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RESEARCH ARTICLE

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Coefficient of variation of sea surface temperature (SST) as an indicator of coral bleaching

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Abstract Coral bleaching has become a major problem on reefs around the world in recent decades. It is believed that mean temperature alone is the primary force driving this ecological phenomenon. We propose that variance in temperature in the short term is just as important as the mean. Thirty years of daily sea surface temperature (SST) data have been collected by the University of Puerto Rico at Mayaguez Marine Laboratory in La Parguera, PR. These data were collated and analyzed initially (by Amos Winter) for their relationship to coral bleaching in this area. We found that the data fell into three categories: high mean temperatures associated with severe bleaching, cooler mean temperatures associated with no bleaching, and years of high SSTs but with no coral bleaching. Here, we examined the relationship between mean temperature during those months in which bleaching occurred, temperature variance (as measured by standard deviation), and coefficient of variation (CV; i.e., SD standardized by the mean). We also derived a critical threshold temperature and level of resolution in time for calculating these statistics to clearly describe the circumstances of bleaching versus non-bleaching events, particularly at marginal bleaching temperatures. These characteristics were compared for the four warmest months of the year (July–October) for four warm bleaching years (1969, 1987, 1990, and 1995), four cool non-bleaching years (1984, 1985, 1986, and 1988), and two warm non-bleaching years (1994 and 2000). No relationship was found between the mean SST and SD in terms of predicting bleaching. The two primary statistics which, in concert, did indicate bleaching, however, were the short-term, biweekly mean temperature and its the associated CV. Bleaching occurs in association with both high temperatures and a high CV. The CV becomes a critical determinant of bleaching only when temperatures are ~29.1–29.8°C. The warm, non-bleaching years were generally characterized by a CV of < 1.9 and a temperature range between 28.5 and 29.9°C. We conclude that increased mean SSTs alone are not sufficient to induce coral bleaching; a high variance in SST at marginal, lower bleaching temperatures can induce bleaching, and likewise, a low variance of such will not induce bleaching. This variance is most clearly described by the CV.

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Introduction

Hermatypic scleractinian corals are dependent upon endosymbiotic zooxanthellae (dinoflagellates) which live within their tissues for their survival and growth (Goreau et al. 1979). The zooxanthellae produce oxygen and carbohydrates which can be used by the coral; the zooxanthellae, on the other hand, utilize inorganic carbon in the form of CO_2 and organic nitrogenous compounds produced by the coral (McCloskey et al. 1978; Webb and Wiebe 1978; Zamer and Shick 1987; Allemand et al. 1998; Roberts et al. 1999). It is known that the coral cannot survive well or long without its symbionts. Thus, when the balance in this obligate symbiotic relationship is upset or altered, the survival of the scleractinian coral is threatened (Edmunds and Gates 2003; Baker 2003).

Hermatypic scleractinian corals have a restricted range of temperatures in which they can survive, grow, and reproduce successfully. Coral reefs generally occur between the latitudes of 25°S and 25°N (Levinton 1982). The optimum temperature for adult scleractinian corals is between 25 and 29°C; the minimal temperature for reef development appears to be 18°C (Stoddart 1969). Corals do exist outside of this range, although these are considered to be marginal habitats.

There has been a great deal of discussion about global climate change, including a potential increase in the mean temperature of the atmosphere (Houghton et al. 1990; Atmospheric Environment Service 1994; Keeling et al. 1996; Mortsch and Quinn 1996; Beardall and Raven 2004; Oreskes 2004; see also Vitousek 1994; Christy and Norris 2004; Santer et al. 2005) and the oceans, particularly in the tropics (Glynn and d'Croz 1990; Barnett et al. 2005).

It is now known that localized marine "hot spots" are occurring frequently in the tropics and subtropics (Hayes and Goreau 1991; Goreau and Hayes 1994; Sobel and Gildor 2003; Sarkar and Banerjee 2004). Modeling runs from a coupled ocean-atmospheric model indicate that most coral reef regions lying between 25°N and 25°S latitudes may experience increases in mean sea surface temperatures (SST) of between 1 and 2°C (Mitchell 1988; Manabe et al. 1991). Results of other modelers forecast somewhat lower rates of warming, but these rates are still approximately five times greater than those which have occurred during the past 100 years (Houghton et al. 1990; Wigley and Raper 1992).

