

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 (that is, 'bleaching'), which often leads 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 that represent 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 applied common time-series methods to study the temporal patterning of acute thermal stress and evaluated the effectiveness of conventional and new sea surface temperature 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, which 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 responses². 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}. Exposure to sea surface temperature (SST) histories of acute and chronic stress can determine future sensitivities or tolerances^{7,8}. Therefore, to identify and guide management interventions and policies for safeguarding coral reefs and associated species, a critical challenge is to evaluate and compare the thermal impacts over various scales of time and space.

Factors that influence bleaching have been well studied at local scales, but at global scales there are cases in which locally observed spatial and temporal patterns differ and are even reversed among locations⁹. 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, and perhaps provide insights into the conditions of spatial refuges for stressed corals. A better understanding of temperature mechanisms and their geographical 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 corals¹⁰. 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 geographical covariates (Table 1). In developing these temperature models and mechanisms, we also derived indices from daily SST time series to describe the 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 the bleaching response in coral communities was measured in a coordinated field survey effort in 2016.

Coral bleaching observations were conducted using the same method and within 21 days of the peak thermal anomalies.

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Table 1 | Models, hypotheses and results for the main drivers of coral bleaching across reefs

Variable	Model/mechanism	Variable	Description	Range	Conclusions
Geography	Historical environmental conditions can modify responses to thermal stress ^{13,24}	Longitude and latitude	Geographical positions	140° × 50°	Strongest variable and significantly modified responses to heat stress
Excess heat	The accumulation of temperatures above a threshold (summer maximum + 1 °C) is a standard model to predict coral bleaching, assessed as DHWs ^{10,25}	Maximum DHW	Maximum DHW during 90 days before survey date	0–14.6	Significant positive but weak effect, and interacts strongly with longitude and mean high spells
		Average DHW	Average DHW during 90-day period before survey date	0–14.6	Significant positive but weak effect, and interacts strongly with bimodality and mean high spells
Early acute temperature acclimation	Early exposure to warm water can prime and acclimate corals to subsequent extreme temperature anomalies, which reduces bleaching ⁶	DHDs	Cumulative sum of DHD >1 °C threshold in the first 60 days of the 90-day period before survey date	0–11.2	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 in which a value greater than 0.55 suggests bimodality. The maximum value of 1 identifies a bimodal distribution	0.38–0.82	Weak single variable effect but moderate when combined with longitude and the 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	0–19.8	Weak effect when combined with depth and maximum low spells
Extreme warm temperatures	Corals that experience 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	1–5	Not significant
		High spell duration (days)	Average duration (days) of high spell events	2.2–21	Significant non-linear effect in which bleaching peaks at a duration of ~35 days
		High spell peak (°C)	Average temperature of high spell events	27–31	Moderate independent effect; important with geography
		High spell rate of rise (°C d ⁻¹)	Average rate of daily temperature rise (°C d ⁻¹) during high spell events	0–4	Weak single variable effect but important when combined with other variables
		Standard deviation of 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 geographical 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 the 10th quantile of SSTs at each site within 90 days before survey	1.43–11	Weak single variable effect but important when combined with longitude and mean high spell peak variables

Continued

Table 1 | Models, hypotheses and results for the main drivers of coral bleaching across reefs (continued)

Variable	Model/mechanism	Variable	Description	Range	Conclusions
Coral community composition	Community composition can influence overall bleaching severity and mortality. <i>Acropora</i> -dominated communities typically show greater sensitivity to warm temperature anomalies and bleaching than massive <i>Porites</i> species ^{25,28}	Coral community composition	Multivariate index of coral community composition based on a correspondence analysis (CA1). High values indicate dominance by <i>Acropora</i> , low values indicate dominance by massive <i>Porites</i> species	−1.79 to 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	Weak effect but interacts with location and depth
Depth	Deeper reefs have less surface irradiation and potentially cooler waters than given by 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 (m)	1–18	Weak effect but interacts with location and coral community
Habitat	Lagoons and reef flats can have warmer and more variable environments with more potential for acclimation and taxa that acclimate compared with 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

Temperature characteristics were 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. CA, correspondence analysis.

We evaluated bleaching responses at 226 sites across 50° of latitude and 140° of longitude largely through the tropical belt of the Indian and Pacific Oceans (Fig. 1a–e, Methods and Supplementary Table 1). In 2016, only 32% of the sites ($n=71$) experienced four or more degree-heating weeks (DHWs (°C weeks)) measured by the National Oceanic and Atmospheric Administration (NOAA) at ~5 km×5 km satellite resolution, which is the common thermal stress index used to predict 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 (Fig. 1f,g and Supplementary Fig. 1). The observed bleaching responses were spatially patchy (Fig. 1a–e), which suggests that unevaluated micro-habitat and local currents may have weakened the ability of coarser satellite metrics to predict in situ bleaching (Supplementary Fig. 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 the warm and cold temperature extremes at each site, we characterized SSTs in the 90 days before 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 the variables and hypothesized mechanisms

are described in Table 1. We quantified the effects on coral bleaching intensity using two approaches—boosted regression trees (BRTs) and generalized linear mixed-effect methods that compared and selected the best models among 2,372 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 Fig. 3).

