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New insights into global patterns of ocean temperature anomalies: implications for coral reef health and management

Elizabeth R. Selig^{1,4*†}, Kenneth S. Casey² and John F. Bruno³

¹Curriculum in Ecology, University of North Carolina, Chapel Hill, NC 27599-3275, USA,

²National Oceanographic Data Center, National Oceanographic and Atmospheric Administration, Silver Spring, MD 20910, USA, ³Department of Marine Sciences, University of North Carolina, Chapel Hill, NC 27599-3300, USA, ⁴Conservation International, 2011 Crystal Drive Suite 500, Arlington, VA 22202, USA

ABSTRACT

Aim Coral reefs are widely considered to be particularly vulnerable to changes in ocean temperatures, yet we understand little about the broad-scale spatio-temporal patterns that may cause coral mortality from bleaching and disease. Our study aimed to characterize these ocean temperature patterns at biologically relevant scales.

Location Global, with a focus on coral reefs.

Methods We created a 4-km resolution, 21-year global ocean temperature anomaly (deviations from long-term means) database to quantify the spatial and temporal characteristics of temperature anomalies related to both coral bleaching and disease. Then we tested how patterns varied in several key metrics of disturbance severity, including anomaly frequency, magnitude, duration and size.

Results Our analyses found both global variation in temperature anomalies and fine-grained spatial variability in the frequency, duration and magnitude of temperature anomalies. However, we discovered that even during major climatic events with strong spatial signatures, like the El Niño–Southern Oscillation, areas that had high numbers of anomalies varied between years. In addition, we found that 48% of bleaching-related anomalies and 44% of disease-related anomalies were less than 50 km², much smaller than the resolution of most models used to forecast climate changes.

Main conclusions The fine-scale variability in temperature anomalies has several key implications for understanding spatial patterns in coral bleaching- and disease-related anomalies as well as for designing protected areas to conserve coral reefs in a changing climate. Spatial heterogeneity in temperature anomalies suggests that certain reefs could be targeted for protection because they exhibit differences in thermal stress. However, temporal variability in anomalies could complicate efforts to protect reefs, because high anomalies in one year are not necessarily predictive of future patterns of stress. Together, our results suggest that temperature anomalies related to coral bleaching and disease are likely to be highly heterogeneous and could produce more localized impacts of climate change.

Keywords

Climate change, coral bleaching, coral disease, coral reefs, disturbance, marine protected areas, sea surface temperature, temperature anomalies.

*Correspondence: Elizabeth Selig, Curriculum in Ecology, University of North Carolina, Chapel Hill, NC 27599-3275, USA.

E-mail: e.selig@conservation.org

†Current address: Conservation International, 2011 Crystal Drive Suite 500, Arlington, VA 22202, USA.

INTRODUCTION

Ocean warming related to human-induced and natural climate variability (Rayner *et al.*, 2006; IPCC, 2007) can affect species

distributions, composition and diversity as well as ecosystem productivity (Harley *et al.*, 2006; Brander, 2007). Sea surface temperature anomalies, or deviations from long-term means, can cause physiological stress, mortality and phenological

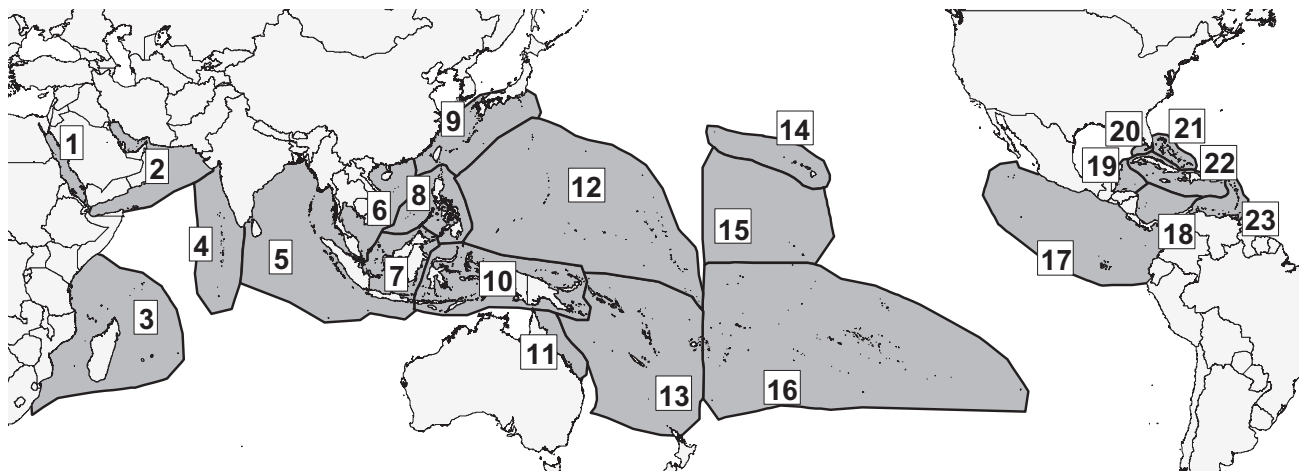


Figure 1 Region delineations for the Coral Reef Temperature Anomaly Database (CoRTAD) analysis (1 = Red Sea, 2 = Persian Gulf, 3 = west Indian Ocean, 4 = Lakshadweep, Maldives and Chagos archipelagos, 5 = east Indian Ocean, 6 = South China Sea, 7 = west Indonesia, 8 = Philippines, 9 = Taiwan and Japan, 10 = east Indonesia and Papua New Guinea, 11 = Great Barrier Reef, 12 = west Pacific, 13 = south-west Pacific, 14 = Hawaii, 15 = central Pacific, 16 = south-east Pacific, 17 = Pacific Central America, 18 = Central America, 19 = Mesoamerican Barrier Reef, 20 = Florida Keys, 21 = Bahamas, 22 = east Caribbean, 23 = Antilles). Although the western Atlantic has reefs (not shown), they were not used in the regional analysis because they cover a relatively small area.

changes that may affect entire food webs (Glynn, 1993; Beaugrand & Reid, 2003; Mackas *et al.*, 2007). Designing conservation strategies for reducing these impacts requires an understanding of the spatio-temporal patterns of ocean temperature anomalies (Halpern *et al.*, 2008). Until recently, efforts to describe these patterns at biologically relevant scales have been limited by the absence of datasets of sufficiently fine spatial resolution. To address this gap, we created the Coral Reef Temperature Anomaly Database (CoRTAD), a 21-year, 4-km resolution global dataset of ocean temperature anomalies using data developed from the National Oceanic and Atmospheric Administration's (NOAA) National Oceanographic Data Center (NODC) and the University of Miami's Rosenstiel School of Marine and Atmospheric Science (Fig. S1 in Supporting Information). Using these data, we calculated baselines for anomaly frequency, size, intensity and duration, and analysed whether and how patterns in these parameters varied across regions (Fig. 1) and years. These data can not only be used to understand typical disturbance regimes, but also act as a starting point for identifying new marine protected areas that may act as potential thermal refugia (Maina *et al.*, 2008).

We focused our analyses on scleractinian or reef-building corals because they already live near their thermal limits (Jokiel & Coles, 1990; Glynn, 1993) and have experienced extensive mortality due to temperature-driven coral bleaching (Arceo *et al.*, 2001; Baird & Marshall, 2002; Arthur *et al.*, 2006) and disease (Selig *et al.*, 2006; Bruno *et al.*, 2007). Declines in coral cover as a result of disease and bleaching can have drastic effects on the entire coral reef ecosystem (Aronson & Precht, 2001; Jones *et al.*, 2004; Graham *et al.*, 2006). Studies of individual reefs that experienced coral mortality during the 1997–98 El Niño–Southern Oscillation (ENSO) event have found subse-

quent parallel declines in fish abundance and diversity (Jones *et al.*, 2004) and erosion of the reef framework itself (Graham *et al.*, 2006).

