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REPORT

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Sea surface temperatures and coral reef bleaching off La Parguera, Puerto Rico (northeastern Caribbean Sea)

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Abstract Much recent attention has been given to coral reef bleaching because of its widespread occurrence, damage to reefs, and possible connection to global change. There is still debate about the relationship between temperature and widespread bleaching. We compared coral reef bleaching at La Parguera, Puerto Rico to a 30-y (1966–1995) record of sea surface temperature (SST) at the same location. The last eight years of the La Parguera SST record have all had greater than average maximum temperatures; over the past 30 y maximum summer temperature has increased 0.7 °C. Coral reef bleaching has been particularly frequent since the middle 1980s. The years 1969, 1987, 1990, and 1995 were especially noteworthy for the severity of bleaching in Puerto Rico. Seven different annual temperature indices were devised to determine the extent to which they could predict severe coral bleaching episodes. Three of these, maximum daily SST, days $> 29.5\,^{\circ}$C, and days $> 30\,^{\circ}$C predict correctly the four years with severe bleaching. A log-log linear relationship was found between SST and the number of days in a given year above that SST at which severe coral beaching was observed. However, the intra-annual relationship between temperature and the incidence of bleaching suggests that no one simple predictor of the onset of coral bleaching within a year may be applicable.

Key words Bleaching · Caribbean · Species · Corals

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Introduction

Coral reef bleaching is caused by the loss of endodermal symbiotic zooxanthellae. Bleaching of corals was first reported in the 1870s (Glynn 1993) and has been observed in the Caribbean since at least 1940 (Goreau 1964). However, most of these early reported bleaching events were spatially localized and clearly linked to discernible factors such as changes in salinity, turbidity, extreme low tides, and outbreaks of *Acanthaster planci* (Goreau 1964; Glynn 1993; Williams and Bunkley-Williams 1990). Since 1980, however, there has been a significant increase in the number of reported large-scale coral reef bleaching events. These events have occurred in most of the world's major coral reef regions (Williams and Bunkley-Williams 1990; Glynn, 1993). Based on laboratory studies, elevated temperatures have been shown to cause coral bleaching (Coles and Jokiel 1977; Hoegh-Guldberg and Smith 1989; Glynn and D'Croz 1991). The increased frequency of widespread bleaching events has given rise to concerns that this may be a serious ecological effect of global climate change (Goreau and Hayes 1994). Correlative field studies have shown that elevated sea temperatures are associated with mass bleaching events (Cook et al. 1990; Jokiel and Coles 1990; Glynn 1991; Goreau et al. 1993; Goreau and Hayes 1994; Montgomery and Strong 1994; Gleeson and Strong 1995; Brown et al. 1996). However, these previous studies were often based on short duration (ten years or less) time series of SST and bleaching observations, and/or used temperature data obtained over broad spatial scales (e.g., hundreds of kilometers) and limited temporal scales (e.g., monthly mean temperature). Several of these studies have further attempted to quantify the relationship between temperature and the onset of mass bleaching events, but they differed about which aspects of extreme temperature variability were affecting coral reef bleaching. For example, Goreau et al. (1993) and Brown et al.

(1996) used mean monthly temperature above a local threshold as a predictor of the onset of bleaching. Hoegh-Guldberg and Smith (1989) predicted bleaching would occur following a 1 °C temperature increase over a two to four-week period. Gleeson and Strong (1995) suggested that bleaching was a function of cumulative heat stress and developed a predictor based on degree heating weeks.

The condition of the reef sites in southwestern Puerto Rico has been almost continuously observed, since the early 1950s when the University of Puerto Rico initiated an active marine biology program at La Parguera. Here we present a long, high-resolution temperature record (1966–1995), obtained in the close proximity to reefs observed over the same time period. This information is used to examine (a) the association of temperature and coral reef bleaching on an inter- and intra-annual basis, and (b) to assess various predictors of coral reef bleaching.

