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New insights into the exposure and sensitivity of coral reefs to ocean warming

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Abstract. Increases in coral bleaching events over the past 20 years are correlated with increases in sea surface temperature (SST). While SSTs have increased everywhere in the tropics, and coral bleaching events have occurred in all coral reef provinces, the frequency and intensity of coral bleaching events have varied considerably from region to region. Unless these patterns are random, we can derive useful information about why some reefs have been less vulnerable to increasing SST, and use this information to guide conservation efforts. Coral reef susceptibility to bleaching is a function of exposure to some stress (elevated SST) and sensitivity to that stress. To better characterize differences in coral reef vulnerability to increases in SST, we analyzed weekly SST records with coral bleaching records for reefs at the global scale. Our results indicate that variability of maximum SSTs is an additional factor that determines reef sensitivity to temperature increases, and taking this into account allows better predictions of coral bleaching in regions with low temperature variability.

Key words: bleaching, thermostat, SST, temperature, vulnerability

Introduction

The most commonly used predictor of when accumulated heat stress will cause coral bleaching is the degree heating week (DHW; (Liu et al. 2006)). The DHW index combines the severity of thermal stress (SST > 1ºC above the climatological maximum) with its duration over a rolling 12-week period. The NOAA Coral Reef Watch Program developed and maintains a very useful real-time bleaching predictive tool that calculates the DHW for reef regions worldwide. These calculations are based on twice-weekly satellite-derived SSTs at a spatial resolution of 50 km. DHW's are commonly used in studies examining the causal relationship between rising sea surface temperature (SST) and coral bleaching, but the method is known to over-predict and under-predict bleaching in some areas (e.g. McClanahan et al. 2007b) due to a range of factors associated with the scale and use of satellite data, to biological traits such as species composition.

When working with either historical or predicted sea surface temperature data, the temporal and spatial resolutions are much coarser; usually the data are weekly to monthly, and at best are gridded at 1x1° resolution. Previous studies that have used global climate model output to predict future bleaching frequency have used either a monthly SST threshold of 1ºC above normal maximum to predict bleaching (Hoegh-Guldberg 1999) or a degree heating month (DHM) index (Donner et al. 2005).

In order to develop a more generalized predictive tool for coral bleaching – one that can be used with more coarsely resolved past SSTs or model-projected SSTs, we examined ways to improve the DHW index toward predictions of coral bleaching. Our examination focuses on the concept of susceptibility, that is, not only a coral's exposure to high temperature event, but also its sensitivity to that exposure.

While it is clear that coral sensitivity to some maximum temperature varies regionally with differences in the climatological maximum, several studies have also suggested that corals from high-variability environments are more temperature-tolerant than those from low-variability environments (McClanahan et al. 2007a; Kleypas et al. 2008). In a rather crude analysis, (Kleypas 2006) found that the threshold of 1ºC above climatological maximum under-predicted coral bleaching in regions where the maxima varied little from year to year (e.g., in the eastern equatorial Pacific; Fig. 1), and that predictions improved if the threshold considered variability of maximum SST (Fig. 2). Here, we more closely examine whether coral sensitivity to elevated temperatures varies as a function of temperature variability.

