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# RESPONSES TO ELEVATED SEA WATER TEMPERATURE AND UV RADIATION IN THE CORAL *PORITES LOBATA* FROM UPWELLING AND NON-UPWELLING ENVIRONMENTS ON THE PACIFIC COAST OF PANAMA

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ABSTRACT

The massive coral species *Porites lobata* from upwelling and non-upwelling environments on the Pacific coast of Panama was exposed to experimentally elevated water temperature and ambient UV radiation to assess the response of the coral-zooxanthella symbiosis. Our experiment demonstrated that elevated water temperature in the range of 30 to 31°C caused bleaching in *P. lobata*, whereas no significant effect on the coral-zooxanthella symbiosis was observed from exposure to ambient UV radiation. Corals maintained under experimental conditions for 31 d showed a significant decrease in zooxanthellae density and chlorophyll concentration as a function of elevated water temperatures. Changes in the concentrations of chlorophylls *a* and $c_2$ per zooxanthella were observed only when corals from the upwelling environment were exposed to high water temperatures. Also, corals from the upwelling environment bleached earlier and more severely than those from the non-upwelling area. Corals returned to ambient conditions showed complete recovery in zooxanthellae density and chlorophyll concentration after 30 d. Bleaching and mortality responses of *P. lobata* indicate a lower threshold to sea warming conditions in coral populations from upwelling Gulf of Panama sites compared to those from the non-upwelling Gulf of Chiriquí. Coral bleaching during the 1997–98 ENSO occurred under similar temperature/time conditions as those examined experimentally in this study, namely 30–31°C per 30 d.

Coral reefs on the Pacific coast of Panama are subject to widely varying environmental conditions, ranging from cold (15–20°C) water due to seasonal upwelling (D'Croz and Robertson, 1997; Glynn and Maté, 1997) to warm (30–31°C) water periods during El Niño–Southern Oscillation (ENSO) events (Glynn, 1988, 1990). Wind-induced upwelling occurs in the Gulf of Panama (Fig. 1) where cool and nutrient-rich waters rise to the surface (D'Croz et al., 1991; Glynn and Maté, 1997). Upwelling reduces coral growth and limits the distribution of corals to the NE sides of islands in the Pearl Islands archipelago where they are sheltered from the coldest waters (Glynn and Stewart, 1973; Glynn, 1977; Glynn and Macintyre, 1977). In contrast, no upwelling occurs in the adjacent Gulf of Chiriquí (Fig. 1), where stable thermal conditions favor the development of the largest known coral reefs in the eastern Pacific mainland region (Glynn and Maté, 1997). The marked differences in the marine thermal climate are evident in Reynolds surface temperatures over an 18 yr period (Fig. 2). Prolonged sea surface warming during El Niño events, especially the 1982–83 event, resulted in the bleaching and mortality of corals in the eastern tropical Pacific Ocean (Cortés et al., 1984; Glynn, 1984, 1990; Robinson, 1985). Coral mortality related to the 1982–83 ENSO showed an increasing trend, from environments with high and stable water temperature, to environments subjected to upwelling and cold ocean currents (Glynn, 1990). Overall mean coral mortality was reported to be 52% at Caño Island (Costa Rica), 75% at Uva Island (Gulf of Chiriquí), 85% at the Pearl Islands (Gulf of Panama) and 97% at the Galápagos Islands (Glynn et al.,

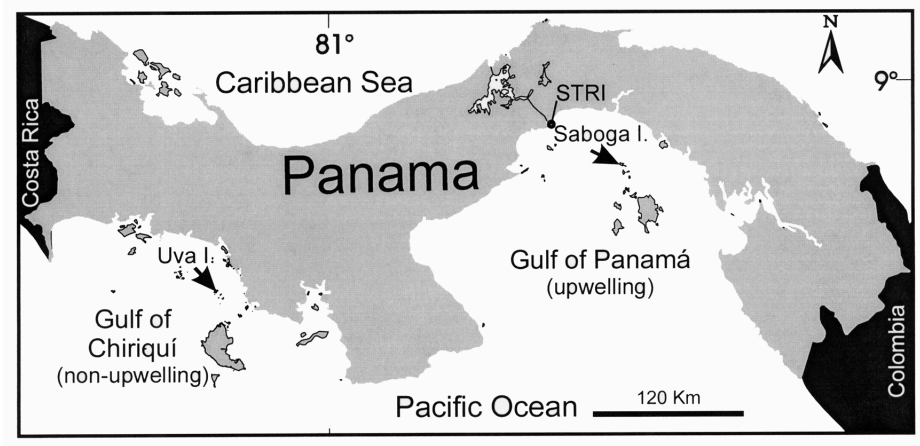


Figure 1. Collection sites for *Porites lobata* on the Pacific coast of Panama. Black arrows indicate locations of the sampled coral reefs.