Bleaching occurs when corals possessing zooxanthellae lose an unusually high proportion of their symbiotic algae, particularly in response to elevated SSTs. Over the past 20 years, this response has become increasingly more frequent phenomenon on a global scale (Brown 1990; Douglas 2003; Beardall and Raven 2004; McWilliams et al. 2005). It is believed that the primary force driving bleaching in corals is SST averaged over some minimum period of time. For example, if the temperature is a) above some critical level, in many cases in the vicinity of 30/31°C (see Berkelmans and Willis 1999; Berkelmans 2002), or 1°C above the maximum monthly mean (Toscano et al. 2002), and b) the duration of the event is long (e.g., on the order of several hours through days to weeks; see Podesta and Glynn 1997; Winter et al. 1998; Craig et al. 2001; Glynn et al. 2001; Vargas-Angel et al. 2001), bleaching has been shown to occur. If bleaching occurs, but some viable zooxanthellae are retained or reinvade the host coral within a certain period of time (Baker 2001; see also Kinzie 1974; Lin Ku-Lin et al. 2000; Estes et al. 2003), then the corals can survive (Hueerkamp et al. 2001; Ridgway and Hoegh-Guldberg 2002). Not all corals bleach, however, if temperatures become elevated to above-normal levels (Craig et al. 2001; Feingold 2001; Hueerkamp et al. 2001; Douglas 2003). It is believed that susceptibility of corals to bleaching due to temperature anomalies, particularly spikes, may vary as a result of acclimation to local environmental conditions (McClanahan et al. 2005) or to gradual temperature increases (Fitt et al. 2001).

If the bleaching event is severe and re-invasion does not occur successfully, the coral often dies. If this type of event is particularly severe, occurring in many species, and if the symbionts do not successfully reinvade their hosts, mass coral bleaching and mortality across a reef or a region can occur (Hoegh-Guldberg 1999; Souter and Linden 2000; Glynn et al. 2001; Licuanan and Gomez 2002; Wilkinson 2002; Aeby et al. 2003; McClanahan et al. 2007). This has been well documented in the Galapogos Islands (Podesta and Glynn 1997; Feingold 2001; Glynn et al. 2001; Reyes-Bonilla et al. 2002) and many other regions of the world's tropical and subtropical oceans (Cumming et al. 2002; Licuanan and Gomez 2002; Wilson et al. 2002). In some cases, local extinctions of certain corals have resulted (Glynn and de Weerdt 1991; see also Hughes and Tanner 2000).

The severe mass bleaching that we are considering here is outside of the range of cycles which occur naturally in the gain and loss of zooxanthellae on a seasonal basis in some regions. For example, some *Montastraea* can lose up to 90% of their zooxanthellae and still not exhibit obvious signs of "bleaching" (Warner et al. 2002; see also Oliver 1985; Nakamura et al. 2004). Here we will focus on those events where loss of zooxanthellae is extreme, resulting in coral mortality. It is these events which are clearly causing damage to coral reefs on a regional and global scale.

Podesta and Glynn (1997) found that neither a high maximum SST nor the duration and the intensity of the SST spike were clearly correlated with bleaching in Panama and the Galapogos Islands. Vargas-Angel et al. (2001) found similar results on Colombian reef corals. The question arises as to whether the most appropriate parameters were being considered as indicators.

What has not been considered thus far, however, is the variance around those high mean SSTs and the potential correlation of that parameter with the onset of bleaching, particularly in cases where temperatures are marginal. We believe that a high variance may be a primary influence in causing bleaching at marginal mean temperatures. Conversely, we also believe that a low variance could result in no bleaching at the same marginal temperatures.

We raise the following questions: what factors differentiate the lack of bleaching in above-normal SST years from those in which bleaching has occurred? Does a statistic exist which can readily describe those factors? Would such a running statistic be capable of predicting near-future bleaching events?

We decided to investigate these relationships using an existing long-term SST data set. One of the longest continuously running global SST data sets has been collected by the La Parguera Marine Laboratory of the University of Puerto Rico at Mayagüez (UPRM). They have been collecting daily SST data since 1958. These data have been analyzed by Winter et al. (1998), and they found a linear log–log relationship between SST and the number of days in a given year above the SST at which severe coral bleaching was observed.

