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Bleaching Patterns of Four Species of Caribbean Reef Corals

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Abstract. Bleaching of reef corals, involving loss of symbiotic algae (= zooxanthellae), loss of algal pigments, or both, has been linked to temperature stress. In this study the effects of high temperature and light on zooxanthellae living in the Caribbean reef corals *Montastrea annularis, M. cavernosa, Agaricia agaricites,* and *A. lamarcki* were studied. Pieces of coral colonies were incubated at ambient seawater temperature (26° ± 1°C), and at 30°, 32°, and 34°C. Symbiotic algae from *M. annularis,* a species of coral from the forereef that commonly bleaches, showed the following sequence of events when exposed to natural light at 32°C: loss of photosynthetic potential measured as fluorescence yield, corresponding reduction of both oxygen production per zooxanthella and P:R (photosynthesis:respiration) ratio, and subsequent reduction in density of algae in relation to surface area of the coral. These parameters were not significantly reduced and no deaths occurred for *M. annularis* or any other coral species maintained at 26° or 30°C. However, the sequence of events was condensed to less than 24 h when *M. annularis* was subjected to 34°C seawater, except that there was little if any reduction in algal density before tissue-sloughing and death occurred between 10 and 24 h. Loss of significant amounts of chlorophyll *a* per alga was not evident for any corals except those maintained at 34°C longer than 10 h. In contrast, symbiotic algae in *M. cavernosa,* a species that rarely bleaches in nature, showed only slight reductions in photosynthesis and fluorescence yield, and no significant loss of algal cells or chlorophyll *a*, when maintained in seawater at 32°C for 2 days. Thus zooxanthellae in *M. cavernosa* appeared to be less affected by sublethal high-temperature stress. Similar contrasting patterns of bleaching were seen in zooxanthellae from the plating coral *Agaricia lamarcki,* which often bleaches during the late summer and fall, compared with zooxanthellae from *A. agaricites,* a coral which bleaches less frequently. In addition, *M. annularis* exposed to sublethal high temperatures and ambient light bleached faster than those kept in dimmer light, supporting past field observations suggesting that light energy is an important component of bleaching in nature. When *M. annularis* was exposed to different wavelengths of natural light at 32°C, the fluorescence yield declined more quickly in the presence of higher energy UV-A and blue light than with other photosynthetically active radiation. Natural levels of UV-B had little effect in this study. These data suggest that the patterns of bleaching seen in nature may be at least partially explained by different tolerances of the symbiotic algae in the corals, and that light plays a significant role in bleaching.

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Introduction

Two major ecological events during the last decade focused the attention of coral reef researchers on the susceptibility of corals and associated reef organisms to the potentially devastating effects of elevated seawater temperatures. The first was the 1982–1983 El Niño Southern Oscillation (ENSO), during which many hard and soft corals from the Great Barrier Reef, the Central Pacific, and eventually the Eastern Pacific bleached as seawater temperatures rose 2°–6°C above normal (Glynn, 1983, 1984; Oliver, 1985; Harriot, 1985; Fisk and Done, 1985; Coffroth *et al.,* 1990; Glynn and D'Croz, 1990). Subsequent coral death was common: up to 97% of the species harboring symbiotic algae were reported dead on some reefs (Glynn and D'Croz, 1990).

The Caribbean-wide "bleaching event" of 1987 again drew attention to warm-water stress in the marine environment, this time coupled with concerns that global warming might be one of the causes (Williams and Williams, 1988). Though bleaching was extensive, total loss

of zooxanthellae from coral tissues was rare, as was death of entire coral colonies (see references in Fitt *et al.*, 1993; Porter and Meier, 1992). Most bleached corals recovered their normal coloration within a year (Szmant and Gassman, 1990; Fitt *et al.*, 1993). The results of both of these events are consistent with the notion that corals and other associated invertebrates are living close to their physiological upper thermal limits during summer months, so that even the smallest increase in seawater temperature may have an effect if the exposure time is long enough (Coles *et al.*, 1976).

Virtually all studies of bleaching support the supposition that summertime bleaching is at least partially linked to the high temperatures (*e.g.*, Yonge and Nichols, 1931a; Jokiel and Coles, 1977; Jaap, 1979; Glynn, 1984; Lasker *et al.*, 1984; Hoegh-Guldberg and Smith, 1989; Glynn and D'Croz, 1991; Gates *et al.*, 1992; Jokiel and Coles, 1990; Fitt *et al.*, 1993). Two of the best examples of the role of temperature involve laboratory experiments, one simulating El Niño conditions in the Eastern Pacific (Glynn and D'Croz, 1990) and the other mimicking the effects of the thermal discharge system of a power generator in Hawaii (Jokiel and Coles, 1977). Both studies clearly showed the immediate, adverse effects on corals of abnormally high temperatures (≥32°C), as well as more subtle bleaching during long-term exposure to temperatures only 1°–2°C above normal ambient (*e.g.*, 30°C).