1988). During 1997–1998, another major ENSO sea warming event reached Panama but affected only the Gulf of Chiriquí where the warm waters arrived in mid-August 1997 and remained at elevated levels until mid-September, causing severe bleaching and mortality of milleporid, pocilloporid, agariciid, and poritid corals (see Glynn et al., this issue). Even though the 1997–98 ENSO sea warming was of short duration along the Panamanian coast and coral bleaching was not so severe as that observed during the 1982–83 event, species such as *Millepora intricata* Milne-Edwards, *Pavona* sp. a and *Porites panamensis* Verrill suffered extensive mortality. Moreover, coral tissue recovery was reversed by a second brief pulse of warm waters which reached the Gulf of Chiriquí in March 1998 (see Glynn et al., this issue). By the end of 1998, most coral species had regained their normal coloration except for the massive species *Porites lobata* Dana and *Pavona clavus* (Dana), and the branching species *Pocillopora elegans* Dana.

Experimental studies of bleaching in the Panamanian Pacific have focused mostly on the branching coral species *Pocillopora damicornis* (Linnaeus), which is one of the main reef-building corals in the region (Glynn and D'Croz, 1990; Maté and Calderón, 1990). Experimental evidence strongly supports the hypothesis that high temperatures are responsible for the loss of zooxanthellae, histopathological abnormalities, and mortality in *P. damicornis* (Glynn et al., 1985; Glynn and D'Croz, 1990). The experimental responses of *P. damicornis* to high water temperature were similar to the field responses observed during the severe 1982–83 ENSO sea warming event. It has also been suggested that corals from the upwelling Gulf of Panama might be more sensitive to elevated water temperatures than corals from the non-upwelling Gulf of Chiriquí (Glynn and D'Croz, 1990).

Although massive coral species are an important frame-building component of eastern Pacific coral reefs, the only information on the bleaching susceptibilities of these corals is derived from scattered field observations performed during sea warming events (Glynn and Wellington, 1983; Cortés et al., 1984; Glynn and Maté, 1997; see also Hueerkamp et al., this issue). Fossil records have shown *Porites* to be one of the most important reef-building corals since the Miocene (Foster, 1986), and it is also among the most widespread coral genera on modern reefs (Veron, 1995). In the eastern Pacific, *P. lobata* is the

