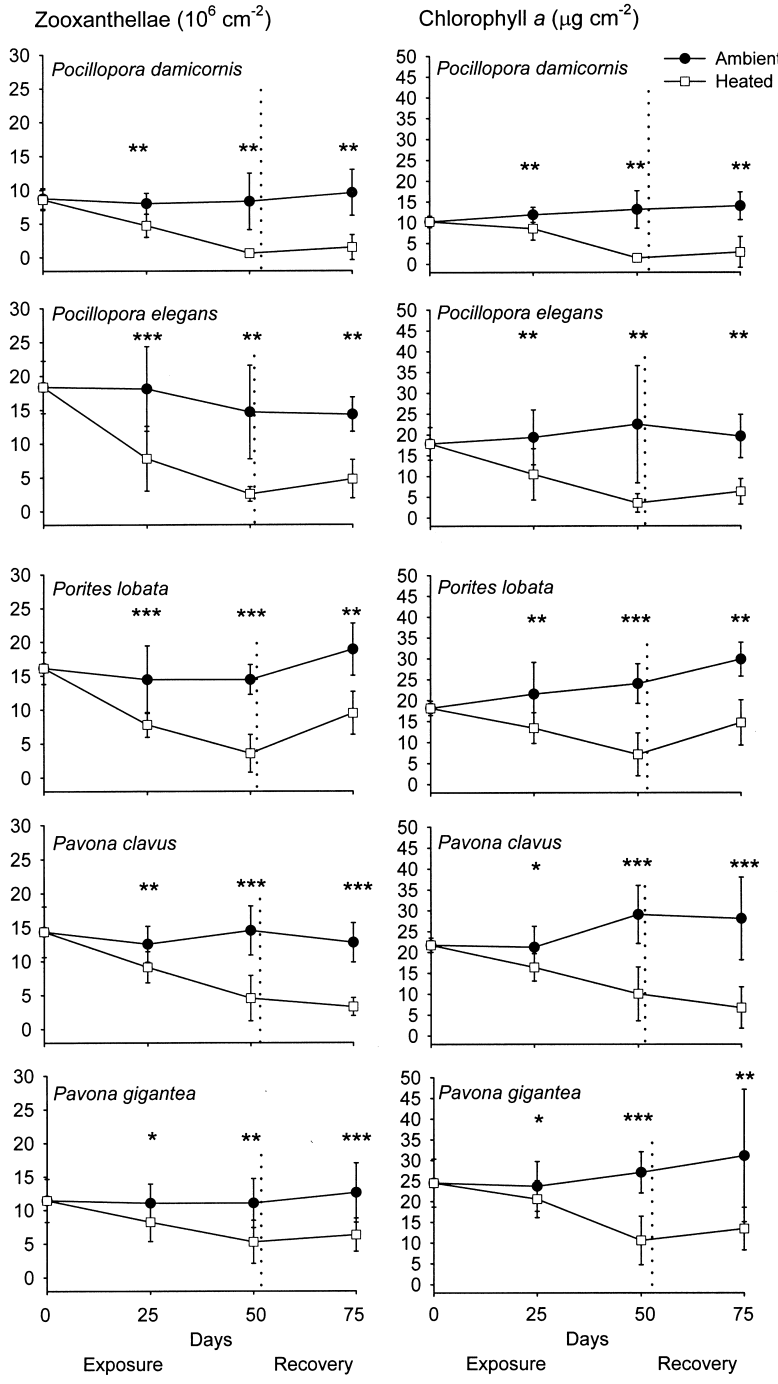

Figure 5. Intraspecific trends of mean (± 1 SD) zooxanthellae density and mean (± 1 SD) chlorophyll *a* concentration over the course of the experiment. Significance levels: * P <0.05, **P <0.01, ***P <0.001. Paired t-test of surviving pairs at each 25 d sampling interval. Slightly offset dotted line at day 50 represents end of exposure period.