The relative importance of other environmental factors on bleaching is more contentious. Low salinity and high levels of natural light sometimes show synergistic effects in connection with high temperatures near the limits of tolerance for corals (Coles and Jokiel, 1978; *cf.* Hoegh-Guldberg and Smith, 1989). In addition, high doses of ultraviolet light induce bleaching without increased temperature (Jokiel, 1980; Gleason and Wellington, 1993). Although the role of light in bleaching is interesting, little is currently known about the role of light quantity and quality, especially in relation to photosynthetic action spectra of the symbiotic algae. For instance, UV-B blocking compounds have been described and characterized (Dunlap and Chalker, 1986), and show the expected decrease in concentrations with depth (Dunlap *et al.*, 1988). However, protection by these compounds from UV-A light (*ca.* 320–400 nm) is generally limited at wavelengths greater than 350 nm, where photosynthetic pigments in zooxanthellae begin absorbing light (Jeffrey and Haxo, 1968; Dunlap *et al.*, 1988). This leaves the coral and symbiotic algae exposed to longer UV-A wavelengths and blue light (*ca.* 400–450) (Dunlap *et al.*, 1988), as well as to other photosynthetically active radiation (PAR).

One of the most perplexing aspects of coral bleaching is that some species seem to lose color frequently and quickly during bleaching events, whereas others never seem to bleach. For instance, the Caribbean reef-building coral *Montastrea anularris* is one of the first species to appear discolored during bleaching events, whereas *M. cavernosa* rarely bleaches (Jaap, 1979, 1985). Although differential tolerance of host tissue to environmental stress may explain these patterns, it is also possible that different species or types of zooxanthellae (see Trench, 1993) exhibit different tolerances to temperature and light (*cf.* Fitt, 1985).

One explanation proposed for high-temperature bleaching is that the host digestive cells detach from the mesoglea, carrying zooxanthellae out of the coelenteron, in a fashion seen in cnidarians exposed to cold water stress (Gates *et al.*, 1992). Other investigators have found that cultured zooxanthellae placed in temperatures equal to or higher than 32°C show decreased photosynthetic efficiency (Iglesias-Prieto *et al.*, 1992); this observation suggests that the algae, and not just the host, are responsible for the breakdown of the symbiosis during bleaching. There is still no consensus as to which of the symbiotic partners is more affected by high temperature. In this study we address some of these issues by documenting the sequence of events occurring in zooxanthellae living symbiotically with four species of Caribbean reef corals, and show that both light quantity and quality can be important environmental factors in bleaching.

Materials and Methods

Collection and maintenance of animals

Intact colonies of the reef corals *Agaricia agaricites, A. lamarcki, Montastrea annularis,* and *M. cavernosa* were collected from a depth of 14–16 m on the forereef off the Discovery Bay Marine Laboratory in Jamaica in the early morning (0700–0800) in February and March of 1993 and 1994. Within 1 h of collection each colony was broken into eight pieces, each with a surface area of 5–10 cm^2, and placed into one of four water-jacketed acrylic incubation chambers containing about 3.5 l of seawater. The clear plastic chambers were exposed to ambient light; their open tops were covered with three layers of screen to reduce the maximum light intensities to slightly less those found at 14–16 m on the reef. Light intensities at noon on a cloudless day on the reef at 15 m were measured on three occasions and ranged between 500–600 $\mu E\ m^{-2}s^{-1}$, maximum intensities measured in the chambers under the screen were 400–475 $\mu E\ m^{-2}s^{-1}$. During the experiments, fresh unfiltered seawater flowed into the chambers at *ca.* 150 m min^{-1} and vigorous aeration from aquarium pumps and air stones kept the water well mixed. Ambient seawater temperatures were 26.0° ± 1.0°C. Coral pieces were allowed to equilibrate in the chambers for 5–15 min at ambient temperature before the start of each experiment. Under ambient temperature and light, control

pieces maintained in chambers showed no adverse or visible effects for at least 4 days.

Experimental protocol

Coral pieces were placed in one of four chambers, each starting out at ambient seawater temperature (26.0°C ± 1.0°C). In three of the chambers, aquarium heaters were used to raise the temperature over a period of about 1 h. Temperatures were kept at 30°, 32°, and 34°C ± 0.5°C. A minimum of four replicate colonies were tested from each species. At least two pieces of each replicate colony were placed into each of the four chambers so that samples could be taken at different times. Coral pieces maintained at 26°, 30°, and 32°C were processed at about 24 and 48 h. Coral pieces exposed to 34°C were sampled 3–5 times during the first 24-h period. Pieces of coral were processed for physiological testing and biomass determinations as detailed below.

Light quality and quantity experiments

Pieces of six replicate heads of *M. annularis* used in experiments testing the effects of light quality and quantity were collected from a patch reef (1–2 m deep) off Key Largo, Florida. Coral pieces were placed in glass petri dishes in a 32°C temperature bath with aeration, where the seawater was changed at least every 4 h throughout the experiment. The quality and quantity of natural ambient light were adjusted with screens and glass cut-off filters (Melles Girot). Corals were exposed to one of the following conditions: natural light with no filters, natural light without UV-B (>320 nm), natural light without UV-A and B (>395 nm), or natural light without UV or blue light (>495 nm). Two layers of window screen covered the entire waterbath to reduce the maximum exposure level to slightly lower than that found *in situ* (<700 μE m^2s^{-1}). Some coral pieces (control) were maintained under two layers of window screen without filters, but at 26°C.

Physiological testing and biomass determinations

Coral tissue and zooxanthellae were removed from the coral skeleton with a Water-Pik and subsamples of the homogenate taken for zooxanthellae counts and chlorophyll *a* determinations. The remaining homogenate was filtered through three layers of cheesecloth and centrifuged at 1500 × *g* for 3 min. The pellet was resuspended and washed (recentrifuged) with fresh filtered (0.45 μm) seawater (FSW) at least three times, or until few animal fragments were seen amongst the zooxanthellae in microscopic observations.

