

Seawater temperature and sublethal coral bleaching in Jamaica

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Abstract. Permanent study sites were established at 6 m, 12 m and 18 m on the West Fore Reef at Discovery Bay, Jamaica. Colonies of *Montastrea annularis*, *Porites astreoides*, *Porites porites* and *Agaricia* spp. were assessed for presence and extent of bleached tissue at two month intervals between October 1986 and September 1987. In 98% of all corals exhibiting a bleaching response, less than 25% of the colony appeared pale. In the remaining 2%, more than 25% of the tissue appeared pale. *M. annularis*, *P. astreoides* and *Agaricia* spp. showed a significant positive correlation between the percent of colonies exhibiting a partial bleaching response and seawater temperature. There was no significant difference in the percentage of colonies bleached between the three depths. *M. annularis* and *Agaricia* spp. exhibited a significantly higher percentage of colonies bleached than *P. astreoides* and *P. porites*. For *M. annularis* 15% of coral colonies studied showed 1–2 cm² randomly scattered patches of pale tissue which remained constant throughout the study. The partial bleaching patterns observed in this study were never lethal and are considered, in part, to be a response to seasonal variations in seawater temperature.

Introduction

Zooxanthellae (*Symbiodinium microadriaticum*) are marine dinoflagellates found in symbiosis with reef building corals and other tropical invertebrates (Trench 1979). The symbionts are important primary producers (Muscatine 1980). A substantial portion of the host respiratory requirement is met by the translocation of photosynthetically fixed carbon from symbiont to host (Muscatine et al. 1983).

In the majority of coral species the presence of zooxanthellae in the gastrodermal tissue layer is considered to account for the external colouration of the host tissue. Under normal environmental conditions the algal population is maintained at a relatively constant level (Drew 1972) by a regulatory mechanism which is not clearly understood. The paling (bleaching) of hermatypic coral colouration is a well documented phenomenon (Glynn 1983, 1984; Lasker et al. 1984; Roberts 1987; Williams et al. 1987). Environmental parameters reported to elicit a bleaching response in reef corals include elevated seawater temperatures (Shinn 1966; Jokiel and Coles 1974; Glynn 1984; Lasker et al. 1984), high levels of ultraviolet radiation (Harriot 1984), reduced salinity (Goreau 1964; Egana and Disalvo 1982), photoperiod (Franzisket 1970), oil pollutants and oil dispersants (personal observation).

The loss of colouration is thought to be associated with an overall reduction in the algal population, involving either active expulsion of the algal symbionts by the host, or migration of the zooxanthellae out of the host tissues and into the surrounding seawater (Hoegh-Guldberg et al. 1987). The duration and scale of the environmental disturbance dictates the severity of the bleaching response and the ability of the coral to recover its colouration (Jaap 1979; Glynn 1984). In the field, bleaching of reef corals has been correlated with large scale temperature disturbances such as the 1982–83 El Nino warming event. Widespread coral bleaching and subsequent mortalities were reported in Panama in response to the highest elevation of equatorial waters this century (Glynn 1983, 1984). In 1987 reef organisms in the Caribbean lost their colouration, and this was attributed, in part, to prolonged exposure to seawater temperatures at the extreme of the normal range (Roberts 1987; Williams et al. 1987).

To date, bleaching in reef corals has only been documented when the response was dramatic and highly visible. The loss of colouration has been discussed with the prior assumption that all corals exhibiting a bleaching response were of normal colouration prior to the event. No

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information exists regarding the uniformity of reef coral colouration over an extended period of time, under normal environmental conditions. This study investigates the suggestion that paling and darkening of reef coral colouration is a dynamic seasonal phenomenon in response to annual variations in seawater temperature.

