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Bleaching in reef corals: Physiological and stable isotopic responses

(zooxanthellae/global warming/carbonate skeleton/stable isotope)

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ABSTRACT **During the late summer to fall of 1987, Caribbean reef corals experienced an intense and widespread discoloration event described as bleaching. Contrary to initial predictions, most bleached corals did not die. However, energy input from zooxanthellae decreased, as estimated from: (*i*) $\delta^{13}C$ values, a measure of the discrimination against ^{13}C in $^{12}C/^{13}C$ assimilation, of skeletal aragonite; (*ii*) *in situ* photosynthesis–irradiance measurements; (*iii*) and tissue biomass parameters of *Montastraea annularis* and *Agaricia lamarcki*. The $\delta^{18}O$ signal, a measure of the discrimination against ^{18}O in $^{16}O/^{18}O$ assimilation, from *M. annularis* skeletons demonstrated that this event coincided with abnormally elevated water temperatures.**

During the late summer and fall of 1987, approximately 40% of the algal-bearing reef invertebrates in the Caribbean lost their pigmentation (1), a phenomenon commonly referred to as bleaching (2). Similar events have been reported from the Indo-Pacific (3–6) and eastern Pacific (7–9) oceans, where bleaching has resulted in mass mortality of reef corals and associated reef fauna. While there have been numerous studies documenting the species-specific and geographical extent of these events (2, 4, 8, 9), data are not currently available on the physiological response of these organisms to bleaching. In this study we present physiological, stable isotopic, and population data from two species of reef-building Caribbean corals (Fig. 1) to document their biological response.

Bleached and unbleached heads of *Montastraea annularis* (Ellis and Solander) (n = 6) and *Agaricia lamarcki* (Milne-Edwards and Haime) (n = 3) were collected from 6 and 31 m in the U.S. Virgin Islands in November 1987 and early April 1988, respectively. Photosynthesis–irradiance relationships were established by *in situ* underwater respirometry (10) to determine integrated ratios of photosynthesis to respiration (P/R) (11). Coral tissue was removed from the skeleton (12) and analyzed for zooxanthellae density, chlorophyll a content, protein, lipid, carbohydrate, and dry weight (13–16). Stable isotope values, $\delta^{13}C$ and $\delta^{18}O$ in parts per thousand were determined by mass spectrometry (17–19) on skeletal aragonite deposited before, during, and after the bleaching event for two bleached and two unbleached colonies of *M. annularis*; $\delta^{13}C$ and $\delta^{18}O$ are measures of the discrimination against ^{13}C in $^{12}C/^{13}C$ assimilation and against ^{18}O in $^{16}O/^{18}O$ assimilation relative to the Pee Dee Belemnite carbonate standard—e.g.,

$$\delta^{18}O = \left[\frac{^{18}O/^{16}O\ (\text{sample})}{^{18}O/^{16}O\ (\text{standard})} - 1\right] \times 1000.$$

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Reduced salinity (20, 21), increased sedimentation (22), increased UV light (23), oxygen stress, and disease (1) can cause a loss of pigmentation in reef corals through reduced zooxanthellae density (6, 9, 24, 25), reduced chlorophyll per algal cell (9, 26), or possibly a combination of both. Our data (Table 1) show that, for *M. annularis* and *A. lamarcki*, bleaching was due to a reduction of both algal densities (86% and 57% loss, respectively) and chlorophyll a content per cell (48% and 56% loss). The loss of photosynthetic potential was also reflected in photosynthetic responses for intact corals (Fig. 2). At saturating light intensities (300 $\mu E \cdot m^{-2} \cdot s^{-1}$; 1 einstein (E) = 1 mol of photons), the maximum net photosynthetic rates for bleached corals were 17% and 74% of those of unbleached *M. annularis* and *A. lamarcki*, respectively. While the respiration rates of bleached corals were slightly lower than for unbleached corals, the other photosynthetic characteristics were also less (Fig. 2), resulting in bleached corals with P/R ratios significantly lower than those of unbleached heads. By assuming that approximately 95% of the fixed carbon is translocated from zooxanthellae to the host coral (27, 28), calculations of the contribution of carbon from the zooxanthellae to meet animal metabolic requirements (10, 11) showed a reduction from approximately 112% in unbleached *M. annularis* to 51% in bleached heads. Likewise for *A. lamarcki*, the zooxanthellae produced 111% of the carbon needed to meet basal metabolic requirements in unbleached colonies but only 53% for bleached colonies.