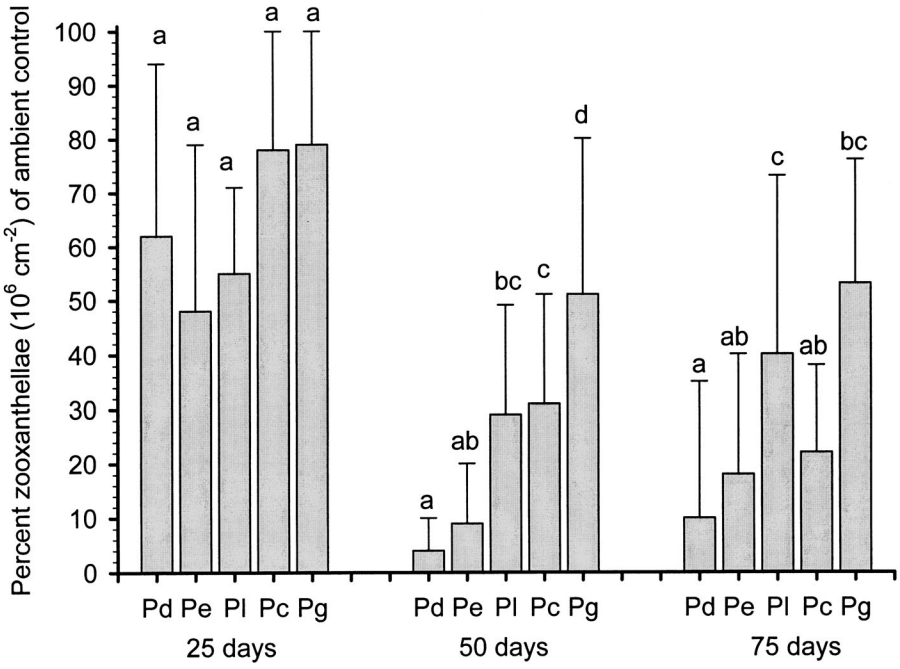

Figure 6. Interspecific ANOVA comparison of zooxanthellae density from the heat treatment expressed as a percent of the corresponding ambient control. (Pd = *Pocillopora damicornis*, Pe = *Pocillopora elegans*, Pl = *Porites lobata*, Pc = *Pavona clavus*, Pg = *Pavona gigantea*). Species with the same letter (a–d) in a given sampling period are not significantly different (P >0.05, Fisher test).

stable chlorophyll c_2/a ratios throughout the experiment. All measured ratios were generally within the range of 0.6 to 0.8, indicating a relatively low chlorophyll c_2 concentration compared with that of chlorophyll *a*. These pigment ratios did not generally vary at either temperature over the experimental period.

Chlorophyll Concentration per Zooxanthella.—The differences in mean chlorophyll *a* concentrations per zooxanthella within each species were generally non-significant in the two treatments over the course of the experiment (Fig. 8). A tendency towards increasing chlorophyll *a* and c_2 concentrations per cell occurred in *P. damicornis*, *P. lobata* and *P. clavus* during the warming treatment, but statistically significant differences were found only in *P. lobata*. A significant decline in chlorophyll *a* cell^{-1} occurred in *P. gigantea* by day 50. By the end of the recovery period, however, chlorophyll concentrations per zooxanthella were in all cases almost identical to those at ambient temperatures.

After 25 d of exposure, all coral species in the heat treatment showed a slight, but non-significant increase of at least 10% in chlorophyll *a* cell^{-1}. After day 50, the most obvious and statistically significant differences among species were for *P. damicornis* and *P. gigantea*. In *P. damicornis* chlorophyll *a* cell^{-1} was 180% of its ambient value and 80% in *P. gigantea*.

