Bleaching Induced Mortalities in Reef Corals from La Parguera, Puerto Rico: A Precursor of Change in the Community Structure of Coral Reefs?

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Abstract. – An unprecedented Caribbean bleaching event occurred in the summer of 1987. Preliminary observations revealed extensive tissue discoloration in zooxanthellate cnidarians at all depths of reef front environments at La Parguera, southwestern Puerto Rico. These included scleractinians, zoanthids, encrusting and arborescent octocorals, anemones, and hydrocorals. Zooxanthellate sponges were also affected. Recovery by all taxa, except for a few species within the Scleractinia, has been almost complete. A grid extending from the reef crest to the reef base on Cayo Enrique, La Parguera, was photographed before and after the event to determine the extent to which scleractinians had been affected.

Four months after the event: 1) 22% of the observed colonies ($n = 326$) were white or pale, 2) 44% of those that were white or pale showed tissue necrosis within or near the discolored tissues and, 3) bleaching was unrelated to depth. The large majority of the affected colonies (78%) belong to *Montastrea annularis*.

The data suggest that a light related phenomenon was responsible for the bleaching event. Over 60% of the affected colonies were bleached only on their upper surfaces. We hypothesize that exceptionally calm seas coupled with high water transparency and increased water temperature were a major factor causing the expulsion of zooxanthellae. It is possible that the 1987 coral bleaching event, together with other recent, large scale events, will modify the community structure of Caribbean coral reefs.

Resumen. – El el verano de 1987 registro un evento de blanqueamiento de corales sin precedentes en la región del Caribe. El fenómeno afectó múltiples especies de escleractinios, zoantideos, octocorales, anémonas e hidrocorales hermatípicos en los frontones arrecifales de La Parguera, Puerto Rico. También se afectaron esponjas con zooxantelas. Informamos sobre el blanqueamiento de corales en el verano de 1987 mediante el análisis de fotografías previas y posteriores al evento en un cuadrante permanente establecido en el Cayo Enrique, La Parguera.

Veintidós por ciento de las colonias observadas, pertenecientes a 7 especies, sufrieron blanqueamiento en parte o la totalidad de sus tejidos. *Montastrea annularis* fue la especie mas frecuentemente afectada y la mas lenta en recuperarse. Sesenta y nueve por ciento de las colonias afectadas se blanquearon sólo en las porciones superiores de sus tejidos. Observamos necrosis parcial en 51% de las colonias afectadas. No observamos correlaciones significativas entre la número de colonias blanqueadas y la profundidad ni entre el número de colonias necróticas y la profundidad.

Postulamos que condiciones adecuadas para una penetración máxima de la luz ultravioleta (alta transparencia del agua y condiciones de calma en el mar durante un período extenso), en conjunto con temperaturas por encima del promedio mensual, propiciaron éste fenómeno en Puerto Rico. Sugerimos que este blanqueamiento, unido a otros incidentes recientes también de gran alcance geográfico podrían ocasionar cambios en la estructura de los arrecifes coralinos caribeños.

Introduction

Scleractinian corals are major, modern reef builders and have been so repeatedly since Triassic times. Although coral reefs are generally known for their beauty and complexity, their socioeconomic importance (Salm and Clark, 1982; Goenaga, 1986) is well established and cannot be overemphasized.

Widespread coral bleaching occurred throughout the Caribbean from July to September, 1987 (Goenaga, 1987; Roberts, 1987; Williams et al., 1987). Bleaching or tissue discoloration is usually related to stress events and occurs when cnidarian hosts expel their dinoflagellate endosymbionts, *Symbiodinium* spp. (Trench and Blank, 1987) (commonly called zooxanthellae) and/or the zooxanthellae partially

lose their pigments (Hoegh-Guldberg and Smith, 1988). Zooxanthellae are important in the nutrition and calcification of many reef building corals (Muscatine, 1980; Cook, 1983) and tissues with reduced densities of zooxanthellae are, therefore, at a disadvantage and likely to die in some instances (e.g., Goenaga and Canals, 1979; Glynn, 1983).

