Temperature patterns and mechanisms influencing coral bleaching during the 2016 El Niño

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Under extreme heat stress, corals expel their symbiotic algae and colour (i.e. "bleaching"), often leading to widespread mortality. Predicting the large-scale environmental conditions that reinforce or mitigate coral bleaching remains unresolved and limits strategic conservation actions[1,2]. Here, we assessed coral bleaching at 226 sites and 26 environmental variables representing different mechanisms of stress responses from East Africa to Fiji through a coordinated effort to evaluate the coral response to the 2014-2016 El Niño - Southern Oscillation thermal anomaly. We apply common time-series methods to study the temporal patterning of acute thermal stress and evaluate the effectiveness of conventional and new sea surface temperature (SST) metrics and mechanisms in predicting bleaching severity. The best models indicated the importance of peak hot temperatures, the duration of cool temperatures and temperature bimodality explained ~50% of the variance, compared to the common degree-heating week temperature index that explained only 9%. Our findings suggest that the threshold concept as a mechanism to explain bleaching alone was not as powerful as the multidimensional interactions of stresses, which include the duration and temporal patterning of hot and cold temperature extremes relative to average local conditions.

The resilience and persistence of coral reefs to increasingly extreme and changing oceans will depend on how corals respond to stressful exposure events and the factors that influence these responses[2]. Predicting the responses of corals to exposures of light and temperature and increasing climate variability is challenged by how these and other environmental conditions interact in time and space[3,4]. Additionally, the coral holobiont composed of the host, symbionts, and the overall microbiome can further modify responses and be modified by environmental exposure[5,6]. Additionally, exposure to sea surface temperature (SST) histories of acute and chronic exposure can determine future sensitivity or tolerance[7,8]. Therefore, evaluating and comparing thermal impacts over various scales of time and space is a critical challenge needed to identify and guide management interventions and policies for safeguarding coral reefs and associated species.

Factors that influence bleaching have been well studied at local scales, but at global scales there are cases where locally observed spatial and temporal patterns differ and are even reversed among locations[9]. This implies that there may be complex and interactive responses to thermal stresses that can be further modified by the local biological and environmental context, perhaps providing insights into the conditions of spatial refuges for stressed corals. A better understanding of temperature mechanisms and their geographic context is needed to improve predictions of the future state of reefs, as current models largely assume that thermal stress threshold anomalies and subsequent impacts are similar and modified by a limited number of adaptive responses of corals[10]. To address this assumption, we used multivariate models to test common and previously untested variables of acute thermal exposure against our observations of bleaching responses, with and without geographic covariates (Table 1). In developing these temperature models and mechanisms, we also derived indices from daily time series SST to describe thermal stress experienced by reefs during an acute, short-term window (90 days), similar to indices that are used widely in hydrology and stream ecology. The ability of metrics to predict bleaching response in coral communities was measured in a coordinated field survey effort in 2016.

All coral bleaching observations were conducted using the same method and within 21 days following peak thermal anomalies. We evaluated bleaching responses at 226 sites across 50 degrees of latitude and 140 degrees of longitude largely through the tropical belt of the Indian and Pacific Oceans (Figure 1a-e, Methods, Supplementary Table 1). In 2016, only 32% of the sites (n = 71) experienced four or more Degree-heating Weeks (DHWs, °C-weeks) measured at the NOAA ~5x5 km satellite resolution, which is the common thermal stress index used for predicting bleaching. However, in 56% of the sites (n = 127) we observed substantial bleaching (>5 bleaching intensity score), even when satellite-derived DHWs were lower than an expected bleaching threshold of 4 DHWs (Figure 1f-g; Supplementary Figure 1). Observed bleaching responses were spatially patchy (Figure 1a-e), suggesting that unevaluated microhabitat and local currents may have weakened the ability of coarser satellite metrics to predict *in situ* bleaching (Supplementary Figure 2 and Supplementary Table 2).