Measurements of tissue protein, lipid, carbohydrates, and dry weight standardized to surface area of the bleached coral showed 39–73% decreases compared to values from unbleached coral tissue (Table 1). Since zooxanthellae comprise only 5–12% of the biomass of coral (27, 28), these reductions reflect loss from the coral tissue as well as loss of zooxanthellae. This measured loss of biomass follows logically from the reduced photosynthetic potential of bleached coral (Fig. 2).

Another way of evaluating the contribution of zooxanthellae to coral nutrition is to examine carbon isotopic ratios recorded in the carbonate skeleton (Fig. 3 *Upper*). Carbon dioxide used during the secretion of skeletal aragonite may come from two sources, diffused seawater HCO_3^- or respired CO_2. Zooxanthellae photosynthesis increases the $^{13}C/^{12}C$ ratio in the pool of available CO_2 via the selective utilization of $^{12}CO_2$ during carbon fixation (29, 30). Thus, the loss of photosynthetic capability in bleached corals should be recorded as a decrease in the $^{13}C/^{12}C$ ratios of their skeletons (31, 32). Our data show that the carbon isotopic ratios of bleached corals decreased by approximately 1.5 parts per thousand relative to unbleached corals (Fig. 3 *Upper*).

Two models have been proposed to describe the mechanism by which algal photosynthesis influences coral skeletal isotopic signals: (*i*) zooxanthellae either enrich the $^{13}C/^{12}C$ ratio of the skeleton (more ^{13}C) through preferential removal of lighter $^{12}CO_2$ during photosynthesis (31, 32) or (*ii*) trans-