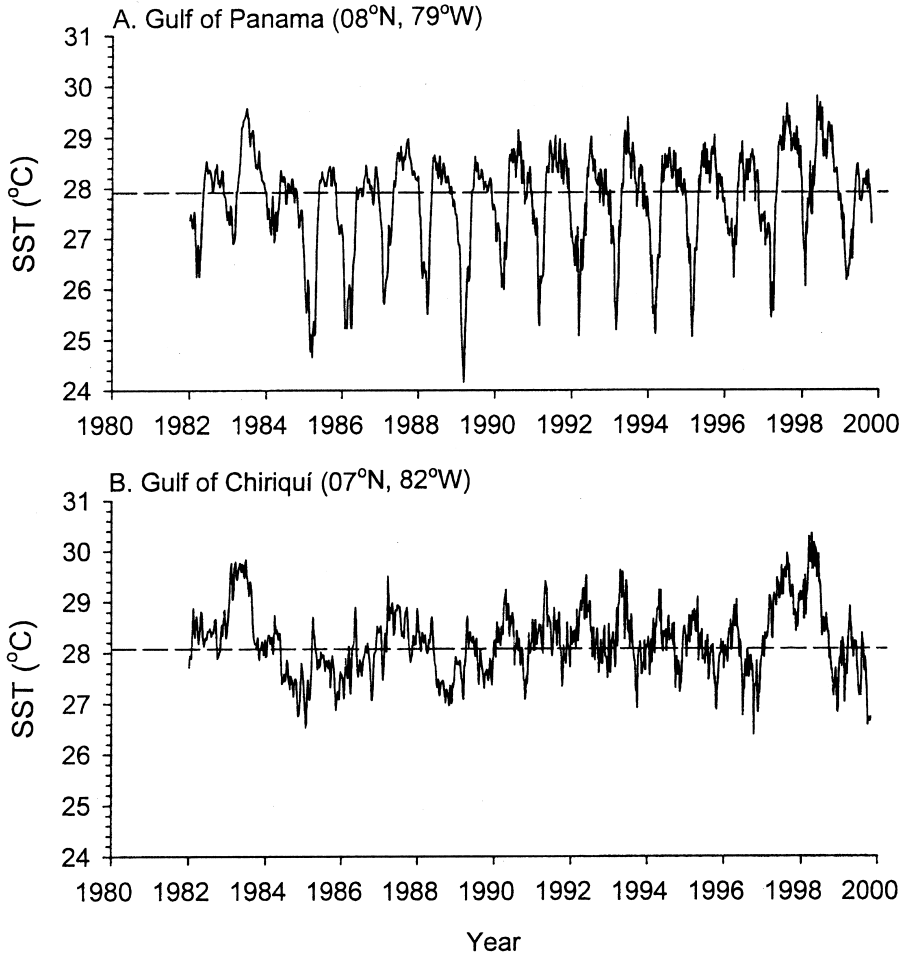


Figure 2. Reynolds sea surface temperatures (1982–2000) on the Pacific coast of Panama. A, Gulf of Panama; B, Gulf of Chiriquí. Data are NOAA/NCEP weekly SST fields (Reynolds and Smith, 1994) using the NOAA-CIRES Climate Diagnostics Center, Boulder, Colorado, USA, from their Web site at http://www.cdc.noaa.gov/. Long term means are denoted by dashed lines.

most abundant and widely distributed poritid species (Glynn and Wellington, 1983; Glynn and Ault, 2000). This massive species may reach large dimensions (2–3 m diameter), and is often abundant on coral reefs in Costa Rica, Panama, and the Galápagos Islands (Glynn and Wellington, 1983), as well as at Clipperton Atoll (Glynn et al., 1996). In Panama, *P. lobata* is found on rubble/sand bottoms and along the deep reef base with colonies reaching 3–4 m high (Guzmán et al., 1991; Glynn and Maté, 1997).

Here we describe the results of an experiment designed to test the simultaneous effects of high temperature and ambient UV radiation on the coral-zooxanthella symbiosis of *P. lobata* from upwelling and non-upwelling environments in Panama. Experimental conditions were controlled to simulate as closely as possible the thermal and irradiance levels typically observed during ENSO events.

## Study Species and Methods

Fragments of *P. lobata* were collected using SCUBA from coral reefs in the upwelling Gulf of Panama and the non-upwelling Gulf of Chiriquí from 4–11 July 1995. All experimental fragments were obtained with hammer and chisel from different colonies, ranging from 10–200 cm in diameter. Fragment sizes ranged from 10–20 cm in diameter with the smallest fragments containing about 5000 live polyps. The corals were collected from 4–6 m below mean low water (MLW) at Uva Island in the Gulf of Chiriquí, and at Saboga Island in the Gulf of Panama (Fig. 1). Immediately after collection, corals were transported in insulated coolers with a continuous air supply to the Naos Marine Laboratory, Smithsonian Tropical Research Institute (STRI), Panama City. Transportation time from the Gulf of Chiriquí to the marine laboratory was 10 h, and 2 h from the northern Pearl Islands in the Gulf of Panama. After arrival at the laboratory, approximately 120 coral fragments from each site were placed in two large water tables at the STRI marine aquarium pavilion. The corals were supplied with continuously running seawater and shaded from direct sunlight with translucent roofing panels. Corals were allowed 2 wks to acclimate to the laboratory conditions before commencement of the experiment. Only corals that appeared healthy (normal coloration and expanded polyps) were used.

