



REPORT

Skeletal records of bleaching reveal different thermal thresholds of Pacific coral reef assemblages

Nathaniel R. Mollica¹ · Anne L. Cohen² · Alice E. Alpert^{1,3} · Hannah C. Barkley^{1,4,5} · Russell E. Brainard⁵ · Jessica E. Carilli^{6,7} · Thomas M. DeCarlo^{1,8} · Elizabeth J. Drenkard^{1,9} · Pat Lohmann² · Sangeeta Mangubhai¹⁰ · Kathryn R. Pietro² · Hanny E. Rivera^{1,11} · Randi D. Rotjan¹¹ · Celina Scott-Buechler^{2,12} · Andrew R. Solow² · Charles W. Young^{4,5}

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Abstract Ocean warming is negatively impacting coral reef ecosystems and considerable effort is currently invested in projecting coral reef futures under 21st century climate change. A limiting factor in these projections is lack of quantitative data on the thermal thresholds of different reef communities, due in large part to spatial and temporal gaps in bleaching observations. Here we apply a coral bleaching proxy, skeletal stress bands, to reconstruct the history of bleaching on eight coral reefs in the central

equatorial Pacific (CEP) and use this information to constrain the thermal thresholds of their coral communities. First, three genera of massive corals collected on both Pacific and Caribbean reefs are used to derive a calibration between the proportion of corals that form stress bands during a bleaching event, and the total observed bleaching incidence in the community of mixed coral taxa. The correlation is highly significant, indicating that stress bands in massive corals reflect community-level bleaching severity ($R^2 = 0.945$, $p < 0.001$). We applied the calibration to stress band records from eight Pacific reefs, reconstructing their bleaching histories over the period 1982 to 2015. A percentile-based method of estimating thermal stress (Degree Heating Weeks) for CEP reefs was

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✉ Nathaniel R. Mollica
nmollica@whoi.edu

✉ Anne L. Cohen
acohen@whoi.edu

¹ MIT-WHOI Joint Program in Oceanography, Woods Hole Oceanographic Institution, Woods Hole, MA 02536, USA

² Woods Hole Oceanographic Institution, Woods Hole, MA 02536, USA

³ Present Address: U.S. Department of State, Washington, DC 20520, USA

⁴ Present Address: Joint Institute for Marine and Atmospheric Research, University of Hawaii at Manoa, Honolulu, HI 96822, USA

⁵ Ecosystem Sciences Division, NOAA Pacific Islands Fisheries Science Center, Honolulu, HI 96818, USA

⁶ Australian Nuclear Science and Technology Organization, New Illawarra Rd, Lucas Heights, NSW 2234, Australia

⁷ Present Address: Energy and Environmental Sciences, Naval Information Warfare Center Pacific, 53475 Strothe Rd., San Diego, CA 92152, USA

⁸ Present Address: Red Sea Research Center, Division of Biological and Environmental Science and Engineering, King Abdullah University of Science and Technology (KAUST), Thuwal, Saudi Arabia

⁹ Present Address: Geophysical Fluid Dynamics Laboratory, NOAA, Princeton, NJ 08540, USA

¹⁰ Wildlife Conservation Society, 11 Ma'afu Street, Suva, Fiji

¹¹ Biology Department, Boston University, Boston, MA, USA

¹² Department of Earth and Atmospheric Sciences, Cornell University, Ithaca, NY 14850, USA

developed and applied. Comparing the level of thermal stress experienced by each coral community during each event with the reconstructed bleaching response, we characterized the thermal sensitivities of each reef community and quantified the thermal threshold ($b_{1/2}$) at which 50% of the coral community bleached. Our analysis reveals a unique non-linear thermal response curve for each reef. The most thermally tolerant reefs in the study (Jarvis and Kanton Islands) experienced 50% bleaching at seven to nine times more thermal stress than did the least resistant reef in the study (Maiana Island). An exploration of the potential drivers of thermal tolerance revealed a strong correlation between $b_{1/2}$ and the history of thermal stress events in each reef system. Thermal tolerance was also correlated with concentrations of dissolved inorganic nitrate in the water column and with estimates of coral energetic reserve.

Keywords Coral reef · Coral bleaching · Coral skeleton · Stress bands · Thermal tolerance · Equatorial pacific

Introduction

Reef-building corals exist in an obligate symbiosis with single-celled dinoflagellates called zooxanthellae, which provide a significant component of the host energetic needs. When sea surface temperatures (SSTs) exceed a physiological threshold, the relationship between corals and zooxanthellae breaks down, the symbionts are expelled, and the coral loses pigmentation in a process called “bleaching” (e.g., Coles and Jokiel 1977). Prolonged or severe bleaching can lead to coral starvation and, eventually, death. Regional-scale or mass bleaching of coral communities and reefs was first reported during the 1982/1983 El Niño (Hoegh-Guldberg and Smith 1989). As the oceans continued to warm over the subsequent three decades, episodes of mass bleaching increased in frequency and extent, and now occur with each strong El Niño (Hughes et al. 2018). By 2008, bleaching had caused irretrievable loss of an estimated 19% of coral reef area worldwide (Wilkinson 2008), and losses following the 2015–2016 El Niño are expected to exceed this estimate. As global temperatures rise, by a projected 1–2.5 °C over this century (IPCC AR5 2014), there is mounting concern that coral communities will soon experience bleaching at a frequency that precludes recovery.

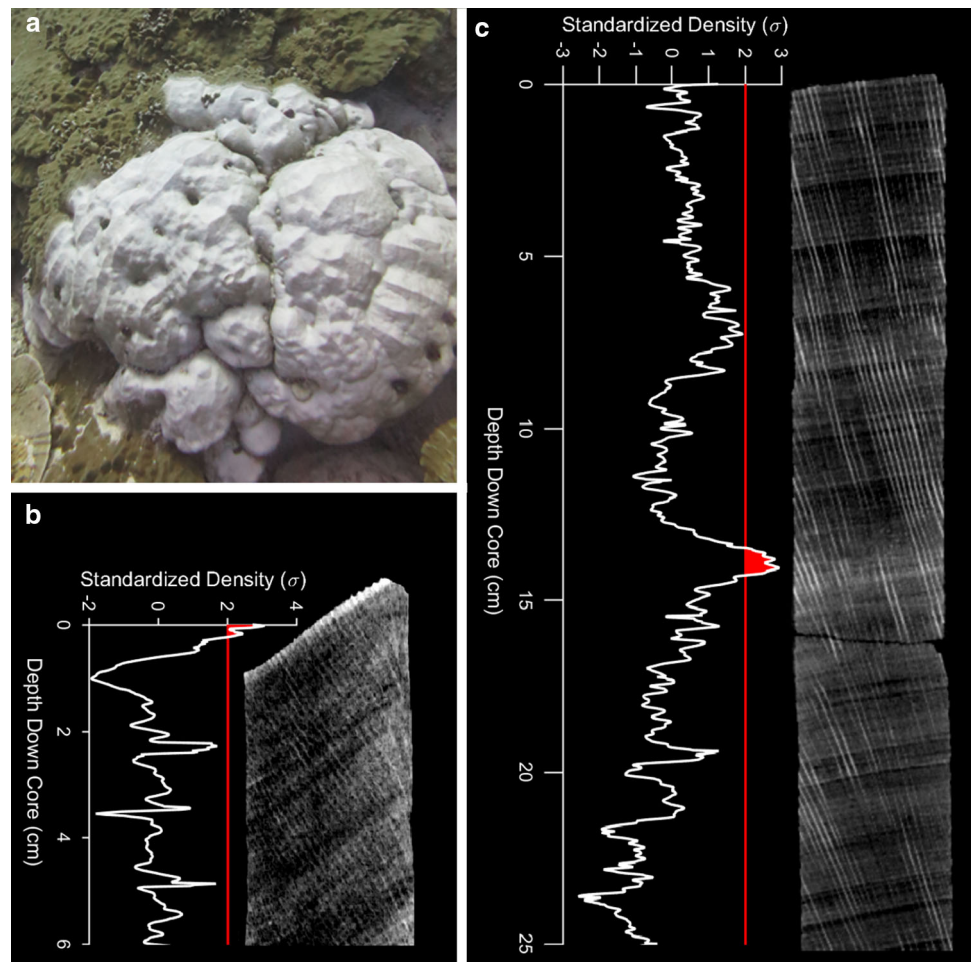
Significant effort is currently invested in identifying coral reef ecosystems or communities that might survive ocean warming (Pratchett et al. 2008; Frieler et al. 2012; van Hooidonk et al. 2016; Beyer et al. 2018). These efforts are limited in large part, however, by two unknowns. First, the spatial resolution of general circulation models (GCMs)