Methods

Bleaching was assessed by examination of established transects, periodic photographs of marked coral heads, and by general underwater observations. Because the La Parguera bleaching data were not collected in a standardized quantitative manner, bleaching in any given year was qualitatively classified in one of three categories: severe, minor, and non-occurring. Sea surface temperatures (SSTs) to the nearest 0.5 °F (0.28 °C) were recorded nearly daily by members of the marine station since the late 1950s. A plastic bucket was lowered at the dock to a depth of 3 m where it remained for 5 min. Upon retrieval water temperature was measured immediately in the shade with a mercury thermometer. To reduce the effect of daily variations only those readings collected between 0700 and 0900 local time were used. These constitute about 85% of all readings since 1966. On average, 25 different daily readings comprise the monthly average. Missing temperature data were interpolated to calculate number of days that temperature was above a certain threshold. Dock temperatures were compared to daily reef temperatures in 1997. Temperatures were measured at Mario Reef (2.5 km offshore) hourly using a StowAway XTI temperature logger at 4 m depth. While maximum dock temperatures exceeded reef temperatures, minimum daily temperatures at the dock occurred between 0700 and 0900; temperatures sampled at the dock during this time were closest to the mean daily reef temperature ($\pm$ 0.4 °C) than any other time of the day and were always less than maximum daily reef temperatures ($\pm$ 0.49 °C). Tidal variations in La Parguera are diurnal and of low amplitude (10 cm daily). Least-squares regression analysis was used to determine the existence of significant linear change in maximum monthly, minimum monthly, and average monthly SSTs.

At present, the exact physiological mechanism causing bleaching in corals is not known, nor is the manner in which temperature may affect this process. With respect to temperature, three factors of possible importance can be considered: absolute temperature (acute temperature stress), duration at some temperature (cumulative heat stress), and rate of change in temperature (temperature shock). All of these could be expressed in absolute terms or in relationship to some minimum temperature threshold. Unfortunately, there is no a priori way to determine the existence of such a threshold and what its value might be, although its existence is biologically reasonable. Because of this uncertainty, we explore a range of thresholds when examining cumulative heat stress. We devised nine indices of annual temperature variation as potential predictors of bleaching events. Maximum daily SST examines the effect of temperature per se. Maximum average monthly SST, the standard used in previous studies (Goreau et al. 1993; Brown et al. 1996), encompasses aspects of temperature and duration. Additionally, a 30-day daily running mean was used to factor out any bias introduced by artificial divisions between months. To examine the cumulative effect of temperature above a threshold, we calculated the number of days per year that SST was above five arbitrary temperatures: 29.0 °C, 29.5 °C, 30 °C, 30.5 °C, and 31 °C. Lastly, annual temperature range (from daily measurements) examines the effect of the extent of annual temperature change. Given the number of ways temperature may affect corals, an almost infinite variety of temperature indices (predictors) could be devised, yet all of them would be variations on the above factors. We feel that the indices we used cover the range of potential factors and take advantage of the detailed (i.e., daily) nature of our temperature record.

Results

The monthly mean SST record from La Parguera for the thirty-year period 1966–1995 is shown in Fig. 1. The record shows a clear increase in yearly average temperatures during this period by about 0.7 °C. Most of this increase has taken place during the last 10 y (regression analysis for the first 20 y of data showed no significant trend). Maximum average monthly temperatures have consistently exceeded 29 °C since 1987. The year 1990 had the highest monthly average temperature of 30.50 °C. This was followed by the years 1987 (30.09 °C), 1992, (29.86 °C), 1995 (29.84 °C) and 1969 (29.76 °C).

