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Coral Reefs

Reduced growth rate of *Montastrea annularis* following the 1987–1988 coral-bleaching event

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Abstract. *Montastrea annularis*, the major Caribbean reef building coral, was severely affected by the unprecedented 1987–1988 bleaching event. Most colonies on the fore reef were affected but few were bleached in the back reef. Skeletal growth rates of *M. annularis* populations were measured non-destructively in the field at Discovery Bay, Jamaica, from the peak of bleaching in Nov. 1987 until recovery was almost complete, in May 1988. Unbleached corals grew at normal rates. Partially bleached corals survived but skeletal growth ceased throughout this period.

Introduction

In Jamaica, colonies of *Montastrea annularis*, the predominant Caribbean reef building coral (Goreau 1959; Goreau and Goreau 1973), first began to lose their pigmentation ("bleach") in mid July, 1977 (R. Gates, personal communication). Around the same time, bleaching began to be noted elsewhere around the Caribbean (Williams et al. 1987). In early August, 1987, two weeks after the start of bleaching, colonies of normal and bleached *Montastrea annularis* growing in waters from 2 to 5 meters depth in adjacent fore-reef and back reef locations at Discovery Bay, Jamaica, were fitted with stainless steel nails ("growth monitors") implanted into uppermost inter-stomadeal surfaces, as part of a Caribbean-wide cooperative study of *M. annularis* growth rates (Goreau 1987; Macfarlane and Goreau 1988).

Histochemical comparison of bleached and normal corals from Discovery Bay by Dr. R. Hayes showed that bleached corals suffer a reduction in numbers of zooxanthellae and in their biochemical functioning (Hayes 1988). Bleaching, or expulsion of zooxanthellae, has been reported to result from a wide variety of stresses to the integrity of symbiosis between hermatypic corals and zooxanthellae (Trench 1986), such as unusually low salinity (Goreau 1964), high salinity (Reimer 1971), high temperature (Mayor 1918; Yonge and Nicholls 1931 a), low light levels (Yonge and Nicholls 1931 b), and high light levels (Dustan 1982). Previous bleaching episodes have been localized in areas with clearly identifiable stresses, such as sedimentation, hurricane runoff (Goreau 1964), or unusual temperatures (Yonge and Nicholls 1931 a; Glynn 1983). In contrast, the 1987–1988 event occured over most of the Caribbean reef province, affected an unprecedented number of corals and other reef organisms, occurred to depths greater than 30 m (the first time this has been recorded) and showed no obvious cause, although both temperature and light levels may be implicated (Williams et al. 1987). Recovery from bleaching took much longer than reported in previous cases, except for corals bleached by the El Niño phenomenon in the Pacific, which largely died (Glynn 1984).

Materials and methods

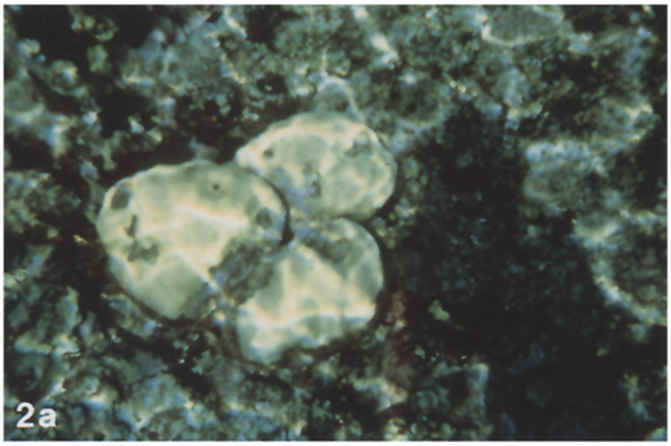
Coral populations studied were in 2–5 meters depth in adjacent 100 m by 25 m back-reef and fore-reef quadrats oriented parallel to the reef crest, about 0.5 km north of the Discovery Bay Marine Laboratory, Jamaica. No bleached colonies were found in the back-reef quadrat, although large *Montastrea annularis* were abundant. In the fore-reef tract most colonies had bleached by November. This is not reflected in the proportion of corals studied because in August the phenomenon had just begun and we were not yet aware of its occurrence in other parts of the Caribbean, so we deliberately chose to under-represent bleached colonies in order to avoid possible further stress to what looked like dying corals.