is too coarse to resolve reef-scale hydrodynamics, meaning that projections of future open ocean conditions may not apply to many shallow water reef systems. Statistical and dynamical downscaling of GCM output is one approach taken to specifically address this issue (Donner 2009; Frieler et al. 2012; van Hooidonk et al. 2016). Second, the thermal thresholds for bleaching of different reef systems are not well characterized. Currently, a single bleaching threshold based on 1 °C warmer than the maximum monthly mean (MMM) SST is used to predict whether, and with what severity, bleaching will occur during heat waves and in model projections of future global change scenarios (Heron et al. 2015). However, thermal thresholds vary between individuals of the same species (e.g., Coles and Jokiel 1977), between populations within and among reefs (e.g., Fisk and Done 1985; Rowan et al. 1997; Van Woesik et al. 2011), and examples exist of thermal thresholds changing over time (Maynard et al. 2008). A few studies have incorporated inter-reef differences in thermal tolerance (van Hooidonk and Huber 2009; Donner 2011) and the potential for coral acclimatization (e.g., Logan et al. 2014) into projections of coral reef futures. Nevertheless, these efforts have all been limited by a paucity of observational bleaching data which precludes accurate and comprehensive estimates of bleaching thresholds (van Hooidonk and Huber 2009).

Bleaching histories for reef locations around the globe have been compiled (e.g., Donner et al. 2017; Hughes et al. 2018), but all are limited by the paucity of observational data, especially but not limited to, remote reef locations. Here, we make a start at filling spatial and temporal gaps in bleaching records using signatures of bleaching archived in the skeletons of massive long-lived corals that survived, and recorded multiple bleaching events extending back in time (Fig. 1). Skeletal “stress bands” have long been linked, qualitatively, with anomalously high summertime SSTs and coral bleaching (Smithers and Woodroffe 2001; Hendy et al. 2003; Cantin et al. 2010; Carilli et al. 2010, 2012; Cantin and Lough 2014; Mallela et al. 2015). Recently, Barkley and Cohen (2016) and Barkley et al. (2018) demonstrated a statistically significant relationship between the prevalence of stress bands in massive *Porites* spp. corals and the severity of observed bleaching in the coral community on multiple reefs within the Palau archipelago and on Howland and Jarvis Islands in the CEP. These observations support the utility of skeletal stress bands as proxies for historical bleaching severity in the absence of observational data.

In this study, we first build on the original calibration of bleaching incidence within a coral community (hereafter “observed bleaching incidence”) against the prevalence of stress bands in massive coral skeletons (hereafter “stress band prevalence”) (Barkley et al. 2018) by including new

Fig. 1 Incorporation of signatures of bleaching into a coral skeleton. **a** *Porites lobata* colony #1032 (Phoenix Islands) bleached in 2015. **b** The CT image of a core removed from the bleached colony revealed a high-density stress band at the top of the core. The density anomaly associated with the stress band is quantified using an automated image analysis routine written in MATLAB (CoralCT, DeCarlo and Cohen 2016). Here, the stress band is identified as a 2σ excursion above the mean skeletal density (red shading). **c** If the coral recovers and continues to grow, the stress band is incorporated into the skeleton and serves as a record of the bleaching event



data from the Pacific and the Caribbean. The new calibration includes 11 reef systems, multiple massive coral genera, and represents multiple coral community compositions. Second, we apply the calibration to stress band records constructed from eight central Pacific reef systems, spanning the time period 1982–2015. Third, we refine the NOAA thermal stress index (Degree Heating Weeks, DHW) calculation to enable estimates of thermal stress in the CEP, where SST variability on inter-annual timescales is dominant. We use a percentile-based method, independent of seasonality, to calculate the DHWs and cumulative thermal stress (total Hotspot) for each heat wave at each site over the corresponding time period 1982–2015. We then compare the severity of the bleaching response with the level of thermal stress imposed on each reef during each event and construct reef-specific thermal sensitivity curves and a thermal tolerance index ($b_{1/2}$) for each reef system. Finally, we assess the thermal tolerance indices against multiple physiological and climatological factors to evaluate the potential mechanisms underpinning the different thermal tolerances exhibited by different reefs.

Materials and methods

Collection of coral cores and identification of stress bands

A total of 247 skeletal cores were collected and analyzed from colonies of three massive coral genera (*Porites* spp., *Orbicella* spp., and *Siderastrea siderea*) on 11 coral reefs in the Pacific Ocean and Caribbean (Fig. 2). A subset of data from each core, specifically those years for which observational bleaching data exist, was used in the calibration. These cores are listed in Table S2. 122 *Porites* cores were then used to construct thermal histories for the eight Pacific reefs back to 1982 and generate the thermal sensitivity curves. These cores are listed in Table S3.

All cores were collected and analyzed using the same methods. Only live colonies were cored, establishing the top age. Cores were removed vertically, i.e., parallel to the upward growth axis, using either a pneumatic drill fitted with 3-cm-diameter diamond tip coring bit or a hydraulic drill fitted with an 8-cm-diameter bit. Core holes were sealed with a cement cap and underwater epoxy, secured

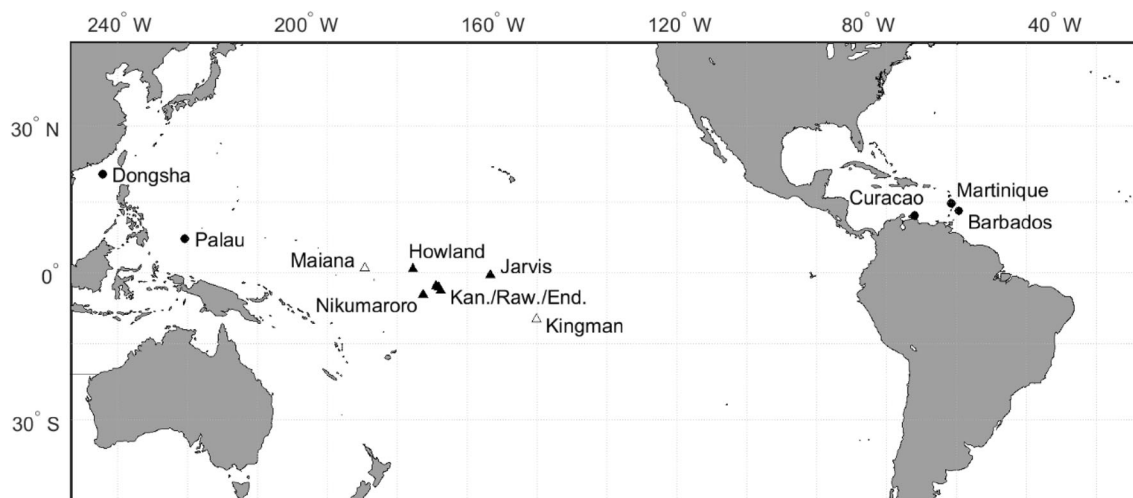


Fig. 2 Location of coral reefs included in this study. Cores collected on reefs denoted by black circles contributed to the stress band-bleaching severity calibration only. White triangles denote reefs that did not contribute to the calibration due to absence of observational

data, but for which bleaching histories were reconstructed. Black triangles denote reefs that both contributed to the calibration and for which bleaching histories were reconstructed. Kan./Raw./End. refers to the Kanton, Rawaki, and Enderbury Islands

flush with the colony surface to facilitate overgrowth of tissue and wound closure (e.g., Matson 2011), a 6- to 36-month process depending on the rate of coral growth and diameter of core. All cores were first air-dried in the field, then oven-dried at 60 °C, and CT-scanned intact, together with density standards, on the Siemens Volume Zoom Helical Computerized Tomography (CT) Scanner at Woods Hole Oceanographic Institution or the Siemens Biograph mCT scanner at the Biomedical Research Imaging Center (BRIC) at the University of North Carolina (protocol as per Barkley et al. 2015; DeCarlo et al. 2015).

