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Coral Reefs

Bleaching of Reef Coelenterates in the San Blas Islands, Panama

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Abstract. Starting in June 1983, 25 species of hermatypic corals, gorgonians, hydrocorals, anemones and zoanthids in the San Blas Islands, Panama, began showing signs of a loss of colour leading in some cases to a white "bleached" appearance. Histologic examination of six coral species indicated that bleaching was associated with drastic reductions in the density of zooxanthellae and with the atrophy and necrosis of the animal tissue. The severity of the bleaching varied among species and many species were unaffected. The species most extensively affected were: *Agaricia* spp., which became completely bleached and frequently died; *Montastraea annularis* which bleached and continued to survive; and *Millepora* spp. which bleached white but quickly regained their colouration. Shallow reefs dominated by *Agaricia* spp. suffered the most extensive bleaching. At one site, Pico Feo, 99% of the *Agaricia* (32% of the living cover) was bleached. On fore reefs, which were dominated by *Agaricia* spp. and *M. annularis,* the proportion of *M. annularis* bleached ranged from 18 to 100% and that of *Agaricia* spp. from 30 to 53%. Transetcs at Sail Rock and House Reef were surveyed in August 1983 and January 1984. At those sites, 53% of the *Agaricia* cover died between August and January. The remaining living cover of *Agaricia* and of all other species exhibited normal colouration in January. Salinity and temperature were monitored every second day at 4 m depth between May 10 and August 28, 1983 at one of the localities. Bleaching was first observed within two weeks of a 2 °C rise in temperature which occurred in late May 1983. Temperatures remained at or above 31.5 °C for the following 3 weeks and were at or above 30 °C for an additional 4 weeks. The bleaching of corals in the San Blas was most likely due to those elevated temperatures.

Introduction

Numerous cases of coral bleaching, the whitening and on occasion death of corals, occurred throughout the Pacific and Caribbean during 1983. Glynn (1984) has documented these episodes on the Pacific and Caribbean coast of Panama and has collected reports demonstrating the widespread nature of these bleaching events. Throughout much of the Pacific the bleaching has been associated with coral mortality. On the Pacific coast of Panama, where the bleaching was first reported (Glynn 1983; Lessios et al. 1983), mortality was as great as 95% of the living coral cover (Glynn 1984). At localities in the Caribbean, mortality was less severe (Glynn 1984; Lasker et al. 1983). In this study we report on bleaching in the San Blas Islands on the Caribbean coast of Panama and document the incidence of bleaching, the histologic condition of corals during the bleaching event, and the long term effects of the bleaching.

Bleaching of hermatypic corals occurs when the coral loses its zooxanthellae. When expulsion of zooxanthellae is incomplete the colony may take on a mottled appearance and when complete the colony takes on a pale white colouration. Bleaching usually affects all or most of a colony, but cases of small areas becoming bleached have also been reported (Lasker 1979; Peters, unpublished observations). Bleaching of natural populations has been observed in association with elevated water temperatures (Shinn 1966; Jokiel and Coles 1974; Coles 1975; Jaap 1979) or reduced salinity (Goreau 1964). Field and laboratory treatments of starvation and/or darkness (Yonge and Nichols 1931; Franzisket 1970; Rogers 1979; Clayton and Lasker 1982) and long term treatment with photosynthetic inhibitors (personal observations) also induce bleaching. The long term effect of the bleaching differs depending on species and environmental conditions. Goreau (1964), Jaap (1979) and Lasker (1979) report normal feeding behavior among bleached corals and these authors as well as Shinn (1966) and Jokiel and Coles (1974) report the recovery of bleached corals following the return of normal environmental conditions. Some authors have reported loss of function among bleached corals (Yonge and Nichols 1931; Clayton and Lasker 1982) and prolonged exposure to thermal stress induces mortality in some corals (Jokiel and Coles 1974, 1977).

Methods

Bleaching on the Caribbean coast of Panama was first noted in June 1983. Observations of researchers at the San Blas field station of the Smithsonian Tropical Research Institute were used to ascertain which species were affected and when they first became bleached. Initial observations were restricted to reefs within several kilometers of the field station (Fig. 1).