Cleaned zooxanthellae were resuspended in FSW at densities between 0.5 and 1.0 × 10^6 zooxanthellae per milliliter. Respiration rates in the dark and photosynthetic rates at 450 μE $m^{-2}s^{-1}$ (above saturation) were determined with a YSI oxygen meter equipped with low-volume (2–10 ml) chambers and magnetic stirrers. Respiration and net photosynthesis rates were added together to give gross photosynthesis rates and standardized to number of zooxanthellae. Gross photosynthesis:respiration (P:R) ratios were calculated from these rates.

Chlorophyll fluorescence of zooxanthellae suspensions was measured with a Turner fluorometer, after a 10-min incubation in darkness. The ratio of fluorescence obtained with additions of DCMU (10^{-5} *M*) in relation to that without DCMU was calculated. Long-term kinetics of chlorophyll fluorescence of zooxanthellae living within the host were recorded with a pulse amplitude modulation fluorometer (model PAM 101, 103; Waltz). The corals were dark-adapted for 10 min under the fiber optic bundle of the fluorometer prior to measurement. The initial fluorescence (Fo) was measured by exposing the coral to a weak pulse of red light (<1 μE m^2s^{-1}). Maximum fluorescence (Fm) was then determined by applying a 1-s pulse of intense white light (>500 μE m^2 s^{-1}). The maximum variable fluorescence was calculated as Fv = Fm − Fo. The value Fv/Fm is used to indicate the photosynthetic efficiency and is proportional to the quantum yield.

Chlorophyll *a* was extracted with acetone by the method of Jeffrey and Humphrey (1975). Total chlorophyll *a* was calculated from absorbance at 663 and 630 nm and standardized per algal cell extracted.

Zooxanthellae densities were calculated from the total number of zooxanthellae and the surface area of the coral. Number of zooxanthellae was determined from replicate (8–10) hemacytometer counts. Surface area was determined by covering the surface of the coral with aluminum foil, weighing the foil, and applying a standard curve relating aluminum weight to area.

Results

High-temperature stress in ambient light

The response of corals and their symbiotic algae to high-temperature stress varied with species of coral, but followed a similar pattern (Figs. 1–4). The pattern is best illustrated with *Montastrea annularis* maintained at 32°C: photosynthetic rates and potential (fluorescence ratio F^{+DCMU}/F^{-DCMU}) as well as P:R (photosynthesis: respiration) ratio all decreased before any significant change in density of zooxanthellae was evident. At 34°C it took less than 24 h for photosynthesis, fluorescence ratios, and the P:R to decrease to 0. The zooxanthellae density and chlorophyll *a* content per zooxanthella changed little at 34°C before coral death was first observed at 19 h. Zooxanthellae from *M. annularis* maintained at 30°C differed little from zooxanthellae isolated from freshly collected