In this study, we attempt to identify a simple, easily calculated statistic which will be a good descriptor of whether temperature changes constitute necessary and sufficient conditions for bleaching to occur in corals. We used the large data set compiled by UPRM to identify not only the appropriate statistic but the most appropriate level of resolution in time to consider when calculating those statistics, in order to optimize the indicator. Here we will demonstrate that the coefficient of variation (CV) calculated over a period of 14 days (during the warm months of the year) acts as an indicator of whether bleaching will or will not occur at SSTs considered marginal for bleaching in marginal cases. The CV is defined as

$$CV = \frac{SD \times 100}{\text{mean}}.$$

The CV can deliver information which the standard deviation (SD) cannot. The value of the CV can have exactly the same value with a high mean with a high SD versus a low mean with a low SD. It is a unit-less statistic delivering an estimate of variance independent of the mean; thus, any influence of low versus high means is removed (Sokal and Rohlf 1981). It removes any covariance which may be present between the mean and its variance (Snedecor and Cochran 1967). The CV describes the SD as a function of the mean, presented as a percentage.

Here, we will demonstrate how the CV can assist as an indicator and a potential predictor of bleaching or the absence of such at marginal SSTs.

Materials and methods

The data used for this study were derived from the long-term SST data set collected by the La Parguera Marine Laboratory of the University of Puerto Rico at Mayagüez, as described above. Temperatures were collected almost daily between 7:00 and 9:00 a.m. off Isla Magueyes at La Parguera by hand with a mercury-based thermometer and logged. The temperatures measured at the laboratory were within ± 0.4°C of temperatures measured at a nearby reef for the period 1997–1998 (see Winter et al. 1998).

The coral communities of the southwestern side of Puerto Rico have been widely studied, and a general description may be found in Goenaga and Cintrón (1979) and Weil et al. (2002). Data on coral bleaching events (see Winter et al. 1998) were incorporated into the database, and additional data on bleaching and its extent were supplied by Weil (UPRM) and colleagues.

We searched this data set for three different types of years: (1) a set of cooler years in which corals did not bleach; (2) a set of warmer years in which severe bleaching did occur; and (3) a set of warmer years in which severe bleaching did not occur.

Initially, we examined 8 months of the raw daily SST data set, extending from March through November, to determine the warmest months of the year for further investigation. These were identified as July, August, September, and October. Further analyses were restricted to these months for this reason. They were also the only months in which bleaching occurred. We then attempted to determine what level of temporal resolution would be most appropriate to describe a relationship between SST and bleaching. Five different levels of resolution in time were considered for calculations of means: (1) the full 4-month period; (2) bimonthly; (3) monthly; (4) biweekly; and (5) weekly. We calculated standard descriptive statistics—mean, standard deviation, variance, 95% confidence limits, and CV—from the data over these periods and graphed them, respectively.

The above statistics were plotted through time at each level of temporal resolution described above for each sample year. Biweekly data exhibited the most promise in terms of patterns; thus, we plotted the SD at the biweekly level of resolution in time against its associated mean to examine any relationship which might exist between the two. Then the CV was plotted against its associated mean for the same purpose.

The data were logged into and stored in EXCEL 2000. Statistical analyses, including Pearson's product–moment correlation analysis and discriminant function analysis (DFA), were performed with the aid of BIOMStat and SAS V8e, respectively. The PROC DISCRIM routine was used for DFA. Probabilities of points belonging to a given group were estimated using Bayes' theorem. Data were cross-validated for DFA using a linear discriminant function. Posterior probabilities were estimated and plotted along with classification results. Graphics were performed with the aid of SigmaPlot® 2001 and MS-PowerPoint®.

Results

Examination of the effects of different levels of temporal resolution on calculation of the basic descriptive statistics revealed that a period of 14 days (biweekly) provided the clearest patterns. It also afforded a relatively low variance, which was essential to the study. When using longer time intervals, differences in these parameters were indiscernible. When using shorter time intervals, the resulting variance was too high.