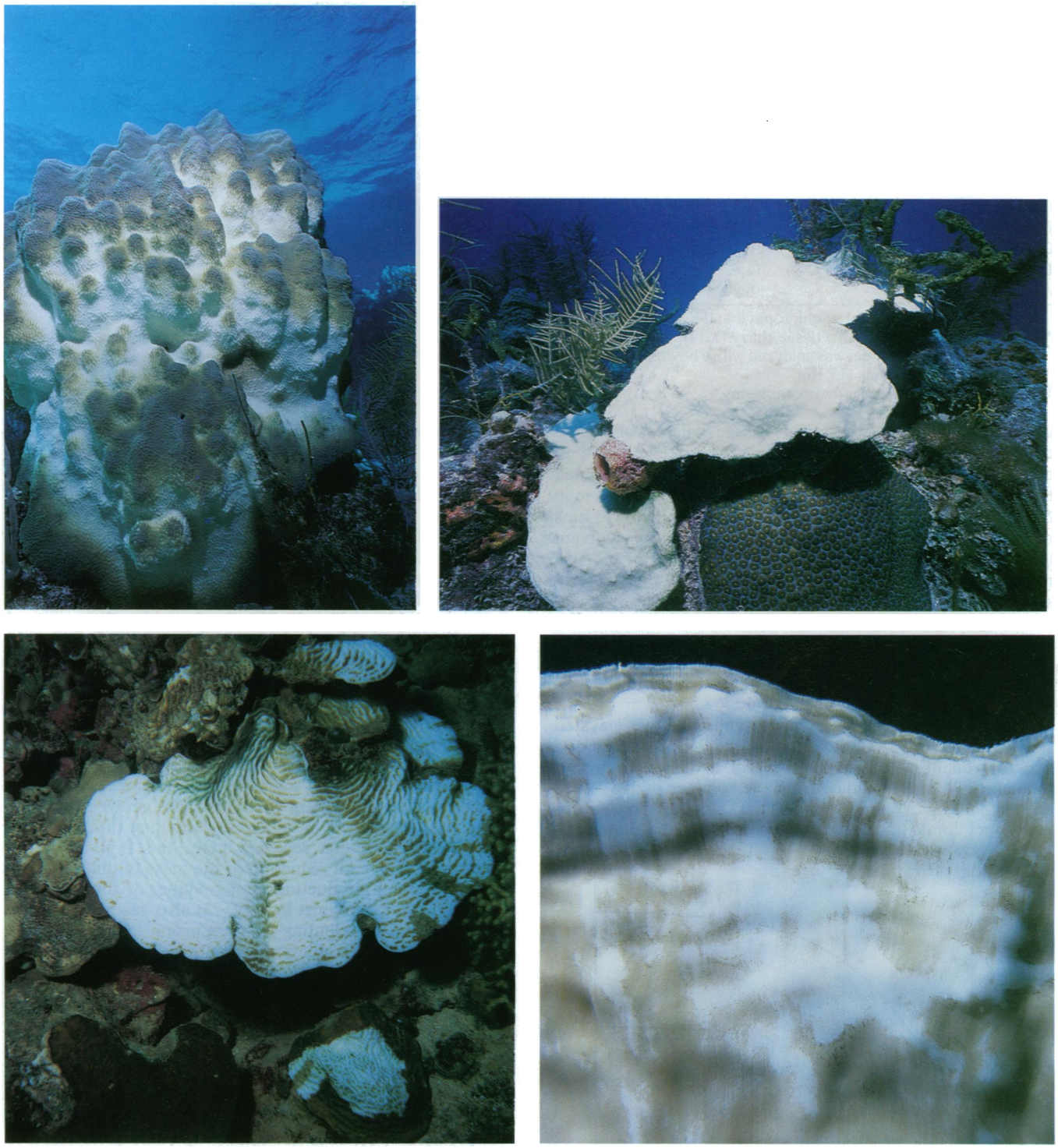

FIG. 1. Widespread bleaching of Caribbean reef corals appears to have been associated with elevated water temperatures during the late summer of 1987 throughout the Caribbean basin. Although most corals, such as the *M. annularis* colonies [*Upper Left* and at the top of *Upper Right* (from 10-m depth in Florida)], and the *A. lamarcki* colonies [*Lower Left* and *Lower Right* (from 31-m depth in Saint Croix)] survived, these individuals lost most of their symbiotic zooxanthellae and hence their photosynthetic capacity. Some coral species, such as *M. annularis* (top in *Upper Right*) were differentially susceptible to these oceanographic conditions, whereas other species, such as the congener *Montastraea cavernosa* (bottom in *Upper Right*), bleached infrequently. Bleaching on the undersides of *A. lamarcki* colonies from recessed cave environments (*Lower Right*) argues against UV light as a direct cause of bleaching in these instances. (Photographs in *Upper* were by John Halas, Key Largo National Marine Sanctuary; photographs in *Lower* were by J.W.P.)

location of zooxanthellae photosynthate depletes the skeletal $^{13}C/^{12}C$ ratio by increasing the coral's respiration rate and enhancing the release of isotopically light $^{12}CO_2$ (33). Our data support model *i*.

The ultimate cause of these bleachings is still under study, but high temperatures have been implicated as a major factor (6, 9, 24, 25, 34–38). Oxygen isotope ratios ($^{18}O/^{16}O$) in a coral skeleton record environmental temperatures during deposition (17, 18) as well as the $\delta^{18}O$ value of the seawater in which calcification occurred (19). In the present study, bleached and unbleached corals were collected from the same depth (6 m) and within 15 m of each other; however, bleached

Table 1. Tissue biomass values* for bleached (B) and unbleached (UB) specimens of *M. annularis* and *A. lamarcki* from 6 m and 31 m, respectively, in the U.S. Virgin Islands (mean ± SE)