Longitude, as a covariate, had the highest relative influence as a single variable in both the BRT and linear mixed-effects models (Fig. 2a and Table 2). However, geographical bias in our data limits the extent to which we can make credible tests and deductions on the 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 and Supplementary Table 3). These results were consistent for inferences from both BRT and linear multimodel approaches (Fig. 2). When geographical variables were excluded, the mean extreme warm temperatures and the mean and cumulative DHWs were the strongest variables associated with increased bleaching (Fig. 2c). Nevertheless, our findings indicate complex and interacting responses of temperature and geography for coral bleaching.

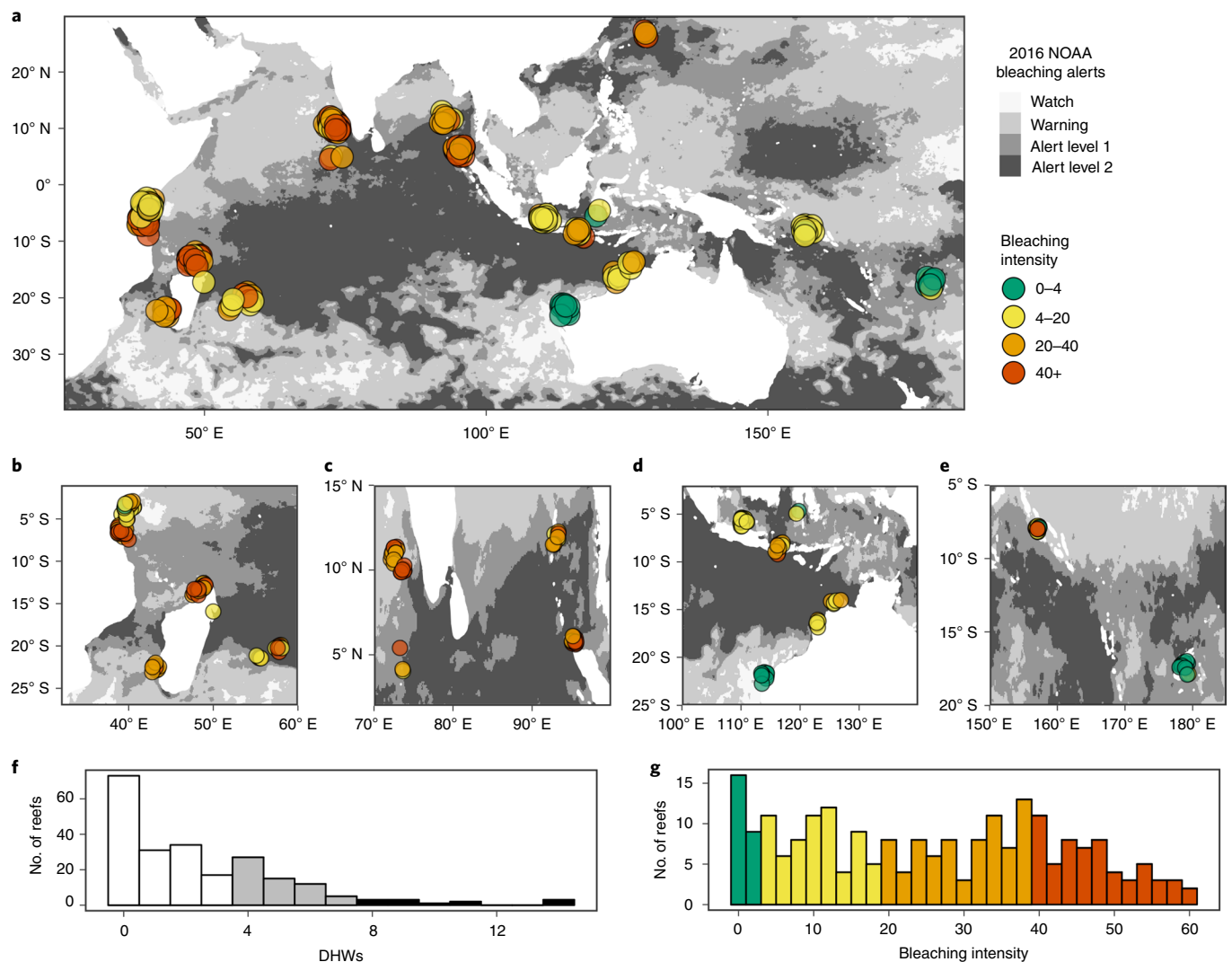


Fig. 1 | Indo-Pacific scale and severity of coral bleaching during the 2016 El Niño/Southern Oscillation event. **a**, The severity of coral bleaching at 226 sites in 12 countries measured from standardized underwater surveys ($n = 60,591$ coral colonies) during the peak of the warm season. Higher bleaching intensity scores indicate more frequent and severe bleaching (Methods). The grey scale indicates the NOAA bleaching alert levels at each site in 2016. **b–e**, As in **a** but for Western Indian Ocean (**b**), Eastern Indian Ocean (**c**), Australia–Indonesia (**d**) and eastern Melanesia (**e**). **f**, Frequency distribution of 2016 maximum DHWs in the 90 days before each survey. **g**, Frequency distribution of bleaching intensity scores for the 226 sites (colour key as in **a**).