Field research and remote sensing analyses suggest that the spatial patterns of bleaching (Marshall & Baird, 2000; Berkelmans *et al.*, 2004) and disease (Kuta & Richardson, 1996; Willis *et al.*, 2004) can be relatively heterogeneous. Bleaching events can be quite localized, and during major events may cluster at scales of only *c.* 10 km or less (Berkelmans *et al.*, 2004). Consequently, coarse-scale 50-km resolution remote sensing data have failed to detect some bleaching events (McClanahan *et al.*, 2007b; Weeks *et al.*, 2008) and higher-resolution data can be more accurate in predicting bleaching (Maynard *et al.*, 2008; Weeks *et al.*, 2008). However, accuracy in predicting bleaching can also be affected by finer-scale phenomena, including coral species composition, symbiont type and visible and ultraviolet light, all of which affect susceptibility to bleaching (Loya *et al.*, 2001; Baird & Marshall, 2002; Lesser & Farrell, 2004; Sampayo *et al.*, 2008). Spatial patterns of disease are less well documented, but also suggest localized spatial clustering, where outbreaks may affect only one reef or part of a reef (Kuta & Richardson, 1996; Willis *et al.*, 2004; Bruno *et al.*, 2007). This patchiness in disease and bleaching may result in part from the documented high local spatial variability of temperature on coral reefs due to diurnal warming, stratification and internal waves (Leichter *et al.*, 2006).

In the past few years, higher-resolution satellite datasets spanning more than a decade have become available. Although these data cannot capture all fine-scale physical dynamics like ponding or internal waves, we can now better determine the scales at which temperature anomalies are occurring, as well as develop a better understanding of the relationship between

Table 1 Metrics of thermal stress.

Metric	Definition	Application	Related references
Thermal stress anomalies (TSAs)	Observed weekly averaged temperature is ≥ 1 °C warmer than the maximum climatological week (the warmest week of the 52 climatological weeks averaged over 21 years); TSAs are deviations from typical summertime temperatures	Bleaching	Glynn (1993), Podesta and Glynn (2001), Liu <i>et al.</i> (2003)
Weekly sea surface temperature anomalies (WSSTAs)	Observed weekly averaged temperature is ≥ 1 °C warmer than the weekly climatological value (averaged over 21 years); WSSTAs are deviations from typical weekly temperatures	Disease	Selig <i>et al.</i> (2006), Bruno <i>et al.</i> (2007)

temperature and biological responses at regional scales. For example, if temperature anomalies are relatively homogeneous across large spatial scales we would expect biological responses to be relatively uniform as well. However, if temperature anomalies are spatially variable, biological responses may also be very heterogeneous. Spatial variability also presents an opportunity to establish new marine protected areas in sites that may act as potential thermal refugia (Maina *et al.*, 2008).

We quantified the spatial and temporal patterns of temperature anomalies associated with coral bleaching and disease (Table 1) using data in the CoRTAD from 1985 to 2005. These data not only enabled us to establish a baseline from which we could compare extreme events like the 1997–98 ENSO, but also allowed us to test how these anomaly characteristics varied by region. For each anomaly metric, we calculated three generally accepted measures of disturbance intensity: frequency, magnitude and duration (Connell, 1978). In addition, we quantified the distribution of anomaly sizes across all years and regions. These analyses described fine-scale spatial structure and variability in temperature anomalies, findings which have broad implications for the design of marine protected areas and future work aimed at understanding how changing ocean temperature could affect ecosystem health.

METHODS

Temperature dataset

The CoRTAD was developed using data from the Pathfinder Version 5.0 collection produced by the NOAA's NODC and the University of Miami's Rosenstiel School of Marine and Atmospheric Science (<http://pathfinder.nodc.noaa.gov/>). Sea surface temperature (SST) data are derived from the Advanced Very High Resolution Radiometer (AVHRR) sensor and are processed to a resolution of approximately 4.6 km at the equator (Kilpatrick *et al.*, 2001; Casey *et al.*, in press). These data have the highest resolution covering the longest time period of any satellite-based ocean temperature dataset (Fig. S1) and cover more than 98% of reefs world-wide, doubling the coverage of coarser resolution datasets (K. S. Casey, personal communication). We created a day–night average database using data with a quality flag of 4 or better, which is a commonly accepted, conservative cut-off for 'good' data (Casey & Cornillon, 1999;

Kilpatrick *et al.*, 2001). Where both day and night data were available, these values were averaged. If only day or night data were available, we used those data. With a day–night average approach, we reduced the number of missing pixels by 25%.

The standard Pathfinder algorithm eliminates any observation with a SST differing by more than 2 °C from a relatively coarse resolution SST value based on the Reynolds Optimum Interpolation Sea Surface Temperature (OISST version 2.0) value, a long-term, satellite and *in situ*-based dataset (Kilpatrick *et al.*, 2001; Reynolds *et al.*, 2002). We added observations back into the analysis if the weekly SST was less than 5 °C warmer than the OISST. The 5 °C threshold is a reasonable selection that allows diurnal warming events (Kawai & Wada, 2007) or other spatially limited warm spots back into the dataset without including unrealistic and erroneously warm values. Values less than the OISST were not included because they may have been biased by the presence of cloud and other satellite errors, which tend to result in cooler SST estimates. The processes of including the day–night average and some data warmer than the OISST resulted in a dataset with only 21.2% missing data.

To create a gap-free dataset for analysis, we used a 3×3 pixel median spatial fill, where the median of adjacent pixels was used to calculate a value for a missing pixel. This process preserved the original resolution of the data and no pixels with an available value were modified. The remaining gaps were filled temporally using the piecewise cubic Hermite interpolating polynomial (PCHIP) function in Matlab (The Mathworks Inc., 2006). We chose this conservative approach because it provided interpolated SSTs that were bounded by the nearest available values in time. Using these gap-filled data, we then created site-specific climatologies for each 4-km grid cell to describe temperature patterns over the 21-year dataset (Eqn. 1). The climatology was generated using a harmonic analysis procedure that fit annual and semi-annual signals to the time series of weekly SSTs at each 4-km grid cell:

$$\text{SST}(t)_{\text{clim}} = A \cos(2\pi t + B) + C \cos(4\pi t + D) + E \quad (1)$$

where t is time, A and B are coefficients representing the annual phase and amplitude, C and D are the semi-annual phase and amplitude and E is the long-term temperature mean. Similar approaches have been used for generating climatologies because they are more robust than simple averaging techniques, which

Table 2 Validations of the Coral Reef Temperature Anomaly Database (CoRTAD) data using *in situ* data loggers at different depths and locations.