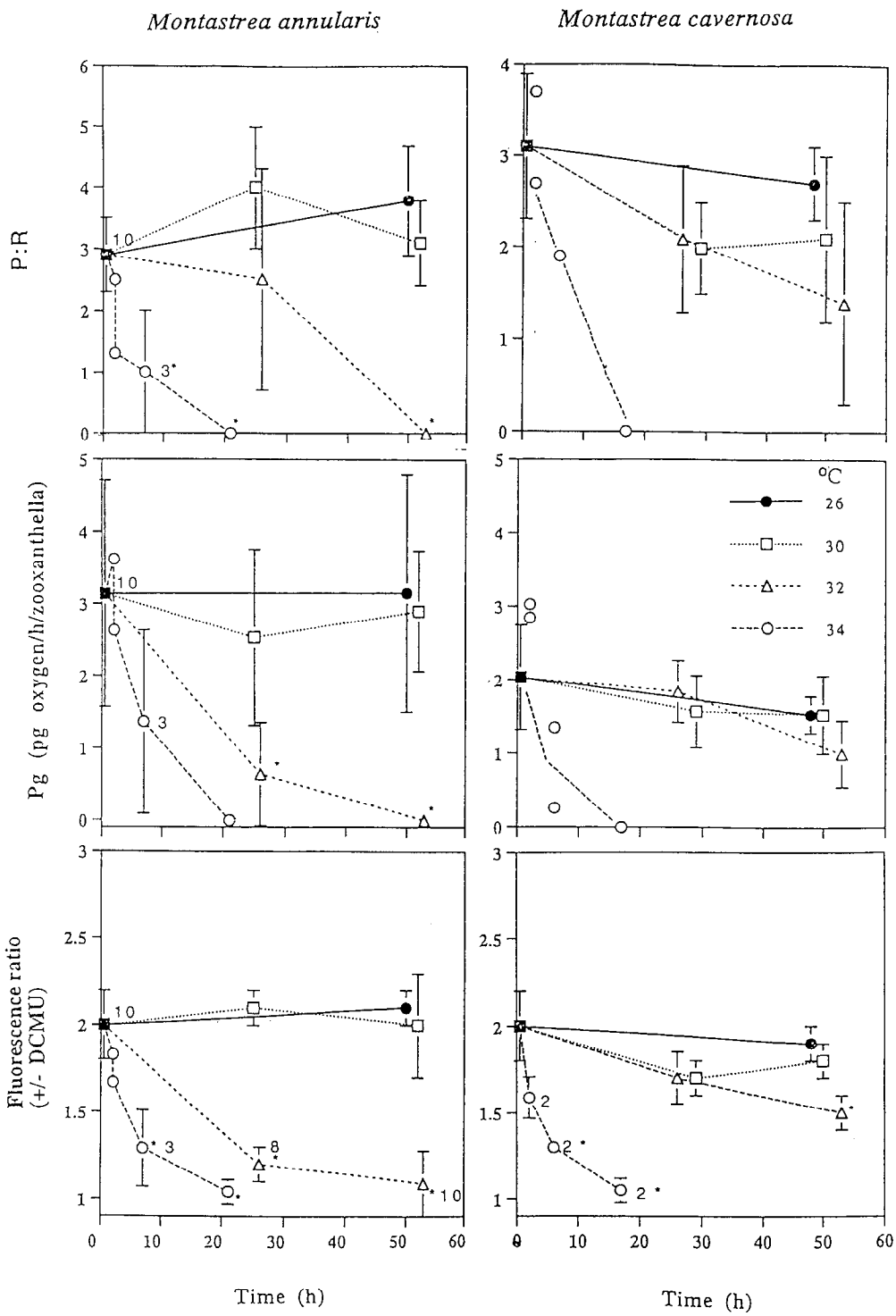

Figure 1. Patterns of bleaching of zooxanthellae in the corals *Montastrea annularis* and *M. cavernosa* exposed to seawater temperatures of 26°C (control), 30°, 32°, and 34°C: gross photosynthesis: respiration ratio (P:R), gross photosynthesis (P_g), and fluorescence ratio (F_{+DCMU}/F_{-DCMU}) in relation to exposure time. All data points are means ± SD, $n = 4$, unless otherwise noted. * = significantly ($P < 0.05$, ANOVA) different from controls.

corals or those maintained at ambient seawater temperature (26° ± 1°C) for 2 days. Chlorophyll *a* per zooxanthella increased slightly over the 2-d experiment, probably due to photoadaptation to the experimental light intensities, which were slightly lower than the light intensities *in situ* (Fig. 2).

M. cavernosa responded somewhat differently to increases of temperature in the light than did *M. annularis*. No significant reductions in the density of zooxanthellae were observed over 53 h at any temperature (Fig. 2). Photosynthesis, fluorescence, and the P:R ratio at 26°, 30°, and 32°C remained relatively stable, except that there was a 25%–50% decrease in these parameters at 53 h at 32°C (Fig. 1). In contrast, photosynthesis, fluorescence, and P:R of the zooxanthellae from *M. cavernosa* declined rapidly at 34°C in a fashion similar to that seen in zooxanthellae from *M. annularis*. Chlorophyll *a* per zooxanthella increased slightly throughout the experiment at all temperatures except 34°C, at which values remained the same or decreased slightly (Fig. 2). Zooxanthellae from *Agaracia lamarcki* appeared to be less tolerant to seawater temperatures of 32° and 34°C than were zooxanthellae from *A. agaricites* (Figs. 3–4). Photosynthesis and the fluorescence ratio of zooxanthellae from *A. lamarcki* declined faster at 34°C than zooxanthellae from *A. agaricites* (Fig. 3). At 32°C, photosynthesis and fluorescence ratios decreased significantly for both species (Fig. 3), and zooxanthellae density was about half of that from corals maintained at 30° or 26°C (Fig. 4). Chlorophyll *a* per zooxanthella did not change significantly ($P > 0.05$, ANOVA) at any temperature for either coral, except for a marked decrease for *A. lamarcki* at 32°C for 48 h (Fig. 4).

High-temperature stress and light

When pieces of *M. annularis* were exposed to different wavelengths of light at 32°C, those experiencing the largest decrease in fluorescence ratio (Fv/Fo) received wavelengths in the UV-A range (320–400 nm) or blue to blue-green light (395–495 nm) (Fig. 5A). Rates of decrease in fluorescence ratio were no different with or without natural levels of UV-B light (<320 nm) in these experiments (ANOVA, $P > 0.05$). Control corals (those maintained at 26°C in natural light with no filters) showed no change in fluorescence ratio throughout the experiment.

Fluorescence ratios (Fv/Fo) of intact *M. annularis* exposed to 32°C declined faster when exposed to higher intensity than lower intensity of natural light (Fig. 5B). Interestingly, a "recovery" trend was observed in the same experiment and in three similar experiments (not included) during periods of cloudy weather.

Discussion

This study shows that symbiotic dinoflagellates living inside of reef corals exhibit a marked decline in their photosynthetic capacity and oxygen evolution when exposed to higher than normal temperatures (32°, 34°C) in natural light for relatively short periods of time. Reductions in photosynthesis and corresponding flow of electrons between photosystems II and I, as indicated by fluorescence ratios, preceded any significant reductions in density of zooxanthellae in the reef-building corals *Montastrea annularis, Agaricia lamarcki,* and *A. agaricites*. In addition, zooxanthellae from *M. cavernosa* and *A. agaricites* appeared to be more tolerant to the experimental temperature regimes, showing reduced photosynthetic competence after longer exposure times (>24 h). There was no significant reduction in symbiont density in *M. cavernosa* over the course of the experiment (48–55 h), though probably they too would eventually lose symbiotic algae that were not photosynthetically functional. The data correspond to the bleaching patterns seen in the field; *M. annularis,* and *A. lamarcki* commonly lose color during bleaching events, whereas *M. cavernosa* rarely bleaches and *A. agaricites* sometimes bleaches. The results of this study suggest that the differences seen in nature in bleaching of coral species may be due to the different physiological tolerances of their specific symbiotic algae.