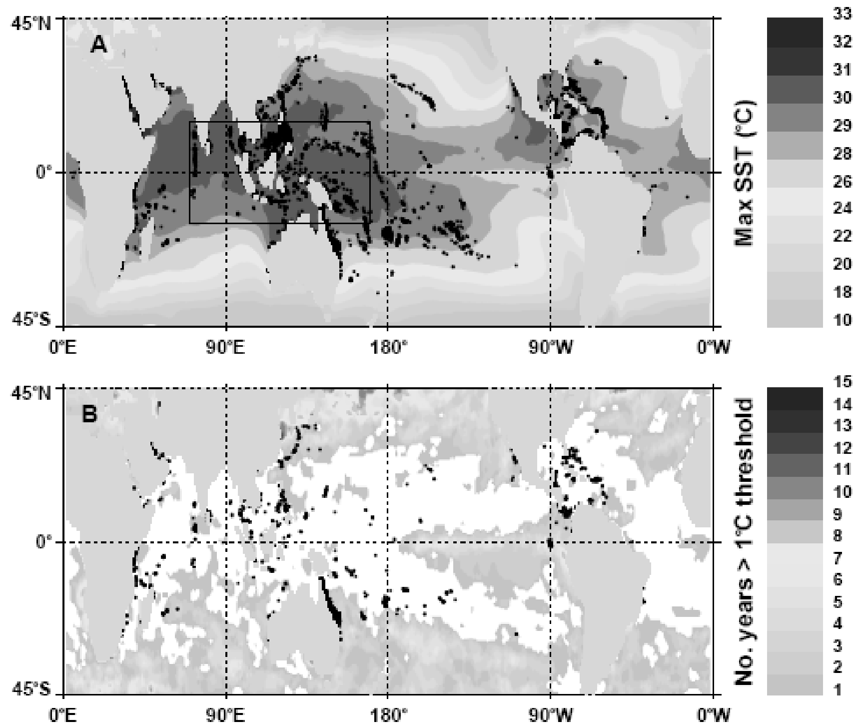

Figure 1: (A) Average annual maximum sea surface temperatures contoured showing locations of all coral reefs. (B) Number of years that the SST maximum exceeded the climatological maximum + 1ºC for at least one week. Black dots indicate reefs that have experienced bleaching (from Kleypas 2006).

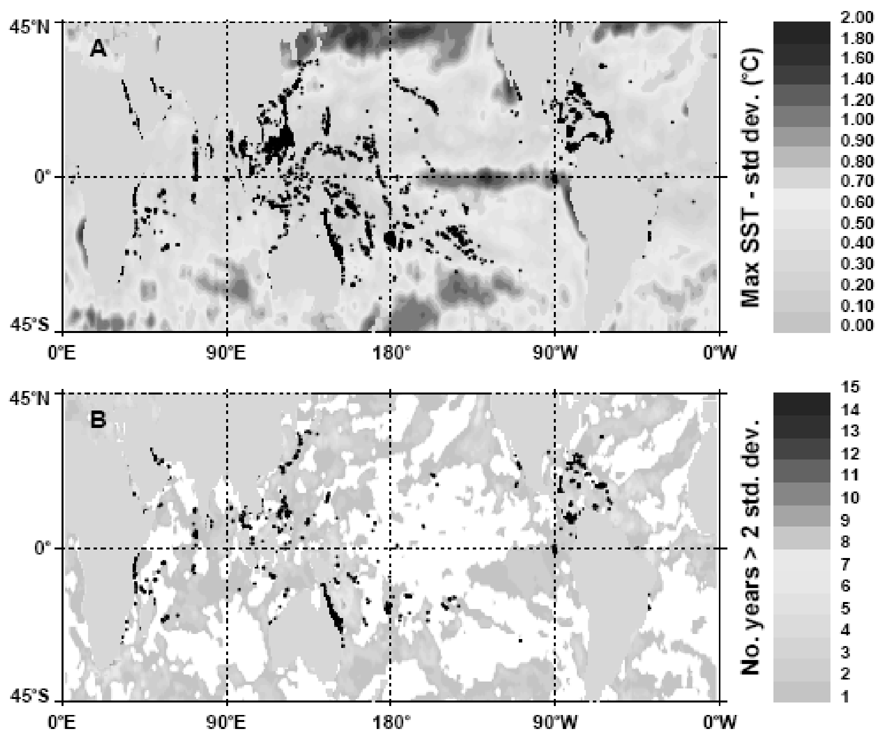

Figure 2: (A) Standard deviation of the average annual maximum sea surface temperature, showing locations of all coral reefs. (B) Number of years that the maximum exceeded the climatological maximum + 2 standard deviations for at least one week. Black dots indicate reefs that have experienced bleaching (from Kleypas 2006).