Location	Country	Depth (m)	Weekly nighttime (Pathfinder v. 5.0)				Weekly CoRTAD			
			Mean diff. (°C)	RMS	<i>n</i>	<i>r</i> ²	Mean diff. (°C)	RMS	<i>n</i>	<i>r</i> ²
42025	United States (Florida Keys)	1–1.5	−0.04	0.57	109	0.94	0.17	0.52	152	0.95
Agincourt	Australia (Great Barrier Reef)	6–9	0	0.54	194	0.91	0.14	0.53	367	0.92
Barracuda Rocks	Bahamas	3	−0.11	0.81	374	0.9	0.07	0.85	471	0.9
Davies	Australia (Great Barrier Reef)	6–9	0.19	0.44	230	0.96	0.26	0.51	317	0.95
DRYF1	United States (Florida Keys)	1–1.5	0.09	0.59	389	0.97	0.32	0.79	465	0.95
East Cay	Australia (Great Barrier Reef)	6–9	0.2	0.45	298	0.96	0.18	0.49	397	0.94
Kure Atoll	United States (Hawaii)	1–1.5	−0.11	0.62	41	0.96	0.04	0.71	61	0.95
Lisianski	United States (Hawaii)	1–1.5	0.23	0.71	25	0.89	0.24	0.67	28	0.9
MLRF1	United States (Florida Keys)	1–1.5	0.01	0.61	604	0.93	0.17	0.69	931	0.93
Myrmidon	Australia (Great Barrier Reef)	6–9	0.01	0.51	247	0.92	0.09	0.51	361	0.93
Night Island	Australia (Great Barrier Reef)	6–9	−0.28	0.72	50	0.89	0.03	0.67	207	0.91
Norman Pond	Bahamas	3	−0.49	0.8	224	0.9	−0.11	0.65	299	0.89
Rainbow Garden	Bahamas	4	−0.39	0.78	376	0.89	−0.01	0.73	512	0.88
St John	United States (Virgin Islands)	9	−0.44	0.51	275	0.72	−0.25	0.66	873	0.76
Turner Cay	Australia (Great Barrier Reef)	6–9	0.28	0.49	264	0.96	0.31	0.52	355	0.96

Data presented include mean diff. (the mean difference between the logger data and the satellite data), RMS (root mean square), *n* (number of observations) and *r*². Logger data came from the Perry Institute for Marine Science (Bahamas), the National Data Buoy Center (Florida Keys, Hawaii), Erich Bartels/MOTE Marine Laboratory (Florida Keys), Peter Edmunds (US Virgin Islands) and the CRC Research Centre (Great Barrier Reef).

can be more susceptible to data gaps from periods of cloudiness (Podesta *et al.*, 1991; Mesias *et al.*, 2007).

SSTs from AVHRR quantify only the temperature of the ‘skin’ of the ocean, roughly the first 10 µm of the ocean surface (Donlon *et al.*, 2007). Most field surveys of coral cover occur between 1 and 15 m depth. To be useful for coupling with coral reef biological data, these temperature data must be relatively accurate beyond the ‘skin’ of the ocean. We used linear regression to examine how data from *in situ* reef temperature loggers compared with data from the CoRTAD. Results from these analyses were then used to determine how accurate the CoRTAD temperature data were at a variety of depths and locations around the world and to assess the selection of day–night averaged data (Table 2).

Temperature anomaly metrics

Several metrics could be used to link the health of the coral reef ecosystem with temperature, including trophic structure, coral or fish diversity or percentage coral cover (Roberts *et al.*, 2002; Newman *et al.*, 2006; Bruno & Selig, 2007). However, we focused our analysis on coral bleaching and disease because they are key drivers of coral decline and their relationships with temperature patterns are more clearly understood (Glynn, 1993; Aronson & Precht, 2001; Bruno *et al.*, 2007). Analyses were performed on two metrics (Table 1): one that is commonly known to lead to bleaching (Glynn, 1993; Liu *et al.*, 2003), and one that is correlated with increased disease severity (Selig *et al.*, 2006; Bruno *et al.*, 2007).

Bleaching is often associated with thermal stress anomalies (TSAs), which are defined as temperatures that exceed the cli-

matologically (long-term average) warmest week of the year for a given 4-km grid cell by 1 °C or more (Table 1, Glynn, 1993). To identify the long-term warmest week, we created weekly climatologies (long-term averages) for each grid cell so that we had 52 weekly long-term averages. The warmest week of these 52 values is considered the warmest climatological week. Therefore bleaching is likely to occur only in summertime because temperatures rarely exceed the long-term average warmest week at any other time of the year. The temperature anomaly thresholds relevant to disease have been studied in only one pathogen–host system, namely white syndrome on the Great Barrier Reef (Selig *et al.*, 2006; Bruno *et al.*, 2007). Changes in white syndrome cases were correlated with weekly sea surface temperature anomalies (WSSTAs), defined as temperatures that are 1 °C or more than the weekly climatological value for that 4-km grid cell. The weekly climatological values can vary substantially since there are 52 different values, one for each week of the year. If the temperature is 1 °C or more than a particular long-term weekly average, it is defined as a WSSTA. These two metrics are quite different in that bleaching-related anomalies are likely to occur only in the warmest weeks of the year, whereas disease-related anomalies can occur at any time of year (Selig *et al.*, 2006; Bruno *et al.*, 2007).

The best metric for predicting bleaching or disease may vary according to location, species and pathogen (Berkelmans, 2002; Selig *et al.*, 2006; Bruno *et al.*, 2007). For example, previous research has found relatively good accuracy with a variety of different bleaching metrics including the maximum SST over a 3-day period (Berkelmans *et al.*, 2004), degree heating weeks (Liu *et al.*, 2003; McClanahan *et al.*, 2007b) or a combination of different stress indices that incorporate heating rate and dura-

tion like the ReefTemp product (Maynard *et al.*, 2008). Although the 7-day averaging approach in the CoRTAD may be too temporally coarse to capture all bleaching events, it is necessary to maintain consistency and minimize gaps in the dataset across broad spatial scales. In addition, the data will be less likely to yield false positives for TSAs and will probably capture most WSTA events, which have a lower temperature threshold.

CoRTAD validation

We found that temperature data in the CoRTAD were accurate when compared with *in situ* loggers over a wide range of coral locations and depths down to at least 10 m (Table 2, Fig. S2). The accuracy of the CoRTAD will depend on local atmospheric (Kilpatrick *et al.*, 2001) and oceanographic conditions, particularly the degree of stratification, local upwelling and depth at a particular location (Leichter & Miller, 1999; Leichter *et al.*, 2006). As depth increases, the CoRTAD is likely to be less accurate because the AVHRR sensor measures only the 'skin' of the ocean, although the Pathfinder processing attempts to create a 'bulk' SST more representative of the temperature at a depth of approximately 1 m.

The CoRTAD typically had $r^2 > 0.90$ when compared with *in situ* temperature loggers (Table 2). The mean difference of the CoRTAD compared with *in situ* loggers was 0.11 °C, which is within the range of the typical accuracy of the *in situ* temperature loggers themselves (± 0.2 °C) (Leichter *et al.*, 2006). In some cases, correlations based on only a few comparisons (< 50) between satellite and *in situ* data (Table 2) may yield artificially low or high correlations.

We chose to calculate the CoRTAD based on day-night averaged data because previous work has shown both daytime and nighttime Pathfinder data to be accurate (Kearns *et al.*, 2000; Casey, 2002; Reynolds *et al.*, 2007). By using a day-night average, we reduced the number of missing pixels by 25%, which allowed us to maximize the number of actual observations and include fewer gap-filled values in the analyses. Nighttime-only data have been the standard for coral researchers because of observed warm differences in the operational AVHRR 50-km daytime data. The operational AVHRR 50-km data have been one of the most widely used datasets for coral reef temperature analyses in the last 10 years (Arceo *et al.*, 2001; Bruno *et al.*, 2001; Strong *et al.*, 2004; McClanahan *et al.*, 2007b). Operational AVHRR data are produced in near real-time and are subject to strong, variable temporal and spatial biases and errors that can only effectively be reduced in retrospective reprocessing efforts like Pathfinder. In addition, operational AVHRR data are produced using different algorithms between day and night. By contrast, Pathfinder 4-km data use the same algorithms from day to night, making the observations more consistent. Previous work has found that daytime Pathfinder data generally have fewer differences than nighttime data when compared with *in situ* measurements (Casey, 2002; Reynolds *et al.*, 2007).