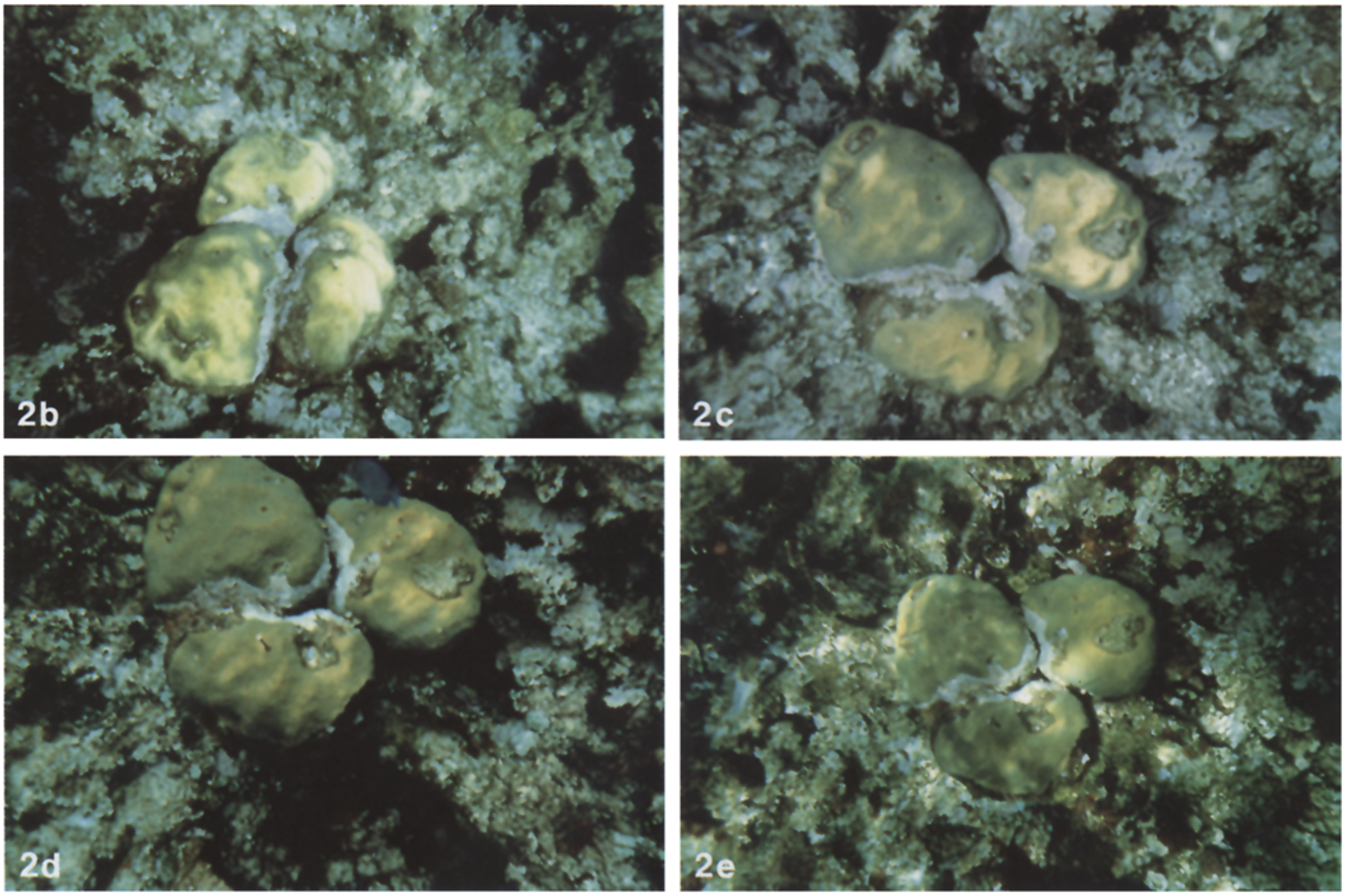
Montastrea annularis is highly variable in pigmentation, with light brown, yellow-brown, green-brown, dark brown, grey, and bluish colonies common. Most are uniform in color but some have clearly demarcated color differences within different parts of the same colony. Populations of zooxanthellae from Discovery Bay *Montastrea annularis* are also known to be extremely variable in morphology and in their photosynthetic response to light (Trench personal communication; Trench and Blank 1987; Sandeman 1988). Bleaching was largely confined to the most abundant light brown and yellow-brown colonies, and relatively uncommon in corals with dark pigmentation, whether brown, green, or blue-grey. Because we deliberately undersampled bleached colonies, we oversampled darker colonies, especially in the fore-reef.