Stress bands and annual growth bands were identified in the CT scan images of each core and quantified using the automated code coralCT for MATLAB which traces the density of individual corallites within the three-dimensional core (DeCarlo and Cohen 2016). Revisions to version 1.1 of coralCT, which was designed primarily for *Porites* spp., were made to accommodate the skeletal architecture of the Atlantic corals which have more prominent thecal walls than *Porites*. Specifically, a linear quadratic estimation algorithm (i.e., Kalman filtering) improved polyp tracing along the core axis. The code was also revised to enable automated identification of stress bands (Barkley et al. 2018). Specifically, the density time series for all corallites in the core (see DeCarlo et al. 2015, Data Repository Figure DR2) were averaged to create an “ensemble” mean density time series for all traceable corallites. The averaged density profile time series was then detrended to account for shifts in mean density that may occur over time. Regions where skeletal density exceeded 2 standard deviations above the whole-core mean, a threshold chosen to account for the range in natural seasonal and

inter-annual density variability, were identified as stress bands (Fig. 1c). To exclude fine-scale density anomalies, stress bands were defined as having a minimum width of 1 mm. Each CT scan was visually inspected to validate the presence and location of stress bands identified by the automated program.

The age model for each core was developed using annual growth bands also identified in the CT images. In corals with clear annual banding, the age model was constructed by counting the bands from the top of the core. Where banding was unclear or ambiguous, the band-based age model was validated using dissepiments. Specifically, the distance between successive monthly dissepiments was quantified from photographs taken under a dissecting microscope (Fig. S2). The estimate of annual extension derived from dissepiments was used to confirm the estimate derived from annual bands, following DeCarlo and Cohen (2017) (i.e., 12.4 dissepiments per year).

The thickness of the tissue in each core used in the bleaching history reconstruction was measured as an index of biomass or energetic reserve. The vertical distance between the top of the core and the topmost dissepiment upon which the base of the tissue rests (e.g., Barnes and Lough 1992) was measured on a cut slab using a Nikon SMZ1500 stereomicroscope and SPOT imaging software (e.g., Barkley et al. 2018).

Bleaching survey data

Published bleaching accounts were used to calibrate the proportion of skeletal stress bands per event identified in the suite of cores against the observed bleaching incidence

(represented by the percent coral cover observed to be bleached) recorded during that event (Table S4). In all cases, with the exception of the Phoenix Islands surveys in 2015 (Kanton, Rawaki, Enderbury, Nikumaroro Islands), bleaching was observed during or after the peak SST anomaly obtained during each event. In the Phoenix Islands, ecological surveys and skeletal cores were obtained two months prior to the peak SST anomaly, and it is likely that the full extent of bleaching in 2015–2016 was not captured by those surveys. However, since coring and surveys were conducted simultaneously, we expect the stress bands to track the severity of bleaching at the time, and we used this information in the calibration.

On Dongsha Atoll and Jarvis Island, bleaching estimates were obtained from photographic surveys conducted in June 2015 (DeCarlo et al. 2017) and November 2015 (Barkley et al. 2018), respectively. On Jarvis and Howland Islands in 2010, bleaching severity was assessed from Rapid Ecological Assessments (REA) and towed-diver surveys (Vargas-Ángel et al. 2011). In the Phoenix Islands (Kanton, Rawaki, Enderbury, and Nikumaroro) in 2015, bleaching information was estimated from photographic surveys (Mangubhai et al. 2015; Table S4). In the Caribbean, coral bleaching observations on Martinique, Barbados, and Curacao in 1998, 2005, and 2010 were used in the calibration (Wilkinson 2008; Eakin et al. 2010; Estep et al. 2017). Because results were reported as percent coral cover bleached (Jarvis, Howland, Dongsha, and the Caribbean sites), or percent colony bleached (Phoenix Islands), we standardized the data as follows:

$$\text{Observed Bleaching Incidence} = \frac{\text{bleached coral (m}^2\text{)}}{\text{total coral (m}^2\text{)}}$$

Sea surface temperature data and data products

We used daily satellite SSTs (November 1981–December 2016) from the AVHRR Pathfinder Version 5.3, 4 km dataset (nighttime only) (Casey et al. 2010). For reefs from which cores were collected across multiple cells, the grid cells were averaged. Average weekly SSTs were calculated, and temporal gaps in the Pathfinder data were filled with mean-adjusted values from the IGOSS OIv2 $1^\circ \times 1^\circ$ resolution dataset (Reynolds et al. 2002). In situ temperature loggers deployed at Jarvis by Barkley et al. (2018), as well as our loggers deployed at Kanton, Enderbury, Nikumaroro, and Rawaki from June 2012 to September 2015, were used to validate satellite-derived SSTs for these central Pacific sites (Fig. S3). Average in situ temperatures were within $\pm 0.25^\circ\text{C}$ of satellite SSTs, with two exceptions. First, on the west side of Jarvis Island, upwelling of the Pacific Equatorial Undercurrent (EUC) lowers local

temperatures relative to the east side of the island and satellite-derived SSTs, which consistently capture east-side SSTs (Alpert et al. 2016). However, during El Niño, weakening of the EUC occurs, upwelling is diminished or entirely absent, and temperatures are homogenous around the island. Thus, during bleaching events, temperatures on Jarvis' west side are consistent with satellite-derived SSTs (Barkley et al. 2018). Second, in Kanton Lagoon, loggers deployed during the 2015 El Niño revealed that daytime temperatures in the lagoon consistently exceeded both satellite-derived SSTs and logged outer reef SSTs by up to 1°C . Kanton lagoon cores were used in the calibration because bleaching severity in the lagoon was recorded in 2015 at the same time the cores were collected. However, we did not include lagoon cores in the down-core historical bleaching reconstruction to evaluate thermal sensitivity because we could not accurately constrain historical lagoon SST back to 1982 from the satellite data alone.

Estimation of the error on the calibration of stress band proportion against observed bleaching

The presence of a stress band in a single core during a known thermal stress event indicates that bleaching occurred, and stress bands have been used as a binary indicator of historical bleaching (e.g., Smithers and Woodroffe 2001; Carilli et al. 2010). Here, we use stress bands to determine when reef-scale bleaching occurred and quantify its severity. However, significant uncertainty exists in estimating the proportion of stress bands in the population of the sampled massive genera (e.g. *Porites spp.*) based on cores extracted from a relatively small number of colonies. Further, because bleaching is variable even on small spatial scales within a reef, there are non-trivial uncertainties associated with both the stress band proportion and the observed bleaching incidence. To best account for these uncertainties in calibrating the proxy, we used the Mantel–Haenszel estimator of the common odds ratio, $\hat{\psi}$ (Mantel and Haenszel 1959) (see SI for detailed methods). To use the odds ratio to predict bleaching incidence, a functional estimate of bleaching incidence was constructed by inverting the odds ratio:

$$p_{bi} = \left(1 + \frac{1 - p_{sb}}{\hat{\psi} p_{sb}} \right)^{-1}$$

where p_{bi} is the proportion of reef community bleached and p_{sb} is the proportion of stress bands (*sb*) observed. From the variance in both p_{sb} and $\hat{\psi}$, the associated variance of the prediction was calculated as follows:

$$\text{Var } p_{\text{bi}} \cong \left(\frac{\partial p_{\text{bi}}}{\partial p_{\text{sb}}} \right)^2 \text{Var } p_{\text{sb}} + \left(\frac{\partial p_{\text{bi}}}{\partial \hat{\psi}} \right)^2 \text{Var } \hat{\psi}$$

We use the variance on the predicted bleaching incidence ($\text{Var } p_{\text{bi}}$) to define a 2σ confidence interval for reconstructed bleaching incidence levels. The width of this confidence interval depends therefore on three things: the number of cores collected, the prevalence of stress bands among those cores, and the effectiveness of the common odds ratio at explaining the calibration data (or the quality of the fit).

Development and application of a percentile-based estimate of thermal stress

The NOAA Coral Reef Watch Degree Heating Week (DHW) index uses the amplitude and duration of the SST anomaly to estimate levels of thermal stress experienced by corals (Gleeson and Strong 1995) and assumes that thermally stressful conditions occur when temperatures exceed 1°C above the maximum monthly mean SST (MMM) to which corals are normally exposed. However, in the CEP, the SST regime is dominated by inter-annual variability rather than regular seasonal cycles, and consequently the maximum temperature to which corals are normally exposed does not occur during the same month every year. This means that the MMM does not effectively describe the “upper end” of temperatures in the CEP or other regions where seasonal variability is not dominant. The traditional DHW metric, therefore, consistently overestimates the level of thermal stress in such regions.