Our use of both daytime and nighttime data in the CoRTAD significantly increased the number of observations with no significant change in the accuracy. The overall mean difference

between the average of nighttime-only and CoRTAD when compared with *in situ* data was less than 0.05 °C (Table 2). On average, the root mean squared (RMS) differences between the two datasets were less than 0.01 °C. Together these results suggest that there is no major difference in accuracy between the CoRTAD and nighttime-only data, but the CoRTAD provides more observations, reducing the need for interpolations, which could make a difference in some locations. Validating the dataset over the whole range of temperatures was important, because disease-related anomalies occur over a wide range of temperatures and bleaching can occur in winter (Hoegh-Guldberg & Fine, 2004; Bruno *et al.*, 2007).

To complement this analysis, we also conducted a validation of the data for our 14 *in situ* logger sites for the summer warm period (warmest climatological week for the *in situ* site ± 6 weeks), when bleaching is most likely to occur. This additional analysis highlights the accuracy of the CoRTAD and the advantage of using a day-night average for increasing the number of actual observations and reducing the need for gap-filling. Across the 14 *in situ* locations, the CoRTAD had a mean difference (-0.05 ± 0.02 °C) less than that of the nighttime-only data (-0.21 ± 0.02 °C). Similarly, the mean RMS was nearly identical (0.64) for both datasets. However, the nighttime-only data had only 62% of the number of matchup observations that CoRTAD had for the *in situ* data.

Region delineations

We delineated regions within ocean basins to better understand how anomaly patterns varied at regional scales (Fig. 1). These regions were different in total spatial area, but they represent general regions of similar biodiversity and biogeography (Roberts *et al.*, 2002), major bathymetric changes or management. Region demarcations are similar to marine ecoregions recently defined by several conservation organizations (Spalding *et al.*, 2007). We restricted our analysis to coral reef regions that were large enough not to cause edge effects in the calculation of anomaly sizes. Thus, we did not include reefs off the coasts of Brazil, West Africa, Bermuda and parts of south-eastern and western Australia.

Coral reef location data

Location data for shallow coral reefs were compiled from a variety of freely available datasets. The initial data were developed from *Reefs at Risk* (Bryant *et al.*, 1998) and *Reefs at Risk in Southeast Asia* (Burke *et al.*, 2002), which used data from the United Nations Environment Programme – World Conservation Monitoring Centre (UNEP-WCMC) as a base dataset. These data were improved with additional data from scientists and government agencies. We then added GIS data from ReefBase and ReefCheck to capture additional reefs world-wide. Data included both polygons and points, which were gridded at a resolution of 1 km. These data were then regridded to 4 km to match the resolution of the CoRTAD data so that 'reef' grid pixels within the CoRTAD could be identified.

Anomaly frequency, temporal duration and magnitude

We calculated both the frequency of TSAs and WSSTAs based on the number of anomalies in each calendar year and cumulatively over the 21-year study. Anomaly magnitude and duration, two important predictors of coral bleaching and disease, may also play roles in the percentage mortality during a thermal event (Glynn, 1993; Winter *et al.*, 1998; Berkelmans *et al.*, 2004). Magnitudes were calculated over the whole time series. We quantified anomaly duration by each anomaly event, which we defined as beginning when ocean temperatures exceeded the threshold value for TSA or WSSTA and ending when temperatures returned below the threshold again. Only 4-km grid cells that had an anomaly and overlapped a known coral reef location were included in the analysis. The mean and standard deviation of anomaly frequency, temporal duration and magnitude were calculated for each region (Fig. 1) using ordinary linear regression models.

Calculation of anomaly sizes

We calculated patterns in anomaly sizes for both WSSTAs and TSAs for the tropics. For each metric, we first created 1096 weekly grids of anomaly presence and absence for all the weeks in the database. We only calculated total area (km²) for anomalies that contained at least one 4-km grid cell that overlapped a known coral reef location. We used the `bwlabel` function in the Image Processing Toolbox in Matlab 7.3 (The Mathworks Inc., 2006) to identify each anomaly and determine whether it was connected to a neighbouring thermal event in any of the eight adjacent grid cells. Anomaly sizes (km²) were then calculated as the total sum of all of the connecting 4-km grid cells.

RESULTS

Anomaly frequency

Anomaly frequencies varied by year and by region for both TSA (bleaching) and WSSTA (disease) metrics (Table 1, Figs 2 & 3). By definition, TSAs have higher temperature thresholds than WSSTAs (Table 1), which generally results in fewer TSAs than WSSTAs. From 1985 to 2005, there were 398,931 TSAs and 1,000,525 WSSTAs. Each anomaly represents 1 week at one 4-km grid cell when the temperature exceeded the TSA or WSSTA threshold (Table 1). Over the 21-year period analysed, TSA frequency varied from a cumulative regional average of 13 anomalies in the Florida Keys to an average of 83 anomalies in the central Pacific (Fig. 2a,b). Across all 4-km grid cells that contained reefs, the average TSA frequency across 21 years was 37 anomalies and the maximum was 444 anomalies. In a typical year, there were an average of one to four TSAs and four to eleven WSSTAs (Fig. 4a,b) on 4-km reef grid cells. However, frequencies changed considerably for some regions during major events, such as the ENSO.

We also examined patterns in anomaly frequencies by year to provide insight into whether more recent years had more TSAs

than earlier years in the database (Figs 5 & 6). In the Pacific, the signature for the 1998 phase of ENSO was very clear (Fig. S3), particularly in the central Pacific, but the Indo-Pacific still had areas that did not have their maximum frequency in that year (Fig. 5). For example, much of the territorial waters of Indonesia between Kalimantan and West Papua experienced greater anomaly frequencies during the 1987–88 ENSO (Fig. 5). In the Caribbean, the Mesoamerican Barrier Reef, Gulf of Mexico and Eastern Caribbean regions all had the highest number of anomalies in 1998 (Figs 1, 6 & S3). There were also a considerable number of anomalies in 2005, particularly in the Antilles region (Figs 1, 6 & S4). Nonetheless, the severity of the 1998 ENSO in the Indo-Pacific and the 2005 event in the Caribbean was clear both in the number of bleaching-related anomalies and in the ratio of anomalies in those years compared with other years (Figs S3 & S4).

Anomaly durations

The duration of temperature anomalies has long been known to increase mortality from bleaching events (Glynn *et al.*, 1988), although its effect on coral disease severity remains poorly understood. Mean TSA and WSSTA durations varied considerably by region (Fig. 4c). The Central America, Persian Gulf, and Pacific Central America regions had the longest mean anomaly durations, averaging approximately 1.8 weeks (Figs 4c, S5 & S6). During the 1998 portion of the ENSO, TSA anomaly durations were markedly higher in Pacific Central America, the South China Sea and the Persian Gulf, where durations averaged approximately 6, 3 and more than 4 weeks, respectively (Fig. S7; Persian Gulf not shown). Although anomaly durations were higher for other regions during ENSO years, they were within the standard deviation of the long-term averages. Anomaly durations for WSSTAs were longer, particularly in Pacific Central America and Taiwan and Japan, where they averaged more than 2 weeks (Fig. 4d). Like TSAs, WSSTA durations were greater during ENSO events in nearly every region except those in the Caribbean (Fig. S8).

Anomaly magnitudes

Absolute anomaly magnitudes between WSSTAs and TSAs were not directly comparable because of the different temperature thresholds. Anomaly magnitudes were highest for the Red Sea and Persian Gulf regions. Typical mean TSA magnitudes over the whole time series varied between 1.4 °C in the western Pacific to 1.8 °C in the Persian Gulf (Fig. 4e). WSSTAs displayed a similar overall pattern to TSAs. Over the whole time series mean magnitudes of WSSTAs ranged from 1.3 °C in the western Pacific to 1.8 °C in the Persian Gulf (Fig. 4f).