Materials and methods

Three study sites were established in September 1986 on the West Fore Reef at Discovery Bay, on the North coast of Jamaica. Thirty meter transects were laid along the 6 m, 12 m and 18 m depth contours on the Long Term Survey reef – LTS. A float was permanently secured at both ends of each transect to allow the measuring tape to be moved and replaced at a later date. The coral reef adjacent to each of these transects was initially surveyed using Loya's line transect method (Loya 1972). A series of 10 m transects were laid 0.5 m above and below the depth contour (6 transects per depth). Each coral colony that intersected the transect line was identified and the length of each intersect measured to the nearest centimeter. Total percent coral cover for each transect was calculated by dividing the sum of the coral intersect lengths by the total length of the transect. Relative percent cover was calculated using the total intersected length for a particular species divided by the total intersect lengths of all the species present along each transect.

Each 30 m transect was then surveyed using a continuous strip of 1 m² quadrats according to the Belt Quadrat method (Dodge et al. 1982). For each quadrat the area occupied by each coral colony and the species was mapped in situ onto waterproof paper (Wienberg 1981). No attempt was made to identify the closely related *Agaricia* species. The maps were traced onto acetate sheets in permanent ink and used to record, in situ, the degree of bleaching at the permanent study locations in October 1986. A coral was considered to be exhibiting a bleaching response if one or more areas of the colony were pale in comparison to the rest of the colony. Each coral colony was assigned to a category dependent on the area of pale coral tissue relative to the colony as a whole:

- I 1– 25% of the colony
- II 26– 50% of the colony
- III 51– 75% of the colony
- IV 76–100% of the colony
- V Dead

A coral colony without pale areas was not assigned to one of the above categories. The study sites were reassessed for presence and extent of bleaching in November 1986 and thereafter at two month intervals up to and including September 1987. Seawater temperature was taken every day at a depth of 3 m on the West fore reef at Discovery Bay from October 4th 1985 to October 1st 1987. Readings were obtained using a standard thermometer (encased in PVC pipe) accurate to 0.1° C.

Results

Total and relative coral cover

Total coral cover (%) and relative coral cover (%) for the four most abundant species of coral at 6 m, 12 m and 18 m depths are given in Table 1. Total coral cover decreased with depth from 14.42% at 6 m to 6.7% at 18 m. At 6 m and 12 m the reef was dominated by the massive coral *Montastrea annularis*. At the 18 m site plating *Agaricia* spp. and branching *Porites porites* were the most common species present. The four selected species represented over 50% of live coral cover at each depth.

Table 1. Total percent coral cover and relative percent cover of the 4 most abundant coral species at 6 m, 12 m, and 18 m depths on the Long Term Survey Reef at Discovery Bay, Jamaica, in September 1986. Values for relative (%) cover do not sum to 100% due to the exclusion of corals species not included in this analysis

		6 m	12 m	18 m
% Coral cover	\bar{x}	14.42	11.48	6.7
	SD	4.71	3.38	2.0
% Relative cover				
<i>Montastrea annularis</i>	\bar{x}	69.40	22.06	12.42
	SD	14.12	17.55	3.61
<i>Porites astreoides</i>	\bar{x}	9.91	9.38	7.14
	SD	2.44	6.9	3.45
<i>Porites porites</i>	\bar{x}	2.92	9.47	28.40
	SD	2.78	3.98	18.83
<i>Agaricia</i> spp.	\bar{x}	9.56	12.49	25.70
	SD	8.76	4.05	5.75

Patterns and severity of bleaching

The observed patterns of partial bleaching differed between the four species studied. *M. annularis* exhibited two distinct patterns. Coral colonies looked either "blotchy" in appearance with randomly scattered 1–2 cm² areas of pale tissue, or one small area (on the top or sides of the colony) appeared pale in comparison to the rest of the colony. *P. astreoides* showed an individual patch of pale tissue usually associated with the edge of the coral colony. In *Agaricia* spp. the ridges of colonies appeared white. Bleached tissue in *P. porites* was restricted to one or two branches at the top of the colony, all other branches showing normal colouration. Over the course of the study, 92% of coral colonies placed in categories were assigned to Category I (1–25% bleached). Corals assigned to Categories II and III (2%) were located in areas of heavy sedimentation and were periodically covered with sand. Corals exhibiting a 26–75% bleaching response were only encountered after a storm. Of the initially recorded corals, 6% died during the course of the study. Coral mortality was caused by storm damage and macroalgal overgrowth. For the purpose of the following analysis only corals assigned to Category I will be considered.