We evaluated a number of hypothesized mechanisms associated with coral bleaching using 26 variables that included: thermal stress exposure and patterning, habitat, depth, management, and coral community composition (Table 1). To assess warm and cold temperature extremes at each site, we characterized sea surface temperatures (SSTs) in the 90 days prior to our surveys at each site. From each site, we quantified the frequency, duration and patterning of extreme temperatures based on the 10th SST quantile ('cold spells') and 90th SST quantile ('hot spells'). All variables and hypothesized mechanisms are described in Table 1. We quantified the effects on coral bleaching intensity using two approaches: boosted regression trees (BRT) and generalized linear mixed-effect methods that compared and selected best models among 2372 possible models. We also accounted for the possible effect of the non-random sampling of geography on observed bleaching impacts, by including longitude and latitude as independent and interactive covariates with thermal metrics in all models (Supplementary Figure 3).

Longitude, as a covariate, had the highest relative influence as a single variable in both the BRT and linear mixed-effects models (Figure 2a; Table 2). However, geographical bias in our data limits the extent to which we can make credible tests and deductions on geographical gradient. Furthermore, the importance of longitude has not been identified in past studies and therefore requires future evaluations using geographically balanced samples. The strongest linear models were those that included interactions with temperature bimodality, extreme warm temperatures, and the duration of extreme cold temperatures with longitude (Fig. 2b; Supplementary Table 3). These results were consistent for inferences from both BRT and linear multi-model approaches (Figure 2). When geographic variables were excluded, mean extreme warm temperatures and the mean and cumulative DHWs were the strongest variables associated with increased bleaching (Figure 2c). Nevertheless, our findings indicate complex and interacting responses of temperature and geography for coral bleaching.

Model quality increased substantially when geography was included (∆AICc improvement of 38). For example, the top models achieved predictability (R^2) of ~50%, and had a greater strength of evidence than models composed of single variables (Table 2; R^2 based on two resampling approaches, see Methods). Independently, single SST variables were relatively weak predictors of bleaching (Table 2). For example, the number of extreme warm events and rate of daily temperature rise during extreme warm events predicted only 13% of the variance (Table 2). However, four model combinations predicted >45% of the total variance (Table 2; Supplementary Table 3) when these variables were combined with geographic covariates of longitude and latitude, which are likely proxies for other environmental and historical conditions. Several models suggested conditions that reduce bleaching, including interactions between extreme warm temperatures and bimodality, and between the duration of cold events, the mean extreme warm temperatures and longitude (Fig. 2b,c). DHW metrics have historically been good predictors of bleaching[4,11] but were not chosen among the top multivariate models (Table 2; Supplementary Table 3) and as a single variable, mean and maximum DHW metrics predicted only 5 and 9% of the variance, respectively.

Models with the strongest ability to predict bleaching comprised the interaction of mean SSTs of extreme warm events with temperature bimodality, low spell duration and longitude (Table 2; Supplementary Table 3). Across our sampled sites, coral bleaching was highest from East African to the central Indian Ocean and declined towards the Coral Triangle and Fiji, moderated by interactions between temperature variables (Supplementary Figure 4). The bimodality coefficient had more impact in the central to western Indian Ocean and declined to little effect east of the western edge of the Coral Triangle. These results suggest that the coral responses to heat stress are not constant but can vary in terms of other stressors and geographically. This is likely because geography can be a proxy for past thermal changes, local stressors, and other historical and present environmental conditions (Table 1). Compilations of coral bleaching responses pooled on large spatial scales suggest that bleaching is, for example, less frequently reported in the western warm pool Pacific[12,13] but there are important exceptions[14]. An increasing number of studies are also showing that the same coral taxa are becoming more tolerant to temperature extremes with repeated stress events, which is likely to be a local response based on complex and interacting factors[15,16].

The strength of DHW predictions have been variable in the past[4,17,18], and, while there are instances where DHW predictions are good, as in Australia's Great Barrier Reef (GBR) during the 2016 bleaching event ($R^2 = 0.55$)[2], our study indicates that prediction success is highly dependent on geographical context. Some of this variation may be due to the inability of satellite data to predict the temperatures that corals experience *in situ* (Supplementary Figure 2). Results also indicate that many currently unmeasured environmental variables represented by geography are important[19].