Methods

Data. Coral bleaching data were obtained from the ReefBase Global Bleaching Database (ReefBase-Project 2007). This data set is a compilation of mostly volunteer reporting of observations. NOAA's Coral Reef Watch Program has facilitated the ability to verify and qualify bleaching in areas where temperatures have exceeded certain thresholds, but coral bleaching has almost certainly been under-reported. The bleaching reports were summarized for each 1x1° cell, yielding a total of 516 unique reef locations that have experienced at least one bleaching event of any severity between 1982 and 2006.

SST data were obtained from the weekly Reynolds Optimally Interpolated SST (OISST) data set (Reynolds et al. 2002) for the years 1982–2006. The OISST has a spatial resolution of 1°x1°, and incorporates in situ observations as well as satellite-based observations.

Analysis. Using the weekly OISST data, the climatalogical maximum SST was determined for each grid cell as the average maximum for the first ten years of the OISST data (1982–1991). The standard DHW index (DHW_1), which uses an absolute threshold (1ºC above climatological maximum), and a modified DHW index (DHW_2) in which the threshold bleaching temperature is based on natural variability (for example, when SST > 2 standard deviations (SD) above climatological maximum), were then calculated for the entire OISST record. For DHW_2, we considered the variability of the annual maxima rather than that of the entire SST record. For both indices, we assumed that a bleaching event was possible once the DHW exceeded a designated threshold.

To account for the fact that bleaching is often observed some time after a temperature excursion, we assumed that a bleaching observation reported within 3 months following a predicted bleaching event was part of that event, and multiple observations within that 3-month time period were consolidated as one event. This was determined as the optimal time period for capturing most bleaching observations following a temperature maximum. Thus, a total of 725 bleaching events were identified for the 516 grid cell locations.

We determined "best fit" by maximizing the number of correct bleaching predictions (bleaching predicted and observed), while minimizing false negative (Type II error; bleaching not predicted but observed) and false positive predictions (Type I error; bleaching predicted but not observed). False positive predictions are particularly difficult to evaluate in this analysis because of the incomplete nature of the ReefBase data; that is, we do not have a good estimate of the number of bleaching events that occurred but were not observed or reported.

Results

Applying the standard bleaching index (DHW_1) with the weekly OISST data predicted 159 bleaching events over the 25-year period, but fails to predict 566 bleaching events (1.0ºC above maximum; Table 1). The number of predicted bleaching events that were not observed (438) is more than twice the number of correctly predicted bleaching events. If one assumes that, when bleaching occurred within a grid cell, at least one report was made and included in the ReefBase dataset, then the DHW_1 method correctly predicted bleaching 14% of the time [% correct = number of correct predictions/(total number of correct + incorrect predictions)]. If the temperature threshold is lowered to 0.7°C, then the method correctly predicts bleaching 19% of the time.

Table 1: Comparison of DHW_1 versus DHW_2 predictions of coral bleaching. Bold rows are predictions using the standard threshold (DHW_1), and the best results when using standard deviation of the annual monthly maximum (DHW_2).

DHW_1 ºC above climatological maximum	Correct	Incorrect		% correct	DHW_2 SD above climatological maximum	Correct	Incorrect		% correct
	Predicted and Observed	Type II Not Predicted but Observed	Type I Predicted but not Observed			Predicted and Observed	Type II Not Predicted but Observed	Type I Predicted but not Observed	
0.5	452	273	2048	16.3	1.5	434	291	1673	18.1
0.6	397	328	1490	17.9	1.6	407	318	1465	18.6
0.7	338	387	1069	18.8	1.7	382	343	1247	19.4
0.8	273	452	778	18.2	1.8	356	369	1087	19.6
0.9	210	515	578	16.1	1.9	326	399	926	19.7
1.0	**159**	**566**	**438**	**13.7**	**2.0**	**308**	**417**	**788**	**20.4**
1.1	107	618	303	10.4	2.1	276	449	670	19.8
1.2	69	656	213	7.4	2.2	262	463	583	20.0
1.3	54	671	161	6.1	2.3	236	489	492	19.4
1.4	43	682	111	5.1	2.4	212	513	423	18.5
1.5	35	690	81	4.3	2.5	189	536	374	17.2

DHW_2 performed best (20.4% correct predictions) using a 2.0 standard deviation threshold. 308 bleaching events over the 25-year period were correctly predicted, 417 bleaching were not predicted, and 788 events were predicted but not observed (Table 1). The % correct predictions dropped off at higher and lower standard deviation thresholds.