Growth.—Since the 75-d experimental period was too short to discern skeletal growth in the massive coral species with the Alizarin staining technique, only the branching species were measured. No skeletal elongation occurred in either species of *Pocillopora*

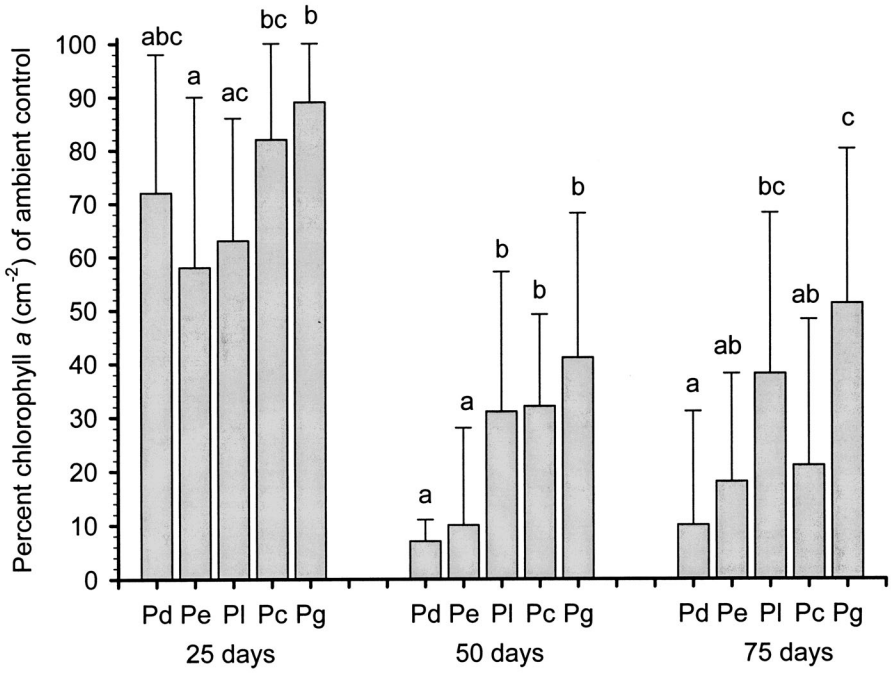

Figure 7. Interspecific ANOVA comparison of chlorophyll *a* concentration from the heat treatment expressed as a percent of the corresponding ambient control. Species abbreviations and statistical testing as in Fig. 6.

during the heat treatment of 50 d. Under ambient conditions, mean skeletal growth was 0.39 mm mo^{-1} in *P. damicornis* and 0.32 mm mo^{-1} in *P. elegans*. These differences were non-significant (P = 0.26, t-test). Tissue growth covered the broken skeletal edge of fragments under ambient conditions, but not in corals in the heat treatment

Discussion

Much work has been carried out relatively recently on temperature related coral bleaching involving field observations (e.g., Ogden and Wicklund, 1988; Brown and Suharsono, 1990; Glynn, 1990; Jokiel and Coles, 1990; Williams and Bunkley-Williams, 1990) and aquarium-based experiments (e.g., Coles et al., 1976; Coles and Jokiel, 1977; Jokiel and Coles, 1977; Hoegh-Guldberg and Smith, 1989a; Glynn and D'Croz, 1990; Glynn et al., 1992; Berkelmans and Willis, 1999). A relationship between high temperature and coral bleaching was observed, however, in the early study of Yonge and Nicholls (1931). In our study, we have documented under controlled conditions interspecific differences in high temperature bleaching and initial recovery responses of five Panamanian reef-building corals.

Decline in Zooxanthellae Densities.—A decline in zooxanthellae is a well known stress response of corals to elevated temperatures and other suboptimal conditions (Brown and Howard, 1985; Glynn and D'Croz, 1990). Glynn (1996) noted that most reef-building coral species normally host from 1×10^6–5×10^6 zooxanthellae cm^{-2}, a lower density