Anomaly sizes

Although there were more WSSTAs than TSAs, the frequency distributions of WSSTA and TSA sizes were relatively similar (Fig. 7) with most anomalies having small sizes and a large

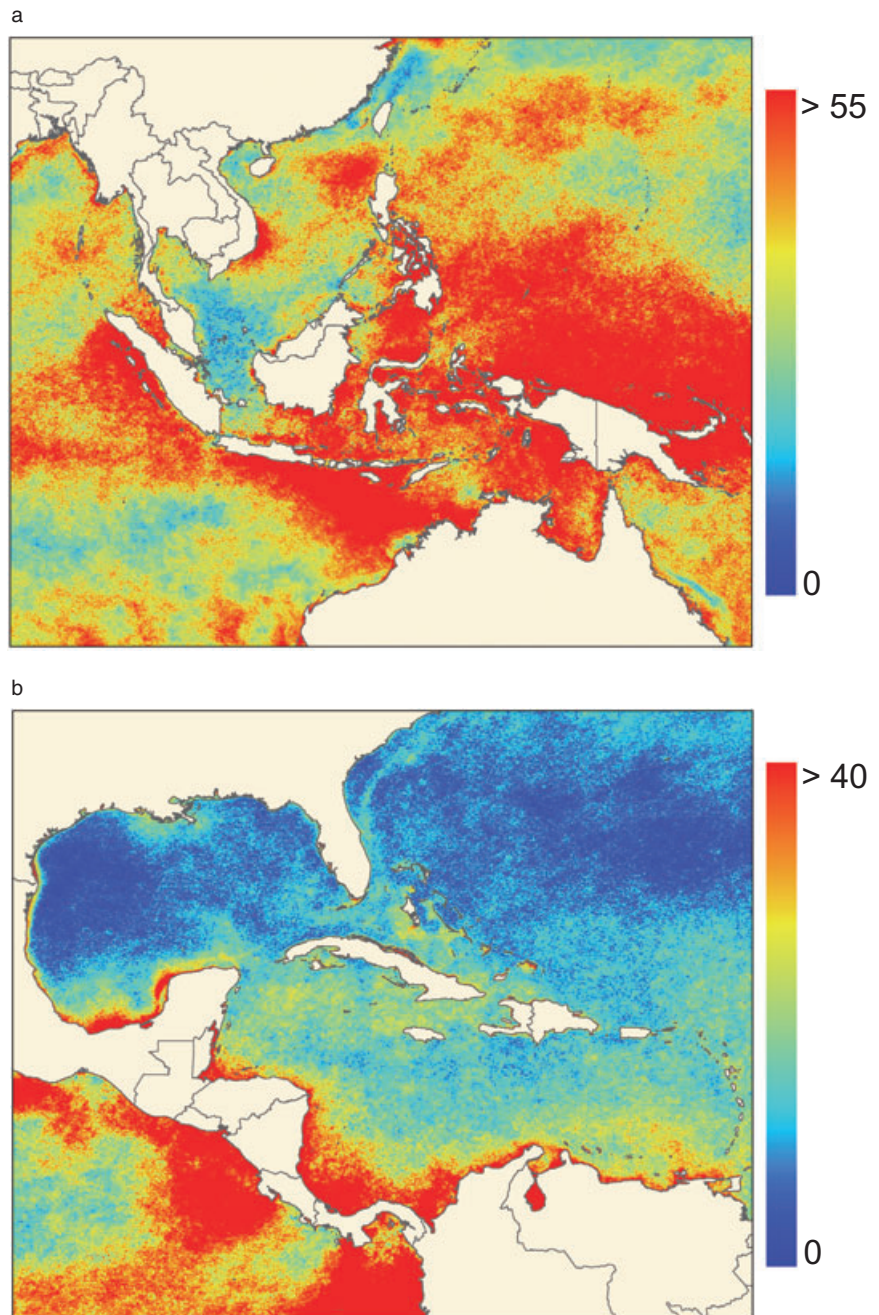


Figure 2 Cumulative number of weeks with thermal stress anomalies (TSAs) (1985–2005) in (a) the Indo-Pacific and (b) the Caribbean.

number of occurrences. Very large anomalies ($> 500 \text{ km}^2$) occurred particularly during ENSO events, but represented less than 10% of the data. For example, 33% of TSAs and 29% of WSSTAs were between 1 and 25 km^2 in size, the smallest size category, which corresponds to roughly one grid cell. More than 90% of TSAs and WSSTAs were $1\text{--}425 \text{ km}^2$ and $1\text{--}500 \text{ km}^2$, respectively.

DISCUSSION

Our work provides the first global- and regional-scale analyses of ocean temperature anomalies related to bleaching and disease across 21 years, a key step in understanding the spatial and

temporal relationships of ocean temperature and biological responses. We found substantial fine-scale variability in temperature anomaly location, size and metrics of intensity between years and regions. Anomalies occurred across the tropics even in years that did not experience a major climatic event such as the ENSO. In addition, we determined that 48% of bleaching-related anomalies and 44% of disease-related anomalies were smaller than 50 km^2 (Fig. 7). Together these results suggest that biological responses to ocean temperature changes could be quite heterogeneous across years, which may complicate efforts to identify consistent thermal refugia.

The fine-scale variability of anomaly events has important implications for coral reef conservation and climate research.