Samples of several species of stony, soft and hydrocorals were collected by hammer and chisel from 2 m depth at House Reef on 3 July 1983. The samples were selected on the basis of apparently healthy (normal) colouring, or mottling of colour, or total bleaching. Corals were fixed in Helly's fixative (Barszcz and Yevich 1975) for 20 h rinsed in seawater for 24 h, and shipped to the University of Rhode Island in 70% undenatured ethanol. Tissues were decalcified in an EDTA-HCl solution (Yevich and Barszcz, in press), washed in running water for 24 h, and trimmed for processing by standard techniques (Peters et al. 1983; Yevich and Barszcz, in press). After embedding tissues in Paraplast, 6 µm sections were placed on clean glass slides and dried overnight in a 60 °C oven. The sections were then stained with Harris' hematoxylin and eosin, Heidenhain's aniline blue method for connective tissue (to show the mesoglea and condition of the zooxanthellae), and modified Movat's Pentachrome technique (for demonstrating the mucus secretory cells) (Luna 1968). Slides were examined with a Zeiss Photomicroscope III.

At House Reef 20 colonies each of *Agaricia* spp. (mostly *A. tenuifolia*), *Millepora alcicornis, Montastraea annularis, Porites astreoides* and *P. furcata* were labelled with aluminium tags on July 15, 1983. The *Agaricia, M. alcicornis* and *P. furcata* colonies used in the study formed clumps 20–50 cm in diameter. *P. astreoides* colonies were 10–30 cm in diameter. Biweekly observations of the colonies were conducted through August 23 and again on January 20, 1984. Colonies were scored on the basis of their colouration: 5, normal colouration; 4, some mottling or lightening evident; 3, less than 50% of the colony bleached white; 2, 50% –99% of the colony bleached white; 1, 100% of the colony bleached white. The extent of bleaching was estimated visually. All of the labelled colonies were at depths of 1–3 m. Temperature and salinity were measured every second day at 4 m depth at House Reef from May 10, 1983 through August 27, 1983.

Permanent 10 m long transects were established at both House Reef and Sail Rock. At House Reef six transects were established, following the depth contours at 1.0, 2.1, 2.9, 3.6, 4.3 and 5.6 m. At Sail Rock transects were established at 1.5, 4.6, 10.0 and 13.6 m. The positions of the transects were chosen by arbitrarily picking depths along a line which had previously been set between the reef crest and reef base. Transects were permanently marked at the 0, 5 and 10 m positions enabling resampling on three occasions, July 1983; August 1983 and January 1984. The extent of damage caused by bleaching was estimated by determining the species located under the transect line at 10 cm intervals and noting whether the coral was healthy, bleached, or recently dead.

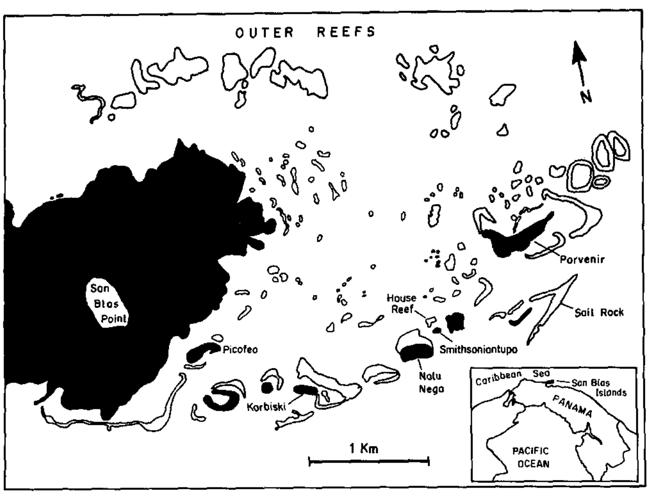

Fig. 1. Map of the San Blas Islands, Panama showing study sites. Two sites not shown Salar and the Hollandes are located 30 km to the east of the inset area. *Open areas* are reefs and *filled areas* islands. With the exception of House Reef names refer to island and their associated reef

Additional transects were examined during August 1983 on the reef-flats at Korbiski and Pico Feo (Fig. 1). Transects were also examined over a range of depths at Salar and the Hollandes. These two sites are located approximately 20 km east of the other sites. Data from Salar and the Hollandes were obtained by J. Morin (University of California, Los Angeles) and M.J. Shulman (Smithsonian Tropical Research Institute).