Coral colonies were exposed to an experimental design which consisted of the following treatments: high water temperature and ambient UV radiation (HT/AUV), high water temperature and low UV radiation (HT/LUV), ambient water temperature and low UV radiation (AT/LUV), and ambient water temperature and ambient UV radiation (AT/AUV). Corals were maintained under the treatment conditions for 31 d, from 26 July to 25 August 1995. The surviving corals were returned to ambient water temperature and ambient UV radiation (AT/AUV) for 30 d in order to assess their capacity to recover. The experimental set-up consisted of six holding tanks (450 L capacity each) located at the STRI aquarium pavilion, open toward the east to receive morning sunlight (07:00–12:00). Raw seawater was fed to two 60-L glass aquaria in series used as reservoirs to supply seawater at a flow rate of 3.4 L $min^{-1}$. Seawater was aerated and filtered through Strainrite polyester-felt bags of 1 μm pore size before its distribution from the reservoirs to the holding tanks. Aquarium heaters were placed in one series of reservoirs in order to achieve an increase of 1–2°C above ambient temperature. Three holding tanks were supplied with heated water from the feeder reservoirs and the other three tanks from the unheated reservoirs. Water temperature was monitored daily in the holding tanks at 12:00 using a calibrated microprocessor-based thermometer (LabComp SCT-100) with a precision of 0.05°C. Actual mean water temperatures (±1 SD) were 30.45° C ± 0.22 for the heated tanks, and 29.14° C ± 0.07 for the ambient tanks (Table 1). One-way ANOVA indicated significant differences between these mean temperatures ($P < 0.05$). The placement of the holding tanks was adjusted so that corals would be exposed to light levels approximating those in the field. One-half of each holding tank was covered by an acrylic panel (1 cm thick) which blocked 99% of the ambient UV radiation while transmitting 99% of PAR (photosynthetically active radiation). The other one-half of each tank remained uncovered and thus exposed to ambient radiation. The acrylic panels were wiped clean daily in order to prevent a buildup of algae. Irradiance measurements were performed adjacent to the corals at about 12:00 with an IL 1400A radiometer (International Light, Inc) equipped with underwater sensors. Over the course of the experiment, mean ambient PAR was 193.8 W $m^{-2}$ (Table 1). Mean PAR at 2–3 m depth on the Uva Island coral reef (Gulf of Chiriquí) in January, under clear skies near noontime, was 230.8 W $m^{-2}$ (±26.0, n = 15 readings). Mean experimental ambient UVA was 1.12 W $m^{-2}$ compared with mean field values of 1.18 W $m^{-2}$ (±0.24, n = 25) under overcast skies and 2.09 W $m^{-2}$ (±0.15, n = 18) under clear skies. An ANOVA test indicated a significant difference in the exposure of corals to UVA ($P < 0.001$) but not to PAR ($P > 0.05$) in tanks with and without acrylic panels (Table 1). No measurements of UVB were recorded due to the malfunctioning of the sensor.

Thirty-two corals were placed in each holding tank with a total of 192 colonies in six tanks. Eight colonies from each locality were placed by strict random assignment on the side of the tank covered by the acrylic filter, and thus protected from ambient UV radiation. Measurements with the radiom-

Table 1. Mean values of water temperature, UVA and PAR measured daily at noon during the experiment. *** $P < 0.001$, ns: non-significant.

| Experimental condition | Mean ± SEM | n | P |
|---|---|---|---|
| High temperature (ºC) | 30.45 ± 0.22 | 125 | *** |
| Ambient temperature (ºC) | 29.14 ± 0.07 | 125 | |
| Ambient UVA (watts $m^{-2}$) | 1.12 ± 0.74 | 130 | *** |
| Acrylic reduced UVA (watts $m^{-2}$) | 0.04 ± 0.01 | 130 | |
| Ambient PAR (watts $m^{-2}$) | 193.84 ± 15.27 | 130 | ns |
| Acrylic reduced PAR (watts $m^{-2}$) | 150.61 ± 12.03 | 130 | |

eter indicated that the corals were exposed to only about 4% ambient UVA. The other eight colonies from each locality, also positioned randomly, were exposed to direct morning sunlight on the unshielded side of each tank.

The condition of the corals was monitored weekly during the experiment. All surviving coral colonies were sampled after exposure using a hammer and chisel to obtain 1–2 cm diameter fragments. These samples were wrapped in aluminum foil and frozen (−20°C) until processing. Tissues were removed from the skeleton with a jet of distilled water from an air brush at low pressure (60 psi). Two aliquots of the resulting suspension were thoroughly mixed and then the zooxanthellae were counted in a haemocytometer (Neubauer chamber) to determine cell densities. The suspension was then centrifuged at 2500 G for 10 min, the clear supernatant discarded, 90% acetone added to the settled zooxanthella pellets, which were then ground with a hand held homogenizer. After centrifugation, tubes holding the solution were wrapped with aluminium foil and stored in a refrigerator for 24 h. The extracts were then analyzed spectrophotometrically and the concentration of chlorophylls *a* and $c_2$ calculated according to Jeffrey and Haxo (1968).