Model quality increased substantially when geography was included (an Akaike's information criteria (ΔAICc) 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 (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 and Supplementary Table 3) when these variables were combined with geographical covariates of longitude and latitude, which are probably proxies for other environmental and historical conditions. Several models suggested conditions that reduce bleaching, which included 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 and 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 and Supplementary Table 3). Across our sampled sites, coral bleaching was highest from East Africa to the central Indian Ocean and declined towards the Coral Triangle and Fiji, moderated by interactions between temperature variables (Supplementary Fig. 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 probably 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},

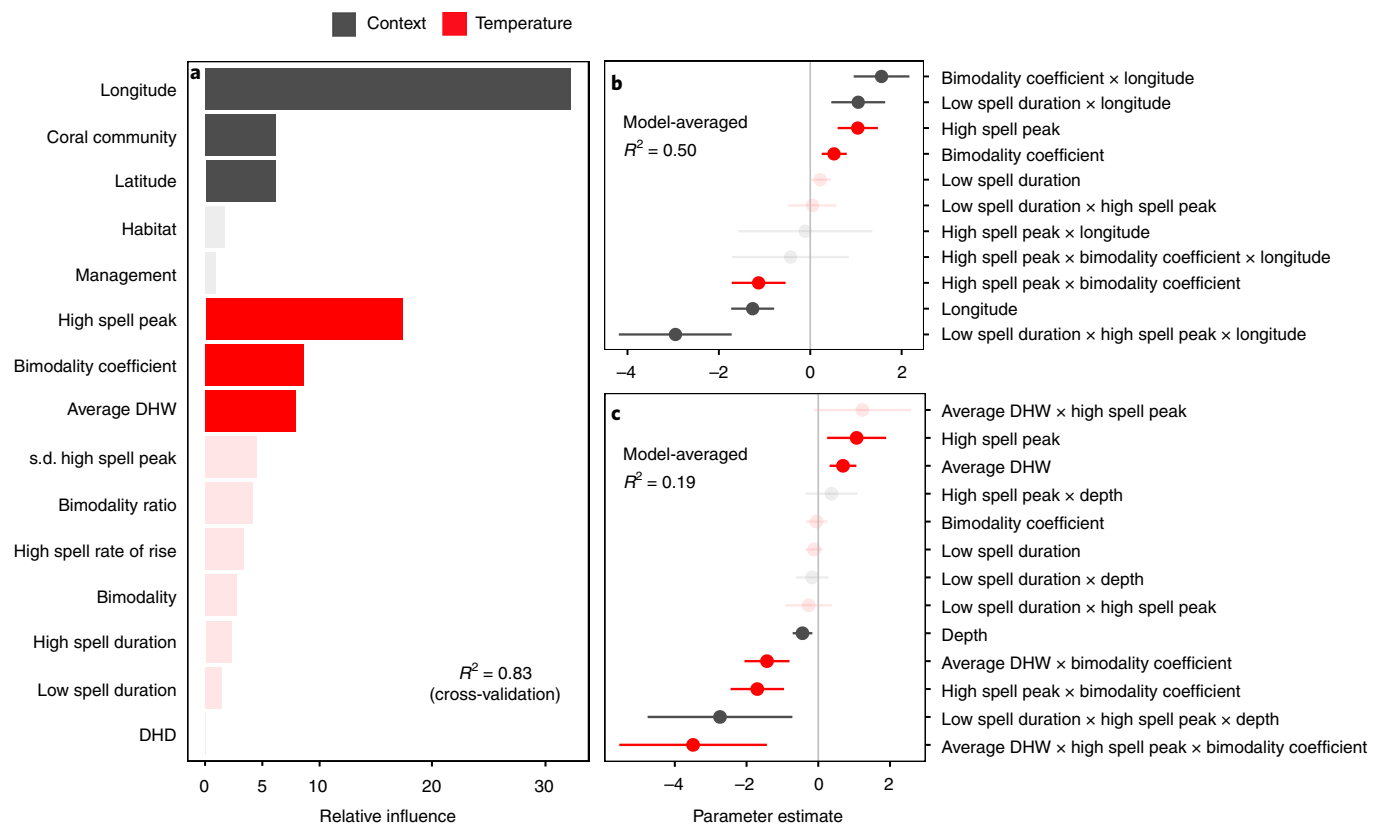


Fig. 2 | Effect of environmental variables on coral bleaching. **a**, Relative influence of variables on the bleaching response from a boosted regression tree approach. **b**, Model-averaged parameter estimates and 95% confidence intervals of the top models (<2AICc) of the environmental and site factors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