The annual SST data in the UPRM data files were distributed in the following way between the 3-year categories: (1) 29 years characterized by normal SSTs in which corals did not bleach; (2) four warm years in which severe bleaching occurred (1969, 1987, 1990, and 1995; the only years of their type in this data set; see Winter et al. 1998); and (3) 2 years, 1994 and 2000, which were warmer than average, but in which no bleaching occurred; (again, the only years of this type in the data set). Four years were chosen from the first group (normal SSTs) on the basis of completeness of the data set (n_i) for the target months considered; these were 1984, 1985, 1986, and 1988.

For each of the above years, spanning the 4-month period under consideration, the mean, SD, and mean with 95% confidence limits, and CV were plotted through time at biweekly intervals. Variances were high among the three groups of years, and no major differences were apparent between them.

We then examined the relationship between the statistics themselves to determine if there was any pattern which could be related to the different groups of years. There did not appear to be any relationship between the mean and the SD.

An interesting pattern appeared, however, when the CV was considered as a function of the mean. In the cooler, non-bleaching years, the points fell within a triangular pattern, spreading out from the low center portion of the graph to the upper left (Fig. 1a). In this set of years, the CV was significantly negatively correlated with mean temperature ($P < 0.01$, correlation analysis). In the warmer, bleaching years, the points showed a very different relationship and forming another triangle—akin to a mirror image to the first one, fanning out from the center to the upper right (Fig. 1c). In this case, however, there was no significant correlation between the CV and mean temperature ($P > 0.05$). In the warmer, non-bleaching years, the cluster of points was much more compact, forming a third area between the other two (Fig. 1b). In this last group, an outlier occurred at values of 29.5°C, CV = 2.9. Again, within this data subset, there was no significant correlation between CV and mean temperature ($P > 0.05$). Correlation analysis yielded some insight into the relationship between CV and temperature, but additional, more powerful and sensitive analyses were required.

The data describing the cool, non-bleaching category extended into higher values of CV at lower SSTs. The data describing the warmer, bleaching category extended into higher values of CV as the SSTs got higher. The points describing the warmer, non-bleaching years were defined by a tight cluster, which overlapped both of the other categories where both the CVs are low. Almost none of the points in this third category extend into the high CV area where many points from the warmer, bleaching data may be found, clearly distinguishing these two categories.

Discriminant function analysis yielded the percent of observations classified into the prescribed bleaching/temperature categories and the generalized squared distance to each group (Table 1). The analysis showed that 69.4% of the cooler, non-bleaching data was assigned back to its own category, and 55.5% of the warm bleaching was assigned back into its own. The warm non-bleaching data seemed to be assigned relatively uniformly to the three categories, overlapping both other categories. In general, however, the warm bleaching and cooler non-bleaching data were found be quite separate, exhibiting an overlap of only 0–13.9%.