Data on bleaching from 270 additional corals on Sail Rock (Fig. 1), were made available by H. Lessios (Smithsonian Tropical Research Institute). The colonies which were examined monthly for an independent study were scored for the presence or absence of bleached tissue. The colonies were distributed between 0.5 and 15 m depth and included specimens of *Colpophyllia natans, Diploria strigosa, Montastraea annularis, M. cavernosa* and *Porites astreoides.*

Results

The first sign of bleaching in a colony was usually the appearance of an area of lighter and/or mottled colouration (Fig. 2). The dates species were first observed in this condition are presented in Table 1. *Millepora alcicornis* and *M. complanata* were the first species in which massive bleaching was evident. Bleaching was observed shortly thereafter in *Agaricia agaricites* and *A. tenuifolia.* In the following 4 weeks 21 additional species became bleached. No additional species were observed bleaching after July 11, 1983 although the severity of the bleaching within species increased through August. The manner in which colonies bleached was species specific. *Millepora* and *Agaricia* colonies first whitened at their tips and the

Table 1. Anthozoan species observed bleached in the San Blas Islands and date of first bleaching

Millepora alcicornis Linnaeus	Before June 15, 1983
Millepora complanata (Lamarck)	Before June 15, 1983
Agaricia agaricites (Linnaeus)	Before June 15, 1983
Agaricia tenuifolia Dana	Before June 15, 1983
Plexaunella dichotoma (Esper)	June 28
Eunicea sp.	June 28
Briareum asbestinum (Pallas)	June 30
Diploria labyrinthiformis (Linnaeus)	June 30
Diploria strigosa (Dana)	June 30
Favia fragum (Esper)	June 30
Montastraea annularis (Ellis and Solander)	June 30
Palythoa caribaeorum (Duchassaing and Michelotti)	June 30
Palythoa caribaeorum	
Plexaurella nutans (Duchassaing and Michelotti)	June 30
Porites astreoides Lamarck	June 30
Porites furcata Lamarck	June 30
Condylactus gigantea (Weinland)	July 3
Isophyllastrea rigida (Dana)	July 3
Montrastraea cavernosa (Linnaeus)[a]	July 3
Mussa angulosa (Pallas)	July 3
Stoicactus sp.	July 3
Acropora palmata (Lamarck)[a]	July 7
Siderastrea siderea (Ellis and Solander)	July 9
Acropora cervicornis (Lamarck)[a]	July 11
Colpophyllia natans (Houttuyn)	July 11
Erythropodium caribaeorum (Duchassaing and Michelotti)	July 11

[a] Single observation – may not have been same phenomenon as in other species

Fig. 2. Photograph of bleached corals at 4 m on Macaroon Reef, San Blas Islands. *Back right, Siderastrea* sp.; *left, Agaricia agaricites*. Note *Millepora* sp. in foreground with bleached tip and small unidentified bleached colony to its left

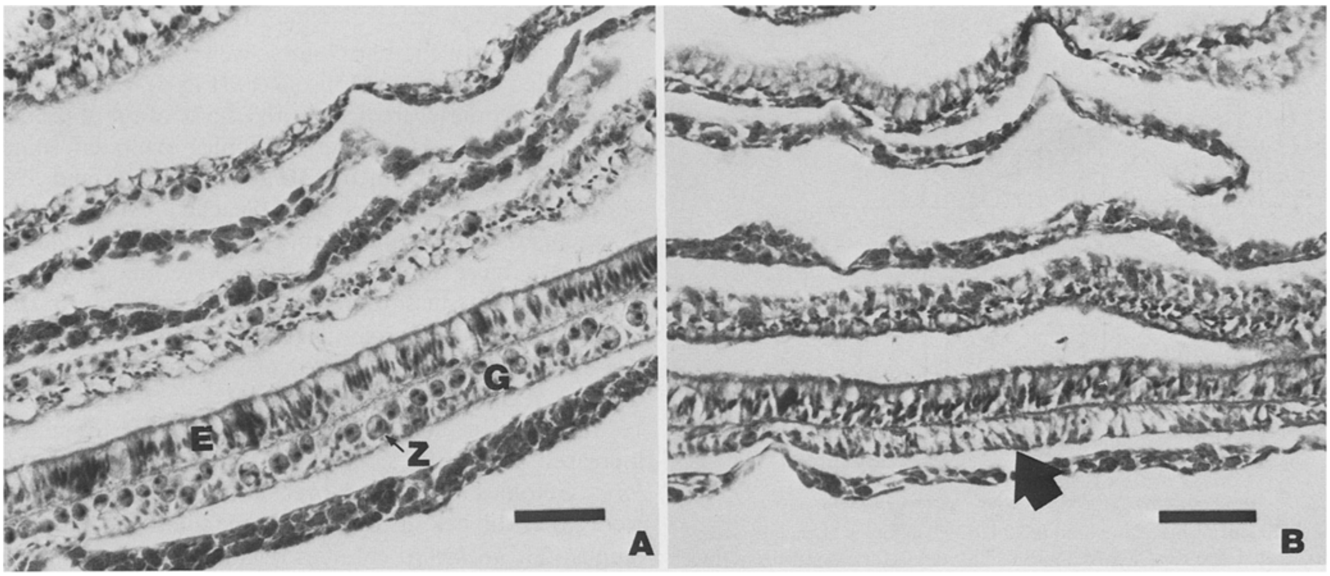

Fig. 3 A, B. Photomicrographs of tissue stained with hematoxylin and eosin. **A** Normal *Agaricia tenuifolia*. Note distinct cellular architecture with deep staining characteristics and zooxanthellae (*Z*) in the gastrodermis (*G*). *E*, mucosecretory epidermis; scale bar, 100 µm. **B** Bleached *A. tenuifolia*. Note atrophy and necrosis of tissue as well as loss of zooxanthellae