but there are important exceptions¹⁴. An increasing number of studies also show 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 strengths of past DHW predictions were variable^{4,17,18} and, although there are instances in which the DHW predictions are good, as in Australia's Great Barrier Reef during the 2016 bleaching event ($R^2 = 0.55$) (ref. ²), our study indicates that prediction success is highly dependent on the 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 Fig. 2). Results also indicate that many currently unmeasured environmental variables represented by geography are important¹⁹.

At the core of the DHW metric is the assumption that the main mechanism of bleaching is a threshold at which symbionts are lost when temperatures exceed the 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 the thresholds were not surpassed (that is, a high bleaching at low DHWs (Fig. 1 and Supplementary Fig. 1). Consequently, common bleaching metrics based on thresholds may fail in future circumstances in which combinations of complex stress initiate the loss of symbionts or historical exposures promote a greater

resistance to heat stress. Understanding past and emerging mechanisms of coral bleaching are, therefore, critical to predict potential strategic refuges for coral reefs²⁰.

To improve the critical global prediction of bleaching and reef status, future analyses should focus on how extreme temperatures interact with location. For example, a 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 Great Barrier Reef⁷, 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 Fig. 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 Fig. 4).

Ultimately, coral bleaching responses can be shaped by both long-term and recent histories of disturbance. For example, time-series studies found that many sensitive reef corals were replaced by weedy and stress-tolerant taxa and genotypes after 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 Great Barrier Reef, where 2016 was among the most severe bleaching years². 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

Table 2 | Multivariate and single variable models of our bleaching observations in 2016

Multivariate model	ΔAICc	Multivariate model R^2	Single variable	ΔAICc	Single variable model R^2
Longitude \times bimodality coefficient \times 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 \times high spell peak \times low spell duration	1.3	0.57	Low spell duration	31.9	0.04
Longitude \times latitude \times high spell peak	6.0	0.55	Latitude	32.2	0.16
Longitude \times maximum DHW \times high spell peak	8.1	0.49	Maximum DHW	29.9	0.09
Longitude \times high spell rate of rise \times high spell peak	8.4	0.34	High spell rate of rise	35.9	0.13
Average DHW \times bimodality coefficient \times high spell peak	10.5	0.23	Average DHW	31.6	0.05
Longitude \times depth \times coral community	11.3	0.16	Depth	29.0	< 0.01
Longitude \times depth \times coral community	11.3	0.16	Coral community	35.8	0.01
Longitude \times high spell peak \times s.d. high spell peak	12.0	0.41	SD high spell peak	34.9	0.02
Longitude \times high spell peak \times management	15.9	0.30	Management	36.2	0.01
Longitude \times coral community susceptibility \times high spell peak	16.0	0.33	Coral community susceptibility	30.7	0.02
Average DHW \times bimodality \times high spell rate of rise	16.4	0.01	Bimodality coefficient	30.4	0.02
High spell events \times high spell peak \times low spell duration	20.9	0.08	High spell events	35.9	0.13
Longitude \times high spell duration \times low spell duration	21.3	0.26	High spell duration	35.9	0.17
Depth \times bimodality ratio \times low spell duration	21.5	0.01	Bimodality ratio	32.2	0.01
Longitude \times high spell peak \times DHD	22.9	0.34	DHD	35.2	0.02
High spell peak \times habitat	29.0	0.13	Habitat	37.7	< 0.01

Multivariate models are ranked using ΔAICc ; the two top models ($\Delta\text{AICc} < 2$) are highlighted. We also present R^2 as an indication of each model's predictive ability. The multivariate models are a subset of the 2,372 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. DHD, degree heating days.

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 before the 90-day acute evaluations may increase coral sensitivities⁸. Second, a number of other non-thermal factors, such as sunlight, turbidity, water flow and water quality strongly influence bleaching¹⁶. Third, different bleaching responses may arise from the duration and magnitude of stress, which are unique components of stress that are poorly reflected by the DHW metric²³. 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 Fig. 2)¹⁸. Predictions will not be improved without further evaluating these issues and the changing thermal sensitivity over time at appropriate spatial scales²⁴. Ultimately, we find that integrating complex environmental interactions can improve predictions of coral bleaching, and show the importance of large-scale coordinated field monitoring for documenting emerging and changing patterns of global climate change.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, statements of code and data availability and

associated accession codes are available at <https://doi.org/10.1038/s41558-019-0576-8>.