At the core of the DHW metric, is the assumption that the main mechanism of bleaching is a threshold where symbionts are lost when temperatures exceed local historical summer maximum temperatures. This assumption may be true for some taxa and locations, but our results also suggest a more complex pattern of stress and bleaching responses. Notably, stress does not always act in a single temperature threshold-dependent way, but can be associated with the frequency, duration, and patterning of both high and low extreme events at local sites. For example, corals in 2016 seemed to be unable to tolerate a combination of complex interacting stressors even if thresholds were not surpassed (i.e., high bleaching at low DHWs; Fig. 1, Supplementary Figure 1). Consequently, common bleaching metrics based on thresholds may fail in future circumstances where combinations of complex stress initiate the loss of symbionts or historical exposures promote greater resistance to heat stress. Understanding past and emerging mechanisms of coral bleaching are, therefore, critical for predicting potential strategic refuges for coral reefs[20].

Future analyses should focus on how extreme temperatures interact with location to improve the critical global prediction of bleaching and reef status. For example, more severe bleaching was predicted by the exposure of corals to two distinct temperatures regimes (bimodality). The bimodality metric used here is not the pre-exposure to severe SSTs shown to modify bleaching responses in the GBR[7], which was not observed in our sites. Rather, bimodality characterizes the distribution of temperatures within a 90-day window, which may represent stressful (rather than acclimating) thermal variability for corals (Supplementary Figure 5). We did not find evidence that bleaching was reduced with pre-exposure acclimation; rather, bimodality increased bleaching in the western but not eastern coral reefs of our East Africa-Fiji transect (Supplementary Figure 4).

Ultimately, coral bleaching responses can be shaped by both long-term and recent histories of disturbance. For example, time series studies have found that many sensitive reef corals have been replaced by weedy and stress tolerant taxa and genotypes following repeated bleaching events[16,21]. Many Indian Ocean and equatorial locations surveyed experienced prior thermal stresses in 1983, 1988, 1998, 2005, 2010, and 2013. These years produced severe bleaching in some reefs but less so in the GBR, where 2016 was among the most severe bleaching years[2]. Thus, we hypothesize that the types of stresses that initiate bleaching at any place and time will change based on previous exposures to thermal stresses and interacting factors. As thermal stresses expand and encounter corals less exposed, threshold metrics may still be predictive[13,22]. Conversely, threshold metrics may increasingly make poorer predictions for corals previously and frequently exposed to thermal stresses[15,16].

Future predictive models should reconcile the spatial variability of the environments and taxa-specific responses with those of the coarse resolution satellite temperature predictions (Supplementary Table 2). Corals experience temperatures that differ from those measured by satellites, and their responses also integrate acclimation, adaptation, and histories of stress. These mechanisms are used to explain coral tolerance to increasing heat but it is more difficult to explain why many of our corals bleached when reported DHWs were low to moderate. First, chronic SST stresses prior to the 90-day acute evaluations may increase coral sensitivities[8]. Second, a number of other non-thermal factors, such as sunlight, turbidity, and water flow and quality strongly influence bleaching[16]. Third, different bleaching responses may arise from duration and magnitude of stress, which are unique components of stress that are poorly reflected by the DHW metric[23]. Finally, some variance can be explained by the accuracy, spatial resolution, and frequent underestimates of satellite relative to *in situ* temperatures in different reef types and habitats (Supplementary Figure 2)[18]. Predictions will not be improved without further evaluating these issues as well as the changing thermal sensitivity over time at appropriate spatial scales[24]. Ultimately, our results indicate that coordinated field and environmental monitoring can document emerging and changing patterns of coral responses to global climate change.

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Supplementary Information is available on the online version of this paper.