bleached area then extended toward the colony base. Some colonies uniformly paled, but most retained some pigmented tissue at the base of the colony. Subsequent tissue death was most common at the tips of the blades. Massive *M. annularis* colonies bleached first at the base of the colony and then the bleaching expanded up the face of the colony. Other species became mottled and bleached in a seemingly random pattern. The severity of bleaching on a colony did not appear to be affected by colony size, with the exception that very small colonies, several cm diameter, were more likely to lose all colouration.

Tissues of six species were examined histologically. One colony of *A. tenuifolia* which appeared normal was examined as well as tissues of *A. tenuifolia, A. agaricites, Favia fragum, M. annularis, Millepora* sp., and *Plexaurella nutans* which exhibited various stages of bleaching or were totally whitened from loss of zooxanthellae. The stony corals were compared to control specimens which were collected elsewhere in the Caribbean (Peters 1984).

Histologically, the healthy-appearing *Agaricia* exhibited normal cell structure and composition (Fig. 3A). Mucus secretory cells of the epidermis stained more intensively with hematoxylin, with the mucus gathered into distinct "blobs" in some regions, which differed from the usual "stringy" or clear appearance of the mucus cells. This may be associated with the occurrence of bleaching in the corals from this area although similar cells are found at lower density in *Agaricia* from other Caribbean sites. A colony of *Agaricia* which was mottled in appearance looked similar to the healthy colony, but contained greater numbers of deeply-staining mucus cells and also contained some degenerating zooxanthellae in the gastrodermis. Five other colonies of *Agaricia* in various stages of bleaching exhibited increased atrophy and necrosis of the tissues (Fig. 3B). Bleaching was accompanied by decreased numbers of zooxanthellae in the gastrodermis. Although a few zooxanthellae showed signs of degeneration, possibly due to autolysis of the coral cells, some apparently healthy zooxanthellae remained in all but the

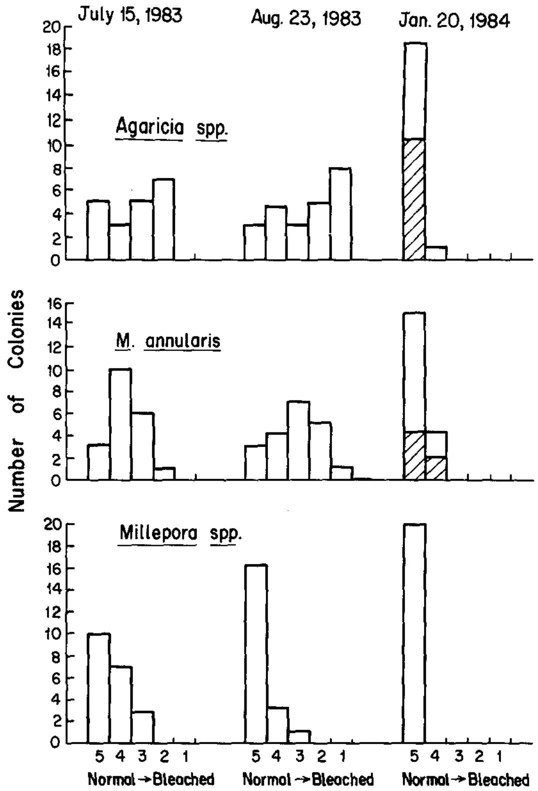

Fig. 4. Extent of bleaching among 20 labelled colonies of each of three species at House Reef. See Methods and Materials for a detailed description of the scale describing bleaching. *Hatched area* indicates colonies with newly dead, overgrown skeleton