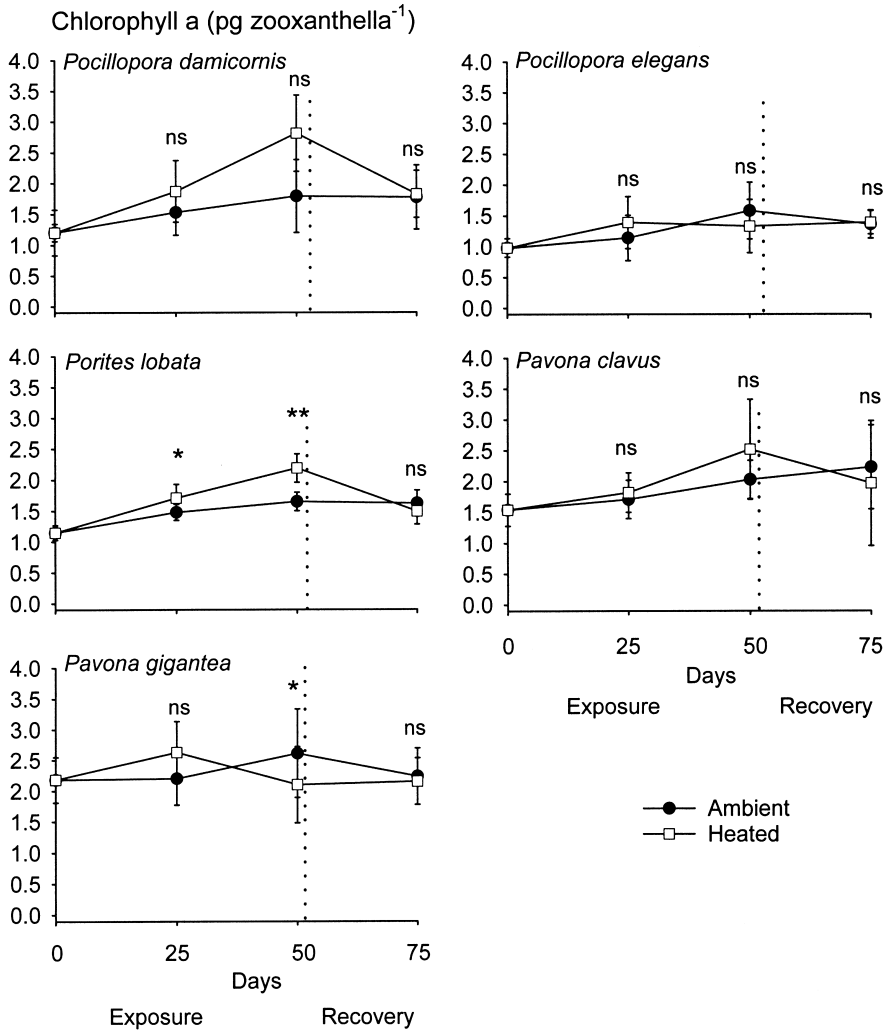

Figure 8. Intraspecific trends of mean (± 1 SD) for chlorophyll *a* concentration zooxanthella^{-1} over the course of the experiment. Significance levels and statistical testing as in Fig. 5, ns = non-significant. Slightly offset dotted line at day 50 represents end of exposure period.

range than demonstrated initially in this experiment. Other workers have found higher values for *P. damicornis* in Panama, e.g., 5×10^6–20×10^6 (Maté, 1997) and 30×10^6 zooxanthellae cm^{-2} (Feingold, 1995). The higher eastern Pacific values could be due to methodological differences, sampling time or the generally elevated nutrient levels in this upwelling region of Panama.

In our heat treatment, chlorophyll *a* concentrations decreased. This can be attributed to the decrease in zooxanthellae densities found, which has also been speculated by many authors as the cause of paling in mass bleaching events (Hoegh-Guldberg and Smith, 1989a). Findings of increased chlorophyll *a* cell^{-1} in three of five experimental species due to elevated temperatures further confirm that zooxanthellae expulsion was

Table 2. Comparison of bleaching and mortality susceptibilities: (spp. more affected > spp. less affected); mortality (% dead), bleached (% white or pale). Species abbreviations as in Fig. 6; exposure n = 20 fragments per species; exposure and recovery n = 30 fragments per species. Pd: *Pocillopora damicornis*; Pe: *Pocillopora elegans*; Pl: *Porites lobata*; Pc: *Pavona clavus*; Pg: *Pavona gigantea*.