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Data availability Data are available at Knowledge Network for Biocomplexity, https://knb.ecoinformatics.org. doi:10.5063/F1WQ024C

Code availability R code is available on GitHub, https://github.com/WCS-Marine/2016-bleaching-patterns

Figure 1. Indo-Pacific scale and severity of coral bleaching during the 2016 El Niño – Southern Oscillation event. a. The severity of coral bleaching at 226 sites in 12 countries measured from standardized underwater surveys (n = 60,591 coral colonies) during the peak of the warm season. Higher bleaching intensity scores indicate more frequent and severe bleaching (see Methods). Grey scale indicates NOAA bleaching alert levels at each site in 2016. **b.** Frequency distribution of 2016 maximum DHWs in the 90-days prior to each survey. **c.** Frequency distribution of bleaching intensity scores for the 226 sites; colours are the same as in **a.**

Figure 2. Effect of environmental variables on coral bleaching. a. Relative influence of variables on bleaching response from a boosted regression tree approach. **b.** Model-averaged parameter estimates and 95% confidence intervals of top models (<2AIC) of environmental and site factors that predict bleaching intensity **c.** The same approach after excluding geographic variables of longitude and latitude. Solid and transparent bars indicate significant and non-significant effects based on 95% CI from a linear mixed-effects modelling approach. Colours indicate variables associated with reef context (grey: location, depth, habitat and management) or acute temperature stress (red).

Table 1. Models, hypotheses, and results for main drivers of coral bleaching across reefs in 11 Indo-Pacific countries during the 2016 El Niño – Southern Oscillation event. Temperature characteristics calculated for each of the 226 survey sites during the 90-day window of acute thermal stress that preceded each underwater survey to assess coral bleaching.

Variable	Model/Mechanism	Variable	Description	Range	Conclusions
Geography	Historical environmental conditions will modify responses to thermal stress[13,24]	Longitude and Latitude	Geographic positions	140° x 50°	Strongest variable and significantly modified responses to heat stress
Excess heat	The accumulation of temperature above a threshold (summer maximum + 1°C) is a standard model to predict coral bleaching, assessed as Degree Heating Weeks (DHWs)[10,25]	Maximum DHW	Maximum Degree Heating Weeks (DHW) during 90 days prior to survey date	0 - 17.2	Significant positive but weak effect, and interacts strongly longitude and mean high spells
		Average DHW	Average DHW during 90-day period prior to survey date	0 - 13.4	Significant positive but weak effect, and interacts strongly bimodality and mean high spells
Early acute temperature acclimation	Early exposure to warm water can prime and acclimate corals to subsequent extreme temperature anomalies, reducing bleaching[6]	Degree Heating Days (DHDs)	Cumulative sum of DHD >1° C threshold in the first 60 days of the 90-day period prior to survey date	0 - 60	Not commonly observed at our sites or significant
Temperature distributions and bimodality	Temperature variability and thermal histories can influence protection or sensitivity of bleaching[6,9,26]	Bimodality coefficient	The bimodality coefficient has a range of 0 to 1 where a value greater than 0.55 suggests bimodality. The maximum value of one identifies a bimodal distribution	0.34 - 0.85	Weak single variable effect but moderate when combined with longitude and mean high spell peak
		Bimodality ratio	A ratio of the two identified bimodality peaks to show the difference in magnitude of the bimodal temperature patterns	0 - 4.43	Weak effect when combined with depth and maximum low spells
Extreme warm temperatures	Reefs experiencing more frequent, more extreme or more variable warm extreme events longer-duration warm events, and faster warming trends will deplete energy reserves and increase the severity of bleaching[4]	High spell events	Total number of temperature events that exceed the 90th quantile of temperatures at each site. Events that occur less than 5 days apart are considered to be within the same event	0 - 4	Not significant
		High spell duration, days	Average duration (days) of high spell events	0 - 91	Significant non-linear effect where bleaching peaks at ~35-day duration
		High spell peak, °C	Average temperature of high spell events	27-31	Moderate independent effect; important with geography