Though it has been clear for some time that the fluorescence patterns and photosynthetic rates of cultured zooxanthellae are altered at moderate increases above control temperatures (e.g., 32° vs. 26°C) (Iglesias-Prieto *et al.,* 1992), there has been debate as to the mechanism of bleaching in relation to mode of release of the zooxanthellae from the coral and the relative health of the symbiont and host (Gates *et al.,* 1992). Hoegh-Guldberg and Smith (1989) clearly showed that bleaching of corals can occur without loss of zooxanthellae, especially when high light intensities "photo-bleach" the algal pigments. However, most bleaching events in nature involve heat stress with full solar radiation, and the loss of both symbiotic dinoflagellates and their photosynthetic pigments has been documented (Kleppel *et al.,* 1989; Porter *et al.,* 1989). In our study, chlorophyll *a* content per zooxanthella varied little, in spite of up to 55 h of exposure to temperatures as high as 34°C. These results are similar to those of Hoegh-Guldberg and Smith (1989), also involving short-term laboratory experiments on corals exposed to elevated temperatures, but in contrast to field observations made during natural bleaching events in the Virgin Islands and southern Florida which showed reductions of chlorophyll *a* ranging from 50% to 80% (Porter *et al.,* 1989; Kleppel *et al.,* 1989). The only reductions seen in chlorophyll content in this study occurred at 34°C at longer exposure times, suggesting that pigment loss during bleaching occurs *after* physiological damage to photosynthesis. During short-term (days) laboratory experiments, zooxanthellae from the more sensitive symbioses appear to leave the host before or during loss of

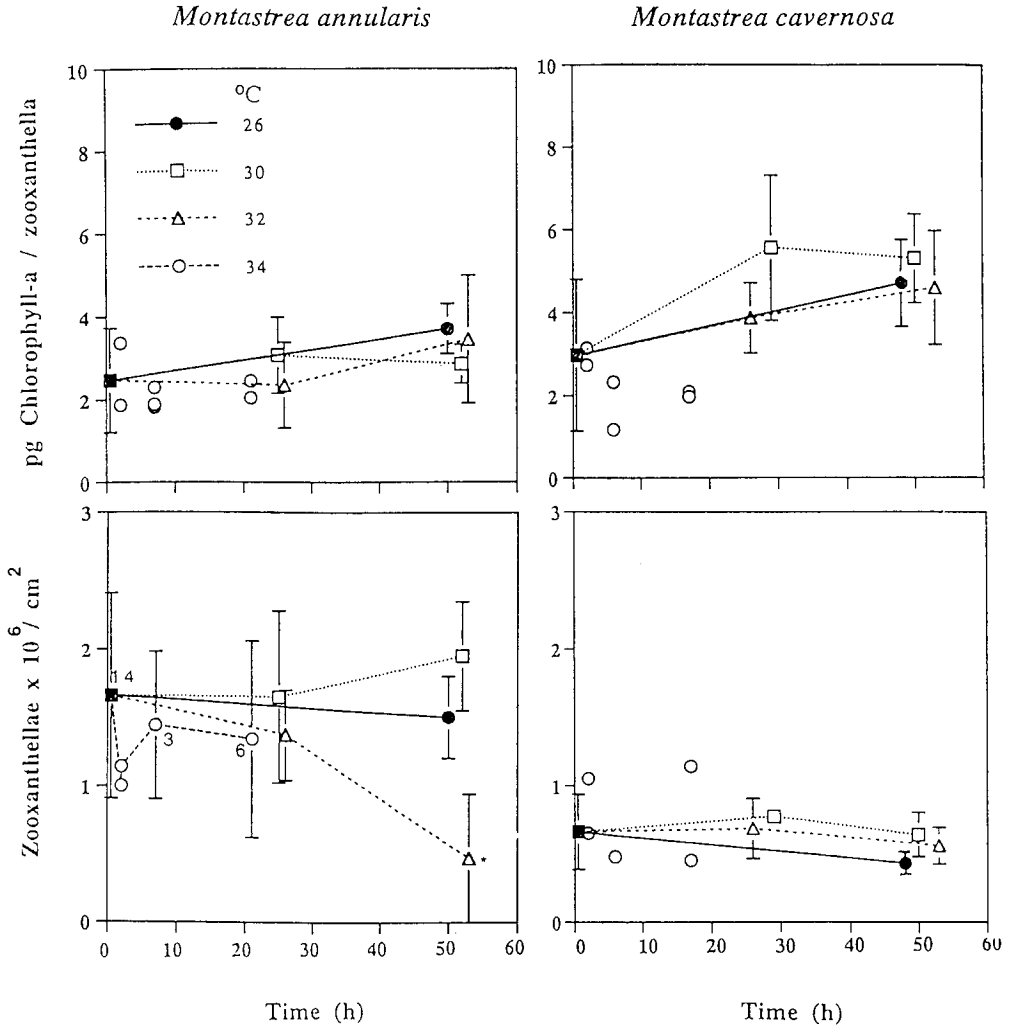

Figure 2. Patterns of bleaching of zooxanthellae in the corals *Montastrea annularis* and *M. cavernosa* exposed to seawater temperatures of 26°C (control), 30°, 32°, and 34°C: chlorophyll *a* per zooxanthella and zooxanthella density in relation to exposure time. All data points are means ± SD, $n = 4$, unless otherwise noted. * = significantly ($P < 0.05$, ANOVA) different from controls.

photosynthetic pigmentation. Longer exposures (weeks) to elevated seawater temperatures (≥30°C) typically involve loss of chlorophyll *a* per zooxanthellae co-occurring with relatively low rates of zooxanthellae expulsion and a decrease in density of zooxanthellae (Glynn and D'Croz, 1990). Thus, loss of photosynthetic pigments appears to be a normal step in warm-water bleaching in nature, and one that indicates algal stress.