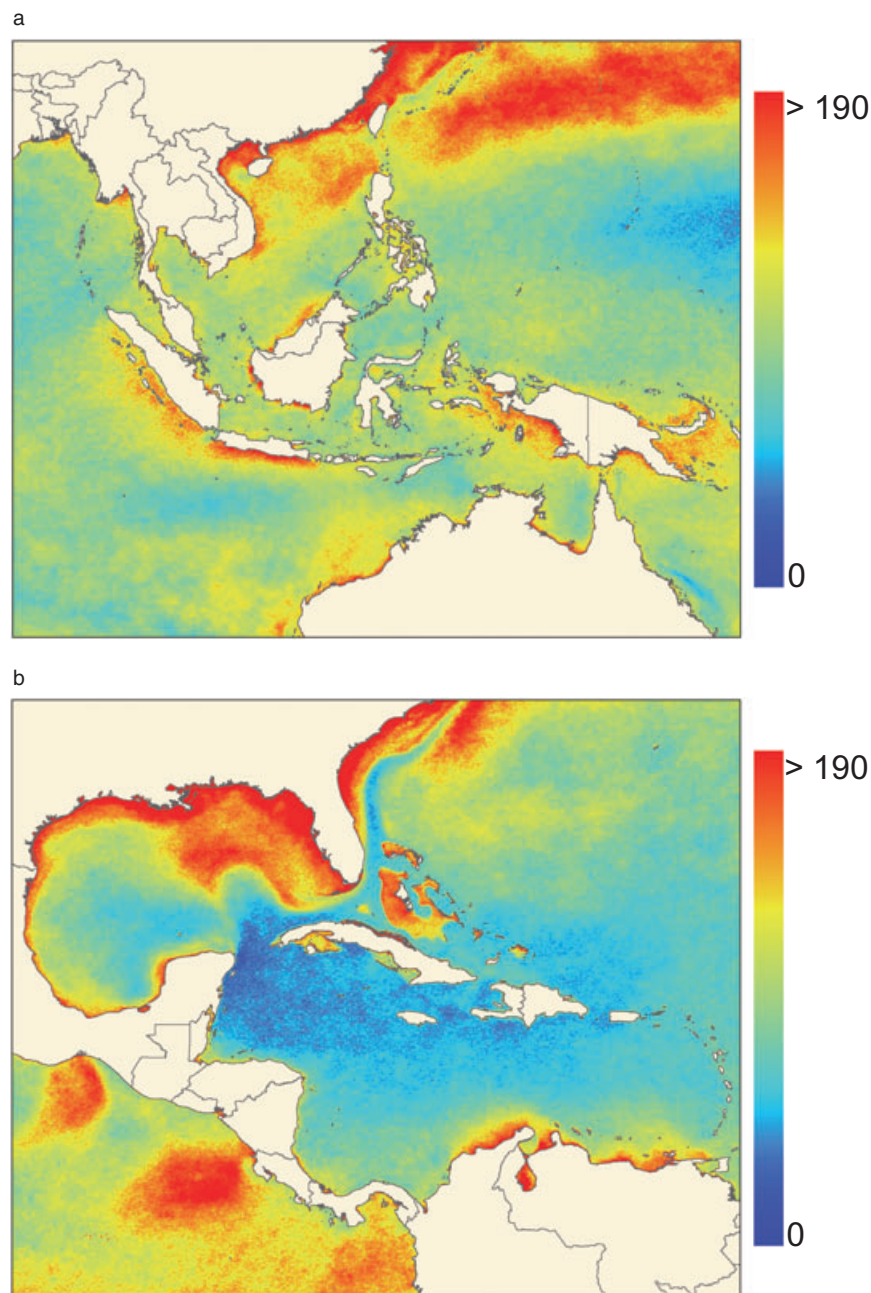


Figure 3 Cumulative number of weeks with weekly sea surface temperature anomalies (WSSTAs) (1985–2005) in (a) the Indo-Pacific and (b) the Caribbean.

Due to the computational constraints of generating global climate models, nearly all ocean climate prediction models are run using at least 100 km by 100 km resolution grids (Rayner *et al.*, 2006; IPCC, 2007; Palmer *et al.*, 2007). The outputs of climate models give critical information about patterns of projected ocean warming, but coarse-resolution data also give the impression of relatively homogeneous patterns of thermal stress. Our results indicate that more than 60% of bleaching- and disease-related anomalies are occurring at scales that are smaller than the resolution of these models. Therefore, finer-scale data are likely to be necessary in order to better understand the biological effects of climate change.

The local and regional variability we observed also provides an opportunity to design management interventions and

monitor both the physical and biological changes predicted to occur with climate change. Some research has advocated protecting coral reefs with particular temperature profiles, which would theoretically enable them to recover more quickly from thermal stress events or remain unaffected (West & Salm, 2003; Obura, 2005; McClanahan *et al.*, 2007a; Graham *et al.*, 2008). Coupled with local data on other important physical and biological factors, our data could be used to identify potential locations for MPAs that may serve as thermal refugia. As an example, we looked at the Antilles in the Caribbean and the Sulu–Sulawesi Seas in the Indo-Pacific (Fig. 8) and calculated how many calendar years the number of TSAs exceeded 1 in each grid cell. This analysis should highlight areas that have had low numbers of anomalies over the time span of our dataset. In the Sulu–

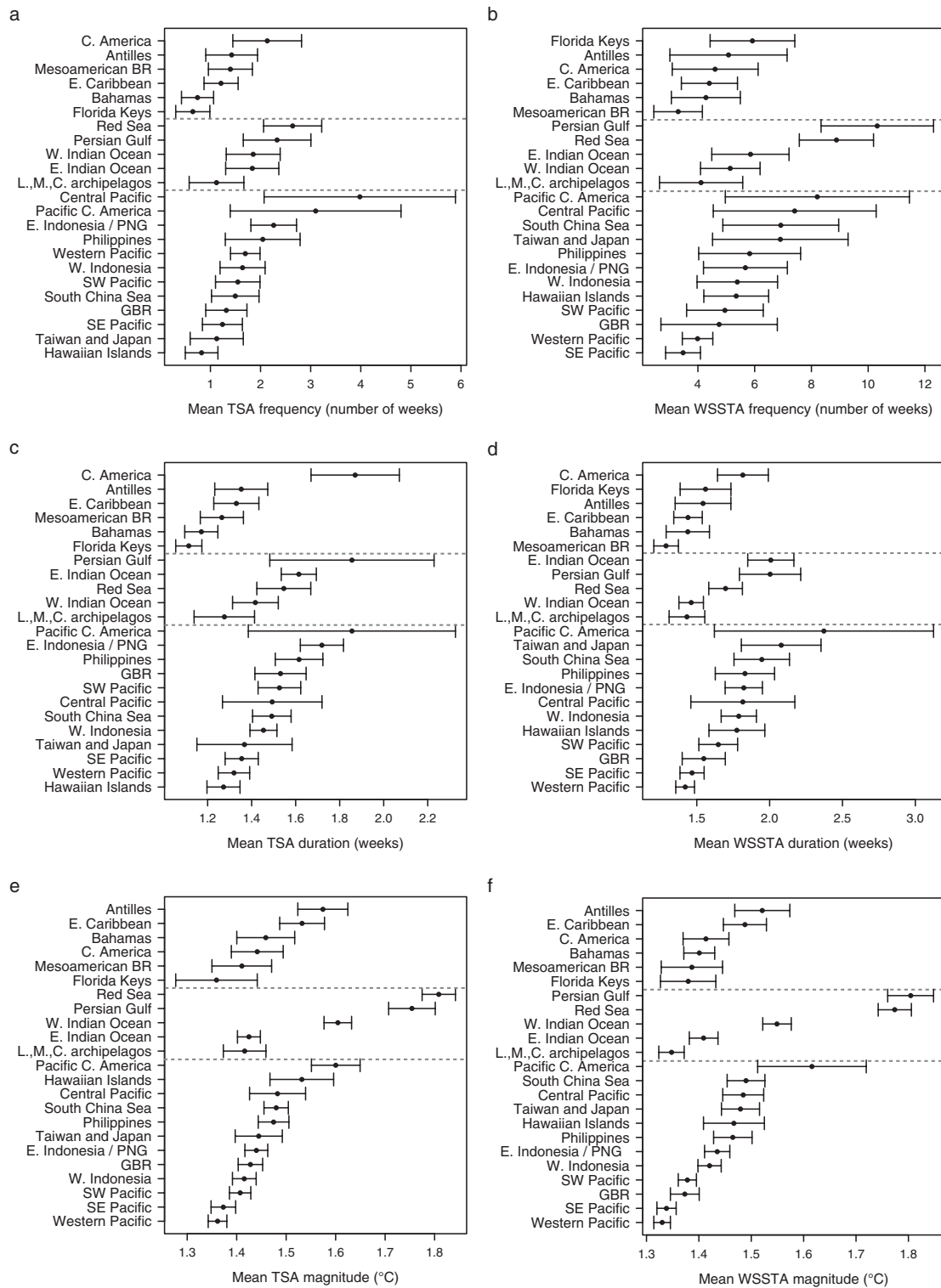


Figure 4 Mean frequency, duration and magnitude of thermal stress anomalies (TSAs) and weekly sea surface temperature anomalies (WSSTAs). Temporal average of mean TSA (a) and WSSTA (b) frequency and 95% confidence intervals (bars) from 1985 to 2005 for the studied regions (see Fig. 1) sorted by ocean basin: Caribbean Sea (top), Indian Ocean (middle) and Pacific (bottom). Mean duration for TSAs (c) and WSSTAs (d) as well as mean magnitude for TSAs (e) and WSSTAs (f) are also shown. C. America = Central America, Mesoamerican BR = Mesoamerican Barrier Reef, E. Caribbean = east Caribbean, W. Indian Ocean = west Indian Ocean, E. Indian Ocean = east Indian Ocean, L., M., C. archipelagos = the Lakshadweep, Maldives and Chagos archipelagos, Pacific C. America = Pacific Central America, E. Indonesia/PNG = east Indonesia and Papua New Guinea, W. Indonesia = west Indonesia, SW Pacific = south-west Pacific, GBR = Great Barrier Reef, and SE Pacific = south-east Pacific.