		High spell rate of rise, °C/day	Average rate of daily temperature rise (°C/day) during high spell events	0 - 0.32	Weak single variable effect but important when combined with other variables
		SD high spell peak, °C	Standard deviation of temperature of high spell events	0.4-1.4	Moderate single variable effect but important when combined with geographic variables
Extreme cool temperature	Cool temperature extremes during warming events can provide a reprieve from bleaching -- longer-duration low spells hypothesized to reduce bleaching[27]	Mean low spell duration, days	Average duration of low spell events that fall below a 10th quantile of SSTs at each site within 90 days prior to survey	1.43 - 11	Weak single variable effect but important when combined with longitude and mean high spell peak variables
Coral community composition	Community composition can influence overall bleaching severity and mortality. *Acropora*-dominated communities typically show greater sensitivity to warm temperature anomalies and bleaching than massive *Porites* species[25,28]	Coral community composition	Multivariate index of coral community composition based on a Correspondence Analysis (CA1). High values indicate dominance by *Acropora*, low values indicate dominance by massive *Porites* corals	-1.79 - 1.33	Weak effect but interacts with location and depth
		Coral community susceptibility	A weighted score of the relative abundance multiplied by bleaching sensitivity in 2016	18.9 – 36.7	
Depth	Deeper reefs have less surface irradiation and potentially cooler waters than predictions from surface measurements and are expected to bleach less than shallow reefs but shallow reefs can have more background temperature variability that promotes acclimation[25,29]	Depth, m	Depth of survey, meters	1 - 18	Weak effect but interacts with location and coral community
Habitat	Lagoons and reef flats can have warmer more variable environments with more potential for acclimation and taxa that acclimate compared to other exposed habitats with more environmental stability[30]	Habitat	Habitat was classified as: reef slope, reef crest, reef flat, lagoon or back reef, reef channel or submerged bank.	Bank, channel, crest, flat, lagoon, slope	Not significant, but associated with mean high spell peak

Management	No-take marine reserves reduce destructive fishing practices that may promote competitive coral life histories sensitive to thermal disturbances[12]	Management	Management was classified as open access (fished), restricted (some gear or access restrictions) or no-take (full restriction on fishing with high compliance)	Open, restricted, no-take	Weak single effect but moderate when combined with longitude and mean high spell peak

370

Table 2. Multivariate and single variable models of bleaching observations in 2016. Multivariate models are ranked using Akaike's information criteria (ΔAICc); the three top models (ΔAICc < 2) are highlighted in bold. We also present R^2 as an indication of each model's predictive ability. The multivariate models are a subset of the 2372 competed models, and the presented model is the strongest multivariate model identified by ΔAICc for its single variable. Supplementary Table 3 presents more information on the top two models.

Multivariate model	ΔAICc	Multivariate model R^2	Single variable	Δ AICc	Single variable model R^2
Longitude x Bimodality coefficient x High spell peak	**0.0**	**0.47**	**Longitude**	**29.2**	**0.19**
			Bimodality coefficient	**33.8**	**0.07**
			High spell peak	**29.0**	**0.08**
Longitude x High spell peak x Low spell duration	**1.3**	**0.57**	**Low spell duration**	**31.9**	**0.04**
Longitude x Latitude x High spell peak	6.0	0.55	Latitude	32.2	0.16
Longitude x Maximum DHW x High spell peak	8.1	0.49	Maximum DHW	29.9	0.09
Longitude x High spell rate of rise x High spell peak	8.4	0.34	High spell rate of rise	35.9	0.13
Average DHW x Bimodality coefficient x High spell peak	10.5	0.23	Average DHW	31.6	0.05
Longitude x Depth x Coral community	11.3	0.16	Depth	29.0	<0.01
Longitude x Depth x Coral community	11.3	0.16	Coral community	35.8	0.01
Longitude x High spell peak x SD high spell peak	12.0	0.41	SD high spell peak	34.9	0.02
Longitude x High spell peak x Management	15.9	0.30	Management	36.2	0.01
Longitude x Coral community susceptibility x High spell peak	16.0	0.33	Coral community susceptibility	30.7	0.02
Average DHW x Bimodality x High spell rate of rise	16.4	0.01	Bimodality coefficient	30.4	0.02
High spell events x High spell peak x Low spell duration	20.9	0.08	High spell events	35.9	0.13
Longitude x High spell duration x Low spell duration	21.3	0.26	High spell duration	35.9	0.17
Depth x Bimodality ratio x Low spell duration	21.5	0.01	Bimodality ratio	32.2	0.01
Longitude x High spell peak x Degree Heating Days	22.9	0.34	Degree Heating Days	35.2	0.02
High spell peak x Habitat	29.0	0.13	Habitat	37.7	<0.01