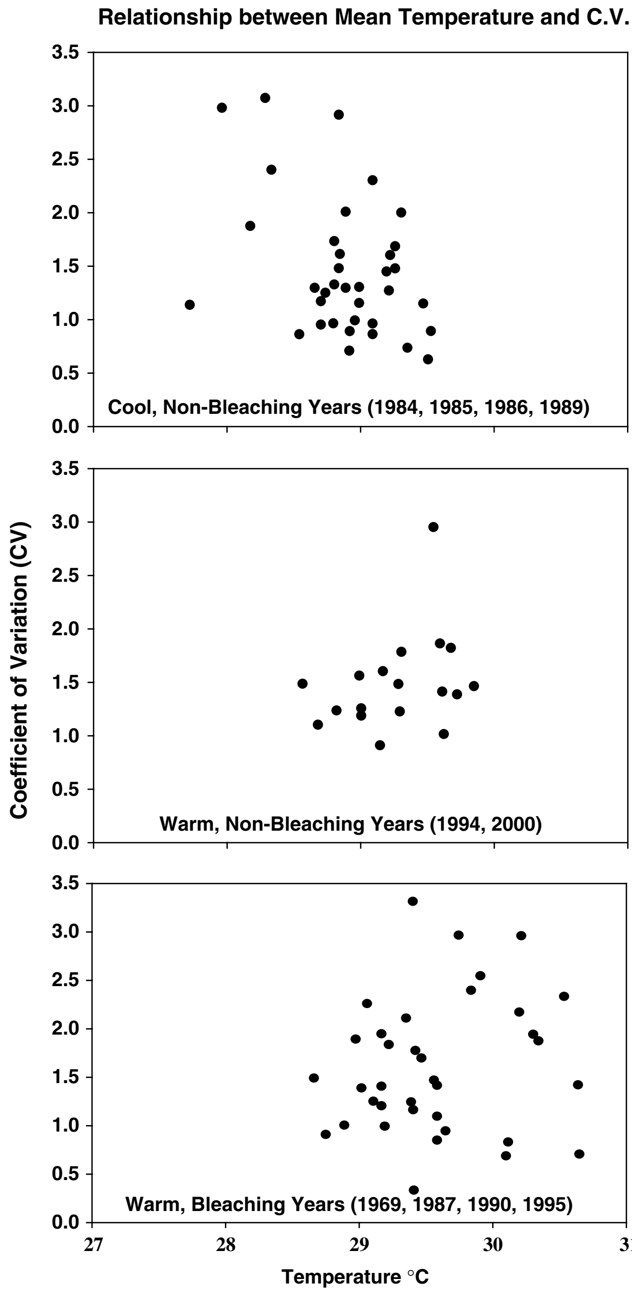

Fig. 1 Relationship between mean SST and CV of that mean in La Parguera, Puerto Rico. Comparisons shown between cool years in which corals did not bleach (1984, 1985, 1986, and 1989; $P < 0.001$, correlation analysis, $r = -0.4030$), warm years in which corals did not bleach (1994, 2000; $P > 0.05$, correlation analysis, $r = 0.3212$), and warm years in which corals did bleach (1969, 1987, 1990, 1995; $P > 0.05$, correlation analysis, $r = 0.1547$). Data drawn from the La Parguera Marine Laboratory, University of Puerto Rico at Mayaguez long-term SST database. Mean calculated over consecutive 14-day periods during the four warmest months of the year—July through October. Note distinctive comparative distribution patterns of each

The posterior probability estimates generated by DFA revealed quite discrete distribution patterns for the

Table 1 Results of Discriminant Function Analysis of mean SST data calculated over consecutive 14-day periods and their CVs

	From	To			
	Types of years	Cool, non-bleaching	Warm, non-bleaching	Warm, bleaching	Total
Percent classified into group	Cool, non-bleaching	69.4	30.6	0.0	100.0
	Warm, non-bleaching	33.3	27.8	38.9	100.0
	Warm, bleaching	13.9	30.6	55.6	100.0
	Total	31.5	38.9	29.6	100.0
N	Cool, non-bleaching	25	11	0	36
	Warm, non-bleaching	6	5	7	18
	Warm, bleaching	5	11	20	36
	Total	36	27	27	90
Generalized squared distance to compared category	Cool, non-bleaching	0	0.70757	2.33804	
	Warm, non-bleaching		0	0.48600	
	Warm, bleaching			0	

Data derived from the three types of years: cool, coral non-bleaching years; warm, coral non-bleaching years; and warm, coral bleaching years. Percent of each group re-classified into itself and other groups shown, along with the number of samples those percentages represent. Generalized squared distance from one category to the next also given

three sets of data (Fig. 2). The cool non-bleaching SST data were clearly centered in the lower temperatures with SSTs of ≤ 28.3°C possessing a probability of ≥ 80%. The probabilities fell off sharply with increasing temperature (Fig. 2a). The SSTs decreased slightly along those probability contours as the value of the CV increased. In the warm, bleaching years, a mirror-image pattern emerged, with the 80% probability line falling at an SST of ≥ 30.7°C (Fig. 2c). This SST values in the warm, bleaching years decreased at a sharper rate along those probability contours as the value of the CV increased when compared to the cool, non-bleaching years. The pattern of probability estimates in the warm, non-bleaching years, however, was quite different (Fig. 2b). The temperatures occurring with the highest probability (40%) were centered at 29.5°C, extending from 29.2 to 29.8°C. The upper limit of the CV for this contour was 1.6. The probabilities decreased regularly as the SST values moved away from this central set of points in the direction of both lower and higher temperatures.