Parameter (units)	*M. annularis*			*A. lamarcki*		
	B (n = 3)	UB (n = 3)	% loss	B (n = 2)	UB (n = 1)	% loss
Zoox, 10^6 cells per cm^2	0.43 ± 0.02	3.03 ± 1.08†	85.8	1.84	4.25	56.7
Pigments, pg of Chl a per cell	1.30 ± 0.15	2.50 ± 0.68†	48.0	0.38	1.13	66.4
Pigments, pg of Chl a per cm^2	0.55 ± 0.04	6.14 ± 0.24†	81.0	0.69	4.82	85.7
Nitrogen, mg of TKN per cm^2	0.47 ± 0.06	0.79 ± 0.05†	40.5	—	—	—
Protein, mg/cm^2	2.82 ± 0.19	8.37 ± 0.95†	66.3	4.40	14.48	69.6
Lipids, mg/cm^2	1.39 ± 0.03	2.27 ± 0.29†	38.8	2.05	7.75	72.9
Carbohydrates, mg/cm^2	0.29 ± 0.06	0.52 ± 0.07†	44.2	1.15	2.17	47.0
Dry weight, mg/cm^2	12.8 ± 1.30	22.4 ± 2.70†	42.9	31.6	51.70	38.9
AFDW, mg/cm^2	6.90 ± 0.80	15.5 ± 2.30†	55.5	16.6	32.80	49.5

Zoox, zooxanthellae; Chl a, chlorophyll a; TKN, total Kjeldahl nitrogen; AFDW, ash-free dry weight.
*Replicate aliquots (n = 3) of a tissue slurry (12) were dried to a constant weight at 60°C. Ash-free dry weight was determined after combustion at 500°C overnight. Protein was analyzed with a bovine serum albumin standard (13). Lipids and carbohydrates were determined by modification (14) of standard methods (15, 16).
†$P < 0.05$; t test, difference between means.

corals were collected from a tidal passage, whereas unbleached corals were collected from an area more exposed to offshore oceanic waters. Swart *et al.* (39) has demonstrated that evaporation of backreef water results in an increase in $\delta^{18}O$ of the seawater. Therefore, decreases in the $\delta^{18}O$ ratios of bleached skeletons probably reflect differences in ambient temperature, not differences in the $\delta^{18}O$ signal of the surrounding seawater. A comparison of the $\delta^{18}O$ values corresponding to peak summer temperatures (depleted $\delta^{18}O$ values) (Fig. 3 *Lower*) shows that bleached corals have $\delta^{18}O$ values 0.25–0.50 parts per thousand lighter than unbleached *M. annularis*. This $\delta^{18}O$ difference suggests that bleached corals were exposed to maximum water temperatures 0.5–1.0°C warmer than unbleached corals.

Recent laboratory experiments demonstrate that elevated temperatures (30–34°C) lead to loss of zooxanthellae and eventual death of corals (26, 40). In addition, sea water temperatures in Bermuda during the summer of 1987 were normal, and, unlike in Florida and the Caribbean, no bleaching of reef corals occurred. However, during the summer of 1988, sea water temperatures in Bermuda were the warmest on record for the last 30 yr. Temperatures stayed above 30.2°C for more than 2 weeks in late summer; coral bleaching started 5 days later (C. Cook, personal communication). In our study, analysis of $\delta^{18}O$ values during the last 12 months of skeletal growth showed that calcification decreased or stopped shortly after the summer temperature peak in bleached heads of *M. annularis* (Fig. 3 *Lower*) but continued in unbleached heads. Approximately 1.4 mm more aragonite was secreted by unbleached heads. Assuming that a normal growth rate for unbleached *M. annularis* ranges from 6 to 10 mm/yr for colonies growing at this depth (41, 42), this would suggest approximately 2 additional months of calcification in the unbleached heads. This places the onset of bleaching in late August 1987, which corresponds to the first observations of bleaching in the Virgin Islands and the Florida Keys (1).