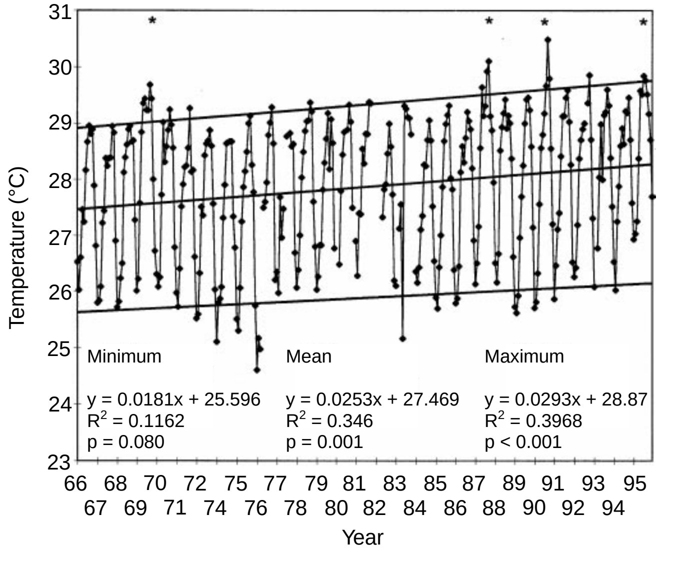

Fig. 1 Thirty-year (1966–1995) time series of monthly means of sea surface temperatures taken from La Parguera, southwestern Puerto Rico. Regression lines are (top to bottom) for maximum annual monthly temperature, mean annual monthly temperature, and minimum annual monthly temperature. Regression equations are given at the bottom. Asterisks indicate years of severe coral bleaching

Severe bleaching occurred in southwestern Puerto Rico in 1969 (Williams and Bunkley-Williams 1990; D.K. Atwood, NOAA personal communication 1993). This bleaching event is well known to coral reef researchers who worked in Puerto Rico at the time but unfortunately there was no description published about this event. The next recorded bleaching event occurred in August 1981, when minor but widespread bleaching occurred in southwestern and western Puerto Rico (Williams and Bunkley-Williams 1989, 1990). In November and December, 1986, widespread, but largely minor bleaching occurred in the mangroves and shallow water areas around La Parguera (Williams and Bunkley-Williams 1989,1990). *Agaricia agaricites* was the species most severely damaged, with half the colonies killed in some areas. Minor bleaching also occurred off Culebra Island just east of Puerto Rico. In 1987, widespread bleaching began in Puerto Rico in late August, became severe by mid-September, and did not decline until December (Fig. 2, top). Not all coral reef photosymbionts bleached, and most were only partially bleached, but extensive partial mortalities of colonies occurred. Although bleaching was not recorded until August, temperatures over 30 °C occurred as early as June, and temperatures well above the long-term mean temperature occurred over a three-month period (Fig. 2). The occurrence of severe bleaching in September coincided with a sharp, but short-lived rise in temperature to its annual maximum (31.11 °C). Minor or residual widespread bleaching lingered through much of 1988 (Bunkley-Williams et al. 1991; Williams and Bunkley-Williams 1990). Widespread minor to moderate bleaching also occurred in the warm-water period of 1989 (Williams and Bunkley-Williams 1990).

In 1990 bleaching began in September and was severe, with most corals being bleached over their entire surfaces (Goenaga and Canals 1990). Some of the shallow-water *Millepora* and scleractinian colonies were killed almost immediately, and extensive partial and total colony mortalities followed. This severe bleaching occurred when temperature rose rapidly to its annual maximum (31.67 °C) (Fig. 2, middle). Bleaching stayed severe until the temperature dropped sharply from 31 °C to below 28 °C in the latter half of October. No bleaching was reported associated with the very sharp, but brief increase in temperature (to over 31 °C) observed at the end of April. Residual or minor bleaching occurred in 1991. Widespread bleaching did not occur in southwestern Puerto Rico again until mid-May, 1992. This event was short-lived and did not develop into severe bleaching. Only sporadic, minor but short-term bleaching was noted from 1993 through 1994 and the photosymbionts quickly recovered.

In 1995, widespread moderate to severe bleaching occurred throughout the western Caribbean from Venezuela to the Flower Garden Banks off Texas, when SSTs exceeded 30 °C (Wolfgang 1995). In La Parguera, minor bleaching first occurred during May and June as temperature rose to over 30 °C (Fig. 2, bottom). At this time, bleaching was primarily among *Montastraea faveolata* and *Diplora labyrinthiformis*. Corals were pale, and bleaching was often confined to small patches. In July, a significant increase in bleaching was observed to 10 m depth coincident with a sharp peak in temperature to 31.7 °C. Species affected include *Millepora* spp. *Porites astreoides*, *P. porites*, *Agaricia agaricites*, *Leptoseris cucullata*, *M. annularis*, *Acropora palmata* and *Meandrina meandrites*. Colonies were white in some areas, although no whole-colony bleaching was observed. No further increase in bleaching was noticed during August as temperature fell to below 29 °C; some previously bleached colonies regained some pigmentation by the end of August despite a short peak in temperature during this period. Severe bleaching reoccurred from September until the end of October, associated with a broad temperature peak, again to 31.7 °C.