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References

- Hoegh-Guldberg, O. et al. Coral reefs under rapid climate change and ocean acidification. *Science* **318**, 1737–1742 (2007).
- Hughes, T. P. et al. Global warming and recurrent mass bleaching of corals. *Nature* **543**, 373–377 (2017).
- Anthony, K. R. N., Hoogenboom, M. O., Maynard, J. A., Grottoli, A. G. & Middlebrook, R. Energetics approach to predicting mortality risk from environmental stress: a case study of coral bleaching. *Funct. Ecol.* **23**, 539–550 (2009).
- McClanahan, T. R. et al. Western Indian Ocean coral communities: bleaching responses and susceptibility to extinction. *Mar. Ecol. Prog. Ser.* **337**, 1–13 (2007).
- Littman, R., Willis, B. L. & Bourne, D. G. Metagenomic analysis of the coral holobiont during a natural bleaching event on the Great Barrier Reef. *Environ. Microbiol. Rep.* **3**, 651–660 (2011).
- Ziegler, M., Seneca, F. O., Yum, L. K., Palumbi, S. R. & Voolstra, C. R. Bacterial community dynamics are linked to patterns of coral heat tolerance. *Nat. Commun.* **8**, 14213 (2017).
- Ainsworth, T. D. A. et al. Climate change disables coral bleaching protection on the Great Barrier Reef. *Science* **352**, 338–342 (2016).
- Grottoli, A. G. et al. The cumulative impact of annual coral bleaching can turn some coral species winners into losers. *Glob. Change Biol.* **20**, 3823–3833 (2014).
- McClanahan, T. R., Weil, E., Cortes, J., Baird, A. H. & Ateweberhan, M. in *Coral Bleaching* (eds van Oppen, M. J. H. & Lough, J. M.) 121–138 (Ecological Studies Vol. 205, Springer, 2009).
- Frieler, K. et al. Limiting global warming to 2 °C is unlikely to save most coral reefs. *Nat. Clim. Change* **3**, 165–170 (2013).
- Eakin, C. M. et al. Caribbean corals in crisis: record thermal stress, bleaching, and mortality in 2005. *PLoS ONE* **5**, e13969 (2010).
- Kleypas, J. A., Danabasoglu, G. & Lough, J. M. Potential role of the ocean thermostat in determining regional differences in coral reef bleaching events. *Geophys. Res. Lett.* **35**, L03613 (2008).

13. Hughes, T. P. et al. Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. *Science* **359**, 80–83 (2018).
14. Brainard, R. E. et al. Ecological impacts of the 2015/16 El Niño in the central equatorial Pacific. *Bull. Am. Mineral. Soc.* **99**, S21–S26 (2018).
15. Guest, J. R. et al. Contrasting patterns of coral bleaching susceptibility in 2010 suggest an adaptive response to thermal stress. *PLoS ONE* **7**, e33353 (2012).
16. McClanahan, T. R. Changes in coral sensitivity to thermal anomalies. *Mar. Ecol. Prog. Ser.* **570**, 71–85 (2017).
17. Heron, S. F. et al. Validation of reef-scale thermal stress satellite products for coral bleaching monitoring. *Remote Sens.* **8**, 59 (2016).
18. Kayanne, H. Validation of degree heating weeks as a coral bleaching index in the northwestern Pacific. *Coral Reefs* **36**, 63–70 (2017).
19. Maina, J., McClanahan, T. R., Venus, V., Ateuwerhan, M. & Madin, J. Global gradients of coral exposure to environmental stresses and implications for local management. *PLoS ONE* **6**, e23064 (2011).
20. Beyer, H. L. et al. Risk-sensitive planning for conserving coral reefs under rapid climate change. *Conserv. Lett.* **11**, e12587 (2018).
21. Edmunds, P. J. et al. Persistence and change in community composition of reef corals through present, past, and future climates. *PLoS ONE* **9**, e107525 (2014).
22. Zhang, N., Feng, M., Hendon, H. H., Hobday, A. J. & Zinke, J. Opposite polarities of ENSO drive distinct patterns of coral bleaching potentials in the southeast Indian Ocean. *Sci. Rep.* **7**, 2443 (2017).
23. Skirving, W. J. et al. The relentless march of mass coral bleaching: a global perspective of changing heat stress. *Coral Reefs* **38**, 547–557 (2019).
24. Hughes, T. P. et al. Climate change, human impacts, and the resilience of coral reefs. *Science* **301**, 929–933 (2003).
25. Hoegh-Guldberg, O. Climate change, coral bleaching and the future of the world's coral reefs. *Mar. Freshw. Res.* **50**, 839–866 (1999).
26. Thompson, D. M. & van Woesik, R. Corals escape bleaching in regions that recently and historically experienced frequent thermal stress. *Proc. R. Soc. B* **276**, 2893–2901 (2009).
27. West, J. M. & Salm, R. V. Resistance and resilience to coral bleaching: implications for coral reef conservation and management. *Conserv. Biol.* **17**, 956–967 (2003).
28. McClanahan, T. R., Muthiga, N. A. & Mangi, S. Coral and algal changes after the 1998 coral bleaching: interaction with reef management and herbivores on Kenyan reefs. *Coral Reefs* **19**, 380–391 (2001).
29. Graham, N. A., Jennings, S., MacNeil, M. A., Mouillot, D. & Wilson, S. K. Predicting climate-driven regime shifts versus rebound potential in coral reefs. *Nature* **518**, 94–97 (2015).
30. McClanahan, T. R. & Maina, J. Response of coral assemblages to the interaction between natural temperature variation and rare warm-water events. *Ecosystems* **6**, 551–563 (2003).