Supplementary Information for

Temperature patterns and mechanisms influencing coral bleaching during the 2016 El Niño

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The file includes:

Methods
Supplementary Figures 1-8
Supplementary Tables 1-3

Methods

Study sites and field methods

Between March and September 2016, we conducted 235 bleaching surveys in 12 countries across the Indian and Pacific Oceans using a standard rapid roving observer methodology. To evaluate how survey timing was related to accumulated temperature stress, we extracted daily 5 km Degree Heating Week time series from NOAA Coral Reef Watch for each site from 1 September 2015 to the date of survey and calculated the date of maximum observed DHWs for each site. Based on these satellite temperature time-series, 45 sites did not experience excess heating (i.e., 0 DHWs). For the remaining 190 sites, we calculated the number of days between the date of the bleaching survey and the date of maximum DHW. For 181 sites, bleaching surveys occurred within 21 days of maximum DHW, well within suggested timelines to assess bleaching-related stress and mortality for corals (~30 days[31]). Nine sites where bleaching surveys were assessed >21 days after maximum DHW were excluded from further analyses, leaving 226 sites across 11 countries for further analysis. Further details on study reefs and bleaching notes are provided in Supplementary Table 1.

During each survey, an observer assessed coral bleaching across a series of haphazard replicate quadrats (~1.5 m^2) to assess the frequency and severity of bleaching. Within each quadrat, hard coral colonies (>5 cm) were identified to genus (using Veron's classifications[32]), and scored for bleaching severity using the following categories: $c0$ – normal; $c1$ – pale; $c2$ – 0-20% bleached; $c3$ – 21-50% bleached; $c4$ – 51-80% bleached, $c5$ – 81-100% bleached; $c6$ – recently dead. From each survey, we calculated the relative abundance of coral colonies with each category. Within each quadrat, observers also estimated the average percent cover of live hard coral, live soft coral and macroalgae (e.g., fleshy or calcareous algae taller than filamentous turf). On each survey, observers conducted an average of 17.8 quadrats (±4.7 SD). In some surveys, quadrats were recorded using photographs and colonies identified and scored for bleaching *post-hoc* by the observer. Observers also recorded depth, habitat type, and management for each survey site.

Bleaching metrics

For each survey, we calculated two standard bleaching metrics: (1) the percentage of bleached coral colonies, and (2) bleaching intensity, a weighted average of the relative abundance of coral colonies within each category of bleaching severity (Fig. 1b):

$$\text{Bleaching intensity} \quad = \frac{\left((0\times c0)+(1\times c1)+(2\times c2)+(3\times c3)+(4\times c5)+(5\times c5)+(6\times c6)\right)}{7}$$

Both metrics of bleaching produced similar results, and both provide simple, repeatable, and comparable methods to quantify bleaching. We chose the intensity metric for further analyses as it is separated sites across a wider bleaching gradient and resulted in better distinctions for modelling. On each survey, we evaluated total bleaching intensity across all coral colonies.

Temperature and site covariates

At each location, we calculated a suite of temperature characteristics informed by specific hypotheses of how thermal stress affects corals (Table 1). Excess thermal stress is among the commonly used models to predict coral bleaching[33-35]. To assess thermal stress, we downloaded daily Degree Heating Weeks (DHWs) that are based on a rolling 14-day average from the NOAA Coral Reef Watch website[33] and calculated the maximum and mean DHWs during the 90-days prior to each survey. We also derived an estimate of early exposure to thermal stress as Degree Heating Days (DHDs), calculated as the sum of DHDs during the first 60 of the 90-day SST time series; an early pulse of exposure to high temperatures has been hypothesized to provide corals with a protective early pre-bleaching stress exposure[7]. All temperature-based variables, including DHW, were derived from NOAA daily SST products[33].