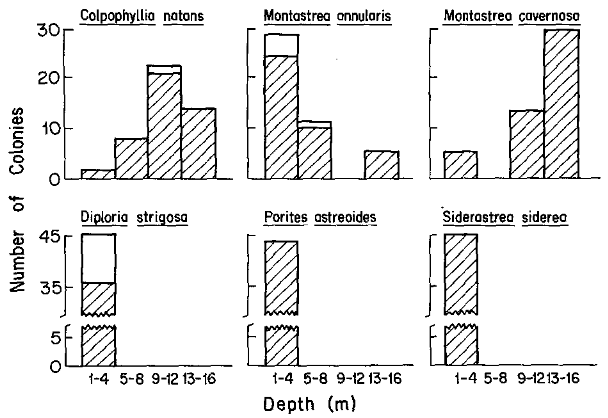

Fig. 5. Depth distributions of labelled corals at Sail Rock. Normal corals are indicated by hatched area and bleached by open areas

most severely necrotic colonies. All but one of the colonies showed signs of gonad development, but the overall condition of the colony was reflected in these tissues. One colony contained an ovoid granular basophilic body similar to those observed in acroporid corals afflicted with "white band disease", which has been noted in other colonies of *Agaricia* (Peters 1984).

The two specimens of *F. fragum* showed an increase in mucus secretory cells in the epidermis compared to controls, with loss of zooxanthellae and atrophy of the tissues. The most-bleached colony was necrotic. The mesoglea appeared swollen and those zooxanthellae remaining in the gastrodermis were degenerating. Ova, sperm and larvae in that colony were also necrotic but not so in the less-bleached sample. The *M. annularis* tissues also exhibited increased mucus secretion from the epidermis and loss of zooxanthellae. Controls were not available for the *Millepora* sp. and *P. nutans* for comparison. These species also showed signs of tissue atrophy and necrosis. Many zooxanthellae remained in the *Millepora* sample, but some were degenerating. No other bacteria or microorganisms were observed in any of the specimens.

The extent of the bleaching is well illustrated by the 100 marked colonies at House Reef (Fig. 4). On July 15, when the colonies were first scored, 75% of the *Agaricia* and 85% of the *M. annularis* colonies exhibited some bleaching. Only 50% of the *Millepora* colonies and 5% of the *P. furcata* colonies were bleached. None of the *Porites astreoides* colonies appeared bleached. Bleaching might not have shown in *Porites* since fine granular brown pigments in chromophore cells contribute to the colouration of this species. *Agaricia* colonies were most heavily affected in the degree of bleaching as well as number of colonies affected.

In the subsequent five weeks the extent of bleaching increased on affected colonies of *Agaricia* and *M. annularis*. Colonies which had been unaffected on July 15, were either still healthy or had become slightly mottled by August 23. *Millepora* colonies regained colouration between July 15 and August 23, and 80% appeared normal on August 23. All *Porites* colonies appeared normal on August 23.

Five months later most of the colonies had recovered from the bleaching. All 20 *Millepora* colonies were normally coloured on January 20, 1984, and there were no visible signs that they had been bleached. Only one of the *Agaricia* colonies exhibited any bleaching, a slightly mottled appearance, but 11 of the 20 *Agaricia* colonies had areas of dead and overgrown tissue which were previously absent. In two cases over 50% of the colony had died, and all 11 had tufts of algae growing on the tips of the blades. Of the 17 affected *M. annularis* colonies, 13 had recovered by January 20. Six of the colonies exhibited dead spots and 25% of one colony was overgrown by algae.

Labelled corals at Sail Rock exhibited less bleaching than those at House Reef (Fig. 5). Only 9% of the label-

Table 2. Percent cover and percent area bleached (bleached/total cover) at House Reef

Species	Date	Depth (m)						Mean
		1	2.1	2.9	3.6	4.3	5.6	
Agaricia spp.	7–83	19/41	22/53	22/46	26/63	25/60	12/59	21/54
	8–83	11/27	14/34	23/50	20/64	17/62	14/63	17/50
	1–84	3[a]/16	10[a]/27	7[a]/17	21[a]/44	10[a]/38+	7[a]/41	10/31
Millepora spp.	7–83	5/15	1/9	1/20	3/9	3/14	1/3	2/12
	8–83	0/24	0/17	1/23	0/8	0/18	0/4	0/16
	1–84	0/27	0/11	1[a]/26	0/4	0/11	0/2	0/14
Porites furcata	7–83	0/15	0/9	–	–	–	–	0/4
	8–83	0/6	0/7	0/1	–	–	–	0/2
	1–84	0/8	0/10	0/3	–	–	–	0/4
Other[b]	7–83	0/15	0/1	0/3	0/3	–	0/4	0/4
	8–83	0/8	–	–	–	0/3	0/1	0/2
	1–84	0/1	–	–	–	–	–	0/0

[a] Injured, overgrown or dead
[b] *Montastraea cavernosa, M. annularis, Briareum asbestinum*

led *M. annularis* colonies at Sail Rock bleached and at depths comparable to House Reef, 0-3 m, only 10% of the colonies bleached. As at House Reef none of the *P. astreoides* were bleached. Among the other species both *D. strigosa* and *C. natans* exhibited bleaching, 28 and 7% respectively. There was no clear relationship between depth and bleaching among the labelled colonies.