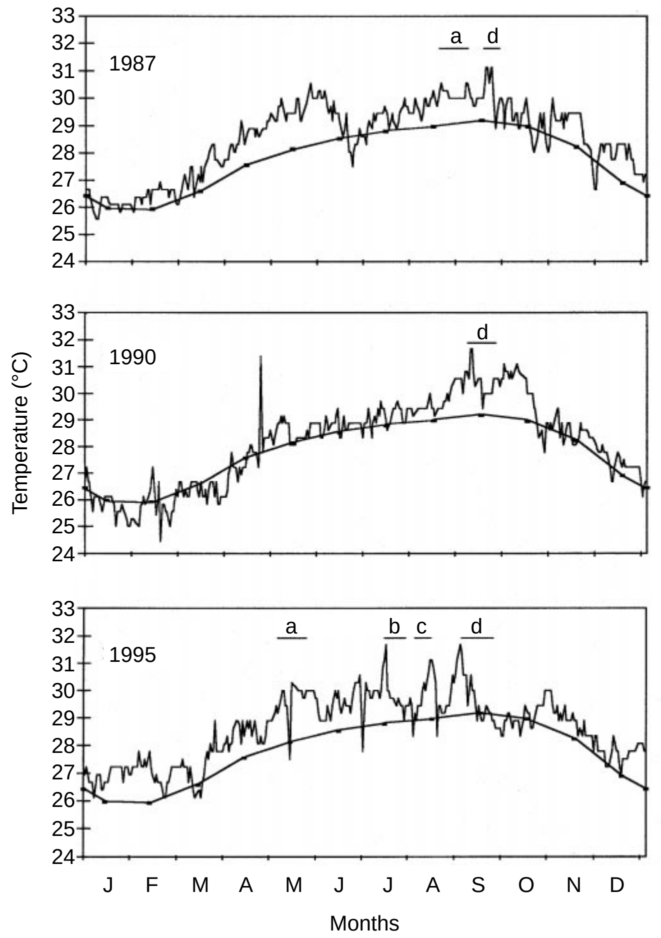

Fig. 2 Daily temperature from La Parguera, Puerto Rico for 3 y when severe bleaching occurred. Horizontal bars indicate the incidence of coral bleaching obtained from field observations: a, minor bleaching; b, increase in incidence of bleaching; c, recovery of corals from bleaching; d, onset of severe bleaching. Smooth curve is average monthly temperature over the period 1966–1995

A large number of colonies bleached; entire colonies were pale, some were patchy, and a few were completely white. The majority of branching, plating and massive coral species were affected. By January 1996 most colonies started to regain their pigmentation. Few corals died during the 1995 bleaching event.

The nine indices of annual temperature variation (Table 1) were evaluated for their ability to predict the occurrence of severe bleaching events (1969, 1987, 1990 and 1995). The ability of the indices to predict minor bleaching events was not considered, as it is known that factors other than temperature may cause localized, minor bleaching. Furthermore, the occurrence of minor bleaching in early years is not well documented. Indices were sorted by days or temperature in descending order and the resulting rankings of the severe bleaching years were determined. For all the indices, the probability was very small ($P < 0.001$, randomization test) that the four years of severe bleaching were ranked among the top four to eight positions. Given the small number of years when severe bleaching occurred, the best criterion for accessing the relative effectiveness of the various indices was their ability to segregate these years into the top four rank positions.

Five of these indices (maximum daily SST, days $>29.5\,^{\circ}$C, days $>30\,^{\circ}$C, days $>30.5\,^{\circ}$C, days $>31\,^{\circ}$C) correctly segregated the four years with severe bleaching. Maximum average monthly SST, as well as the 30-day running mean, did not perfectly segregate the years of severe bleaching because they included 1992. Yearly temperature range was a relatively poor indicator of bleaching severity.

Based on these results, we developed a general function relating number of days above a given temperature to the occurrence of severe bleaching. Because the exact minimum number of days for coral bleaching to occur is not known, we plotted temperature against both the minimum days at which bleaching was observed (e.g., 54 days above 29.5 °C, Table 1) and the maximum number of days at which bleaching was not observed (e.g., 37 days above 29.5 °C, Table 1) on a log-log plot (Fig. 3). The resulting relationship is nearly linear. A least-squares regression predicts that 104 days above 29 ° C would be necessary to cause severe bleaching, which compares favorably with our observations (Table 1).