Experimental period	Observation	Ranking of species susceptibilities
Exposure only	Bleaching	Pd> Pe> Pl> Pc> Pg
(April–June 1997)	Mortality	Pd= Pe> Pl= Pc= Pg
Exposure and recovery	Bleaching	Pe> Pd> Pl> Pc> Pg
(April–July 1997)	Mortality	Pd= Pe> Pl> Pc> Pg

responsible for the pigment declines. Results from another eastern Pacific temperature simulation study with *P. damicornis* did not exhibit an increase in chlorophyll *a* cell^{-1}, and it was concluded that the bleaching was due to both the loss of zooxanthellae and a reduction in chlorophyll concentration zooxanthella^{-1} (Glynn and D'Croz, 1990). The increase in intracellular pigment in the majority of the corals in the high temperature treatment might be explained by nutrient limitation, possibly nitrogen limitation. Hoegh-Guldberg and Smith (1989b) found that chlorophyll *a* cell^{-1} increased in bleached corals and suggested that the zooxanthella endosymbionts at low densities within the host may be more nutrient sufficient. Zooxanthellae at low densities in bleached corals may receive proportionally more nutrients than at higher densities. Increases in chlorophyll concentration zooxanthella^{-1}, due to increasing nutrient concentration, have been reported in other studies (Hoegh-Guldberg and Smith, 1989b; Dubinsky et al., 1990).

Hoegh-Guldberg and Smith (1989b) showed increasing growth rates with nitrogen addition. The opposite trend was observed when the particulate food supply to coral hosts was blocked under low nutrient conditions (Muller-Parker and D'Elia, 1997). Experiments with enriched nitrogen, in the absence of thermal stress and bleaching (Marubini and Davies, 1996), demonstrated both higher chlorophyll concentration per cell and higher zooxanthellae densities.

Recovery.—The relatively brief 25-d period of ambient temperature following the high temperature treatment allowed only an indication of the potential for recovery. In this El Niño warming simulation, all species showed some degree of recovery except for *P. clavus*, whose tissues remained bleached. The greatest capacity for recovery was demonstrated by *P. lobata* and *P. gigantea*. These massive corals had the highest concentrations of chlorophyll, zooxanthellae and chlorophyll zooxanthellae^{-1} after the high temperature exposure period. Not surprisingly, recovery of individual fragments was related to the degree of zooxanthellae and/or chlorophyll loss during the high temperature treatment.

Recovery duration in the field is highly variable, ranging from 3 mo (Brown and Suharsono, 1990) to more than 2 yrs (Glynn and D'Croz, 1990), for a variety of zooxanthellate coral species. Partial recovery under field conditions on Pacific and Caribbean reefs has occurred after 3–7 mo (Lang et al., 1992; Glynn et al., 1992; Gleason, 1993; Berkelmans and Willis, 1999). Full recovery on a Caribbean reef has been reported after 8–11 mo (Lang et al., 1992).

Growth Rate Reduction.—Several studies have demonstrated the negative effects of bleaching on skeletal growth (Goreau and MacFarlane, 1990; Leder et al., 1991; Glynn, 1996; Vargas-Ángel et al., this issue). The skeletal extension rates reported here, 0.3–0.4 mm mo^{-1}, are low compared with field studies (Glynn, 1977; Guzmán and Cortés, 1989).