Data from the transects at Sail Rock and House Reef are contained in Tables 2 and 3. House Reef was dominated by *Agaricia* spp., primarily *A. tenuifolia*. *Agaricia* occupied an average of 54% of the transect points and 21% of the transect points were bleached in July 1983 (39% of the *Agaricia* points). Similar proportions of the *Agaricia* on the transects were bleached in August 1983. However, the percent cover of *Agaricia* on the 1.0 and 2.1 m transects was lower in August than July. This decrease may be attributable to variance in resampling the identical transect, but the continued decrease in percent cover evident in the January 1984 transects indicates that the percent cover declined. The January 1984 transects had lower *Agaricia* cover than the August transects (38% lower on average). Furthermore, many of the remaining colonies contained areas which had become overgrown by algae. None of the other important species at House Reef exhibited as strong or as persistent bleaching as *Agaricia*. *Millepora* spp. also bleached, but colonies were beginning to recover when the transect was examined in July. Only one point with bleached tissue was observed after July. No additional cases of bleaching were found on the transects at House Reef.

The coral fauna at Sail Rock was more diverse than at House and many more species were observed on the transect. The shallower transects (1.5 and 4.6 m) were dominated by *Agaricia* spp. Total living cover and *Agaricia* percent cover were both lower than at House Reef. In July, 34% of the agaricid cover was bleached, which is virtually identical to that observed at House Reef. The apparent proportion of the transect taken up by bleached *Agaricia* increased in August (18% to 27%) but the percent of bleached *Agaricia* and the total *Agaricia* cover declined by January 1984.

The transects at 10 and 13.4 m were both dominated by large heads of *Montastraea annularis*. As among the labelled corals bleaching was slow to develop among *M. annularis* heads on the transects. In July, 9% of the transect points contained bleached *M. annularis* and that increased to 17% in August. In January 1984, 5% of the transect area still contained bleached or mottled *M. annularis*. In August 77% of the area occupied by *M. annularis*

Table 3. Percent cover and percent area bleached (bleached/total cover) at Sail Rock

Species	Date	Depth (m)				Mean
		1.5	4.6	10.0	13.4	
Montastraea annularis	7–83	–	3/18	3/17	31/63	9/25
	8–83	–	2/3	8/20	57/64	17/22
	1–84	–	1/20	5/18	13/54	50/23
Agaricia spp.	7–83	8/20	6/27	2/2	2/3	5/13
	8–83	9/14	10/33	2/2	6/9	7/14
	1–84	3[a]/12	1/15	1/1	0/2	1/5
Millepora spp.	7–83	4/11	3/10	–	–	2/5
	8–83	0/7	2/9	–	–	1/4
	1–84	0/13	–	–	–	0/3
Porites spp.	7–83	3/4	0/5	0/7	–	1/4
	8–83	–	0/1	2/8	0/2	0/4
	1–84	1/3	3[a]/5	0/6	–	1/4
Colpophyllia natans	7–83	–	0/5	0/9	–	0/4
	8–83	–	0/3	0/8	0/2	0/3
	1–84	–	–	0/10	–	0/3
Acropora cervicornis	7–83	–	–	0/6	–	0/2
	8–83			0/2		0/1
	1–84	–	–	–	–	–
Other[b]	7–83	0/3	–	1/3	0/2	0/2
	8–83	0/5	–	0/3	3/13	1/5
	1–84	0/8	–	2/5	1/9	1/6

[a] Colonies with dead spots
[b] *Erythropodium caribaeorum, Montastraea cavernosa, Mycetophyllia* spp., *Dicocoenia* sp., *Stephanocoenia michelinii, Siderastrea siderea*

Table 4. Percent cover and percent area bleached (bleached/total) at four sites in the San Blas Islands