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Author contributions

T.R.M., E.S.D. and J.M.M. conceived the study with the support of all the authors. T.R.M. led the manuscript writing, with the help of E.S.D. and J.M.M. E.S.D., J.M.M., S.D. and T.R.M. conducted all the analyses. All the other authors contributed data, edited and approved the manuscript.

Additional information

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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 the survey timing was related to accumulated temperature stress, we extracted daily 5 km DHW time series from the NOAA Coral Reef Watch for each site from 1 September 2015 to the date of the survey and calculated the date of the maximum observed DHWs for each site. Based on these satellite temperature time series, 45 sites did not experience an excess heating (that is, 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 the maximum DHW, well within the suggested timelines to assess bleaching-related stress and mortality for corals (~30 days³¹). Nine sites where bleaching surveys were assessed >21 days after the maximum DHW were excluded from further analyses, which left 226 sites across 11 countries for further analysis. Further details on the 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 m²) to assess the frequency and severity of bleaching. Within each quadrat, hard coral colonies (>5 cm) were identified to genus (using Veron's classifications³²) 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 within each category. Within each quadrat, observers also estimated the average percent cover of live hard coral, live soft coral and macroalgae (for example, fleshy or calcareous algae taller than filamentous turf). On each survey, observers conducted an average of 17.8 quadrats (+4.7 s.d.). In some surveys, quadrats were recorded using photographs and colonies identified and scored for bleaching post hoc by the observer. Observers also recorded the 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):

$$\text{Bleaching intensity} = \frac{(0 \times c0) + (1 \times c1) + (2 \times c2) + (3 \times c3) + (4 \times c4) + (5 \times c5) + (6 \times c6)}{7}$$

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 separated sites across a wider bleaching gradient and resulted in better distinctions for modelling. On each survey, we evaluated the total bleaching intensity across all the 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^{25,33,34}. To assess thermal stress, we downloaded daily DHWs that are based on a rolling 14-day average from the NOAA Coral Reef Watch website³³ and calculated the maximum and mean DHWs during the 90 days before each survey. We also derived an estimate of the early exposure to thermal stress as 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 prebleaching stress exposure⁷. All the temperature-based variables, including DHWs, were derived from NOAA daily SST products³³.

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 before the date of sampling for each survey³³. Gap-filled daily SST data based on the NOAA Advanced Very-High-Resolution Radiometer satellite observations at a resolution of ~5 km × 5 km grid cells. At 13 sites in four countries (Tanzania, Kenya, India and La Réunion, France), we compared NOAA 5-km daily SSTs records to in situ temperature gauges placed on the studied reefs. We used linear regressions and dynamic time warp analysis to compare the time series of satellite and in situ records, using the dtw package in R (ref. ³⁵) (Supplementary Table 2).

To describe the frequency, duration and other characteristics of extreme warm and cold temperature events, we used the Hydrostats package in R (ref. ³⁶) 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 the purpose of the 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 the high spells (Table 1).

Studies have suggested that fluctuating temperature distributions before bleaching may expose corals to either additional stress or prestress 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 prestress acclimation⁷. Thus, we used bimodality metrics during the 90 days before each bleaching survey to evaluate bimodal variability in the distributions.

Bimodal probability distributions³⁷ 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 site³⁷. The bimodality coefficient measures the presence of bimodal distributions with a range of (0,1), in which a value greater than 0.55 suggests bimodality; the maximum value of 1 can only be reached when the distribution is composed of separate two-point masses (Supplementary Fig. 5). The bimodality peak proportion describes the ratio between the two peaks, in which values greater than 0 indicate that the amplitude of the hot peak dominates that of the cool peak. These multimodality metrics reflect probability distributions and not the temporal patterning within time series and were calculated using the modes³⁸ package in R.

A correlation matrix was used to evaluate the relationships between all the temperature factors and collinear variables were accounted for in the subsequent analyses³⁹ (Data analysis and Supplementary Fig. 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*^{4,25}. To estimate this metric, we calculated the relative abundance of each hard-coral taxa observed during each survey and used a correspondence analysis ordination to distinguish a strong gradient from *Acropora*- to *Porites*-dominated communities. For each survey, we extracted the value of correspondence analysis 1 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 the 2016 surveys) by the numbers of individuals of that taxon, and summed for all the taxa. Sites with more bleaching-susceptible taxa have higher scores of community susceptibility than sites with more bleaching-tolerant taxa⁴.