To address this issue, we developed a percentile-based bleaching threshold which is independent of the timescale of SST variability and can be applied in any oceanographic environment. First, we calculated gap-filled Pathfinder SSTs from 1982 to 2016 for each grid cell containing the reef locations represented in the global bleaching database of Donner et al. (2017). To establish the maximum heat to which corals are exposed during “normal” or non-extreme years, SSTs during ENSO neutral years between 1982 and 2012 (i.e., 1985–1986, 1990, 1993–1996, 2001, 2003–2006, 2012 based on years when $-1.25 < \text{Nino}$ $3.4 < 1.25$ (Trenberth 1997)) were extracted and the site-specific distribution of weekly SSTs evaluated. A threshold percentile (e.g., 94th, 95th, 96th) was chosen to represent the high end of SSTs typically experienced by each coral community, and the SST value corresponding to that percentile at that site was substituted for the $\text{MMM} + 1^\circ\text{C}$ threshold. We used the new threshold to calculate DHWs at each site. We repeated the exercise with different percentiles and compared the resulting DHWs with the observed bleaching levels at each site during bleaching

years (Donner et al. 2017). The quality of each set of predictions was evaluated using the Gilbert Skill Score (or Equitable Threat Score, ETS) which maximizes predictive power while accounting for the increase in type 2 errors associated with lower thresholds (Fig. S1). A percentile of 94.4th resulted in the maximum ETS (0.68 on a scale of 0–1, see SI). It is important to note that this method is calibrated to maximize the predictive power of the 4 DHW alert level. Other commonly used alert levels, e.g. alert level 2 (8 DHW), under which mortality is likely have not yet been estimated (Liu et al. 2006).

Total Hotspot as an index of cumulative thermal stress

The DHW index was developed as a 3-month running forecasting metric to predict where bleaching is likely to occur. In this study, we compare the cumulative level of thermal stress, experienced by the reef during each event, with the resulting bleaching severity. Thus, rather than DHW, we use the total Hotspot (TH), which is the total number of weeks during which the site-specific thermal threshold is exceeded (Gleeson and Strong 1995). TH is calculated using the percentile-based threshold of 94.4th instead of the traditional $\text{MMM} + 1$ threshold as follows:

$$TH_e = \sum_{w=1}^n H_w$$

where TH is the total Hotspot, for event e from the first week ($w = 1$) to the last week (n) during which SST exceeded the bleaching threshold. We use the TH index below to assess the sensitivity of each coral community to thermal stress.

Results

Stress band: bleaching calibration

Stress bands were identified in the majority of cores (with the notable exception of those collected from Kingman Reef) and only occurred in years in which SSTs were anomalously warm and TH exceeded zero (Table S4, Table S5). No stress bands occurred in years during which thermal stress was zero. For sites and years in which observational bleaching data are available, we regressed the proportion of stress bands against the observed severity of coral bleaching incidence at the same site during the same year (Fig. 3). Stress bands are highly correlated with bleaching severity ($r^2 = 0.945$, $p < 0.001$), consistent with Barkley and Cohen (2016) for Palau, and Barkley et al. (2018). The common odds ratio regression, used to

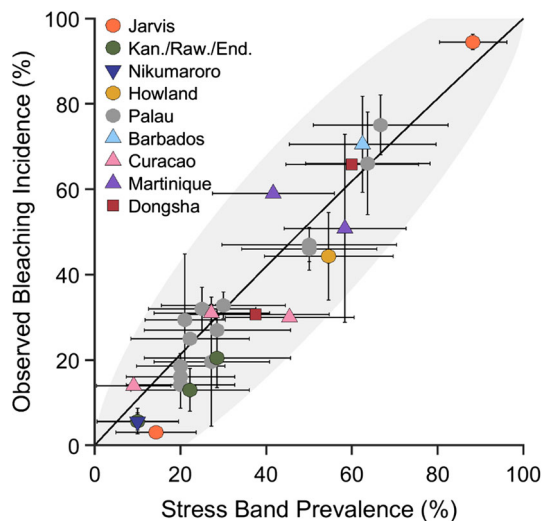


Fig. 3 Stress band prevalence in three massive Pacific and Caribbean coral genera versus observed bleaching incidence at each site for the matching time periods. Vertical error bars show ± 1 standard deviation on the observational bleaching data, and horizontal error bars represent the standard error of a proportion of stress bands in the population of massive corals. The magnitude of the error is a function of the sample size ($n = 10$ to $n = 38$). The regression was computed using the Mantel–Haenszel common odds ratio. Shaded region shows 95% prediction interval in predicting bleaching incidence from a sample of $n = 15$ cores

estimate the error on the relationship between bleaching severity and stress band proportions (Methods, Eq. 1), was $\psi = 1.11 \pm 0.10$ (2σ), implying a near 1 to 1 relationship (Fig. 3). We use this regression to predict bleaching levels at sites and during times where no observations were made. The error on these predictions is calculated using Equation 2 (methods) using the variance in the common odds ratio (ψ), the number of cores sampled, and the fraction of cores that exhibit stress bands. For a sample size of 15 cores, the maximum uncertainty on the estimate of bleaching severity is 28.7% (2σ), which occurs at a stress band proportion of 48.3% (Fig. 3 shaded region).

Thermal stress indices

In Fig. 4, DHW and TH calculated using the traditional threshold method (i.e., 1°C above the MMM, a–h) are compared with DHW calculated using the 94.4th percentile-based (j–q) threshold for our study sites. In addition, we provide DHW and TH estimates for the northern Great Barrier Reef (GBR; 10.8°S and 142.9°E) (i and r), to highlight both the different levels and histories of thermal stress experienced by reefs in the CEP versus reefs in regions dominated by seasonal SST variability, and the relative change in estimated severity when the percentile-based method is applied. DHW events coincide with El Niño years at all CEP sites and their magnitudes are linked

to size and type of El Niño event, i.e., central versus eastern Pacific El Niño (Ashok et al. 2007). Eastern Pacific events are felt most strongly at Jarvis ($\sim 160^\circ\text{W}$), whereas central Pacific events are felt most strongly in the Phoenix Islands. Further west, Maiana Island, is unaffected by eastern Pacific events instead experiencing its major thermal stress events in weak El Niño years (e.g., 2004).

At all our study locations, the percentile-based bleaching threshold was higher than the $\text{MMM} + 1$, causing lower DHW and TH estimates for each event relative to the traditional calculation. At equatorial sites, average DHW and TH for most events were substantially different. For example, DHWs derived by the percentile method were lower by an average of 6.3°C wk and 5.8°C wk at Jarvis and Kanton, respectively, versus 4.5°C wk and 2.3°C wk for Dongsha and the GBR. TH decreased by 10.01 and 4.1°C , versus 2.14 and 0.88°C at the same sites. These results indicate that the traditional $\text{MMM} + 1$ method overestimates thermal stress on CEP coral reefs relative to other reefs confirming the bias observed by others (e.g., Donner 2011; Lough et al. 2018). Conversely, the percentile method provides a non-biased method for all sites.

Reconstructed bleaching histories

We applied the stress band prevalence—observed bleaching incidence calibration (Fig. 3) to reconstruct the history and severity of bleaching at our eight central Pacific reef sites since 1982 (Fig. 5; Table S6). The young end of the reconstruction on each reef is determined by the date the most recent cores were collected (for example 2010 on Kingman, 2016 on Jarvis, 2012 on Howland and Maiana, see Table S3). We do not attempt to reconstruct bleaching in the Phoenix Islands in 2015 because the cores were retrieved two months prior to the peak SST and thus may not capture the full severity of the bleaching that occurred there in 2015. Stress band counts at Jarvis Island back to 1960 were initially published by Barkley et al. (2018).

Bleaching has been directly observed in the Phoenix Islands only in 2015 and on Howland Island only in 2010, and no bleaching observations have been made on Maiana or Kingman, meaning that our reconstructions significantly extend the bleaching database for this region across space and back in time. For all reefs, excluding Kingman, our analysis reveals a history of bleaching events, each occurring in response to El Niño-induced thermal stress. Cores collected on Kingman Reef in 2010 and 2012 revealed no stress bands back to 1982, consistent with the absence of appreciable thermal stress ($\text{DHW} > 4$) over this time period (Fig. S4), and implying that Kingman Reef has never experienced significant bleaching.