	Korbiski[a]	Pico Feo[a]	Salar[b]	Hollandes[c]
Agaricia agaricites and *A. tenuifolia*	18.2/20.2	26.4/26.8	12.4/23.8	8.8/29.4
Colpophyllia natans	2.8/2.8	–	0/4.4	0/4.4
Favia fragum	3.6/4.0	0/0.8	–	–
Millepora alcicornis and *M. complanata*	1.2/9.4	0/20.8	0.4/1.4	0.2/5.8
Montastraea annularis	–	–	8.4/8.4	1.0/5.6
Palythoa caribaeorum	4.2/4.2	–	–	–
Porites astreoides	0/26.8	0/7.6	0.8/1.6	0.2/4.2
Porites furcata	0.2/12.8	0/26.8	0.2/3.2	0/4.6
Siderastrea spp.	0.02/9.6	0/0.4	–	–
Other	0/4.2	–	0.4/2.8	0/4.2

[a] Mean of 5 reef-flat transects
[b] Mean of transects from 3, 6, 9, 12, and 15 m
[c] Mean of transects from 1.5, 3.0, 4.5, 6.0, and 7.5 m

was bleached. This is comparable to the 85% bleaching observed among the House Reef labelled colonies but is much greater than the 9% bleaching rate observed among the Sail Rock labelled colonies.

Millepora spp. only made up 5% of the Sail Rock transect, and in July 33% of that area was bleached. Some bleaching was also observed among *Porites furcata* and *Erythropodium caribaeorum*.

The data from Korbiski and Pico Feo were collected on reef flats (< 1 m depth). These areas were among the first to exhibit bleaching and already exhibited mortality when the transects were examined in August. As at House Reef *A. tenuifolia* dominated the fauna (Table 4) and bleaching was extremely high. The reefs at Salar and the Hollandes were more similar to those at Sail Rock. Like Sail Rock those reefs extended below 15 m, contained a diverse array of species and were dominated at depth by large *M. annularis* heads which exhibited variable degrees of bleaching.

Salinity and temperature data for House Reef are plotted in Fig. 6. Salinity varied as a function of local rains and no large fluctuations or trends are apparent during the 3 month period. Water temperature markedly increased at the end of May reaching 32 °C on June 4, 1983 and temperature remained at or above 31 °C until June 30. Temperatures of 31 °C were also recorded during much of July. Temperatures at 1 m were usually

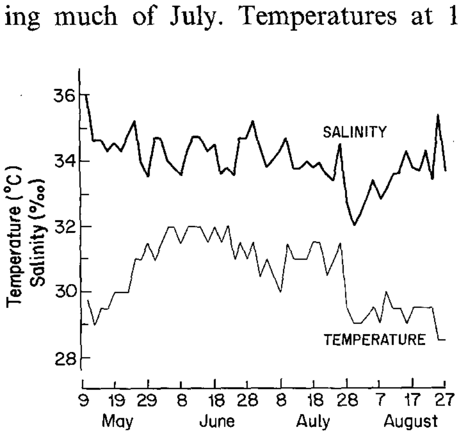

Fig. 6. Salinity and temperature at 4 m depth on House Reef during May to August 1983

within 0.5 °C of these at 4 m, but reef flat temperatures during low tides regularly reached 34 °C (M. A. Coffroth, unpublished data).

Discussion

Much of the coral bleaching which has been reported in the Pacific has been correlated with the extensive warming associated with the 1982–1983 El Niño (Glynn 1984). Although the Caribbean bleaching may not be related to the El Niño event, bleaching in both the Florida Keys and in the San Blas Islands correlate with unusually high water temperatures. Temperatures in the Florida Keys were reported as high as 34 °C (Jaap in Glynn 1984) and reached 32 °C at 4 m depth and 34 °C on reef flats in the San Blas.

The temperatures observed in the San Blas were well within the range of temperatures known to induce bleaching in corals. Healthy corals have been observed in waters of up to 34 °C (Kinsman 1964), but most studies indicate that temperatures above 31°–32 °C induce bleaching. Jokiel and Coles (1977) observed bleaching and mortality among Hawaiian corals maintained at 30 °C and Yamazato (1981, cited in Glynn 1984) reported bleaching at 30 °C. Sensitivity to thermal stress also is affected by local conditions to which corals are adapted. Coles et al. (1976) report that species which die at 32 °C in Hawaii survive at 34 °C in Enewetak. Marcus and Thorhaug (1981) report bleaching in Atlantic and Pacific *Porites* species at 31° and 32 °C respectively.

In the San Blas, May 1983 water temperatures steadily rose to a maximum of 32 °C in early June, and bleaching was first observed approximately one week later. The bleaching progressed through June and July. No additional bleaching was observed after August when temperatures dropped below 30 °C.