Coral surface area was estimated by wrapping the upper side of the colony with aluminum foil. A regression equation was developed from the weight of pieces of aluminum foil of known area in order to calculate the surface of sampled corals. Parametric procedures were used for most statistical testing. When necessary logarithmic, square root and reciprocal transformations were performed to satisfy the assumptions of the statistical analysis. A two-way ANOVA (SYSTAT, 1998) was performed to analyze the effects of seawater temperature and ambient UV radiation on the corals from both sampling locations.

## Results

The initial condition of all corals from the upwelling Gulf of Panama and the non-upwelling Gulf of Chiriquí was similar after the 14-d acclimation period, based on the zooxanthella and chlorophyll biomass measurements (Fig. 3). After experimental exposure (31 d), corals from both locations subjected to high water temperature treatments (with and without ambient UV radiation) were bleached and showed a significant decrease in zooxanthellae densities (Fig. 3, Table 2). However, there was no evidence of zooxanthellae decline in corals from both locations due to the effects of exposure to ambient UV radiation, in either high temperature or ambient temperature treatments (Table 2). As well, no significant effects from the interaction between water temperature and UV radiation were observed for any analyzed attribute (Table 2). After 15 d of exposure to high water temperature treatments (mid-way through the exposure period), corals from the Gulf of Panama had a paler appearance than those from the Gulf of Chiriquí (Fig. 4). Some mortality had occurred by this time. Five colonies from the Gulf of Panama (2, HT/