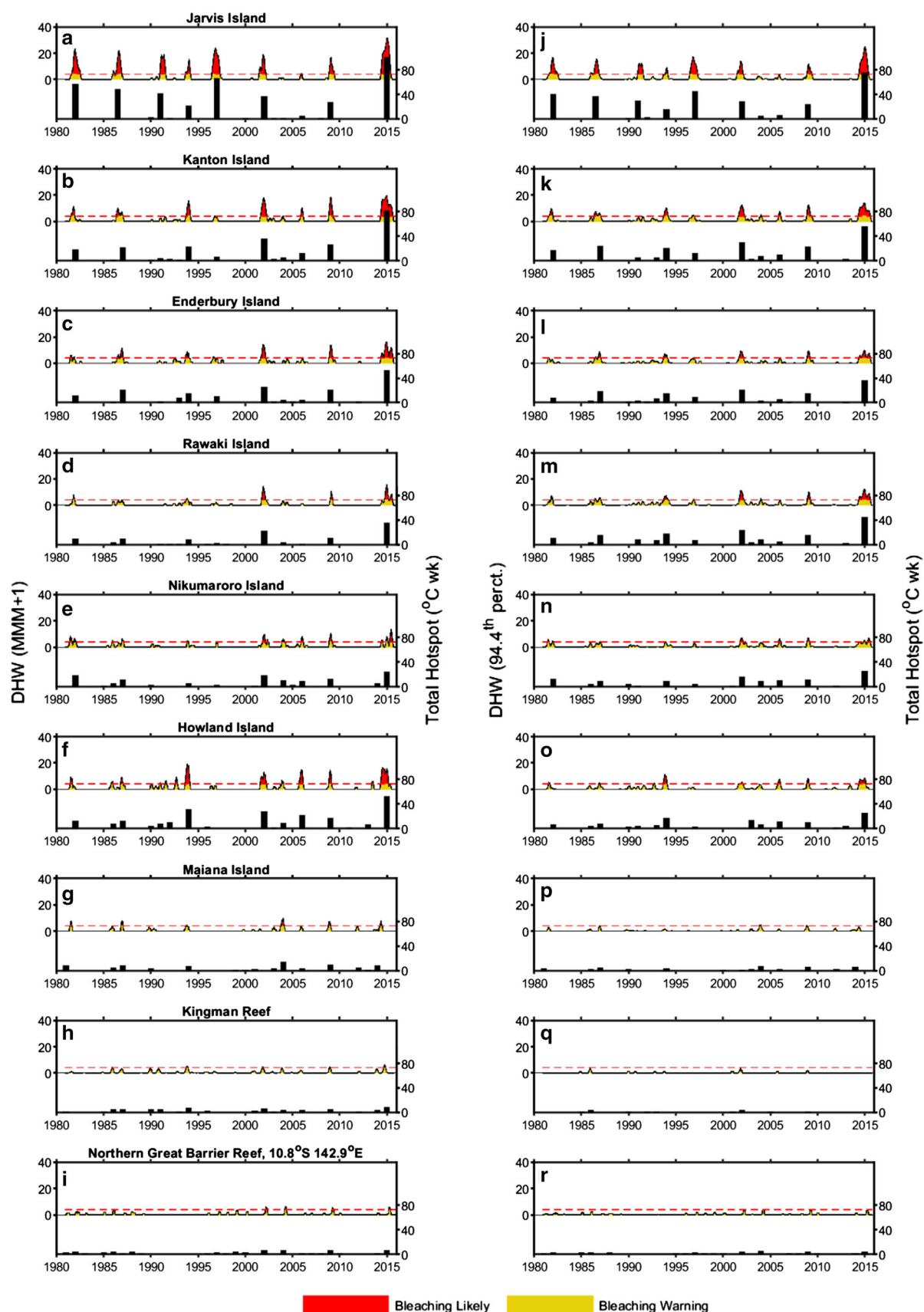


Fig. 4 Degree heating weeks (line curves) and total Hotspot (bars) 1982–2015 calculated using the traditional bleaching threshold (NOAA Coral Reef Watch, MMM + 1) (left panel) and the 94.4th percentile method (right panel). DHW events at locations with strong seasonal temperature cycles (e.g., GBR) are of similar magnitude by both methods, but are less severe at equatorial locations when calculated using the 94.4th percentile method. Pathfinder v5.3 4 km daily resolution dataset (nighttime only) was supplemented with the mean-adjusted IGOSsv2 weekly $1^\circ \times 1^\circ$ gridded data product

Assessment of the thermal sensitivity of coral communities

Using the reconstructed bleaching histories (Fig. 5; Table S6) and the calculated thermal stress experienced by each reef during each bleaching event (Fig. 5), we characterized the sensitivity of the coral community response to thermal stress (Fig. 6). For each site, the relationship between thermal stress and bleaching severity follows a

predictable, nonlinear pattern. Because the bleaching thresholds of individual coral colonies on each reef are assumed to be normally distributed, we used a cumulative density function (CDF) to fit the data. A minimum amount of thermal stress is required to induce bleaching; therefore, we used a lognormal CDF for the regression:

$$BI_j = \frac{100}{\sigma\sqrt{2\pi}} \int_0^{TH_j} \frac{e^{-(\ln(t)-\mu_i)^2/(2\sigma_i^2)}}{t} dt$$

where BI_j is coral bleaching incidence at a given total Hotspot TH_j and μ_i and σ_i are regression parameters corresponding to mean and standard deviation of the associated normal distribution for each reef i . Data from Kanton, Rawaki, and Enderbury were pooled as the relationship between BI and TH was not significantly different between these reefs. For the purpose of this analysis, we excluded reconstructed BI events with greater than 35% error.

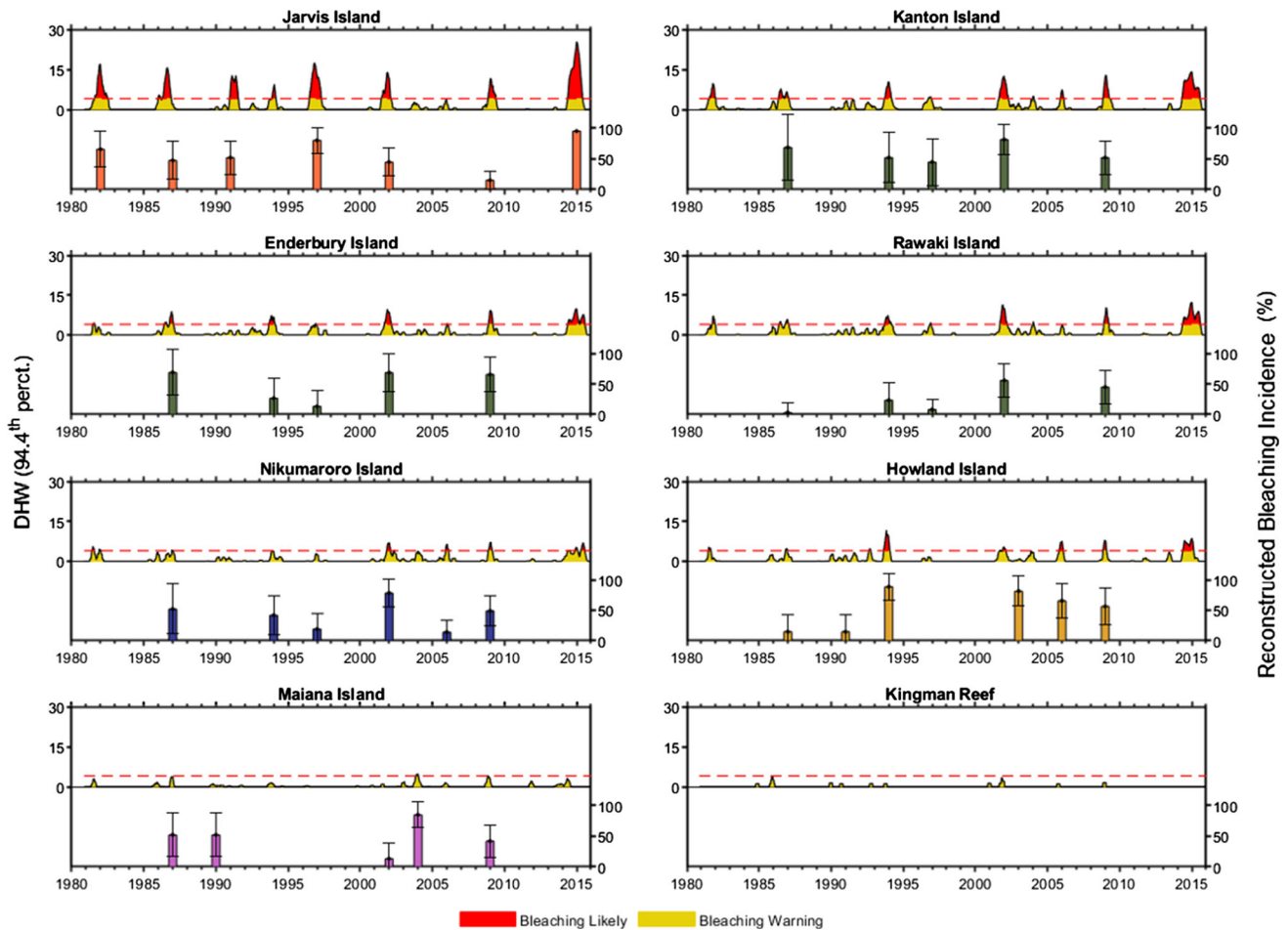


Fig. 5 The history of thermal stress (Degree Heating Weeks) calculated using the percentile method (top panels) shown with the history of bleaching events and their severity reconstructed from stress band records (bottom panels) for eight Pacific coral reefs.