The presence of warm waters in the San Blas Islands during June and July 1983 was probably a consequence of both large scale water mass effects and local events. Glynn (1984) has summarized oceanographic data which reveal the presence in the western Caribbean of oceanic waters of 28°–29 °C during May and 29°–30 °C through

June and July. During 1982 temperatures were 1–2 °C lower. Additional warming probably occurred as a consequence of solar insolation in shallow, semi-restricted areas. This local warming was particularly evident on reef flats where daytime low tides on clear sunny days led to water temperatures of 34 °C. The importance of both large scale and local effects is suggested by the relationship between bleaching and depth reported both here and by Glynn (1984). In most localities bleaching was observed over a wide range of depths and bleached *Agaricia agaricites* colonies were observed as deep as 20 m. This suggests that the warming occurred over a wide depth range, a phenomenon which tidal flat heating would not induce. However, the most severe bleaching occurred on shallow tidal flats (Fig. 7) which suggests that the additional heating observed on reef flats enhanced the bleaching effect.

As has been reported in other studies (Shinn 1966; Jaap 1979) many of the bleached corals recovered, but some of the bleached corals in the San Blas died. Mortality, like bleaching, was both species and location specific. *Millepora* spp. were among the first species to bleach, but mortality was limited and colonies had already begun to recover in July when the first survey was conducted. Recovery was further advanced in August and in September only 0.6% of the *Millepora* colonies were bleached (Glynn 1984). All of the *Millepora* had recovered by January 1984. The recovery of *Millepora* in the Caribbean is in contrast to Eastern Pacific *Millepora* which experienced extensive mortality (Glynn 1984).

Agaricia agaricites and *A. tenuifolia* also exhibited extensive bleaching, but they were slow to recover and exhibited extensive mortality. Of the labelled colonies 60% exhibited mortality which ranged from a portion of the growing tip to 50% of the entire colony. At House Reef and Sail Rock 43% and 62%, respectively of the living *Agaricia* cover died. Almost all of the mortality occurred between August 1983 and January 1984. *M. annularis* colonies also exhibited extensive bleaching and some mortality. However, there were no observable changes in *M. annularis* living cover at Sail Rock, where large (> 1 m diameter) *M. annularis* are common.

Although many species became bleached during 1983, significant mortality only occurred among *Agaricia* colonies. This may be attributable to its abundance in the shallows of some reefs, which presumably experienced the warmest temperatures. The sensitivity of *Agaricia* may also relate to greater reliance on its zooxanthellal productivity than other species which may make *Agaricia* more susceptible to mortality due to the loss of its zooxanthellae. Primary productivity and coral growth rates are reduced at temperatures above 28 °C (Coles and Jokiel 1977; Highsmith 1979) coinciding with the loss of algal pigment in the zooxanthellae (Coles and Jokiel 1978). One species, *Pocillopora damicornis,* which does receive much of its energy from its zooxanthellae (Muscatine et al. 1981); loses biomass when maintained in the dark (Clayton and Lasker 1982); and suffered extremely

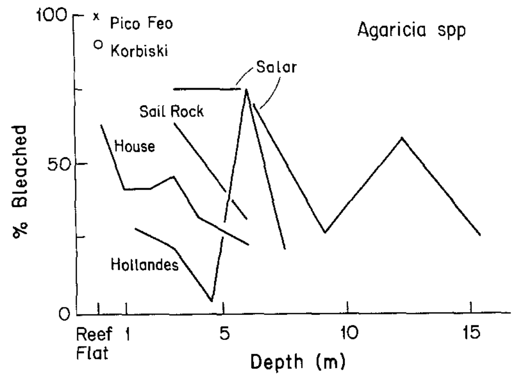

Fig. 7. Percent of *Agaricia agaricites* and *A. tenuifolia* living tissue exhibiting bleaching as a function of depth. Data from transects with less than 5% *Agaricia* cover (i.e. five points) are excluded

high mortality during the bleaching event in the Eastern Pacific (Glynn 1984). Alternatively, *Agaricia* may have a lower temperature limit than other genera. This latter hypothesis is supported by the observation that partially bleached colonies frequently contained healthy appearing zooxanthellae and necrotic animal tissue. This suggests that the initial damage occurred in the coral animal.

The bleaching and subsequent mortality observed in the San Blas Islands during 1983 was less severe than that reported from the Pacific (Glynn 1984). Similarly the scale of destruction was not as great as that of other natural disasters like hurricanes (Woodley et al. 1981). However, mortality in the San Blas Islands was measurable and significant. At Sail Rock there was a 20% decrease in living coral cover between July 1983 and January 1984, at House Reef living coral cover decreased 35%. Much attention has been given to the role of disturbance in structuring reef communities (Connell 1978, 1983). The bleaching event reported here suggests yet another natural process which can disturb reef communities and open up space for other species to utilize.

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