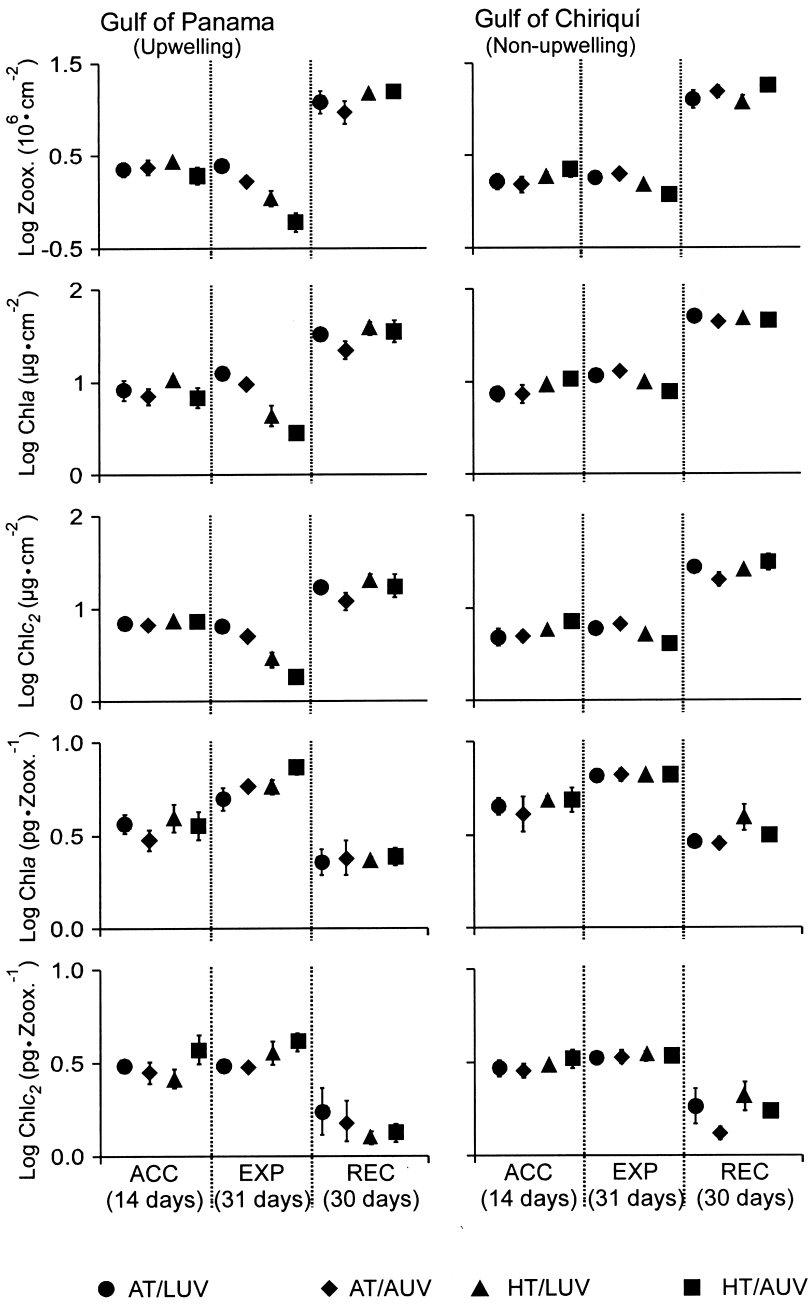


Figure 3. Variations in zooxanthellae densities and chlorophyll pigment concentrations in *Porites lobata* over a 75-d experimental period. ACC: acclimation period (14 d); EXP: exposure to experimental conditions (31 d); REC: recovery under ambient conditions (30 d).Treatment conditions: AT/LUV, ambient temperature and low UV radiation; AT/AUV, ambient temperature and ambient UV radiation; HT/LUV, high temperature and low UV radiation; HT/AUV, high temperature and ambient UV radiation. Error bars denote the SE.

LUV; 2, AT/AUV; 1, HT/AUV) succumbed, as well as one colony from the Gulf of Chiriquí (HT/AUV). No further mortality occurred during the rest of the experiment.

ANOVA tests confirmed a significant difference (decrease) in concentration of chlorophylls *a* and $c_2$ per area in all corals in the high temperature treatment (HT/AUV and HT/LUV) from both localities (Fig. 3, Table 2). However, the observed pigment declines were greater in corals from the Gulf of Panama than from the Gulf of Chiriquí. No significant effect on the concentration of chlorophylls resulted from exposure to ambient or low UV radiation, nor from the interaction between temperature and UV radiation (Table 2).

Chlorophyll *a* content per zooxanthella in corals from both localities was higher in all treaments after the 31 d of exposure (Fig. 3). However, a two-way ANOVA test indicated that the difference in chlorophylls *a* and $c_2$ per zooxanthella was significant only in corals from the Gulf of Panama, and only in those exposed to high water temperature ($P < 0.01$). No significant UV effect on zooxanthellae chlorophyll concentrations from the two localities was evident, nor from the UV-high temperature interactions (Table 2).

Except for the six coral fragments that died within the first 2 wks of the experiment (Fig. 4), all remaining corals showed a notable recovery, regaining their golden-brown coloration by the end of the 30 d recovery period under ambient conditions. This qualitative assessment was supported by an increase in zooxanthellae densities and in the concentrations of chlorophylls *a* and $c_2$ per live tissue area (Fig. 3). Zooxanthellae densities and the concentrations of photosynthetic pigments in experimental corals from both localities were even higher after the recovery period than before the initiation of the experiment (Fig. 3). Unexpectedly, the concentrations of chlorophylls *a* and $c_2$ per zooxanthella decreased when the experimental corals were returned to ambient conditions (Fig. 3). The corals in all treatments and from both localities showed significant recovery after 30 d under ambient conditions when compared to those at the end of the experimental exposure (Mann-Whitney U tests, $P < 0.001$ in all cases). Differences in biomass attributes in all treatments and localities were not significant at the end of the recovery period (Table 2).

Table 2. Results of biomass attributes in relation to the two-way ANOVA analysis of effect of water temperature and UV radiation on *Porites lobata* during the experimental exposure and recovery period. ** $P < 0.01$; *** $P < 0.001$; ns: non-significant.

| Locality | Biological variables | Temperature | UV radiation | Temperature × UV radiation | Recovery |
|---|---|---|---|---|---|
| Gulf of Panama | Zooxanthellae $cm^{-2}$ | *** | ns | ns | ns |
| (upwelling) | Chlorophyll *a* $cm^{-2}$ | *** | ns | ns | ns |
| | Chlorophyll $c_2$ $cm^{-2}$ | *** | ns | ns | ns |
| | Chlorophyll *a* Zoox.$^{-1}$ | ** | ns | ns | ns |
| | Chlorophyll $c_2$ Zoox.$^{-1}$ | ** | ns | ns | ns |
| Gulf of Chiriquí | Zooxanthellae $cm^{-2}$ | ** | ns | ns | ns |
| (non-upwelling) | Chlorophyll *a* $cm^{-2}$ | *** | ns | ns | ns |
| | Chlorophyll $c_2$ $cm^{-2}$ | *** | ns | ns | ns |
| | Chlorophyll *a* Zoox.$^{-1}$ | ns | ns | ns | ns |
| | Chlorophyll $c_2$ Zoox.$^{-1}$ | ns | ns | ns | ns |