When Hoegh-Guldberg and Smith (1989) used chlorophyll data taken from water surrounding the corals to calculate release rates of zooxanthellae from the heat-stressed (30°, 32°C) Pacific corals *Stylophora pistillata* and *Seriatopora hystrix,* expulsion rates increased by a factor of 2 to 10, but only the corals maintained at 32°C showed significant decreases in density of zooxanthellae. In the present study, zooxanthellae density in *Montastrea annularis, Agaricia lamarcki,* and *A. agaricites* decreased significantly only *after* photosynthesis and enhanced zooxanthellar fluorescence decreased. Zooxanthellae from *M. cavernosa* were apparently more resistant to the higher temperatures than zooxanthellae in *M. annularis,* in that zooxanthellae density did not change over the 2 days of exposure to 32°C. However, at least some of the zooxanthellae in *M. cavernosa* held 2 days at 32°C showed reduced photosynthetic capacity, and—on the basis of the experiments with *M. annularis*—densities might be expected to decrease after longer exposure times. Similarly, Glynn and D'Croz (1990), who documented steady decreases in density of zooxanthellae from *Pocillopora damicornis* at 30° and 32°C, found that the effects were evident (significantly different from controls) only after 2 weeks or more.

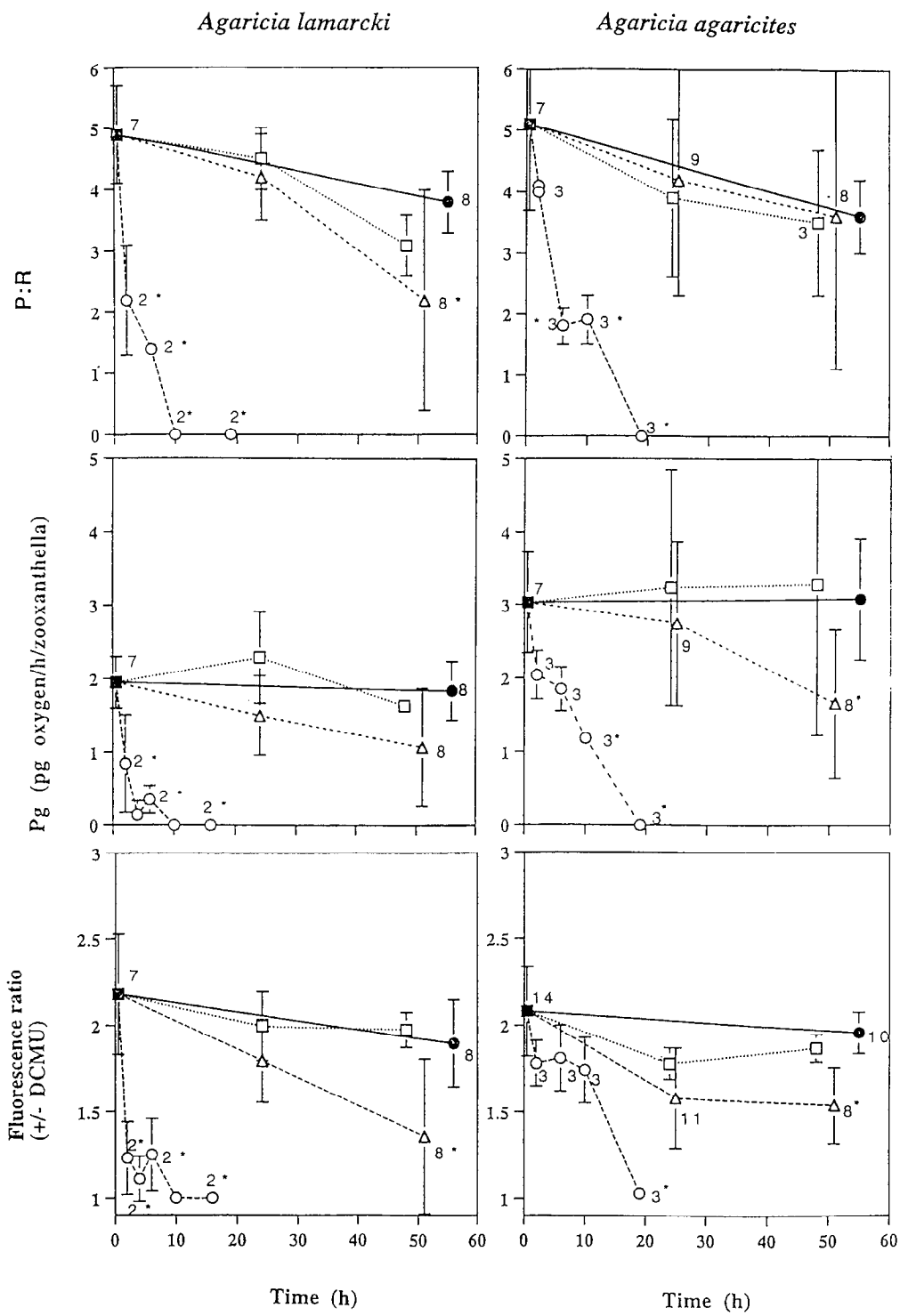

Figure 3. Patterns of bleaching of zooxanthellae in the corals *Agaricia agaricites* and *A. lamarckii* exposed to seawater temperatures of 26°C (control), 30°, 32°, and 34°C: gross photosynthesis: respiration ratio (P:R), gross photosynthesis (P_g), and fluorescence ratio (F_{+DCMU}/F_{-DCMU}) in relation to exposure time. All data points are means ± SD., $n = 4$, unless otherwise noted. * = significantly ($P < 0.05$, ANOVA) different from controls. Symbols as in Figures 1 and 2.

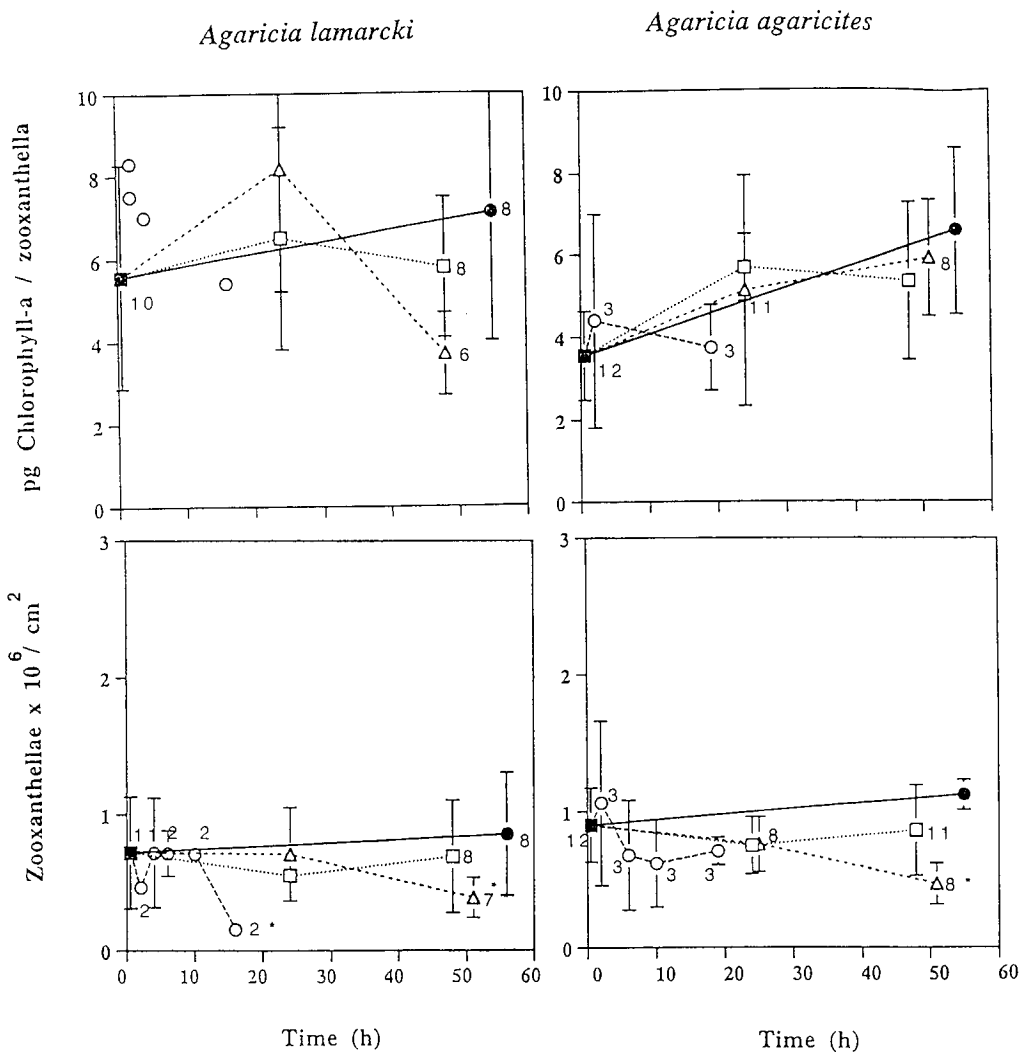

Figure 4. Patterns of bleaching of zooxanthellae in the corals *Agaricia agaricites* and *A. lamarckii* exposed to seawater temperatures of 26°C (control), 30°, 32°, and 34°C: chlorophyll *a* per zooxanthella and zooxanthella density in relation to exposure time. All data points are means ± SD, $n = 4$, unless otherwise noted. * = significantly ($P < 0.05$, ANOVA) different from controls. Symbols as in Figures 1 and 2.