When these probability estimates were combined, DFA indicated that CV values in the warm, non-bleaching group were defined as falling within a range of 29.15–29.70°C at a CV of 0.1 (Fig. 2). The SSTs in this category became more restricted at higher CVs, however, becoming minimal when the CV reached 3.5, with the range reduced to 29.8–29.4°C. Thus, even at SSTs approaching 30°C, corals tended not to bleach as long as the CV of the SSTs was low. At temperatures of just below 29°C, however, the corals would bleach if the CV was high.

Discussion

All analyses and considerations of these data sets indicate the same general relationship between temperature, variance as described by CV, and bleaching. In no case where SSTs were < 29.5°C in the normal years did bleaching occur, irrespective of the CV. In all cases where SSTs were > 29.9°C, bleaching occurred. In these cases, the value of the CV was inconsequential. In other years where the SSTs were high but CVs were low, bleaching did not occur. In fact, there appeared to be a limit regarding the threshold for not only temperature, but for variance around that temperature (as defined by CV), beyond which bleaching would occur. Similar analyses revealed that the SD, a general measure of variance, was found not to distinguish between bleaching and non-bleaching. It was only through use of the CV considered at a temporal resolution of 14 days that this relationship became apparent. This was confirmed by DFA.

All but one of the points describing the warm, non-bleaching data set, fell below a CV value of 1.9, despite the fact that the temperatures at these times fell between 28.5 and 29.8°C (Fig. 1c). On the other hand, during other warm years, severe bleaching was observed at these same temperatures, but only in those cases where the CV was ≥ 2.0. Thus, it appears that we may have identified a combination of statistics which, when used at the appropriate level of resolution in time, act as an indicator of bleaching (Fig. 3).

The fact that there are bleaching and non-bleaching events within the same temperature range indicates that mean temperature alone is not sufficient to describe or predict bleaching. It is the shifts in temperature over short periods of time that apparently have an effect on the probability of bleaching. It would appear that above-normal SSTs which are capable of inducing bleaching will not do so if the variance, as described by CV, is low. The same temperatures with high variances, however, will induce bleaching. The shock of a temperature change within a short period of time may be just as significant to inducing bleaching as the temperature itself. This suggests that additional research is needed on coral physiology regarding