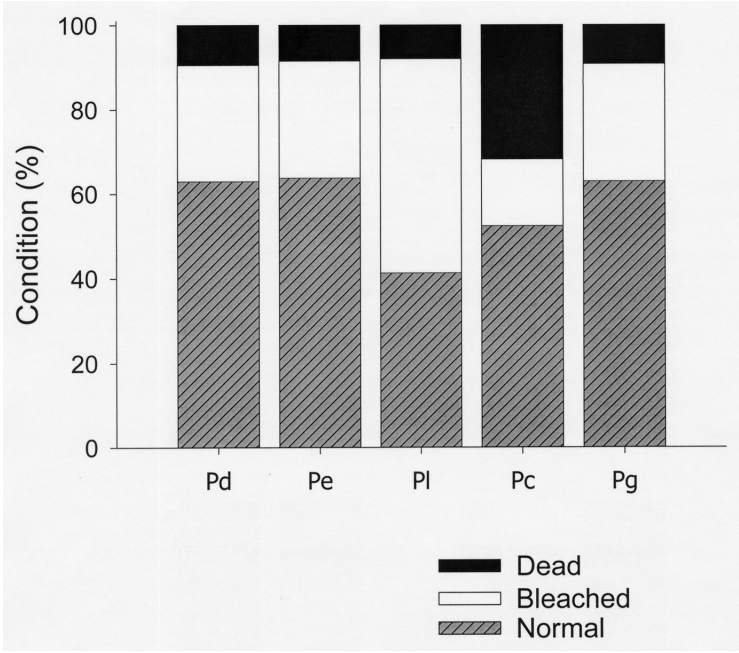

Figure 9. Coral colony condition (in % colonies) at five study sites in the Gulf of Chiriquí, Panama, 10–15 March 1998 (see Glynn et al., this issue). Pd, *Pocillopora damicornis* (n = 197); Pe, *Pocillopora elegans* (n = 314); Pl, *Porites lobata* (n = 227); Pc, *Pavona clavus* (n = 321); Pg, *Pavona gigantea* (n = 178). Study sites include: Silva de Afuera Island, Uva Island, Montuosa Island, Secas Islands, Jicarita/Jicarón Islands.

There was an obvious difference, however, between the skeletal growth of *Pocillopora* spp. in the heat treatment and under ambient conditions. No skeletal growth or tissue regeneration occurred in the heat treatment. Under ambient temperatures, tissue regeneration also accompanied skeletal growth. Field growth rates of branching pocilloporid corals in the eastern Pacific are about 1–3 mm mo^{-1} (Glynn and Stewart, 1973; Glynn, 1977; Glynn et al., 1983, 1992; Guzmán and Cortés, 1989; Maté, 1997). Due to the subdued irradiance levels under experimental conditions, growth rates would be expected to be lower than reported in other studies. In addition, since present growth rates were measured in fragmented corals over a relatively brief period (75 d), some time was required for tissue regeneration before growth could resume.

Experimental vs Field Bleaching and Mortality.—The well-documented 1982–83 El Niño event caused widespread coral mortality in the eastern Pacific (Glynn, 1990; Guzmán and Cortés, 1993). Corals suffered from 50–97% mortality, with 85% mortality (all species) recorded in the Gulf of Panama. During the experimental warming phase of this study, overall mortality was 13%, exclusively among branching corals. This increased to 30% mortality during the 25-d recovery period, which included both branching (*Pocillopora* spp.) and massive species. In the Gulf of Panama, the duration of ENSO-associated SSTs of 30–31°C was 24 wks in 1982–83 (Podestá and Glynn 1997), whereas comparable experimental temperatures in this study lasted only 7 wks. This difference may explain in part the lower overall mortality that occurred experimentally. Mean

pocilloporid field mortality in 1982–83 was 92% (Glynn et al., 1988), but only 50% in our experiment.

Our experimental results agreed with the coral responses observed during the 1982–83 bleaching event. Field bleaching among scleractinian corals was most pronounced in pocilloporid species after 25 d of +1°C anomalous temperatures (Glynn, 1984). *P. damicornis* was the first species to bleach during our study. Futhermore, bleaching was first observed in the field after about 1 mo of increased water temperatures, which also occurred in our experimental tanks. Other workers first observed bleaching in the field 2–3 wks after the initiation of thermal stress (Hoegh-Guldberg and Salvat, 1995). Glynn and D'Croz (1990) also found that mortality began 2–4 wks after the initial bleaching. During a severe natural bleaching event in Indonesia, Brown and Suharsono (1990) reported 40–50% of all corals bleached with 10–15% mortality after about 4–6 wks, ending with 80–90% mortality, mostly of branching species.

Pocillopora spp. have also been shown to be the most susceptible corals in several other bleaching studies. Brown and Suharsono (1990) reported that *Pocillopora* (and *Acropora*) were the most severely affected corals in the Thousand Islands area, Indonesia. *Pocillopora* spp. were also reported to be particularly sensitive to thermal stress in Hawaii (Jokiel and Coles, 1990), on the Great Barrier Reef (Marshall and Baird, 2000), and in Costa Rica (Jiménez et al., this issue) and Colombia (Vargas-Ángel et al., this issue).