The intra-annual relationship between temperature and bleaching was examined for the three years of

Table 1 Comparison of indices of coral reef bleaching. Asterisk, major bleaching years; **bold**, bleaching years

Days > 20 °C		Days > 29.5 °C		Days > 30 °C		Days > 30.5 °C		Days > 31 °C		Maximum daily temperature		Maximum monthly temperature		30-days running average		Temperature average	
Year	Days	Year	Days	Year	Days	Year	Days	Year	Days	Year	°C	Year	°C	Year	°C	Year	°C
87*	167	**87***	91	**90***	42	**90***	37	**95***	8	**95***	31.67	**90***	30.50	**90***	30.53	83	8.89
95*	150	**95***	83	**95***	30	**95***	15	**90***	5	**90***	31.67	**87***	30.09	**87***	30.22	**90***	7.22
69*	138	**90***	64	**87***	21	**69***	11	**87***	4	**87***	31.11	**92**	29.86	**95***	30.20	68	6.67
93	128	**69***	54	**69***	11	**87***	10	**69***	4	**69***	31.11	**95***	29.84	**92**	29.95	76	6.11
88	112	**92**	37	**93**	9	**93**	3	94		**93**	30.56	**69***	29.70	**69***	29.81	**69***	6.11
90*	109	**93**	31	**92**	9	**91**	3	**93**		**92**	30.56	**93**	29.60	**91**	29.74	70	6.11
91	100	**89**	26	**91**	4	**92**	2	**92**		**91**	30.56	**91**	29.56	**93**	29.64	**87***	5.56
89	94	**91**	24	94	3	84	1	**91**		84	30.56	94	29.45	**89**	29.62	**95***	5.56
94	91	94	21	70	2	80	1	**89**		80	30.56	**88**	29.42	94	29.52	**91**	5.56
92	80	79	18	**89**	1	70	1	**88**		70	30.56	**89**	29.40	79	29.47	71	5.56
78	65	**88**	16	**86**	1	68	1	**86**		68	30.56	**81**	29.38	78	29.45	**89**	5.28
83	62	70	14	84	1	94		85		94	30.28	80	29.33	**88**	29.43	**93**	5.00
81	58	78	12	80	1	**89**		84		**89**	30.28	85	29.31	83	29.43	**92**	5.00
70	58	**86**	9	79	1	**88**		83		**86**	30.28	72	29.31	70	29.40	**86**	5.00
86	56	85	8	68	1	**86**		82		**88**	30.00	71	29.00	**81**	29.38	85	5.00
80	56	**81**	8	**88**		85		**81**		85	30.00	83	29.29	**86**	29.38	84	5.00
76	54	80	6	85		83		80		83	30.00	76	29.25	80	29.37	80	5.00
79	46	84	5	83		82		79		**81**	30.00	**86**	29.18	76	29.37	75	5.00
85	43	83	5	82		**81**		78		79	30.00	78	29.17	85	29.33	74	5.00
75	34	71	3	**81**		79		77		78	30.00	75	29.14	71	29.32	66	5.00
68	28	76	2	78		78		78		76	30.00	79	29.11	84	29.26	94	4,72
66	24	66	2	77		77		75		71	30.00	70	29.10	75	29.9	**88**	4.72
71	21	68	1	76		76		74		66	30.00	84	29.05	67	29.13	**81**	4.44
84	20	82		75		75		73		82	29.44	82	28.97	73	29.09	79	4.44
67	18	77		74		74		72		77	29.44	68	28.95	68	29.95	78	4.44
82	17	75		73		73		71		75	29.44	66	28.93	82	29.02	73	4.44
77	13	74		72		72		70		74	29.44	67	28.93	77	28.92	67	4.44
73	9	73		71		71		68		73	29.44	73	28.87	74	28.84	82	3.89
74	5	72		67		67		67		67	29.44	77	28.81	72	28.80	77	3.89
72		67		66		66		66		72	28.89	74	28.66			72	3.89

major bleaching (i.e., 1987, 1990, 1995) for which we have substantial information on the occurrence and severity of coral bleaching (Fig. 2). Although the number of years for comparison are limited and the data on the occurrence and incidence of bleaching are sketchy, there is some consistency among years: Bleaching (minor) was observed only once in the spring or early summer, even when temperatures were above 30 °C, long periods of temperatures above the long-term mean occurred, or when sharp increases in temperature were observed. In each year, severe bleaching occurred in the late summer-early fall when temperatures were near their annual maxima, and the onset of severe bleaching was associated with a sharp rise in temperature.