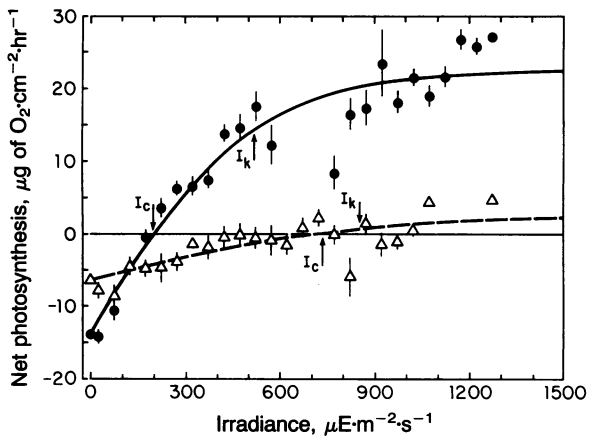

FIG. 2. *In situ* production. Irradiance curves differ for bleached (△) and unbleached (●) colonies of the reef-building coral *M. annularis*. Oxygen flux characteristics based on these curves show significant differences ($\bar{X}$ ± 95% confidence interval; $n = 3, P < 0.05$) for all major parameters, including respiration rate (−6.37 ± 0.21 versus −13.79 ± 0.27 μg of $O_2 \cdot cm^{-2} \cdot hr^{-1}$); maximum net photosynthetic rate (4.64 ± 0.38 versus 27.15 ± 0.58 μg of $O_2 \cdot cm^{-2} \cdot hr^{-1}$); light compensation intensity, I_c, (750 ± 131 versus 212 ± 16 $\mu E \cdot m^{-2} \cdot s^{-1}$); the photosynthesis/irradiance curve break point, I_k, (851 ± 191 versus 511 ± 42 $\mu E \cdot m^{-2} \cdot s^{-1}$); and the initial slope, α, (0.011 ± 0.018 versus 0.071 ± 0.018 μg of $O_2 \cdot cm^{-2} \cdot hr^{-1} \cdot \mu E^{-1} \cdot m^2 \cdot s^1$). The integrated P/R ratios (0.51 ± 0.09 versus 1.12 ± 0.13) are also significantly different ($P < 0.05$).

Our $\delta^{18}O$ data corroborate these observations that bleaching occurred during the warmest period of the year. Alternatively, Hoegh-Guldberg and Smith (26) showed that high light intensity causes an apparent bleaching of corals, but unlike the conditions reported here, this high-irradiance bleaching involved a reduction in the mass of chlorophyll a per cell and not a reduction in the number of zooxanthellae per unit area. Ultraviolet light (2, 23) also has been hypothesized to be a contributing factor. Current hypotheses hold that bleaching may result from a combination of factors, such as temperature and UV light (P. W. Glynn, personal communication) or temperature and oxygen toxicity (38).

Corals in the Florida Keys are on the northern geographic fringe of coral reef development in the New World and are susceptible to both high and low temperature extremes (47). Different species of coral have different susceptibilities to environmental stress. For instance, in the Atlantic, *Agaricia* and *Montastraea* are among the most sensitive to high temperatures (43). It is not clear why some coral colonies bleach and others, even of the same species at the same depth, do not (Fig. 1). Interspecific and/or strain differences between zooxanthellae of the genus *Symbiodinium* (44, 45) may also account for variable bleaching and recovery patterns observed for symbiotic reef invertebrates. Whether reactions to environmental conditions, such as bleaching, are due to physiological stresses on the coral animal, their zooxanthellae, or both, is not known.

High mortality of corals often follows bleaching episodes (3–9). We photographically monitored 24 areas at a 15-m depth on Carysfort Reef in the Key Largo National Marine Sanctuary, Florida, before (1984, 1985, and 1986) and after (1988) the bleaching event of 1987 (46). Despite the fact that every specimen of *A. lamarcki* bleached during 1987, no colony of this species died between 1984 and 1988. Ninety-