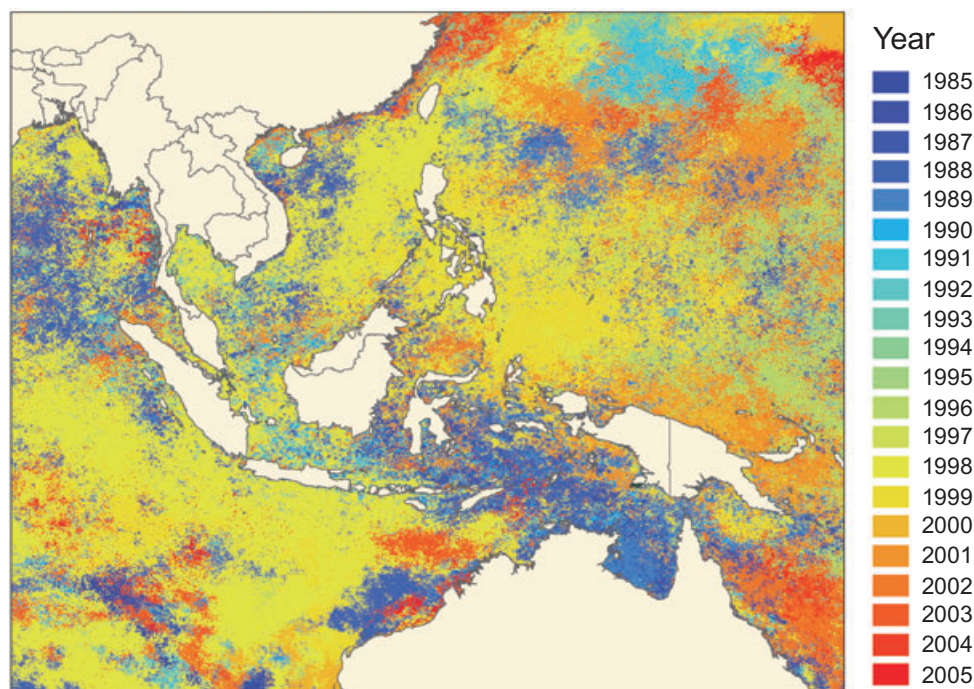


Figure 5 Year of maximum number of thermal stress anomalies (TSAs) in the Pacific. For each grid cell, the year with the greatest number of TSAs was recorded. Although most locations had their maximum TSAs during one phase of the 1997–98 El Niño–Southern Oscillation (ENSO) event (yellow), several other ENSO years including 1988 (light blue) and 2002 are also visible.

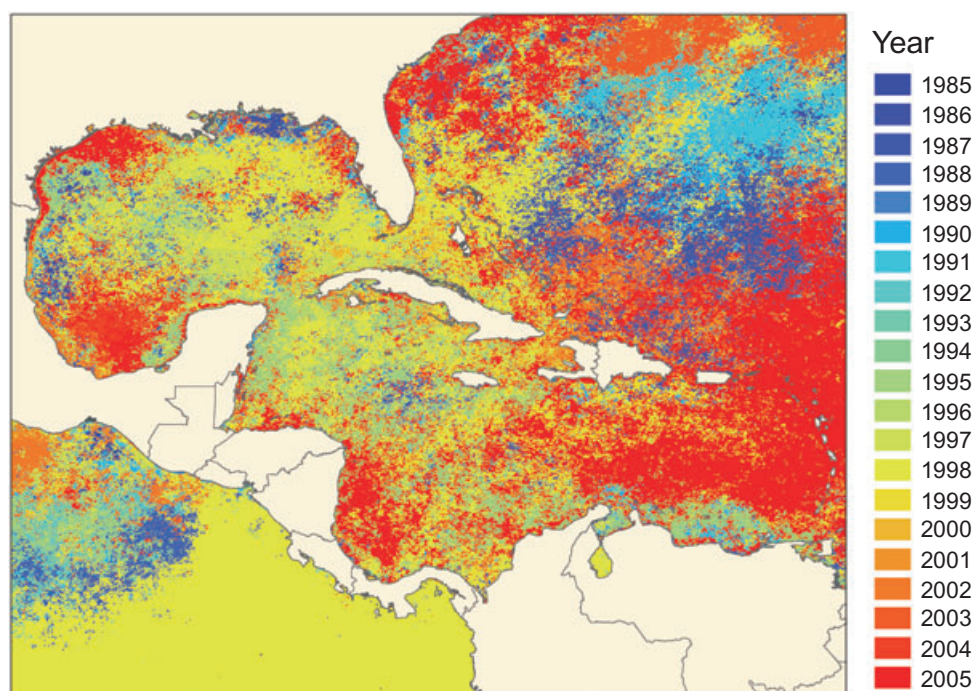


Figure 6 Year of the maximum number of thermal stress anomalies (TSAs) in the Caribbean. For each grid cell, the year with the greatest number of TSAs was recorded. The signature of the 2005 warm event is clearly visible in the Antilles region.

Sulawesi Seas area, there is evidence of considerable variability that could be used for identifying potential refugia (Fig. 8a). The Antilles region, though, was considerably more uniform with most grid cells having 3 or fewer years out of 21 with more than one TSA, indicating that many areas could be thermal refugia

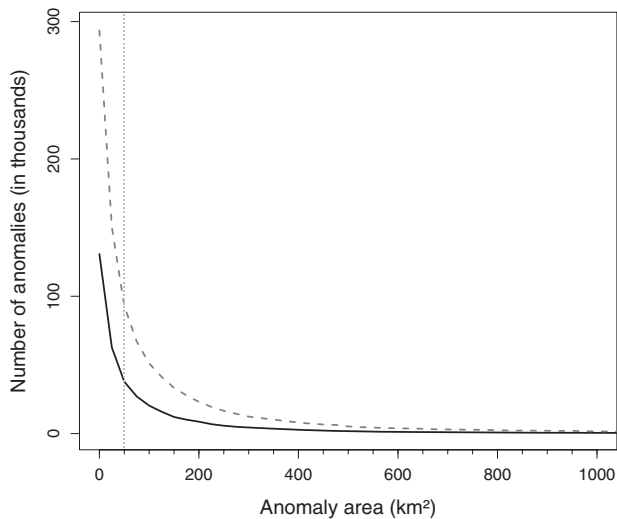


Figure 7 Frequency distribution of anomaly sizes for thermal stress anomalies (TSAs) and weekly sea surface temperature anomalies (WSTAs) for 1985–2005. TSAs are shown with the solid black line and WSTAs with the dashed grey line. Most climate studies occur at a spatial resolution of more than 50 km² (dotted grey line). Raw anomaly areas were categorized into 25 km² bins.

(Fig. 8b). However, during the warm event in 2005, Antilles reefs that had previously experienced very few anomalies, experienced substantial mortality from bleaching (Whelan *et al.*, 2007).

These results, as well as several biological and physical factors, indicate that caution should be exercised when trying to use past patterns of thermal stress for protection prioritization. Indeed, the relationship between past temperature exposure and response to future thermal stress is still relatively unclear (McClanahan *et al.*, 2007a, 2009). Therefore, although our data can be used to identify candidate areas of thermal refugia, during major mass bleaching events even these areas may experience extensive mortality from bleaching and disease.