To characterize other aspects of the acute thermal environment and relate it to our *in situ* bleaching observations, we downloaded SST time series for 90 days prior to the date of sampling for each survey[33]. Gap-filled daily sea surface temperature (SST) data based on NOAA AVHRR satellite observations at a resolution of ~5 x 5 km grid cells. At 13 sites in four countries (Tanzania, Kenya, Indian and la Réunion, France), we compared NOAA 5-km daily SSTs records to in situ temperature gauges placed on the study reefs. We used linear regressions and dynamic time warp analysis to compare time series of satellite and in situ records, using the package '*dtw'* package in R[36] (Supplementary Table 2).

To describe the frequency, duration and other characteristics of extreme warm and cold temperature events, we used Hydrostats package in R[37] to calculate a suite of indices for daily time series data that are widely used in hydrology and stream ecology. These included the frequency and duration of high and low 'spells' – or extreme events – during each 90-day time series (Table 1). We defined 'spells' as extreme SST site-specific characteristics that were greater than the 90th quantile of SST temperatures ('warm spells') or lower than the 10th quantile ('low spells'). Spell events within five days were considered as one event for purpose of calculations. After identifying the high and low spells at each site, we calculated factors to describe the frequency (count), duration, and rate of temperature change within extreme spell events for both warm and cold extreme events, and the maximum temperature within high spells (Table 1).

Studies have suggested that fluctuating temperature distributions prior to bleaching may expose corals to either additional stress or pre-stress acclimation that acts to reduce or protect corals from subsequent thermal stress[7,8]. To evaluate these possibilities we assessed the time series of SSTs at each site by visual inspection but failed to find patterns described to produce pre-stress acclimation[7,]. Thus, we used bimodality metrics during the 90 days prior to each bleaching survey to evaluate bimodal variability in the distributions.

Bimodal probability distributions[38] are defined by two unambiguous peaks of temperatures, cool and hot, separated by an abrupt boundary, in contrast to unimodal (Gaussian) distributions of temperature that fall along a normal distribution from cool to hot temperatures. To quantify bimodality characteristics, we computed two metrics: bimodality coefficient and bimodality peak proportion for each site[38].. The bimodality coefficient measures the presence of bimodal distributions with a range of [0,1]), where a value greater than 0.55 suggests bimodality; the maximum value of one ("1") can only be reached when the distribution is composed of separate two-point masses (Supplementary Figure 5). The bimodality peak proportion describes the ratio between the two peaks, where values greater than 0 indicate the amplitude of the hot peak dominates that of the cool peak. These multi-modality metrics reflect probability distributions and not the temporal patterning within time-series and were calculated using the package *modes*[39] package in R.

A correlation matrix was used to evaluate the relationships between all temperature factors, and collinear variables were accounted for in the following analyses[40] (see *Data Analysis;* Supplementary Figure 6).

Community composition

Coral community composition is an important predictor of bleaching, for example more bleaching may occur when a coral assemblage is dominated by bleaching-susceptible coral taxa. Here, we estimated two metrics of community composition to use as predictor variables in the models. First, we estimated a multivariate metric of coral community dominance from bleaching-sensitive *Acropora* corals to less-sensitive massive genera, such as *Porites*[34,4]. To estimate this metric, we calculated the relative abundance of each hard-coral taxa observed during each survey and used a Correspondence Analysis (CA) ordination to distinguish a strong gradient from *Acropora* to *Porites*-dominated communities. For each survey, we extracted the value of CA1 as a covariate of community composition. Second, we calculated a metric of community susceptibility to bleaching, estimated by multiplying the observed bleaching intensity for each taxon (based on all 2016 surveys) by the numbers of individuals of that taxon, and summing for all taxa. Sites with more bleaching susceptible taxa would have higher scores of community susceptibility than sites with more bleaching-tolerant taxa[4].