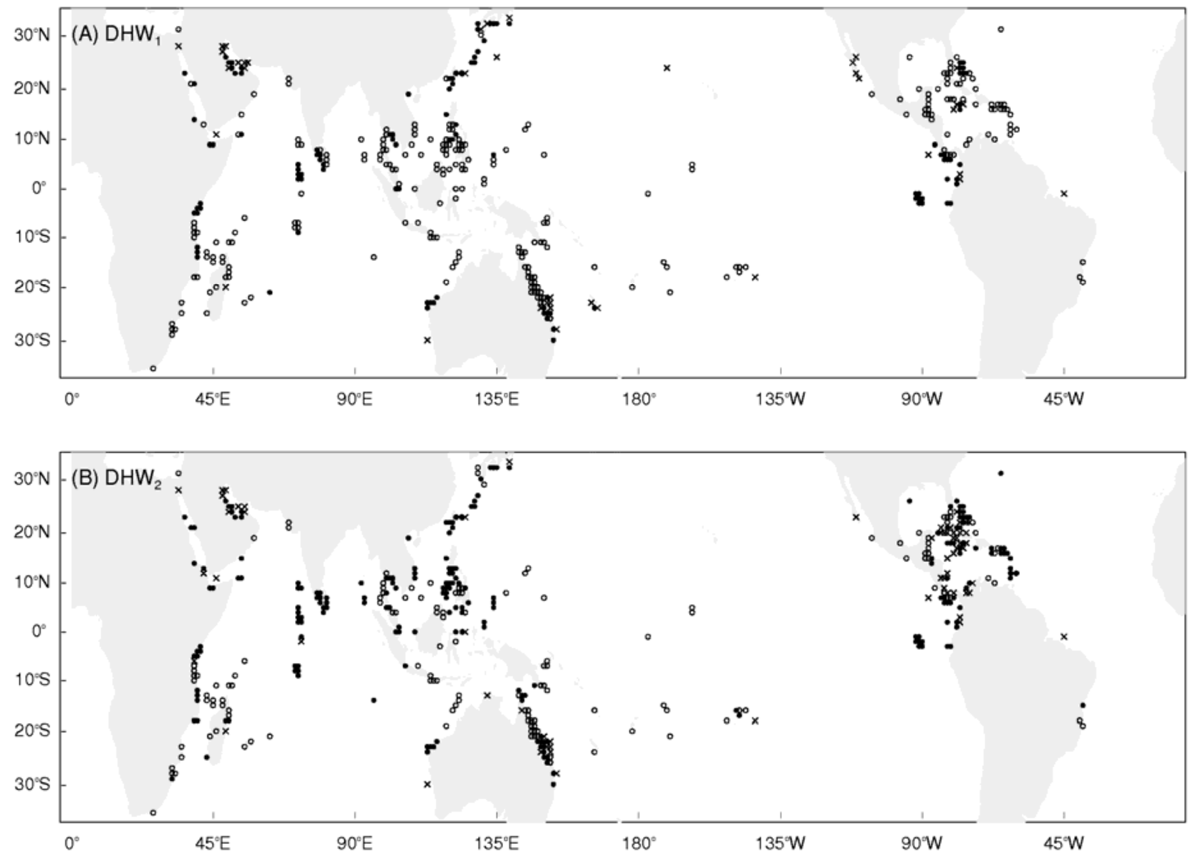

Figure 3: (A) DHW_1 predictions for 1997–1998. Solid black circles indicate a match: bleaching was observed where it was predicted. White circles indicate where bleaching was observed but not predicted (Type II error). The X's show locations where bleaching was predicted but not observed (Type I error). (B) DHW_2 predictions for 1997–1998.