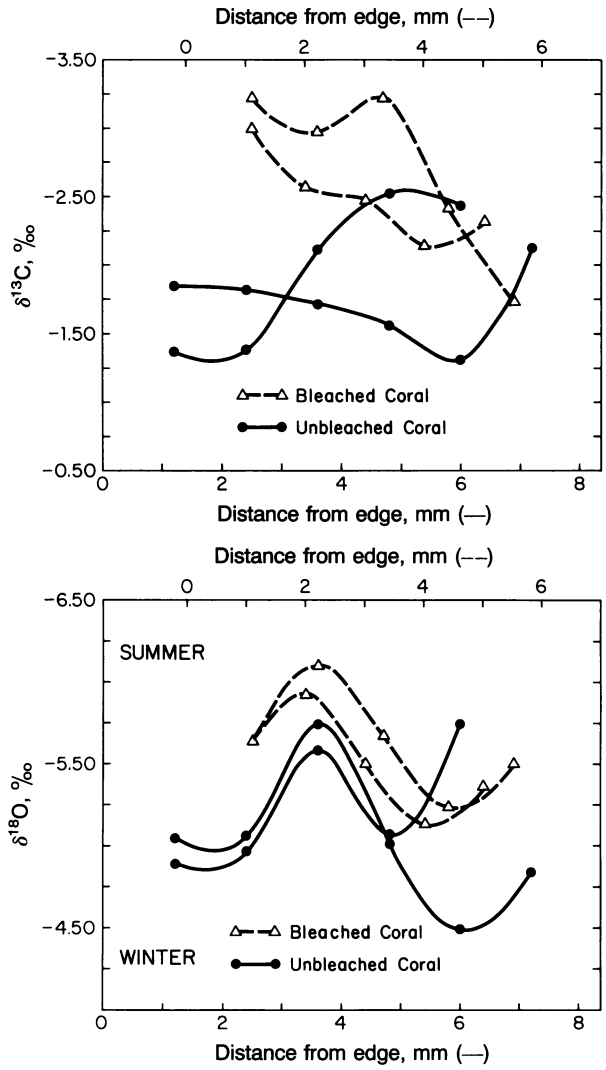

FIG. 3. Stable isotopic profile of $^{13}C/^{12}C$ and $^{18}O/^{16}O$ ratios from *M. annularis* across approximately 1 yr of skeletal growth. Scales for bleached coral (--) and unbleached coral (—) data are offset in order to align $\delta^{18}O$ peaks and facilitate comparison. (*Upper*) $\delta^{13}C$ value versus distance from the coral surface. Depleted $\delta^{13}C$ values are recorded in bleached corals (△) relative to unbleached corals (●) following the summer temperature peak. This reduction in the $\delta^{13}C$ value corresponds to the reduction in zooxanthellae density and productivity during bleaching (Table 1 and Fig. 1) and indicates that the preferential removal of $^{12}CO_2$ by photosynthesis has decreased (29, 30). (*Lower*) $\delta^{18}O$ values versus distance from coral surface. Depleted (more negative) isotope values indicate calcification in warmer waters (summer); positive isotope values indicate calcification in cooler waters (winter). A reduction or cessation of skeletal calcification is evident in bleached corals (△) shortly after the peak summer temperature. Note that resolution of the sampling technique cannot distinguish between reduction and cessation of calcification at the skeletal surface. In contrast, unbleached corals (●) continued to grow, as evidenced by the deposition of aragonite with enriched (more positive) $\delta^{18}O$ values, indicative of calcification in cooler water. Cleaned *M. annularis* skeletons were cut along the corallite axes into slabs 2–3 mm thick, and x-radiographed with a Philips Radifluor 360 instrument for 20 s at 60 kV to illuminate the coral bands. Sequential samples were collected at 1-mm intervals with a dental drill along 10-mm transects oriented in the direction of upward growth. Each isotopic value represents the mean of samples from three transects per colony. The data from two colonies is plotted. Aragonite samples were roasted *in vacuo* at 425°C for 1 hr and then treated with purified orthophosphoric acid at 60°C. The isotopic composition of the CO_2 gas generated by this reaction was determined on a VG SIRA-24 mass spectrometer (sensitivity to 50 μg of calcite CO_2 generated) and is presented in the δ (‰) notation relative to the PDB (Pee Dee belemnite) carbonate standard (std) where $\delta = [(R_{sample}/R_{std}) - 1] \times 10^3$ and R is the $^{13}C/^{12}C$ or $^{18}O/^{16}O$ ratio, respectively.

one percent of all *M. annularis* colonies bleached, but since the number of colonies lost (two) was the same as the number recruited, there was no net change in the population size of this species either during this 4-yr period. Although 29% and 65% of the surface area of *A. lamarcki* and *M. annularis*, respectively, bleached, tissue loss rate for both species did not change between 1984 and 1988.

The long-term ecological implications of coral bleaching are not evident at this time, but the changes in biomass demonstrated in Table 1 and the measured reduction in the contribution of carbon from zooxanthellae to meet animal metabolic requirements suggest an immediate reduction in nutrients for growth, metabolism, and the reproduction of bleached corals. On a larger scale, it is not clear whether coral bleaching is related to global warming trends. However, the widespread stress reactions exhibited in late 1987 indicate that tropical species like corals that are already at or near their physiological temperature limitation, may be highly susceptible to even marginally elevated temperatures.

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