Data analyses

To evaluate our sampling distribution, we compared our empirical with a random sampling of reefs based on the Reefs at Risk mapping[41]. Random sampling of the reefs used the package *dismo*[42] in R to generate coral reef sites on the 500-m resolution the tropical coral reef grid, resulting in a total of 19,700 sites randomly distributed in the same latitude and longitude windows as the empirical sampling. This process indicated higher sampling in East Africa relative to the random distribution (Supplementary Figure 3). To account for the non-random distribution of sampling, longitude and latitude were included as a covariates in all further analyses. We also included the location of sampling as a random intercept in our linear models, where location was defined as an alternative hierarchical structure to country to account for more appropriate geomorphology and environmental groupings of survey sites, as compared to national socioeconomic boundaries (see Supplementary Table 1). Spatial autocorrelation was evaluated using Moran's I and Mantel tests and found to be accounted for by our modelling approaches (Supplementary Figures 7 and 8).

We evaluated hypothesized models and mechanisms of coral bleaching (Table 1) using two quantitative approaches: boosted regression trees (BRTs) and generalized linear mixed-effect models. Boosted regression trees are an ensemble method that relates response variables to predictor variables by using recursive splits 'boosted' with multiple trees[43]. They also account for higher-order interactions and nonlinear relationships and are a complementary approach to linear modelling. We used generalized linear mixed-effect models to examine the direction and magnitude of the relationships between the environmental and site covariates with bleaching intensity. Models with fit using Beta regression models as bleaching intensity is a continuous variable distributed from 0 to 1[44].

Before applying statistical models, we constructed models using all possible combinations of the covariates (up to three covariates and their respective interactions). Within each model combination, we checked for collinearity among covariates by examining the variance inflation factor (VIF) for each model. We used a VIF > 1.5 as a threshold to determine collinearity and removed any models that contained collinear variables above this threshold. A subset of 2372 combinations of independent predictor variables (for a full list of variables, see Table 1 and descriptions above) were then used to construct generalized linear mixed-effect models using the package *glmmADMB*[45] in R. We standardized and centered numerical covariates prior to analysis, so that the resulting coefficients were directly comparable[46].

Models were run in a multimodel selection framework and compared using Akaike's Information Criterion adjusted for small sample sizes (AICc) and Akaike weights (w_i) to represent the relative support for each model[47]. To discriminate more thoroughly among covariates and the mechanisms postulated as important for bleaching (Table 1), we selected a best model set (<2 delta AICc, N=2 top models) and performed AICc-weighted model averaging across the best model set to calculate standardized coefficients (with 95% CI), adjusted standard errors and associated *t*-statistics and *p*-values. To illustrate interactions between continuous variables identified in the top models, we used the package *jtools*[48] to visualize the relationship of two-way interactions.

To validate the best models, we visually evaluated plots of the model residuals versus fitted values, and constructed Moran's I similarity spline correlograms from the residuals of the fitted models to test for bias from spatial autocorrelation[49]. Additionally, we used Mantel tests[50,51] to confirm the lack of spatial autocorrelation between the Pearson residuals of the model averages and the lag distance (in km) between sites, and found that the overall correlation coefficient for the model was low (Supplementary Figures 7 and 8). We used R package *ncf*[52] for estimating Moran's I and Mantel tests.

To evaluate the predictive ability of the best and null mixed models of bleaching intensity, we applied two variants of bootstrapping, 'simple' and 'enhanced' bootstrapping[53] using the R package *boot*[54]. Simple bootstrapping involved creating resamples with replacement from the original data of the same size and applying the models to the resample, then using the model to predict the values of the full set of original data and calculating a goodness of fit statistic (R^2) by comparing the predicted value to the actual value[53]. With the enhanced bootstrap[53], we first estimated the 'optimism' of the goodness of fit statistic (i.e. overfitting). When a model fitted using a bootstrap dataset is applied to the original data, the predictive accuracy is lower than the apparent accuracy when evaluating the fitted model using the same data that was used to fit it. In enhanced bootstrap, the difference in these predictive abilities is calculated for each bootstrap sample, and then averaged across 100 bootstrap samples, before subtracting from the naive estimate of predictive ability. All analyses were run in R 3.3.4[54].

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