After 50 d under our heat treatment conditions, the massive corals began to bleach. Glynn (1984) also noted that *P. lobata* and *Pavona* spp. began to bleach in the field following pocilloporid corals. Field observations in French Polynesia revealed that *Pocillopora* spp. bleached more often than species of *Porites* and *Pavona* (Gleason, 1993), which showed only mild bleaching or no bleaching at all. Marshall and Baird (2000) reported that members of the Poritidae were less susceptible to bleaching and that mortality was rare during their March 1998 survey, conducted approximately 6 wks after bleaching began on the Great Barrier Reef. They also found the susceptibility of *Pavona* to be mixed within their bleaching categories of unaffected to severe. The non-lethal responses of *P. gigantea* in our study also corresponded with the relatively high survivorship of this species in Panama (Glynn, 1984) and the Galápagos Islands (Glynn, 1990) following the 1982–83 ENSO compared to the devastation of pocilloporid corals.

Experimental vs Field Observations in the Eastern Pacific, 1997–98.—Due to upwelling, SSTs did not reach stressful high values in the Gulf of Panama during 1997–98 where the experimental corals were collected. Nonetheless, experimental results can be compared with field observations in the nonupwelling Gulf of Chiriquí, Panama where bleaching and mortality were observed (Glynn et al., this issue).

Considering the 1997–98 ENSO-induced field mortality, as reported by Glynn et al. (this issue), a ranking of the five species under examination was as follows: *P. clavus* (31.8% mortality)> *P. damicornis* (9.5%), *P. gigantea* (9.2)%, *P. elegans* (8.5%)> *P. lobata* (8.0%) (see Fig. 9). Experimental results (Table 2) showed that *Pocillopora* corals were more susceptible to bleaching and mortality than the massive species, however, field results (Fig. 9) showed that the latter suffered greater bleaching and mortality. These differences could be attributed to at least three factors, namely (1) higher irradiance levels in the field compared to the laboratory, (2) location of corals in nonupwelling vs upwelling environments, and (3) history of exposure to elevated temperatures.

Experimental corals received subdued light whereas field corals were subjected to higher illumination concurrent with low cloud cover during the dry season (Glynn, 1977). Recently, physiological studies have reported that a decrease in PS II efficiency occurs when corals and their zooxanthellae are exposed to heat (Hoegh-Guldberg, 1999), and consequently, coral bleaching is related to photoinhibition of zooxanthellae. It has also been reported that light amplifies the extent of damage caused by thermal stress (Jones et al., 1998; Hoegh-Guldberg, 1999). Further, Coles and Jokiel (1978) found that high temperature treatment effects were exacerbated under high light intensities (Oliver, 1985). Therefore, light levels may have played an important role in species-specific bleaching responses in the field and may have had an unexpected effect on our results. The presence of an unique genotype in zooxanthella clade D in eastern Pacific *Pocillopora* spp. is relatively insensitive to high light (Baker, 1999; Glynn et al., this issue). Symbiont genotype differences can not explain the intermediate-ranked field mortality rates (Fig. 9) at this time.

Differences in thermal environments have been previously reported to be associated with varying bleaching responses. D'Croz et al. (this issue) demonstrated that *P. lobata* had a lower bleaching threshold to sea warming in the upwelling Gulf of Panama than in the non-upwelling Gulf of Chiriquí. Variable susceptibility of corals to the 1997–98 ENSO event from geographically separated reefs in Costa Rica was also reported by Jiménez et al. (this issue), who related the differences to varying thermal regimes. Therefore, it is likely that coral populations from the two Panamanian gulfs are acclimatized to these different thermal environments. Interestingly, the experimental response results of this study are in agreement with the 1982–83 field responses, but not with those in 1997–98 (Glynn et al., this issue). Thus, historical effects of high temperature exposure (Coles and Jokiel, 1978; Jokiel and Coles, 1990; Marshall and Baird, 2000) may have altered the thermal tolerances of populations in the Gulf of Chiriquí, where SSTs are generally already higher and more stable than in the Gulf of Panama. Increasing rather than decreasing bleaching response with depth at one site on the Great Barrier Reef was attributed to this phenomenon, i.e., to prior acclimatization (Marshall and Baird, 2000).