Growth monitors were inserted between polyps on the upper surface of colonies in early August, 1987 (Fig. 1). Monitors are non

Fig. 1. Insertion of growth monitors into large coral head. Note partially bleached patch in foreground. Scale indicated by hand. Photograph August, 1987, by Dr. Peter D. Goreau

Fig. 2 a–e. Time series photographs of *Montastrea annularis* colonies showing their recovery from bleaching. **a** 1 December 1987; **b** 21 January 1988; **c** 21 February 1988; **d** 9 April 1988; **e** 16 May 1988. This coral cluster is about one meter across. Photographs by A. H. Macfarlane





corroding stainless steel nails, polished and annealed to a sharply tapered conical point on a bench grinder while held in a cylindrical sleeve permitting free rotation during sharpening. Sharpened monitors have had 100% implantation success, in contrast to some of the first nails deployed which were not sharpened. About a third of unsharpened nails were later found loose, apparently because the relatively blunt nail point shattered coral aragonite crystals during implantation. Measurements on loose nails were tabulated, and while not included in the data discussed in this paper, they gave values (0.00119 ± 0.00139 cm/day for 10 normal corals, and 0.00057 ± 0.00058 for 3 bleached corals) statistically similar to those of well emplaced nails, as determined by Student's *t*-test.

Growth monitors were left in place undisturbed for three months until we could return to begin measurements in November,

1987. No damage to coral tissue around growth monitors could be seen. Monitors in back reef sites acquired up to a centimeter of filamentous algae, primarily *Ceramium sp.*, if not kept clean by periodic gentle rubbing between thumb and forefinger. Clean monitors showed no signs of growth alteration around their base, but a few monitors, which were deliberately left fouled with filamentous algae had a half centimeter deep conical growth depression around the base of the monitor by May, 1988. Fouling by filamentous algae was not common on fore-reef monitors. Monitors are read periodically by measuring the height of the flat head above the surface of the coral tissue, using a ruler glued to the back of a small test tube, which is inverted over the monitor, and through which the ruler is viewed. Measurement errors due to parallax make the minimal detectable change about one millimeter, or around 0.00055 cm/day over the period of study.

Results

Bleaching appeared in irregular patches, being often, but not invariably, on upper surfaces of the coral, as noted elsewhere around the Caribbean (Williams et al. 1987; Goenaga 1988; Goenaga et al., in press). Corals which were partially shaded by other corals were bleached on fully exposed surfaces but not where shaded, suggesting that light exposure played a role in the bleaching phenomenon. Complete bleaching was not seen in *Montastrea annularis* at Discovery Bay. Intensity of pigment loss varied, but all corals retained some low residual level of color in bleached areas and most affected colonies maintained significant fractions of their surface, often around half, with normal pigmentation. All partially bleached corals had monitors emplaced in bleached upper surfaces. No whole colony in the studied populations died: in only one case was a nail implanted in coral tissue replaced by a filamentous green algal mat on dead skeleton, where bleached peripheral tissue had died back about 2 cm. The number of corals bleached increased steadily until November, when most *Montastrea annularis* heads on the fore reef were bleached. In contrast, bleaching was so scarce in the back reef that no bleached colonies could be found in the sample quadrat, although a few were seen elsewhere in the Discovery Bay back reef. Bleached tissue gradually regained pigmentation (Fig. 2), uniformly within individual patches, but at different rates from coral to coral, until by May 1988 recovery was nearly complete, and less than 5% of affected corals showed faint residual traces of bleaching.

Growth rates of *Montastrea annularis* colonies, bleached and unbleached, in fore-reef and in back-reef areas, from November 1987 to May 1988, are shown in Fig. 3. Normal colonies in the back reef grew a mean rate (± standard deviation) of 0.00167±0.00103 cm/day ($n=11$), a rate close to the 6±3 mm/annum normal for the area (Dodge et al. 1974; Goreau 1977; Teal 1986, those measurements consisting of light brown colonies). On the fore reef normal colonies grew 0.00149±0.00083 cm/day ($n=14$), a rate very similar to that of normal colonies in the back reef. Bleached corals on the fore-reef grew at a rate of 0.00057±0.00084 cm/day ($n=7$), only about one third as much as normal unbleached corals. Much of the variability of bleached coral population growth is due to a single colony, which appeared pale throughout the period, but which grew at four times the mean rate of the entire bleached population. All the rest had growth rates at or below the minimum detectable amount over the period of observation, 0.00055 cm/day. If that outlying coral had been a normal, but light-colored morph, mistakenly identified as bleached, and is deleted from the bleached sample population as a statistical outlier, the mean growth rate of the bleached corals was only 0.00031±0.00050 cm/day, about one fifth the average of unbleached corals, and below the minimum detectable growth limit. Student's t-test showed that normal fore-reef corals grew at rates statistically indistiguishable from normal back-reef corals (with probability of belonging to populations with the same mean growth rate is 0.623) but very significantly higher than bleached corals (probability of the null hypothesis that they belong to populations with the same mean growth rate is 0.005).