Light and dark rates of zooxanthellar expulsion are identical in *Stylophora pistillata* and *Seriatopora hystrix* maintained at ambient temperature (Hoegh-Guldberg and Smith, 1989). In contrast, corals maintained at high temperatures in the light exhibit higher rates of expulsion (Hoegh-Guldberg and Smith, 1989), resulting in reduced densities of zooxanthellae at 32°C (Hoegh-Guldberg and Smith, 1989; this study). The quantity of light makes a major difference in the kinetics of warm-water-induced bleaching; zooxanthellae kept in dim light take longer, and often require higher temperatures, to achieve the same level of bleaching as seen in brighter light (Fig. 2 this study, Warner and Fitt, unpub.). The quality of light is also a factor in bleaching. Although the effects of large and sudden increases in UV-B can be devastating to zooxanthellae in corals (Lesser *et al.*, 1990; Gleason and Wellington, 1993), most shallow-water corals have UV-protective mycosporine-like amino acids (MAAs) that screen out such dangerous wavelengths. Much more likely sources of synergistic light energy for bleaching are longer wavelength UV-A (wavelengths not screened out by MAAs) and blue light, both important in photosynthesis and therefore not screened out by the coral host (Dunlap *et al.*, 1988). Preliminary experiments show that blue light also promotes bleaching of some types of cultured zooxanthellae much more effectively than the same amount of light at any other part of the visible spectrum (Fitt and Warner, unpub.).

It is not clear at present whether coral death is solely a function of animal tissue death, or if lack or dysfunction of zooxanthellae may trigger or exacerbate events preceding host tissue sloughing and coral death. That the latter

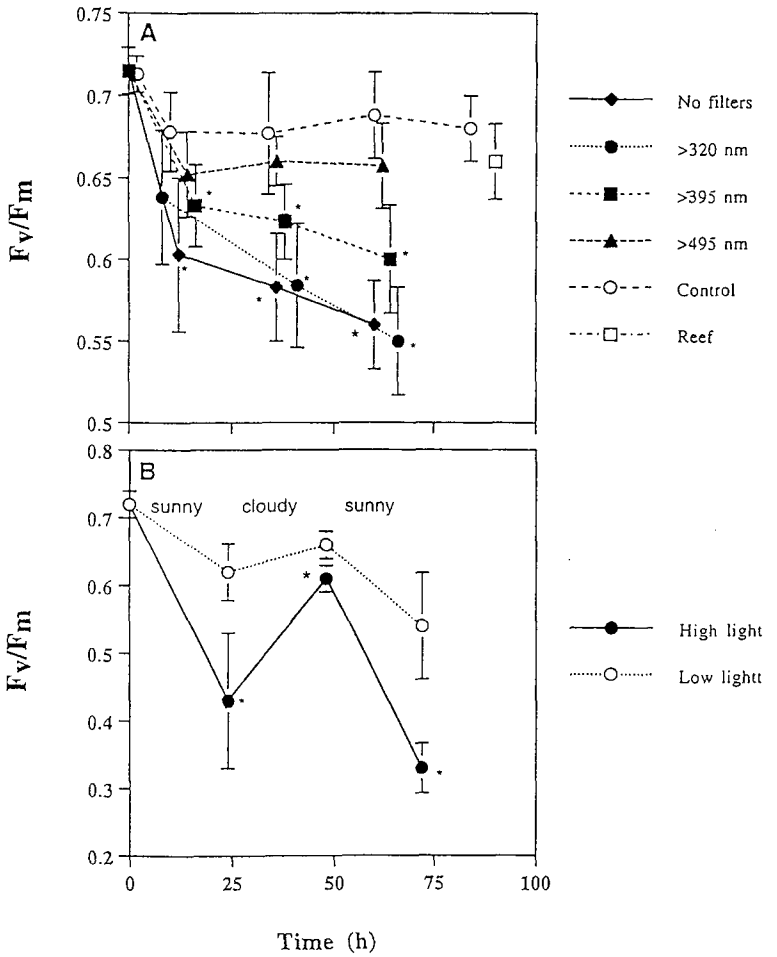

Figure 5. Fluorescence ratios (F_m/F_o) of zooxanthellae in *Montastrea annularis* collected from the reef (28°C) or exposed to seawater temperatures of 26°C (control) and 32°C (all other data) under different wavelengths (A) and intensities (B) of natural light in relation to exposure time. Neutral-density screens were used to adjust maximum intensities to 54% of air ambient (high light) in all experiments. Cut-off filters were used to adjust wavelength (A), and additional neutral-density screens reduced ambient light to 19% of air ambient (low light) in (B). All data points are means ± SD, $n = 6$. * = significantly different from control (A, ANOVA) or low light intensities (B, Student's t test).

can occur in nature was illustrated, on a somewhat longer time scale, in the Eastern Pacific after extensive coral bleaching during the El Niño Southern Oscillation (ENSO) event of 1982–1983 (Glynn, 1983, 1984). Before the widespread local and regional deaths of the corals, no zooxanthellae remained in the tissues of *Pocillopora damicornis* and *Millepora* spp. Temperatures only a few degrees above normal ambient will kill reef corals. Mayer (1914) found that all the reef corals tested in the Dry Tortugas, at the end of the Florida reef tract, died when exposed for an hour to temperatures between 36° and 38°C during the summer. In this early study, the organisms that died at the lowest temperatures tested (*M. annularis, A. lamarcki,* and the hydrocoral *Millepora* sp.) are the same species that are the first to react during natural bleaching events (*e.g.,* Williams and Bunkley-Williams, 1988), lending support to the notion that the differential bleaching of zooxanthellate cnidarians exposed to moderately high temperatures in nature reflects the tolerances of their particular zooxanthellae.

Acknowledgments

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