Discussion

The results shown in Fig. 3 indicate that there is a strong relationship between severe bleaching and cumulative heat stress, but they do not indicate the exact mechanisms relating temperature to the onset or severity of bleaching. The exact relationship between days above threshold temperature and the occurrence of severe bleaching is most likely site dependent, but the linear nature of this relationship should be generally applicable. Moreover, the relationship in Fig. 3 cannot be extrapolated to temperatures that are not stressful. This may explain why the index of days above 29 °C did not perfectly predict the occurrence of severe bleaching.

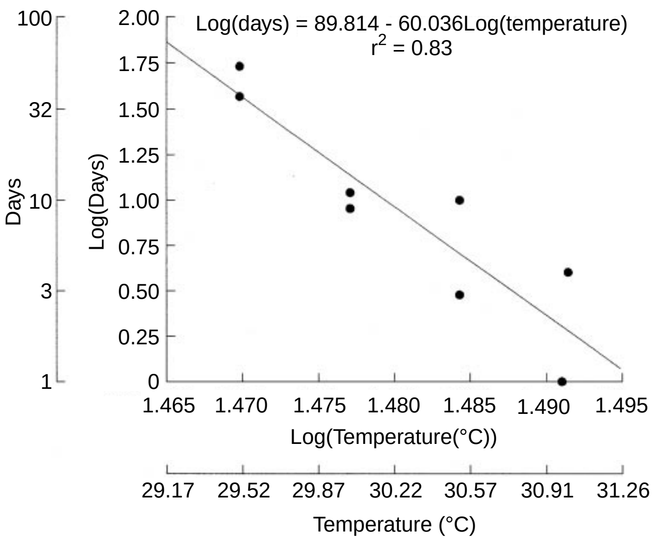

Fig. 3 Log-log plot showing the number of days above a given temperature for severe bleaching to occur in La Parguera, Puerto Rico. For any given temperature, two points are plotted: the upper point is the minimum number of days at which bleaching was observed and the lower point is the maximum number of days at which bleaching was not observed. Solid line represents least-squares regression

Although five annual temperature indices correctly sorted the years of severe bleaching, the analysis of intra-annual dynamics of the incidence of coral bleaching relative to temperature showed that bleaching responded to temperature on a finer temporal scale than indicated by these indices. Thus, the five indices may be viewed best as probability based predictors rather than as causal conditions. For example, while 54 days above 29.5 °C correlated with severe bleaching, the total number of days necessary to induce severe bleaching can be less (e.g., 31 days in 1990; Table 1 and Fig. 2, middle). However, when 54 days above 29.5 °C occur there is a high probability that the conditions associated with the onset of severe bleaching (e.g., daily temperatures above the long term mean and/or sharp temperature increase during the warmest part of the year) will also occur.

The intra-annual relationship between temperature and the incidence of bleaching suggests that no one simple predictor of the onset of coral bleaching within a year may be applicable. While there is some support for Hoegh-Guldberg and Smith's (1989) suggestion that bleaching follows a sharp increase in temperature, this only occurred late in the summer when temperatures were near the annual maximum, and not all such increases were associated with observations of more severe bleaching. There is less support for Gleeson and Strong's (1995) suggestion that the onset of bleaching is a function of cumulative heat stress; severe bleaching often occurred shortly after sharp temperature increases. However, prolonged heat stress appeared to be related to the duration of severe bleaching, and in all three years examined, severe bleaching occurred when temperatures exceeded the long term mean during the period of maximum annual temperature. Prolonged heat stress may be an important precondition for bleaching to occur, with sharp temperature changes acting as an immediate trigger. Goreau et al. (1993) and Brown et al. (1996) suggested that bleaching occurred when average temperature rose above a local threshold. While severe bleaching in Puerto Rico only occurred when temperatures were above the long term mean for the warmest months, severe bleaching did not occur during one of the four years with the highest maximum average monthly temperature (Table 1).

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