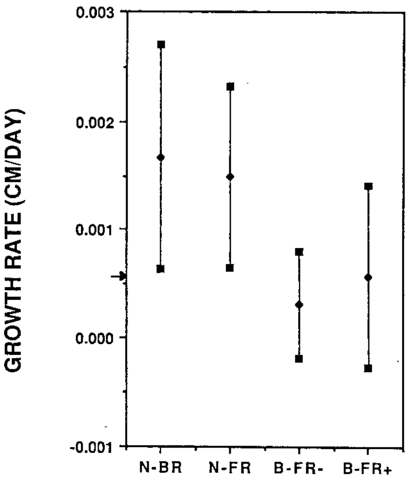


Fig. 3. Mean growth rates plus or minus standard deviations for normal and bleached *Montastrea annularis* populations in back-reef and fore-reef habitats. The population marked + includes one outlier with high growth, which has been removed in the population marked –, as explained in the text. The precision and minimal detectable growth are about 0.00055 cm/day (arrow). N = normal; B = bleached; FR = fore-reef; BR = back-reef

Discussion

Corals depend on translocation of photosynthetic products from zooxanthellae for much of their food (Goreau and Goreau 1960; Trench 1986), and skeletal calcification rates are proportional to photosynthesis (Goreau and Goreau 1959). None of the corals in the populations studied were bleached completely transparent, as were some other less common coral species, and most contained some fraction of tissue with normally pigmented growth. By May 1988 almost all had recovered pigmentation to the point that they looked normal, yet during this half year period as bleached corals regained their pigmentation they practically ceased to accrete skeleton. The presence of normally colored zooxanthellae over much of the colonies over this interval suggests that the phenemenon causing bleaching may have inhibited calcification more than photosynthesis. Ongoing work will document growth rates after recovery, and study of skeletal banding will determine if bleached and normal portions of the same coral showed differential growth.

Back-reef corals, being exposed to higher turbidity from resuspended sediments might be expected to grow more slowly than fore-reef corals (Dodge et al. 1974), but this effect may be countered by nutrients supplied by back-reef groundwater springs at Western Discovery Bay (D'Elia et al. 1981). Corals in the back reef experience greater extremes in temperature than fore reef corals, being exposed to cold groundwater and hot slack water depending on the degree of sunshine and groundwater discharge. Water temperatures were measured in back reef waters during the period of study, decreasing from 29.0 to 25.8 degrees centigrade, in the normal range for this time of year. The time course of bleaching roughly followed the water temperature curve, which peaked in October–November. Considerably higher temperatures, up to 33 degrees, have been measured in the Discovery Bay back reef in the past (Laughlin 1985; Edmunds 1986), without corals bleaching. The spatial patterns of bleaching fit a generalized stress to which back-reef and darker-pigmented corals may have greater tolerance than lighter colonies on the fore-reef. The wide variety in morphology, photosynthetic rates and physiological responses of zooxanthellae isolated from *Montastrea annularis* (Trench and Blank 1987; Sandeman 1988) may have played a role in causing this pattern if zooxanthellae populations in back-reef and dark corals are more tolerant of higher temperatures and light exposure.

Reefs at Discovery Bay, and many places around the world, have changed in recent years from coral-dominated to macroalgal-dominated ecosystems (Lapointe 1989). Much of the Discovery Bay fore-reef, which had over 90% coral cover in 1981, has come to be dominated by the brown alga *Lobophora variegata* (Hughes et al. 1987; Morrison, in press). This alga was formerly so scarce that a two week search for it in the same area in 1973 was unsuccesful (J. Ramus, personal communication). These changes are due in part to 1. catastrophic destruction of reefs in 1980 by Hurricane Allen (Woodley et al. 1981), the second most intense ever recorded in the Caribbean (Kjerfve et al. 1986), 2. the epidemic die-off of dense populations of the herbivorous echnioid *Diadema antillarum* (Hughes et al. 1987; Morrison, in press), 3. alteration caused by a long history of severe overfishing (Munro 1983), 4. increasing eutrophication of the ecosystem by nutrients in submarine groundwater springs, affected by increasing population and land disturbance in the area, and 5. Hurricane Gilbert on September 12 1988 (the strongest ever measured in the Atlantic by the US National Weather Service) which largely stripped algal cover off the reef (they have already regrown extensively). The coral populations of this study were not markedly affected by Hurricane Gilbert: only one was toppled and a few monitors bent by flying debris. Growth rates in relation to both hurricanes will be discussed elsewhere (Goreau and Macfarlane, in preparation).

The virtual cessation of growth in the majority of colonies of the predominant fore-reef Caribbean coral following the 1987–1988 bleaching event can only have aided shifts to algal dominance caused by other factors. Should such bleaching events recur, in the face of increasing stress to reefs from sediment runoff, eutrophication, and overharvesting, and possible global ocean warming there could be significant consequences for the future health of Caribbean reefs, fisheries, and tourism.

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