Discussion and Conclusions

This rather simple analysis illustrates that neither method predicts bleaching well, but it does suggest that natural variability of the annual maximum SST is a factor that determines regional thresholds to bleaching. The most obvious error in both methods is the failure to predict bleaching when it occurs (Type II). The DHW_2 method seems to do a slightly better job at predicting the observed bleaching events. Both methods suffer from high Type I errors, such that bleaching is predicted much more often than it is observed. This over-prediction can occur for two reasons: 1) the coral reef communities did not bleach (a true Type I error); or 2) at least some bleaching events were not reported (and indeed, were probably not even observed) and thus were not included in the ReefBase data set. Thus, the number of over-predicted reefs is almost certainly less than shown here.

The distribution patterns of the correctly and incorrectly predicted bleaching events reveal a potential bias in the DHW_1 method in that it does a better job in high variability regions such as at higher latitudes and in upwelling regions (compare Figs. 1 and 2 with Fig. 3). The DHW_2 method seems to do a better job across regions, and successfully predicts bleaching events in regions with low SST variability (e.g. equatorial regions; Fig. 3). This implies that current bleaching predictions underestimate bleaching in low variability regions, such as in the western Pacific warm pool. It also implies that the conditioning of corals to bleaching is not only a function of the maximum temperatures that they are accustomed to, but also the variability in those maximum temperatures. Fig. 4 presents a clustering of coral reefs based on SST minima, maxima, and variability. We propose that these reef clusters have different thresholds to changes in temperature extremes and variability, and that bleaching indices should take into account these differences. Finally, many other factors besides SST affect the bleaching thresholds in corals, such as solar radiation (Brown, Dunne 2008), mixing (Nakamura, Yamasaki 2005; Fabricius 2006), community structure (McClanahan et al. 2005), and clade-type of the zooxanthellae symbionts (Baker 2003; Berkelmans, van Oppen 2006; Jones et al. 2008). Like SST patterns, these variables also vary from region to region, and many have been shown to be important factors that contribute to regional variations in vulnerability to coral bleaching (McClanahan et al. 2007a; Maina et al. 2008).

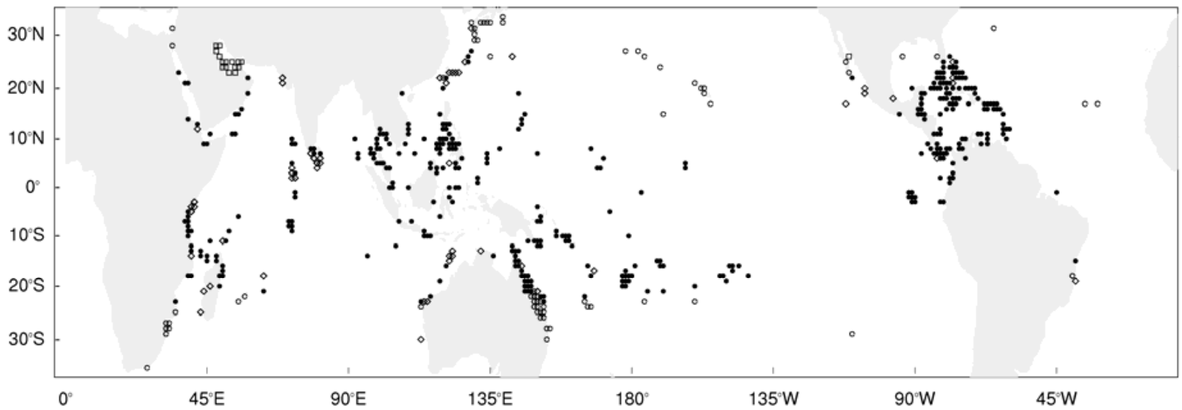

Figure 4: Reefs with common temperature characteristics, based on the minimum, maximum and variance of SSTs from the weekly OISST data (Reynolds et al. 2002).

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