Coral bleaching events are common in the Caribbean and have been attributed to lowered salinities by intense precipitation (Goreau, 1964; Goenaga and Canals, 1979), extreme low tides and raised temperatures (Jokiel and Coles, 1977; Jaap, 1979; Glynn, 1984), low temperatures (Walker et al., 1982) and increased water turbidity (Acevedo and Goenaga, 1986). Until 1982 these events affected few species in localized areas and were bathymetrically restricted. However, the 1987 summer event was unprecedented for several reasons: 1) bleaching occurred in species never reported to have bleached before, 2) bleaching was unrelated to depth (at least within 0-50 m), and 3) the event was widespread throughout the Caribbean (Williams et al., 1987).

Coral bleaching at Cayo Enrique in La Parguera was quantified by analyses of sequential photographs on a permanent grid. The frequency of bleaching among species and with depth is reported here. Only scleractinians and a hydrocoral are included although bleached gorgonians, actiniarians, zoanthids and poriferans were also observed.

METHODS

A 10 by 15 m grid, subdivided into 1 m^2 quadrats, and extending from the reef crest to the reef base of Cayo Enrique, La Parguera, Puerto Rico (Fig. 1; Vicente, 1987; Goenaga, 1988) was monitored for the last five years. Quadrats within the grid were photographed before and after the 1987 summer bleaching event. Quadrats from both dates were projected side by side and the number of bleached and unbleached non-cryptic corals was noted. Physiological isolates derived asexually or through partial mortality were considered as individual colonies in this study. Therefore, several physiological isolates may belong

to a single original sexual recruit. Necrosis, determined by epibenthic growth, was counted as resulting from bleaching only if it was not detected in photographs taken before the bleaching event and only if it was associated with bleached colonies. Photographs with poor resolution were not included in the analyses. It is possible that some colonies bleached but recovered before the grid was photographed (January 1988) and were, therefore, were not counted as affected. To determine whether the incidence of bleaching and necrosis were related to depth, the number of colonies with these conditions was divided by the total number of colonies (of affected species) on each transect and linear regression analyses were applied.

RESULTS

Three hundred twenty-six colonies, belonging to 13 species of scleractinians and one species of hydrocoral (*Millepora complanata* Lamarck), were observed within the study area. Of these, 72 colonies (227. of the total) belonging to seven species had at least some portions of their tissues bleached (Table 1). Bleached colonies of *Agaricia agaricites* (Linnaeus) and *Mycetophyllia lamarckiana* Milne Edwards and Haime occurred outside the study area, near the base of the reef. Most affected colonies of *Siderastrea siderea* (Ellis and Solander) had an iridescent blue color. All other corals bleached white, although not always uniformly over their surface. Histological examination of some bleached corals showed that zooxanthellae were present in reduced quantities within endodermal tissues.

Frequency of bleaching did not occur independently among species ($x^2 = 178.0$; $P < 0.0001$). The Chi square test was performed only for those species with more than 5 bleached colonies. Colonies of *Montastrea annularis* (Ellis and Solander) were the most frequently bleached (Table 1).