Temporal variations in coral bleaching

The percentages of four coral species exhibiting a Category I bleaching response for 6 m, 12 m and 18 m are shown in Fig. 1. For each species values obtained for each month were ranked in ascending order of magnitude and compared with one another using Friedman's Test and Non Parametric Comparison of Multiple Variables – NCMV (Zar 1974). Results are given in Table 2. All species studied showed significant ($P < 0.05$) variations in the percentage of coral colonies exhibiting a partial bleaching response over time. For example, values obtained for *M. annularis* in May were significantly differ-

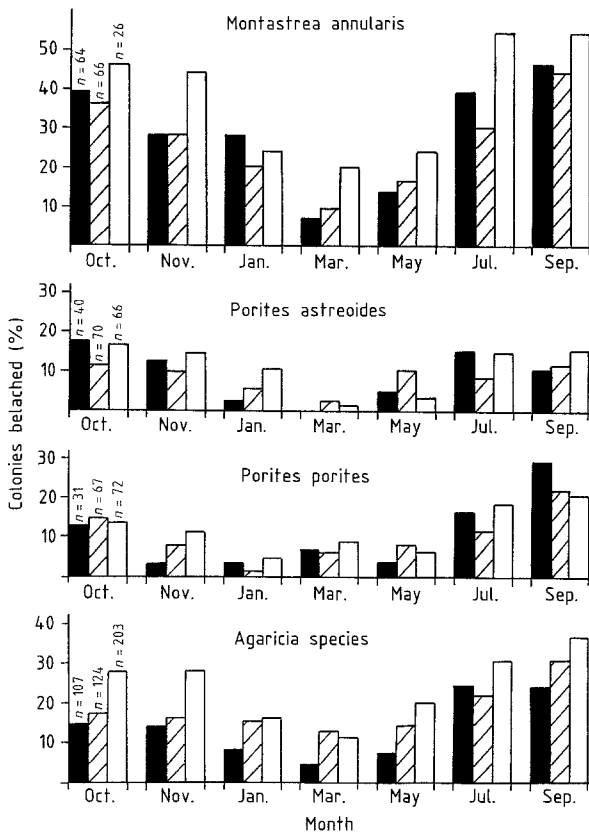


Fig. 1. Percentage of coral colonies of four species exhibiting a Category I bleaching response (see methods for criteria) at 6 m (■), 12 m ▨ and 18 m (□) from October 1986 to September 1987. *n* = The number of corals in the study for each species and depth

ent from those obtained in October, March, January, July and September. There was no significant difference between May and November values.

Comparison of species and depths

The percentage of colonies of *M. annularis*, *P. astreoides*, *P. porites* and *Agaricia* spp. exhibiting a Category I

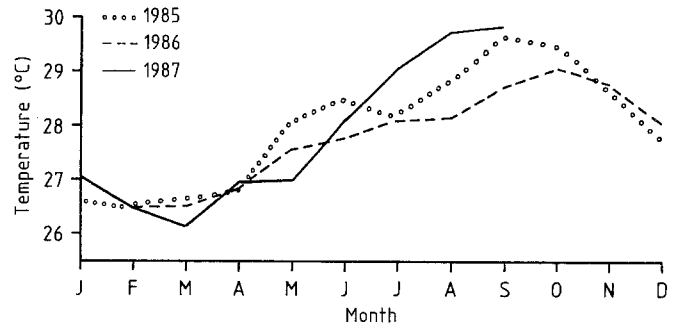


Fig. 2. Mean monthly seawater temperatures ($\pm 0.1^\circ\text{C}$) at 3 m depth on the West Fore Reef of Discovery Bay for 1985, 1986 and January to September 1987 (Data for January to September 1985, Edmunds and Davies 1989)