Broken red line indicates 4°C weeks when bleaching is likely to occur. Error bars denote 2σ based on the variance of the bleaching reconstructions (Eq. 2)

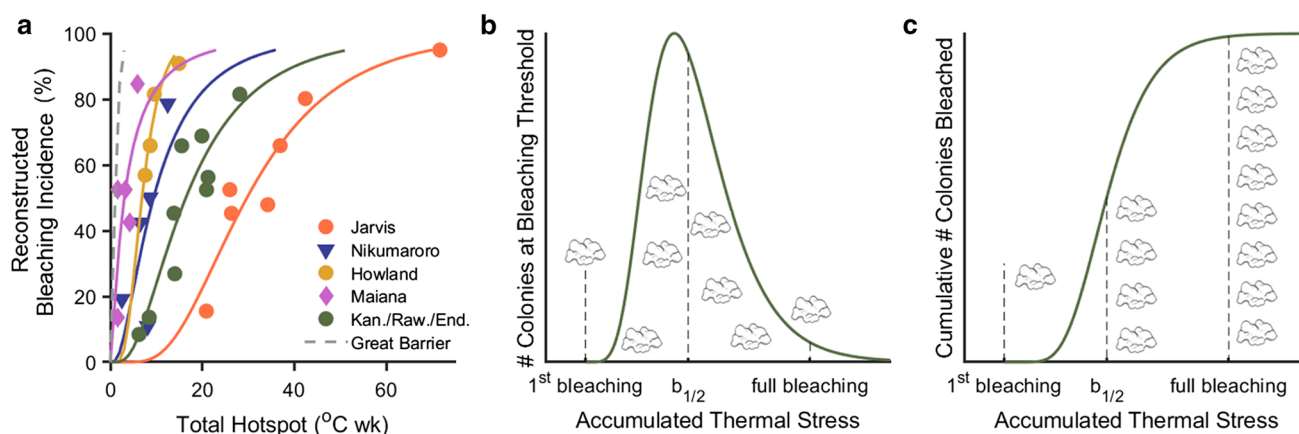


Fig. 6 **a** The site-specific relationship between thermal stress (total Hotspot) and percent bleaching incidence generated from bleaching reconstructions and DHW calculations in Fig. 5. Great Barrier Reef data (gray) are observed bleaching severity recorded during the 2002/2003 and 2015/2016 bleaching events (Donner et al. 2017; Hughes et al. 2017). **b**, **c** Present a conceptual model to explain the mechanism by which massive corals record community bleaching

A single parameter index of the mean thermal tolerance of corals at each reef was estimated by converting μ_i to the half-point of each regression (i.e., the TH at which 50% bleaching is predicted) as follows:

$$b_{1/2} = e^{\mu_i}.$$

Using $b_{1/2}$ as an index of thermal tolerance implies that Jarvis Island coral communities have the highest thermal tolerance ($b_{1/2} = 29.71 \pm 1.06$ SE), followed by the northern Phoenix Islands (Kanton/Enderbury/Rawaki) and that tolerances decrease westward, with Maiana Island exhibiting the lowest thermal tolerance index ($b_{1/2} = 3.04 \pm 1.36$ SE) of the CEP reefs studied here. We also compare the bleaching sensitivity of these CEP reefs with the GBR using spatial (Hughes et al. 2017) and temporal (Donner et al. 2017) bleaching observations versus percentile-based TH estimates. The GBR data help to put the thermal tolerances of the central Pacific reefs in perspective, exhibiting an even lower thermal tolerance index than Maiana ($b_{1/2} = 1.03 \pm 1.04$ SE).

Discussion

The occurrence of mass coral reef bleaching events associated with ocean warming has motivated efforts to better predict coral reef futures (Pandolfi et al. 2011). While some efforts are based predominantly on GCM projections of temperature (Beyer et al. 2018), others are incorporating variable and potentially shifting thermal thresholds, as observed in nature (Coles and Jokiel 1977; Fisk and Done 1985; Rowan et al. 1997; Maynard et al. 2008; Van Woesik

et al. 2012; Hughes et al. 2017). Nevertheless, characterizing the thermal tolerances of different reef communities and evaluating change over time are difficult because they require direct, repeat observations of coral communities during periods of thermal stress. Here, we used skeletal stress bands to fill gaps in observational bleaching data on eight central Pacific coral reef islands since 1982. Our study builds on pioneering work by Emiliani et al. (1978), who identified stress bands in a *Montastrea* coral (now *Orbicella*), and by Hudson et al. (1976) who attributed anomalously high-density bands in the same species to environmental stress. Subsequent work by Cantin and Lough (2014) constructed bleaching histories from the GBR, and Carilli et al. (2009) used stress bands to evaluate effects of local stressors on bleaching incidence in the Caribbean. Subsequently, Barkley and Cohen (2016) showed that the proportion of stress bands reflected the severity of bleaching in the coral reef community. These observations paved the way for the use of skeletal records to provide quantitative information about reef responses to thermal stress in the absence of direct observations (DeCarlo et al. 2017; Barkley et al. 2018).

The stress band–bleaching relationship and a conceptual model of the mechanism

We expanded the original calibration of Barkley and Cohen (2016) using new observational bleaching data and measurements of stress band prevalence in three massive coral genera in the Pacific and Caribbean. These results show that the relationship applies beyond just Pacific reefs and Pacific *Porites* corals and leads naturally to the question:

why is the prevalence of stress bands in massive corals so well correlated with the incidence of bleaching across the community of mixed coral taxa? We propose that within each population of massive corals, a range of thermal thresholds exist (Fig. 6b). At low levels of thermal stress a relatively small fraction of the massive corals bleach along with other more sensitive species. As thermal stress increases, massive corals with higher and higher thermal thresholds succumb to bleaching, as do the rest of the species in the coral community (Fig. 6c). Under this model, long-lived massive corals represent the full range of bleaching thresholds within their communities of mixed species on the reef. The Caribbean corals included in the calibration (Fig. 3) behave as the Pacific *Porites* spp. do, implying that the long-lived massive coral genera play a similar role on Caribbean reefs. While we attempted to avoid colony size bias during field sampling, we recognize that bleaching reconstructions based on stress band prevalence do have the potential to underestimate the severity of bleaching during events in which mortality in the massive corals was high. If a substantial portion of massive colonies died and were not represented in the core samples, the relative proportion of colonies that have stress bands would be lower and underestimate the severity of the event. We can assume that such a bias is minimal during most bleaching events as *Porites* tends to have lower mortality rates than other corals and because our record is relatively short (33 yrs). However, in applying this calibration to longer records, considering and accounting for the compounding of potential bias is necessary.

Generation of bleaching histories

Using the new calibration, we generated bleaching histories for eight central Pacific reefs back through 1982. With the exception of Kingman Reef, each island experienced multiple episodes of thermal stress sufficient to cause coral bleaching (DHW > 4) over this time period and our historical bleaching reconstruction reveals that each of the coral communities responded in a manner consistent with the degree of thermal stress imposed. Critically, seven of the reefs have experienced multiple severe (> 30% bleaching) episodes within the last four decades, most of which had not been observed. For example, Howland Island experienced four substantive bleaching episodes in just 20 yrs, between 1990 and 2010. The Phoenix Islands—Kanton, Enderbury, Rawaki, and Nikumaroro—all experienced multiple episodes of bleaching prior to 2015, but 2002/2003 (which coincided with the central Pacific El Niño) appears to have been the most significant (the upper bound of uncertainty in the reconstructed bleaching levels reaches 100%). While direct observations did not occur in 2002/2003, our results are consistent with those of

ecosurveys conducted several years later that recorded mass mortality of corals across the Phoenix Islands (Obura and Mangubhai 2011).