Necrosis occurred in 51% ($n = 37$) of all colonies that bleached. Of these, 81% belonged to *M. annularis*. There were two incidents of necrotic tissues on portions of colonies that were not bleached.
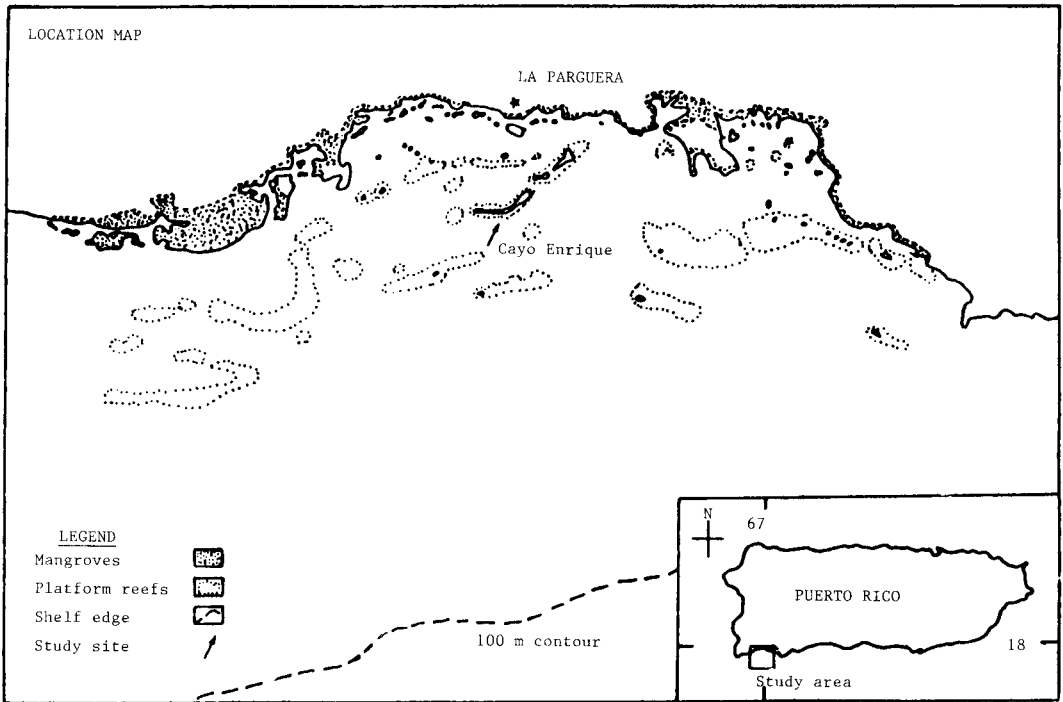
FIG. 1. Location of La Parguera, southwestern Puerto Rico. Arrow shows Cayo Enrique, the study site.

Forty-six colonies (69% of the bleached colonies) bleached only on their upper surfaces (excluding *Acropora palmata* (Lamarck) and *A. cervicornis* (Lamarck) which are branched and, therefore, not easily compared to the other species). Some boulder-like colonies bleached only on the top portions of the corallum (Fig. 2D). Some irregular or corrugated colonies bleached on the top portions of the irregularities (i.e., portions approximately parallel to the water surface), even when these did not coincide with the top of the corallum (Fig. 2C). Other colonies had all their surfaces bleached and only 5% were bleached only on their lateral surfaces.

Total number of bleached and necrotic colonies are presented by transect number in Fig. 3. Transect "A" is 2.7 m deep; transect "O" is deepest at 7.3 m. Depth did not appear to influence bleaching (linear regression; df = 14; $r^2 = 0.11$; $P = 0.20$) or

TABLE 1. Number of colonies from all depths sampled that were bleached or necrotic and bleached on their upper surfaces at the Enrique study site. Only those colonies whose portions became necrotic after bleaching are included in the Necrotic category.