Colony Morphology and Susceptibility to Elevated Temperatures.—Present experimental results generally support the notion that branching scleractinian corals (*Pocillopora* spp.) are more sensitive to elevated temperatures and suffer higher rates of mortality than massive corals. Eastern Pacific field studies in accordance with this relationship range from Mexico (Reyes Bonilla, this issue) to Costa Rica (Guzmán and Cortés, this issue; Jiménez et al., this issue), Panama and the Galápagos Islands (Glynn et al., 1988; Glynn et al., this issue). Oliver (1985) and Marshall and Baird (2000) also found branching species to be more susceptible and more frequently affected than massive species. Coral stress responses during the 1997–98 ENSO warming event have shown some exceptions, however. For example, a high proportion of *Pocillopora* spp. colonies in Panama and Colombia (Glynn et al., this issue; Vargas-Ángel et al., this issue) recovered from the 1997–98 ENSO event, whereas mortality was high among massive coral species. Also, in Colombia, *Pocillopora eydouxi*, with a branching colony morphology, was the least affected of all zooxanthellate species. It is possible that bleaching susceptibility is influenced by the retractability of tissue and the degree of tissue exposure to water column stressors. The tissues of *Pocillopora* form a superficial layer over the corallum, whereas those in *Porites* are deep-seated with ramifying vertical and lateral connections that can

be extensively retracted during periods of stress. The disposition of tissues in *Pavona* is less obvious, but they appear to be more protected than those of *Pocillopora*.

A recent physiological study noted the importance of protein metabolism in the ability of scleractinians to acclimatize to various stressors associated with global environmental change (Gates and Edmunds, 1999). This study suggested that corals with high growth rates and low metabolic rates (branching species) would have a lower capacity to acclimatize than corals with low growth rates and high metabolic rates (massive species). Clearly, it will be necessary to assess the relative resistance of coral hosts, resident symbionts and integrated symbiotic relationships to understand and predict responses to environmental perturbations.

Consequences and Conclusions

Coral bleaching is a major subject of concern because of its increasing frequency and intensity during the last two decades (Glynn, 1993; Flora et al., 1996; Hoegh-Guldberg, 1999; Wilkinson, 2000). The severe 1997–98 ENSO event has precipitated yet unknown coral community responses. If regional and/or local water temperatures continue to increase, due to global warming and/or ENSO-related events, certain zooxanthellate species may become extinct with consequent changes in coral community structure. Chronic sea warming due to a thermal power plant effluent over a 15 yr period in Guam has shown a decrease in reef area, significant changes in coral communities and accelerated bioerosion (Randall, 1992). Reef framework building ceased locally with the development of vermetid gastropod, red algal and foraminiferan communities. Reef building has also been halted in the Galápagos Islands, accompanied by rapid bioerosion and coral framework destruction, following a single (1982–83 ENSO) warming event (Glynn, 1994; Reaka-Kudla et al., 1996).

A global warming scenario was considered by Glynn (1993), suggesting that most coral species at low latitudes would be unable to adapt genetically to a rapid temperature increase. Jokiel and Coles (1990) and Brown (1997b) also suggested that adaptive responses would be limited. Tropical coral reef communities, which are already being degraded by many anthropogenic influences (e.g., Ginsburg, 1994; Hutchings, 1994; Falkowski, 1996), would be particularly affected. Some recent studies (Kinzie et al., 2001; Glynn et al., this issue), however, lend support to the adaptive bleaching hypothesis of Buddemeier and Fautin (1993), who proposed that some bleached coral hosts may acquire symbiont genotypes that are more resistant to sea warming disturbances.

Despite the relatively brief experimental exposure and recovery periods relative to natural events, the present study is suggestive of likely response trends of eastern tropical Pacific reef building corals to possible sea warming events of the future. Whether the predominant, yet sensitive, reef-building pocilloporid corals will be able to cope with likely temperature rise in the eastern Pacific, is a vexing and intriguing question.

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