Data analyses. To evaluate our sampling distribution, we compared our empirical with a random sampling of reefs based on the *Reefs at Risk* mapping⁴⁰. Random sampling of the reefs used the package *dismo*⁴¹ in R to generate coral reef sites on the 500 m resolution tropical coral reef grid, which resulted 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 Fig. 3). To account for the non-random distribution of sampling, longitude and latitude were included as covariates in all further analyses. We also included the location of sampling as a random intercept in our linear models, with location 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 (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 Figs. 7 and 8).

We evaluated hypothesized models and mechanisms of coral bleaching (Table 1) using two quantitative approaches—BRT and generalized linear mixed-effect models. BRT models are an ensemble method that relates response variables to predictor variables by using recursive splits 'boosted' with multiple trees⁴². They also account for higher-order interactions and non-linear 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 were fit using beta regression models, as the bleaching intensity is a continuous variable distributed from 0 to 1 (ref. ⁴³).

Before applying statistical models, we constructed models using all the 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 variance inflation factor greater than 1.5 as a threshold to determine collinearity and removed any models that contained collinear variables above this threshold. A subset of 2,372 combinations of independent predictor variables (Table 1 and the descriptions above five a full list of variables) was then used to construct generalized linear mixed-effect models using the package *glmmADMB*⁴⁴ in R. We standardized and centred the numerical covariates before analysis, so that the resulting coefficients were directly comparable⁴⁵.

Models were run in a multimodel selection framework and compared using AICc adjusted for small sample sizes and Akaike weights (*w_i*) to represent the

relative support for each model⁴⁶. To discriminate more thoroughly among covariates and the mechanisms postulated as important for bleaching (Table 1), we selected a best model set ($<2 \Delta AIC_c$, $N=2$ top models) and performed AICc-weighted model averaging across the best model set to calculate standardized coefficients (with a 95% confidence interval), adjusted standard errors and associated t statistics and P values. To illustrate the interactions between continuous variables identified in the top models, we used the package *jtools*⁴⁷ 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 autocorrelation⁴⁸. Additionally, we used Mantel tests^{49,50} to confirm the lack of spatial autocorrelation between the Pearson residuals of the model averages and the lag distance (km) between sites, and found that the overall correlation coefficient for the model was low (Supplementary Figs. 7 and 8). We used the R package *ncf*⁵¹ to estimate 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'⁵², using the R package *boot*⁵³. 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 value⁵². With the enhanced bootstrap⁵², we first estimated the 'optimism' of the goodness of fit statistic (that is, 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 the fitted model is evaluated using the same data as used to fit it. In an enhanced bootstrap, the difference in these predictive abilities is calculated for each bootstrap sample, and then averaged across 100 bootstrap samples, before it is subtracted from the naive estimate of predictive ability. All the analyses were run in R 3.3.4⁵³.

Reporting summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

Data are available at the Knowledge Network for Biocomplexity (<https://knbi.ecoinformatics.org>) via <https://doi.org/10.5063/F1WQ024C>.

Code availability

R code is available on GitHub: <https://github.com/WCS-Marine/2016-bleaching-patterns>