| Species	Not bleached	Bleached	Necrotic	Bleached upper sfc.	Total
Montastrea annularis (Ellis and Solander)	130	57	30	41	187
Porites astreoides Lamarck	27	3	1	3	30
Colpophyllia natans (Houttuyn)	25	3	2	1	28
Siderastrea siderea (Ellis and Solander)	13	1	1	0	14
Diploria labyrhinthiformis (Linnaeus)	1	3	2	1	4
Acropora palmata (Lamarck)	5	4	1	—	9
Acropora cervicornis (Lamarck)	7	1	0	—	8
Total	208	72	37	46	280
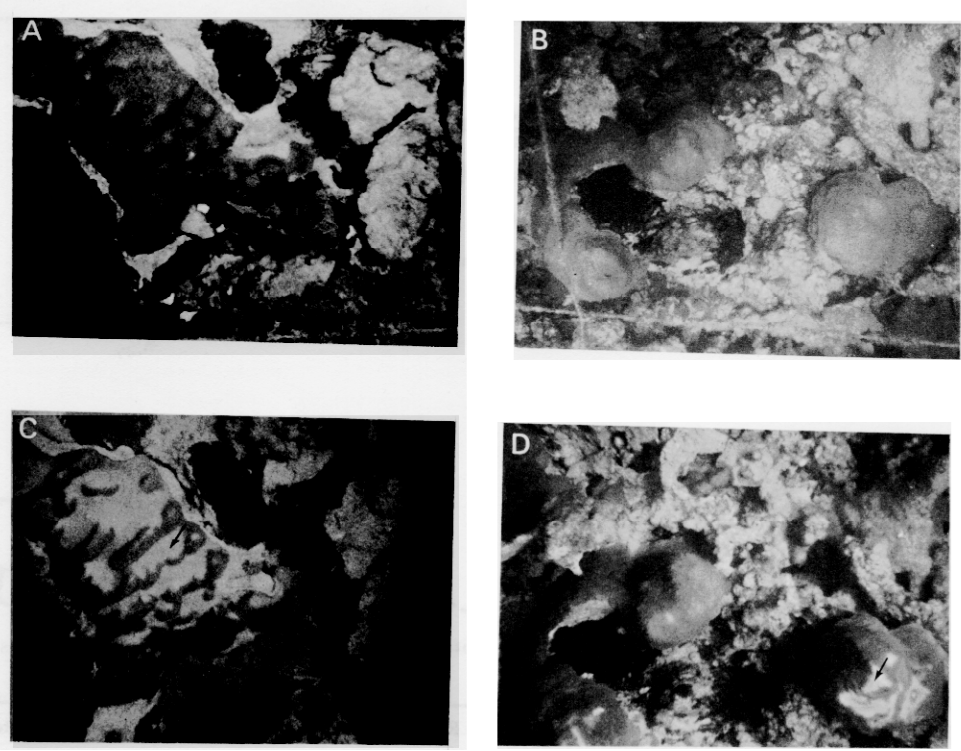
FIG. 2. Colonies of *Montastrea annularis* before (A and B) and after (C and D) the bleaching event. Colony shown in C (top view) is bleached on its upper tissues (arrow). Colony shown in D (lateral view) has an irregular shape and is bleached (arrow) on the top portions of its tissues. Colony in upper part of A is about 10 cm in diameter. Colony in the center of B is about 20 cm long.

necrosis (linear regression; df = 14; $r^2 = 0.28$; $P = 0.52$).

DISCUSSION

Environmental conditions during the bleaching event varied among localities

FIG. 3. Total number of colonies from all species, bleached colonies and necrotic colonies observed on transects A-O.

within the Caribbean. In Puerto Rico it coincided with extended periods of calm seas, high water transparency, clear skies and slightly elevated temperatures. Over half of the affected colonies at our study site were bleached only at their upper surfaces suggesting that a light related phenomenon played an important role. We propose that increased penetration of solar radiation, related to doldrum conditions, and increased water temperature were the causal agents involved in the bleaching of corals in Puerto Rico in 1987. High levels of solar radiation induce the formation of toxic superoxide anions above levels normally encountered (Sandeman, personal communication). Harriott (1985) proposed that UV radiation explained the 1982 mass coral bleachings in the Great Barrier Reef, Australia. Ultraviolet (UV) radiation penetrates ocean water nearly as well as visible light in the absence of dissolved and suspended organic matter (Jerlov, 1950; Smith
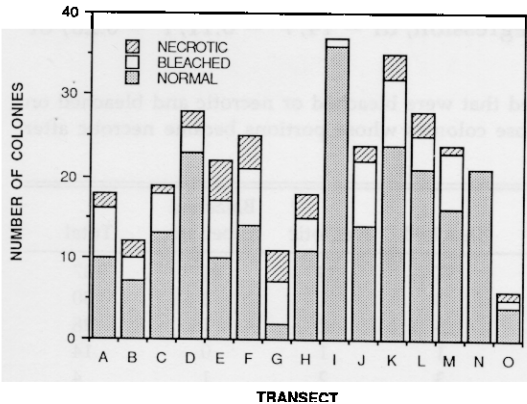
and Baker, 1979) and, by itself, is also known to induce the formation of toxic superoxide anions (Sandeman, pers. comm.). Increased levels of UV radiation can result from depletion of stratospheric ozone (Luther et al., 1982) or, simply, from appropriate oceanographic conditions, such as those observed in the summer of 1987.

It is difficult to elucidate the relative importance of visible light and UV radiation as causal agents of the 1987 bleaching phenomenon. Nevertheless, controlled experiments have shown that levels of UV radiation normally encountered in the field, and not visible light, result in the destruction of photopigments and tissue bleaching of zooxanthellae from "shade-loving" anemones (Jokiel and York, 1982) and of other marine algae (Steemann Nielsen, 1964; Wood, 1987). It remains to be shown, however, if other species of *Symbiodinium* behave similarly.