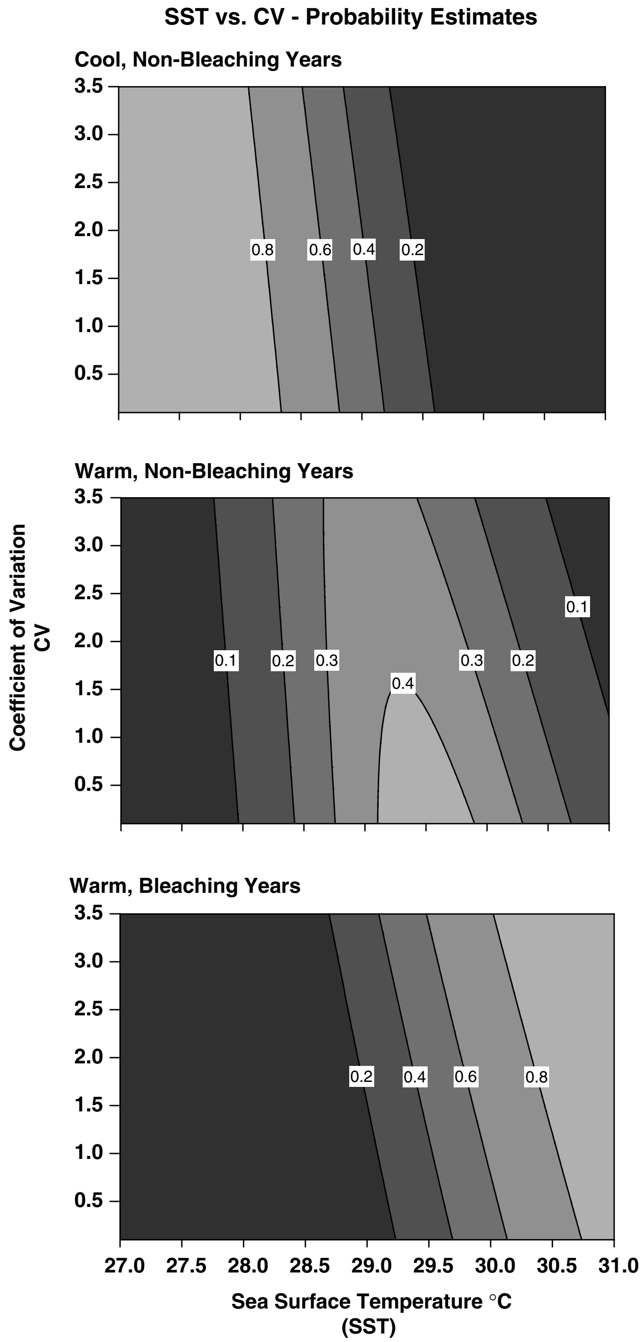

Fig. 2 Posterior probability estimates yielded by Discriminant Function Analysis of mean SST data with their associated CVs. Data derived from the long-term database held at the La Parguera Marine Station, University of Puerto Rico at Mayaguez. Data derived from the three types of years: **a** cool, coral non-bleaching years; **b** warm, coral non-bleaching years; and **c** warm, coral bleaching years. Note that the probability distribution is skewed heavily to the lower temperatures in **a** and to the higher temperatures in **c**, as might be expected. In the warm, non-bleaching years, however, the highest probabilities are centered around 29.5°C and are characterized by distinctly low CVs

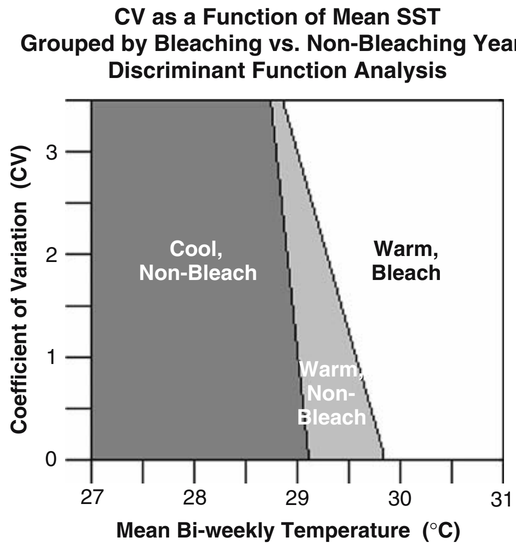

Fig. 3 Classification results of DFA of mean SST data and associated CV data. Means calculated over 14-day time intervals for the four warmest months of the year—July through October. Data derived from the three types of years: **a** cool, coral non-bleaching years; **b** warm, coral non-bleaching years; and **c** warm, coral bleaching years. These results indicate that bleaching will not occur in corals experiencing the same mean temperatures if the CV is low

the ability of corals to withstand high variance in temperature, which includes critical temperatures. A number of observation and modeling studies indicate that the tropical Atlantic SSTs have increased significantly in the last century and that the warming is most likely a consequence of anthropogenic activity (Barnett et al. 2005).

Regional warming is a complex issue covering a wide spectrum of oceanographic phenomena occurring at different time scales and patterns of spatial variability, from advection changes to differences in the rate and flow of eddies. One might expect that as global warming continues, the range of average biweekly SST temperatures will gradually shift from their current values to those somewhat higher. Unless adaptation to this higher range of temperatures occurs in these corals, bleaching frequency may be expected to increase, but, also under those conditions, a window of warm SSTs with low CVs characterized by lack of bleaching may be expected to remain.

We believe that the relationship we have found in Puerto Rico is probably characteristic of this region. We also believe, however, that this general relationship may well be applicable to corals in any region. The specific details of the critical temperature may be expected to vary from region to region. For example, corals occurring in the Red Sea may have higher tolerances, while those in the marginal subtropical areas might have lower ones. As average SSTs rise in the tropics and subtropics, and the frequency of development of hot spots increases, mass coral bleaching on reefs may be expected to increase concomitantly. The occurrence and possibly the severity of these events may to some degree be predictable using running means and running CVs over a fortnightly period. Understanding this relationship may eventually help us to build predictive models regarding bleaching on coral reefs.

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