In addition, the year-to-year variability in temperature anomalies that we observe also suggests that past stress is not necessarily predictive of where and when future thermal stress events will occur. Warm years like 1998 and 2005 clearly led to anomaly frequencies that were higher than the 21-year average for some areas of the Pacific (Fig. S3a,b) and the Caribbean, respectively (Fig. S4a,b). Nonetheless, different areas had greater bleaching-related anomaly frequencies in different years (Figs 5 & 6). For example, during the 1998 ENSO, 21% of reefs in the Indo-Pacific experienced the highest recorded anomaly frequencies. Yet, across much of eastern Indonesia and the Great Barrier Reef, bleaching-related anomaly frequencies were higher during the 1988 and 2002 ENSO events (Fig. 5). The Great Barrier Reef experienced extensive bleaching in 1998, but the most severe and extensive bleaching on record occurred in 2002 (Berkelmans *et al.*, 2004). Similarly, although 33% of reefs in the Caribbean experienced a 21-year peak in number of anomalies during

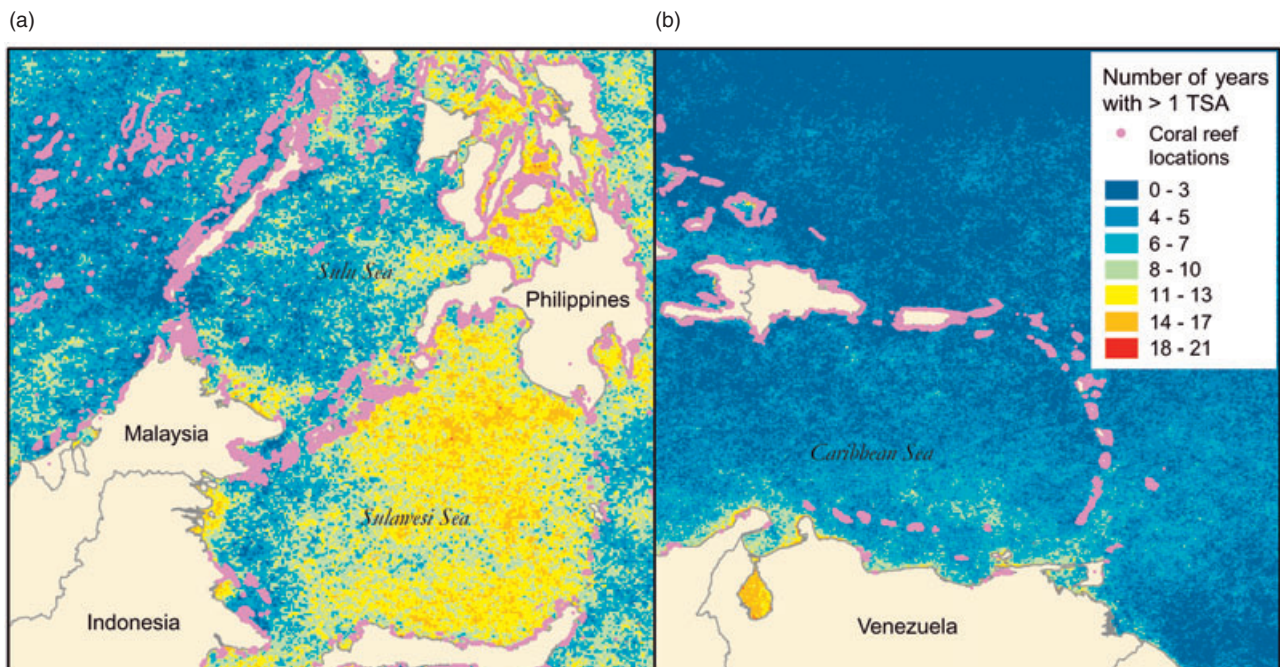


Figure 8 Number of years where more than one thermal stress anomaly (TSA) was recorded from 1985 to 2005 in (a) the Sulu and Sulawesi Seas and (b) the eastern Caribbean. For display purposes, coral reef locations are represented as points, not their actual area.

2005, 18% of reefs had the highest number of anomalies during 1998 (Fig. 6). These results suggest that anomaly frequencies can be spatially and temporally patchy even when associated with large climatic events like ENSO.

Our findings also illustrate that the thresholds that may trigger bleaching or disease are likely to vary considerably by region. Frequencies of both bleaching- and disease-related anomalies (TSAs and WSSTAs) were highly regionally specific (Fig. 4a–f). For example, in the Caribbean, the highest mean frequencies of bleaching-related anomalies were found in Central America, whereas the Florida Keys experienced the highest disease-related frequencies (Fig. 4a,b). Spatial variability between disease- and bleaching-related anomalies could have important ecological and management implications. Regions or locations that are more likely to experience bleaching- versus disease-related anomalies could be more vulnerable to bleaching or disease, respectively. Although the presence of an anomaly is not necessarily predictive of actual changes in coral condition, anomalous temperatures can indicate conditions that may be favourable to the development of bleaching or disease. Future work could focus on identifying region-specific patterns of vulnerability to temperature-driven bleaching mortality and disease outbreaks.

Understanding the scale of variability in temperature anomalies is a critical step towards characterizing ocean temperature patterns, their relationship to ecosystem response, and potential management interventions. Even minor changes in the dynamics of physical factors like temperature can have dramatic effects on ecosystems. For example, coarse-scale analyses in the Caribbean predict that rises of only 0.1 °C in regional ocean temperatures could trigger 35% and 42% increases in the geographic extent and intensity of coral bleaching, respectively (McWilliams *et al.*, 2005). Our work suggests that these general patterns of biological responses to climate change could have substantial regional and local variability due to the fine-scale spatial structure in temperature anomalies. Heterogeneity in temperature anomalies could interact with predicted shifts in community structure and species interactions (Harley *et al.*, 2006) to produce more localized impacts of climate change than are currently resolvable by climate models.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Comparison of the 4-km Pathfinder with other satellite datasets.

Figure S2 *In situ* (black) versus Coral Reef Temperature Anomaly Database (CoRTAD; blue) and nighttime-only data (red).

Figure S3 Severity of the 1998 phase of the El Niño–Southern Oscillation.

Figure S4 Severity of the 2005 warm event.

Figure S5 Mean duration of thermal stress anomalies (TSAs; weeks), 1985–2005 in (a) the Indo-Pacific and (b) the Caribbean.

Figure S6 Mean duration of weekly sea surface temperature anomalies (WSSTAs; weeks), 1985–2005 in (a) the Indo-Pacific and (b) the Caribbean.

Figure S7 Mean duration of thermal stress anomalies (TSAs; weeks) in 1998 in (a) the Indo-Pacific and (b) the Caribbean.

Figure S8 Mean duration of weekly sea surface temperature anomalies (WSSTAs; weeks) in 1998 in (a) the Indo-Pacific and (b) the Caribbean.

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BIOSKETCHES

Elizabeth Selig is an ecologist at Conservation International. Her research focuses on analysing which conservation strategies may be useful in moderating the effects of climate change in coral reef ecosystems. She is also investigating how broad-scale changes in marine and terrestrial ecosystems will affect ecosystem services and human well-being and where conservation efforts should be prioritized.

Kenneth Casey is the Technical Director of the NOAA National Oceanographic Data Center (NODC). He provides the overall technical direction for NODC, which provides scientific stewardship and long-term preservation of ocean data and information. His research focuses on developing climate-quality datasets from satellite and *in situ* observations and applying them to climate change and climate–ecosystem interaction studies.

John Bruno is a marine ecologist and associate professor of marine sciences at the University of North Carolina where his research is focused on understanding and conserving the structure and dynamics of marine communities. His current work investigates the link between global warming and changes in coral reef ecosystems and ocean food webs, the importance of predator biodiversity and marine metacommunity dynamics.

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