bleaching response were compared with one another for each depth over the study period. Values were analysed using the Kruskal-Wallis test and NCMV (Zar 1974). At 6 m, *M. annularis* showed a significantly higher percentage of colonies bleached than *P. astreoides*, *P. porites* and *Agaricia* spp. ($H = 8.48, P < 0.05$). At 12 m, *M. annularis* and *Agaricia* spp. gave significantly higher values than *P. astreoides* and *P. porites* ($H = 14.474, P < 0.01$). At 18 m, *M. annularis* gave a significantly higher result than *Agaricia* spp. ($H = 6.41, P < 0.05$) and both species exhibited significantly higher levels of bleaching when compared to *P. astreoides* and *P. porites* ($P < 0.01$). There was no significant difference in the percentage of each coral species exhibiting a Category I bleaching response between the three depths (NCMV, $P > 0.05$).

Partial bleaching and seawater temperature

Mean monthly seawater temperatures ($\pm 0.1^\circ\text{C}$) from January 1985 to September 1987 are given on Fig. 2 (January to September 1985, Edmunds and Davies 1989). Values obtained for the percentage of corals exhibiting a

Table 2. Comparison of the percent of Category I bleached corals for a given month with all other monthly values for each of 4 species. Months are ranked in ascending order

	Mar.	May	Jan.	Nov.	Oct.	Jul.	Sep.		Jan.	Nov.	Mar.	May	Oct.	Jul.	Sep.		
Mar.		+	+	+	+	+	+	Jan.		+	+	-	+	+	+		
May			+	-	+	+	+	Nov.			-	-	-	-	-		
Jan.				-	+	+	+	Mar.				-	+	+	+		
Nov.					+	+	+	May				+	+	+	+		
Oct.						-	-	Oct.					-	-	-		
Jul.		<i>Montastrea annularis</i>							Jul.		<i>Porites porites</i>						
Sep.								Sep.							+		
	Mar.	Jan.	May	Jul.	Nov.	Oct.	Sep.		Mar.	Jan.	May	Oct.	Nov.	Jul.	Sep.		
Mar.		+	+	+	-	+	+	Mar.		+	-	+	+	+	+		
Jan.			-	-	-	+	+	Jan.			-	+	-	+	+		
May				-	-	+	+	May				+	+	+	+		
Jul.					-	+	+	Oct.					-	-	+		
Nov.						+	+	Nov.						+	+		
Oct.		<i>Porites astreoides</i>							Jul.		<i>Agaricia</i> spp.						
Sep.								Sep.							-		

+ = Significantly different ($P < 0.05$); - = Not significantly different ($P > 0.05$)

Table 3. The correlation coefficients (r) for the percentage of Category I bleached corals and mean seawater temperature from October 1986 to September 1987. $P < =$ level of significance

		6 m	12 m	18 m
<i>Montastrea annularis</i>	r	0.917	0.968	0.978
	$P <$	0.02	0.005	0.001
<i>Porites astreoides</i>	r	0.950	0.774	0.888
	$P <$	0.002	0.1	0.025
<i>Porites porites</i>	r	0.739	0.783	0.869
	$P <$	0.1	0.1	0.025
<i>Agaricia</i> spp.	r	0.953	0.867	0.989
	$P <$	0.002	0.025	0.001

Category I bleaching response for each species (at each depth) were correlated with the mean seawater temperature for each month of the survey using Spearman's Rank Correlation, Two Tailed Test (Zar 1974). Results and significance levels are given in Table 3. *M. annularis*, and *Agaricia* spp. gave highly significant positive correlations ($P < 0.05$) between seawater temperature and percentage of bleached colonies for all depths. An increase in seawater temperature was associated with an increase in the percentage of partially bleached coral colonies. *P. astreoides* gave significant positive correlations ($P < 0.025$) at 6 m and 18 m. *P. porites* only showed a significant ($P < 0.025$) positive correlation at 18 m.