Characterization of thermal sensitivity

Seven of the Pacific reefs studied experienced multiple episodes of bleaching at different levels of severity, and we were therefore able to characterize the reef-specific relationship between thermal stress and bleaching response. In these cases, we use total Hotspot (TH) as a measure of the cumulative thermal stress experienced by each coral community during each event. In the absence of quantitative stress band data, we used observational bleaching data to construct a comparable response curve for the northern GBR, which reveals exceptionally low thermal thresholds of GBR coral communities relative to those in the central Pacific. This observation raises the question: what are the biological and environmental factors underlying the relative thermal tolerance of the central Pacific reef assemblages?

Potential drivers of thermal tolerance in the CEP

We established a thermal tolerance index ($b_{1/2}$) and evaluated the relationship between $b_{1/2}$ and the reef thermal history, water column nutrient concentrations, energetic status of the corals, presence or absence of upwelling, and cloud cover-based differences in irradiance at each of our study sites. For thermal history, we calculated the variance, range, median, and mean SSTs, and the median and mean of the TH per event for each reef over the satellite period. The best correlation with $b_{1/2}$ was the mean TH (OLS, $p < 0.001$). Thermal tolerance was significantly higher on reefs experiencing the most severe thermal stress events on average, i.e., highest mean TH (Jarvis, Kanton, Rawaki, Enderbury), suggesting that thermal thresholds are likely linked to the history of thermal stress exposure (Fig. 7a). While our data do not allow for a mechanistic understanding of this relationship, the link between thermal history and coral thermal tolerance is fairly well established. Indeed, the thermal threshold value used in the DHW calculation is based on the observation that corals living at higher temperatures also bleach at higher temperatures in field and laboratory-based studies (Coles and Jokiel 1977; Van Woesik et al. 2012; Fine et al. 2013). Further, evidence suggests that corals in more variable SST environments, whether diurnal or seasonal or inter-annual time scales, have higher bleaching thresholds than corals living in more thermally homogenous environments (McClanahan et al. 2007; Oliver and Palumbi 2011; Carilli et al. 2012; Safaie et al. 2018).

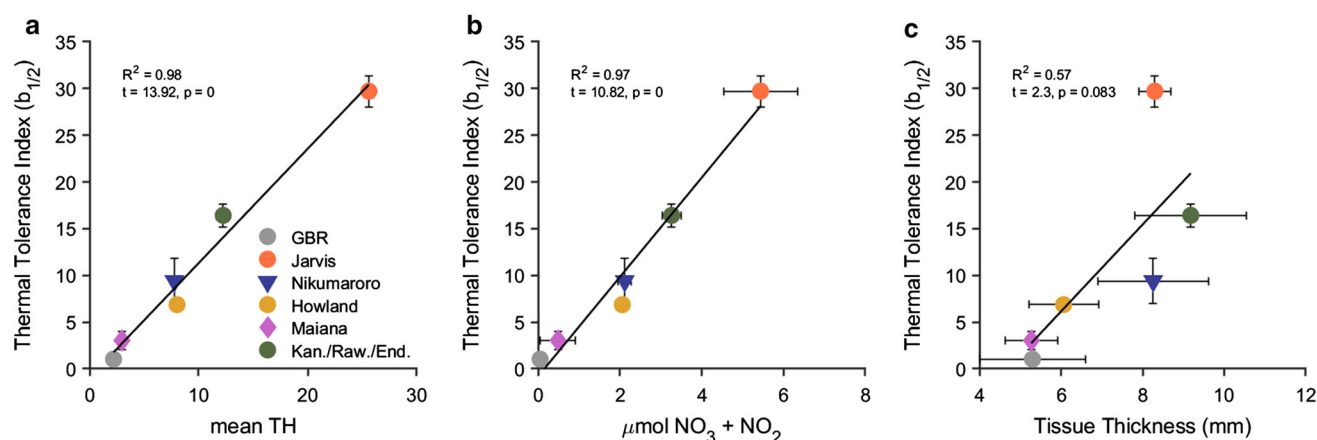


Fig. 7 Thermal tolerance index ($b_{1/2}$) as a function of **a** mean total Hotspot over the instrumental period, **b** nitrate + nitrite concentrations during non-stressful conditions (Table S7), and **c** coral tissue thickness during non-stressful conditions (Table S8). Thermal

tolerance is significantly related to thermal history (mean TH) (linear regression), consistent with evidence that corals experiencing regular, large thermal stress events are more resistant to stress than those experiencing relatively weaker events

We also examined the potential role of water column nutrients and host energetic status in promoting thermal tolerance. High nutrient concentrations are thought to lower the bleaching thresholds of corals (Wooldridge 2009; D'Angelo and Wiedenmann 2014) so we compared average dissolved inorganic nutrient (DIN) concentrations ($\text{NO}_3 + \text{NO}_2$) during ENSO neutral conditions (Table S7) with the derived thermal tolerance of each reef community. We found a significant positive correlation (OLS, $p < 0.001$) between nutrient levels and thermal tolerance, inconsistent with prior hypotheses based on results from laboratory experiments (Fig. 7b). While this evidence may suggest a role for nutrient uptake or heterotrophy in thermal tolerance, it is yet unclear whether the relationship we observe is direct. TH and nutrient concentrations covary across these sites and more testing is required to deconvolve these different factors.

Evidence exists that heterotrophic feeding can alleviate bleaching-induced starvation by supplementing the coral's energy budget (Grottoli et al. 2006; Rodrigues and Grottoli 2006; Hoogenboom et al. 2012). We used tissue thickness as a proxy for biomass and energetic reserve (Carilli et al. 2012) and found that average tissue thickness of cores collected during non-stressful (i.e., ENSO neutral) conditions was correlated with $b_{1/2}$, but the correlation was less significant (OLS, $p = 0.083$) (Fig. 7c). This result suggests that energetic reserve may not be the over-riding factor in establishing thermal tolerance. However, it is likely that energetic status plays an important role in the survival of corals through bleaching and in the post-bleaching recovery.

We also investigated the potential for cloud cover to mitigate the impact of thermal stress on coral bleaching using outgoing longwave radiation (OLR) as a proxy

(Fig. S4A) for cloud cover (Kessler and Kleeman 2000). To compare the relative amount of total cloud cover observed at each site with the total thermal stress, the standardized cloudiness was integrated over each thermal stress episode (TC) and regressed against TH (Fig. S4B). Our analysis reveals that total cloud cover at our study sites is indeed elevated during thermal stress episodes but that cloudiness per $^{\circ}\text{C}$ week (i.e., the slope of the TH–TC regression) is the highest where thermal tolerances are the lowest (e.g., Maiana, the GBR). This suggests that differences in cloud cover cannot explain the differences in thermal tolerance observed in this study.

We conclude that the relatively high thermal tolerances observed on Jarvis and the northern Phoenix Islands most likely have arisen from adaptation over centuries or millennia of exposure to repeated episodes of thermal stress driven by El Niño. Nevertheless, while coral reefs in the CEP have elevated thermal thresholds for bleaching relative to other reefs, they also experienced significantly higher levels of thermal stress than other reefs, and our bleaching reconstructions indicate that CEP coral communities bleach predictably in response to thermal stress. For this reason, elevated thermal thresholds of CEP coral communities are likely only one, albeit important, component of the strategy for coral reef survival in the dynamic, oft-times hostile environment of the CEP. New studies will shed light on questions about how the CEP coral communities survive the repetitive bleaching events they endure.

This study shows that thermal tolerances of coral communities can be constrained using proxy data accrued across space and through time, in the absence of direct observations. Further development and application of this approach, and its expansion to regions outside of the CEP,

will enable better constraints on coral thermal thresholds both within and among reef systems, and allow for the identification of whether and where thermal thresholds may be shifting over time.