References

31. Diaz-Pulido, G. & McCook, L. J. The fate of bleached corals: patterns and dynamics of algal recruitment. *Mar. Ecol. Prog. Ser.* **232**, 115–128 (2002).
32. Veron, J. *Corals of the World Vols 1–3* (Australian Institute of Marine Science, 2000).
33. NOAA Coral Reef Watch (NOAA Satellite and Information Service, accessed 20 January 2017); <http://coralreefwatch.noaa.gov/satellite/hdf/index.php>
34. Donner, S. D., Skirving, W. J., Little, C. M., Oppenheimer, M. & Hoegh-Gulberg, O. Global assessment of coral bleaching and required rates of adaptation under climate change. *Glob. Change Biol.* **11**, 2251–2265 (2005).
35. Giorgino, T. Computing and visualizing dynamic time warping alignments in R: The dtw package. *J. Stat. Softw.* **31**, 1–24 (2009).
36. Bond, N. Hydrostats: Hydrologic indices for daily time series data. R package version 0.2.7 (2019); <https://github.com/nickbond/hydrostats>
37. Freeman, J. B. & Dale, R. Assessing bimodality to detect the presence of a dual cognitive process. *Behav. Res. Methods* **45**, 83–97 (2013).
38. Deevi, S. modes: Find the modes and assess the modality of complex and mixture distributions, especially with big datasets. R package version 0.7.0 (2016); <https://CRAN.R-project.org/package=modes>
39. Graham, M. H. Confronting multicollinearity in ecological multiple regression. *Ecology* **84**, 2809–2815 (2003).
40. Burke, L., Reyter, K., Spalding, M. & Perry, A. *Reefs at Risk Revisited* (World Resources Institute, 2011).
41. Hijmans, R. K., Phillips, S., Leathwick, J. & Elith, J. dismo: Species distribution modeling. R package version 1.1-4 (2017); <https://CRAN.R-project.org/package=dismo>
42. Elith, J., Leathwick, J. R. & Hastie, T. A working guide to boosted regression trees. *J. Anim. Ecol.* **77**, 802–813 (2008).
43. Zimprich, D. Modeling change in skewed variables using mixed beta regression models. *Res. Hum. Dev.* **7**, 9–26 (2010).
44. Skaug, H., Fournier, D., Nielsen, A., Magnusson, A. & Bolker, B. glmmADMB: Generalized linear mixed models using AD model builder. R package version 0.7.7 (2019); <https://rdrr.io/rforge/glmmADMB/>
45. Gelman, A. Scaling regression inputs by dividing by two standard deviations. *Stat. Med.* **27**, 2865–2873 (2008).
46. Burnham, K. P. and Anderson, D. R. *Model Selection and Inference: A Practical Information-Theoretic Approach* 2nd edn (Springer, 2002).
47. Long, J. A. jtools: Analysis and presentation of social scientific data. R package version 0.9.0 (2017); <https://mran.microsoft.com/snapshot/2017-12-11/web/packages/jtools/index.html>
48. Zuur, A., Ieno, E. N., Walker, N., Saveliev, A. A. & Smith, G. M. Mixed effects models and extensions in ecology with R. *Biometrics* **65**, 992–993 (2009).
49. Mantel, N. Ranking procedures for arbitrarily restricted observation. *Int. Biom. Soc.* **23**, 65–78 (1967).
50. Legendre, P. & Fortin, M. J. Spatial pattern and ecological analysis. *Vegetatio* **80**, 107–138 (1989).
51. Bjørnstad, O. N. ncf: Spatial nonparametric covariance functions. R package version 1.1–5 (2013); <https://CRAN.R-project.org/package=ncf>
52. Canty, A. & Ripley, B. boot: Bootstrap R (S-plus) functions. R package version 1.3-22 (2019); <https://cran.r-project.org/web/packages/boot/boot.pdf>
53. R Core Team R: A Language and Environment for Statistical Computing (R Foundation for Statistical Computing, 2018); www.R-project.org/

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Software and code

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Data collection

The open-source software R was used in all analyses.

Data analysis

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

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Ecological, evolutionary & environmental sciences study design

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Study description	An Indo-Pacific survey of coral bleaching during the 2016 El Nino and global bleaching event.
Research sample	Scleractinian coral communities with corals identified to genus using a standard roving diver based protocol to determine percent bleaching of total coral colonies and by genus.
Sampling strategy	Sampling was limited to either 40 minutes of underwater survey per site, or ~20 replicate quadrats, whichever was reached first. Bleaching quadrats were haphazardly chosen along a reefs and separated by ~10 dive fin kicks between quadrats.
Data collection	Trained coral reef scientists recorded the data using a standard roving diver observation method, described at https://c532f75abb9c1c021b8c-e46e473f8aadb72cf2a8ea564b4e6a76.ssl.cf5.rackcdn.com/2017/02/22/9mkks762mz_Bleaching_Survey_writeup_April2016.pdf
Timing and spatial scale	Data collection occurred in 2016 with the onset of coral bleaching at each reef location. Reefs were surveyed once for bleaching during a 3-week window of peak SST that coincided with coral bleaching
Data exclusions	Surveys that occurred outside the 3-week window of peak SST were excluded
Reproducibility	All original raw data are stored with their corresponding R code to compile into a regional dataset
Randomization	NA
Blinding	NA
Did the study involve field work?	<input checked="" type="checkbox"/> Yes <input type="checkbox"/> No

Field work, collection and transport

Field conditions	Field conditions were determined by individual data collectors, and involved assessing conditions of temperature, wind, rain and waves that allowed for the identified and recording of bleaching observations of coral colonies.
Location	226 coral reef locations in the Indian and Pacific Oceans (see Map - Fig 1 in manuscript)
Access and import/export	All data collectors were responsible for obtaining the necessary permissions and permits required for underwater observations of coral reef benthic communities.
Disturbance	Any disturbance to coral communities was minimized by experienced surveyors using proper buoyancy control to avoid disturbing live coral colonies and other organisms.

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Animals and other organisms

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Laboratory animals	NA
Wild animals	Invertebrate coral communities were sampled non-destructively using standard underwater observation protocols and recorded

Wild animals	by experienced scientific divers.
Field-collected samples	No samples were collected from the field
Ethics oversight	NA - invertebrates only

Note that full information on the approval of the study protocol must also be provided in the manuscript.