Discussion

From July to December 1987, reef corals throughout the Caribbean appeared to lose their colouration and it was reported that a bleaching event was in progress (Williams et al. 1987). Prolonged exposure to seawater temperatures at the extreme of the normal range was considered to be a causative factor (Palca 1987; Roberts 1987). It was assumed that prior to the onset of the bleaching event corals were of normal colouration. This assumption was incorrect with respect to the Jamaican reefs. In May 1987, two months prior to the onset of the reported 1987 Caribbean bleaching event, approximately 25% of *M. annularis* and *Agaricia* spp. colonies on the study reef were exhibiting a partial bleaching response. In September of 1987 during the bleaching event, the values obtained for *M. annularis*, *P. porites* and *P. astreoides* were not significantly different from those obtained the previous October when no bleaching event was reported for Jamaica or elsewhere in the Caribbean. However, *Agaricia* spp. appeared to exhibit a significant increase in the percentage of bleached colonies in September 1987. In response to elevated seawater temperatures, *Agaricia* spp. in the San Blas Islands suffered severe bleaching and widespread mortalities as compared to *M. annularis* (Lasker et al. 1984).

Throughout the study a significantly higher percentage of *M. annularis* and *Agaricia* spp. colonies exhibited a bleaching response than *P. astreoides* and *P. porites*.

The brown pigment in the chromophore cells of the *Porites* species (see Lasker et al. 1984) may have masked some of the bleaching events in these species, however partial bleaching was observed and similar to that described by Marcus and Thorhaug (1981). For *P. porites* the periodic production of mucus tunics (Edmunds and Davies 1986) made the assessment of partial bleaching even more difficult. In *M. annularis* approximately 15% of the studied corals exhibited randomly scattered 1–2 cm² areas of pale tissue. Such patterns did not recover or worsen with time and appeared to be independent of seawater temperature. The cause of this type of bleaching is not known, but may have been the result of disease or predation.

For *M. annularis*, *Agaricia* spp. and *P. astreoides*, the percentage of coral colonies exhibiting a bleaching response was positively correlated with seawater temperature. Although coral bleaching in the field is usually associated with a large scale environmental disturbance, no such incident occurred during the study period. The strong relationship between the percentage of partially bleached coral colonies and seawater temperatures, illustrates the acute sensitivity of the above coral species to thermal variation. Depth did not influence the bleaching response in the four species of coral studied. The thermocline at Discovery Bay is at a depth of over 100 m (Woodley, personal communication), therefore the temperature difference between 3 m, 6 m, 12 m and 18 m is negligible. It is suggested that darkening and paling of colouration in these coral species is a dynamic seasonal phenomenon in response to annual variations in seawater temperature.

The loss of zooxanthellae from the host gastrodermis is thought to result in the paling of cnidarian colouration. Little is known about the mechanism involved in the reduction of the zooxanthellae population or the effects of temperature on this mechanism. Steen and Muscatine (1987) have shown that under experimental conditions temperature stress evokes rapid exocytosis of symbiotic algae in the tropical anemone *Aiptasia pulchella*. In the tropical anemone *Phyllactis flosculifera* a rise of 1.5° C and 4° C in seawater temperature results in increased loss of zooxanthellae from the host. These laboratory investigations illustrate the importance of seawater temperature as a factor controlling zooxanthellae populations.

There is a clear need for extensive investigation into this phenomenon as no evidence exists to explain the variation and pattern of coral bleaching in the field. A greater understanding of the basic regulatory mechanism that exists between the symbiotic partners is required before partial bleaching responses in reef corals can be fully understood.

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