## Discussion

Our experiment showed that an increase of water temperature in the range of 30 to 31°C (1.3°C above ambient) caused bleaching in *P. lobata* from the Pacific coast of Panama. However, *P. lobata* from the upwelling Gulf of Panama and non-upwelling Gulf of Chiriquí demonstrated different responses to sea warming. Corals from the Gulf of Panama bleached earlier and more severely than those from the Gulf of Chiriquí (Fig. 4). The following factors may play a role in these differential responses: (1) poritid corals from both locations may exhibit genetic variation (see Weil, 1992), possibly a result of the contrasting environmental settings (coral in the non-upwelling Gulf of Chiriquí are adapted to warmer water conditions, see Glynn and Maté, 1997), and (2) the hosted type of zooxanthellae in the coral colonies may be different, thereby possibly affecting the sensitivity of the symbiotic partnership to stressors (see Rowan and Knowlton, 1995; Rowan et al., 1997; Baker, 1999; Kinzie et al., 2001).

Corals in the Gulf of Panama are subject to seasonal upwelling from mid-December to mid-April (D'Croz and Robertson, 1997). During this time water temperatures may drop to 15°C at 10 m depth for short periods (D'Croz et al., 1991). This can also lead to bleaching (Glynn and Stewart, 1973; Glynn and Maté, 1997), however, intense upwelling conditions do not affect corals so severely as exposure to sea warming episodes (Glynn and D'Croz, 1990). In addition, upwelling itself may retard the effect of ENSO warming in the Gulf of Panama (Podestá and Glynn, 1997, this issue; Glynn et al., this issue). Similar effects have been reported for corals in highly fluctuating thermal environments in the Gulf of Oman, Indian Ocean (Salm, 1993; Glynn, 1993; Coles, 1997).

*P. lobata* from the seasonal upwelling Gulf of Panama when experimentally exposed to high water temperatures showed greater negative effects than corals from the thermally stable Gulf of Chiriquí. This same pattern was reported for *P. damicornis* (Glynn and D'Croz, 1990). Since most coral species live close to their upper limit of thermal tolerance (Coles and Jokiel, 1978; Glynn and D'Croz, 1990), temperature increases of only a few degrees above the normal ambient level may trigger the bleaching response. Our experimental results show that for the massive coral species *P. lobata* an increase of 1 to 2°C above ambient water temperature over a 4 wk period is sufficient to cause both the loss of zooxanthellae and a decrease in the concentration of photosynthetic pigments (Fig. 3). However, this sensitivity to water temperature may vary with the locality and/or microenvironments in which the corals live because corals have the ability to adapt to local conditions (Jokiel and Coles, 1990; Buddemeier, 1992). This may in large measure explain why corals from the upwelling Gulf of Panama, which may be physiologically adapted to colder water temperatures than those from the non-upwelling Gulf of Chiriquí, suffered higher mortality and more severe bleaching during the 1982–83 ENSO sea warming event (Glynn et al., 1988). During the 1997–98 ENSO two coral bleaching episodes (late July–September 1997; March–June 1998) were evident in the Gulf of Chiriquí when sea surface temperatures increased above 30°C (Glynn et al., this issue). Sea water temperatures in the Gulf of Panama, however, remained below 30°C and corals did not bleach. Our experimental results are in agreement with these observations since experimentally induced bleaching occurred only when corals were exposed to water temperatures above 30°C.

High solar irradiance (especially UV radiation) may also be a factor responsible for large-scale coral reef bleaching (Jokiel and York, 1982) and may interact synergistically