Some zooxanthellate reef corals are known to produce a UV absorbing pigment, S-320, in response to UV light (Jokiel and York, 1982). The intensity of UV radiation diminishes with increasing depth and, presumably, less of this protective pigment is required at greater depths. Deeper water corals, therefore, may be susceptible to increases in UV radiation despite attenuation of the latter in the water column.

Sandeman (1988) suggested that elevated summer temperatures could have contributed to the 1987 coral bleaching. In Puerto Rico, monthly mean sea surface temperatures for 1987, recorded at the Magueyes Island tide station during the time of the bleaching were 0.8°C higher than long term averages. However, it is unlikely that temperature alone was the causal factor at La Parguera since a higher temperature anomaly during May 1987 (1.5°C above long term averages) did not result in coral bleaching (Armstrong and Goenaga, unpublished data). The absolute temperature for September was about 0.1°C higher than that for May. Elsewhere, temperature or other factors causing stress to reef corals may have contributed to their bleaching (Causey, 1987).

Our data show that recovery is indepen-

dent of depth if one assumes that the effect was initially uniform. Unquantified personal observations three weeks after the onset of the event suggest that bleaching was uniform among depths on Cayo Enrique. However, it is possible that there was an initial depth-dependent effect obscured by rapid recovery of some bleached colonies.

Intraspecific and interspecific variation in the mode of bleaching and in recovery rates among corals may be related to physiological differences among species of zooxanthellae (cf. Trench and Blank, 1987; Sandeman, personal communication). Zooxanthellate individuals of *M. annularis,* for example, have high relative tissue regeneration capabilities (Bak et al., 1977; Goenaga, 1988). However, colonies of this species bleached and became necrotic more frequently and recovered more slowly than colonies of other species. Grazing scarids commonly inflict tissue injuries to corals at our study site (personal observations) making healing capability an important asset.

Further massive bleaching events may have long term implications for the ecology of coral reefs. Goreau and MacFarlane (personal communication; MacFarlane and Goreau, 1988) recently measured reduced growth rates (i.e., linear extension) in bleached, Jamaican *M. annularis.* Reductions in growth may impair the competitive ability of corals. *M. annularis,* a major Caribbean reef builder (Goreau, 1959; Goreau and Land, 1974; Macyntire, pers. comm.), was the most frequently bleached species at 24 sites in or adjacent to the Caribbean in 1987 (Williams and Bunkley-Williams, 1988). This species, commonly considered spatially dominant, has limited sexual recruitment rates in reefs (Bak and Engel, 1979; Szmant, 1986). Recolonization, therefore, is likely to be hampered if sizable population declines occur.

Coral reef development depends on the survival, growth and reproduction of reef corals. Other regional events in combination with or in addition to the 1987 coral bleaching may induce changes in the reef communities through impact on coral life histories. The massive die off of *Diadema*

antillarum (Philippi) in 1984 (Lessios et al., 1983), an important grazer on coral reefs (Carpenter, 1981), has been associated with sustained macroalgal blooms (Hughes et al., 1987; Vicente, 1987). Macroalgal blooms are known to limit the recruitment and survival of juvenile reef corals (Sammarco, 1982) and to smother adult colonies (Hughes et al., 1987). Large algal biomass, in turn, leads to an increased number of algal propagules that will potentially recruit onto the reef. Necrotic tissues in corals, such as those related to bleaching, are swiftly colonized by fleshy and filamentous algae (pers. obs.). Coral surfaces colonized by algae do not recover easily. Recent deaths of old coral colonies on Puerto Rican reefs (Goenaga, 1988; Vicente, 1987) suggest that environmental changes, unprecedented during the last centuries, are occurring. It is possible that natural phenomena, such as the 1987 coral bleaching event, the 1984 epizootic in *Diadema,* together with nearshore eutrophication, increased runoff from uncontrolled land vegetation clearing (Evans et al., 1986) and rising industrial pollution may be paving the way for long term changes in coral reef community structure in the Caribbean.

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