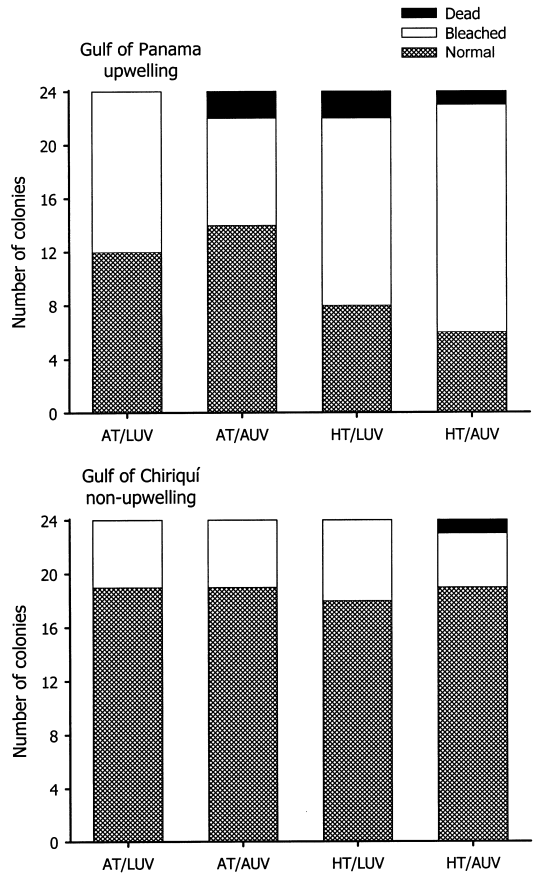


Figure 4. Visual condition of colonies of *Porites lobata* 15 d through the experimental treatments. Treatment conditions as in Figure 3.

with elevated water temperatures (Gleason and Wellington, 1993; Glynn, 1996). In coral species such as *Montipora verrucosa* in Hawaii (Coles and Jokiel, 1978), and *Montastraea annularis* in the Caribbean (Rowan et al., 1997), high solar irradiance was found to exacerbate the damage sustained by elevated water temperature. Also, while the loss of zooxanthellae is more likely to occur when corals are exposed to elevated water temperature (Hoegh-Guldberg and Smith, 1988), the decline of photosynthetic pigments per zooxanthella can be induced solely by exposure to high irradiance (Gladfelter, 1988; Hoegh-Guldberg and Smith,1988; Brown et al., 2000; Salih et al., 2000).

The experimental results with *P. lobata* clearly demonstrate that high water temperature is the more important factor leading to the decline of zooxanthellae and photosynthetic pigments in this coral species. We do not, however, have an explanation for the increase in chlorophyll *a* content per zooxanthella in thermally stressed *P. lobata* from the upwelling Gulf of Panama. A similar response in intracellular pigment concentration has been observed in other coral species (Fitt et al., 1993; Jones, 1997; Brown et al., 2000). Discounting the early mortality of two colonies under ambient temperature and UV radiation (Fig. 4), no further deleterious effects were observed (Table 2). Neverthe-

less, bleached corals showed a high capacity for recovery when returned to ambient water temperature, increasing their zooxanthellae densities and photosynthetic pigment concentrations. However, the pigment content of the zooxanthellae themselves decreased when corals were returned to ambient conditions (Fig. 3). This is most likely due to an increased mitotic rate of the surviving zooxanthellae, leading to the repopulation of the host tissue by smaller cells. The lack of a significant response by *P. lobata* to a major stressor such as UV radiation may be attributed in part to the perforate nature of the skeleton which allows deep polyp retraction, thus providing protection from harmful UV radiation. In addition, corals have UV absorbing compounds like S-320 (Dunlap and Chalker, 1986) and these may further protect *P. lobata* from radiation damage.

Some reef-building scleractinian species have recently been shown to contain more than one taxon of endosymbiotic dinoflagellates [e.g., in the Caribbean coral complex *M. annularis* (Rowan and Knowlton, 1995) and in eastern Pacific *Pocillopora* spp. (Glynn et al., this issue)]. These dinoflagellates have marked intraspecific patterns of photic zonation among colonies at different depths (Rowan and Knowlton, 1995; Baker et al., 1997), and within colonies across sunlit and shaded surfaces (Rowan et al., 1997). The pattern of coral colony bleaching is related to the type of zooxanthella symbiont hosted by a given coral species (Rowan et al.,1997; Baker, 1999; Kinzie et al., 2001). The loss of zooxanthellae may be followed by a new symbiotic consortium with zooxanthellae that are more resistant to the environmental conditions (Kinzie et al., 2001). Thus, zooxanthella diversity within a particular host might be important in understanding variability in coral bleaching during episodes of natural environmental stress (Rowan et al., 1997). However, only one type of zooxanthella is reported in *P. lobata* in Panama (Baker, 1999). Therefore, the differential thermal resistance exhibited by *P. lobata* during this experiment suggests that the coral host genotype may also influence the bleaching patterns in this coral in Panama.

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