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References

- Alpert AE, Cohen AL, Oppo DW, Decarlo TM, Gove JM, Young CW (2016) Comparison of equatorial Pacific sea surface temperature variability and trends with Sr/Ca records from multiple corals. *Paleoceanography* 31:252–265
- Ashok K, Behera SK, Rao SA, Weng H (2007) El Nino Modoki and its possible teleconnection. *J Geophys Res* 112:1–27
- Barkley HC, Cohen AL (2016) Skeletal records of community-level bleaching in *Porites* corals from Palau. *Coral Reefs* 35:1407–1417
- Barkley HC, Cohen AL, Brainard RE, Mollica NR, Rivera HE, Drenkard EJ, Young CW, Vargas-Ángel B, Lohmann GP, Decarlo TM, Alpert AE, Lino KC, Oliver TA, Pietro KR, Luu VH (2018) Repeat bleaching of a central Pacific coral reef over the past six decades (1960–2016). *Nat Biol Commun*
- Barkley HC, Cohen AL, Golbuu Y, Starczak VR, Decarlo TM, Shamberger KEF (2015) Changes in coral reef communities across a natural gradient in seawater pH. *Sci Adv* 1–7
- Barnes DJ, Lough JM (1992) Systematic variations in the depth of skeleton occupied by coral tissue in massive colonies of *Porites* from the Great Barrier Reef. *J Exp Mar Bio Ecol* 159:113–128
- Beyer HL, Kennedy E V., Beger M, Chen CA, Cinner JE, Darling ES, Eakin CM, Gates RD, Heron SF, Knowlton N, Obura DO, Palumbi SR, Possingham HP, Puotinen M, Runtz RK, Skirving WJ, Spalding M, Wilson KA, Wood S, Veron JE, Hoegh-Guldberg O (2018) Risk-sensitive planning for conserving coral reefs under rapid climate change. *Conserv Lett* e12587
- Cantin NE, Cohen AL, Karnauskas KB, Tarrant AM, McCorkle DC (2010) Ocean Warming Slows Coral Growth in the Central Red Sea. *Science* 329:322–325
- Cantin NE, Lough JM (2014) Surviving coral bleaching events: *Porites* growth anomalies on the great barrier reef. *PLoS One* 9
- Carilli J, Donner SD, Hartmann AC (2012) Historical temperature variability affects coral response to heat stress. *PLoS ONE* 7:1–9
- Carilli JE, Norris RD, Black B, Walsh SM, Mcfield M (2010) Century-scale records of coral growth rates indicate that local stressors reduce coral thermal tolerance threshold. *Glob Chang Biol* 16:1247–1257
- Carilli JE, Norris RD, Black BA, Walsh SM, McField M (2009) Local stressors reduce coral resilience to bleaching. *PLoS ONE* 4:1–5
- Casey KS, Brandon TB, Cornillon P, Evans R (2010) The Past, Present, and Future of the AVHRR Pathfinder SST Program. *Oceanogr from Sp Revisit* 1–375
- Coles SL, Brown BE (2003) Coral bleaching-capacity for acclimatization and adaptation. *Adv Mar Biol* 46:183–223
- Coles SL, Jokiel PL (1977) Effects of temperature on photosynthesis and respiration in hermatypic corals. *Mar Biol* 43:209–216
- D'Angelo C, Wiedenmann J (2014) Impacts of nutrient enrichment on coral reefs: New perspectives and implications for coastal management and reef survival. *Curr Opin Environ Sustain* 7:82–93
- Decarlo TM, Cohen AL (2016) coralCT: software tool to analyze computerized tomography (CT) scans of coral skeletal cores for calcification and bioerosion rates. *Zenodo*
- Decarlo TM, Cohen AL (2017) Dissepiments, density bands, and signatures of thermal stress in *Porites* skeletons. *Coral Reefs* 1–13
- Decarlo TM, Cohen AL, Barkley HC, Cobban Q, Young C, Shamberger KE, Brainard RE, Golbuu Y (2015) Coral macro-bioerosion is accelerated by ocean acidification and nutrients. *Geology* 43:7–10
- Decarlo TM, Cohen AL, Wong GTF, Davis KA, Lohmann P, Soong K (2017) Mass coral mortality under local amplification of 2 C ocean warming. *Sci Rep* 7:44586
- Donner S (2011) An evaluation of the effect of recent temperature variability on the prediction of coral. *Ecol Appl* 21:1718–1730
- Donner SD (2009) Coping with commitment: Projected thermal stress on coral reefs under different future scenarios. *PLoS One* 4
- Donner SD, Rickbeil GJM, Heron SF (2017) A new, high-resolution global mass coral bleaching database. *PLoS ONE* 12:1–17
- Eakin CM, Morgan JA, Heron SF, Smith TB, Liu G, Alvarez-Filip L, Baca B, Bartels E, Bastidas C, Bouchon C, Brandt M, Bruckner AW, Bunkley-Williams L, Cameron A, Causey BD, Chiappone M, Christensen TRL, Crabbe MJC, Day O, de la Guardia E, Díaz-Pulido G, DiResta D, Gil-Agudelo DL, Gilliam DS, Ginsburg RN, Gore S, Guzmán HM, Hendee JC, Hernández-Delgado EA, Husain E, Jeffrey CFG, Jones RJ, Jordán-Dahlgren E, Kaufman LS, Kline DL, Kramer PA, Lang JC, Lirman D, Mallela J, Manfrino C, Maréchal JP, Marks K, Mihaly J, Miller WJ, Mueller EM, Muller EM, Toro CAO, Oxenford HA, Ponce-Taylor D, Quinn N, Ritchie KB, Rodríguez S, Ramírez AR, Romano S, Samhouri JF, Sánchez JA, Schmahl GP, Shank B V., Skirving WJ, Steiner SCC, Villamizar E, Walsh SM, Walter C, Weil E, Williams EH, Roberson KW, Yusuf Y (2010) Caribbean corals in crisis: Record thermal stress, bleaching, and mortality in 2005. *PLoS One* 5

- Emiliani C, Hudson JH, Shinn EA, George RY (1978) Oxygen and Carbon Isotopic Growth Record in a Reef Coral from the Florida Keys and a Deep-Sea Coral from Blake Plateau. *Science* (80) 627–628
- Estep A, Sandin S, Vermeij M (2017) The State of Curaçao's Coral Reefs
- Fine M, Gildor H, Genin A (2013) A coral reef refuge in the Red Sea. *Glob Chang Biol* 19:3640–3647
- Fisk DA, Done TJ (1985) Taxonomic and Bathymetric Patterns of Bleaching in Corals, Myrmidon Reef (Queensland). *Proc Fifth Int Coral Reef Congr Tahiti* 6:149–154
- Frieler K, Meinshausen M, Golly A, Mengel M, Lebek K, Donner SD, Hoegh-Guldberg O (2012) Limiting global warming to 2 °C is unlikely to save most coral reefs. *Nat Clim Chang* 3:165–170
- Gleeson MW, Strong AE (1995) Applying MCSST to coral reef bleaching. *Adv Sp Res* 16:151–154
- Golbuu Y, Victor S, Penland L, Idip D, Emaurois C, Okaji K, Yukihira H, Iwase A, Van Woesik R (2007) Palau's coral reefs show differential habitat recovery following the 1998-bleaching event. *Coral Reefs* 26:319–332
- Grottoli G, Rodrigues LJ, Palardy JE (2006) Heterotrophic plasticity and resilience in bleached corals. *Nature* 440:10–13
- Hendy EJ, Lough JM, Gagan MK (2003) Historical mortality in massive Porites from the central Great Barrier Reef, Australia: Evidence for past environmental stress? *Coral Reefs* 22:207–215
- Heron SF, Liu G, Eakin CM, Skirving WJ, Muller-Karger FE, Vera-Rodriguez M, de la Cour JL, Burgess TFR, Strong AE, Geiger EF, Guild LS, Lynds S (2015) NOAA Technical Report NESDIS 145 Climatology Development for NOAA Coral Reef Watch's 5-km Product Suite. 30
- Hoegh-Guldberg O, Smith GJ (1989) The effect of sudden changes in temperature, light and salinity on the population density and export of zooxanthellae from the reef corals *Stylophora pistillata* Esper and *Seriatopora hystrix* Dana. *J Exp Mar Bio Ecol* 129:279–303
- Hoogenboom MO, Campbell DA, Beraud E, DeZeeuw K, Ferrier-Pagès C (2012) Effects of light, food availability and temperature stress on the function of photosystem II and photosystem I of coral symbionts. *PLoS One* 7
- van Hooidonk R, Huber M (2009) Quantifying the quality of coral bleaching predictions. *Coral Reefs* 28:579–587
- van Hooidonk R, Maynard J, Tamelander J, Gove J, Ahmadi G, Raymundo L, Williams G, Heron SF, Planes S (2016) Local-scale projections of coral reef futures and implications of the Paris Agreement. *Sci Rep* 6:39666
- Hudson JH, Shinn EA, Halley RB, Lidz B (1976) Sclerochronology: A tool for interpreting past environments. *Geology* 4:361–364
- Hughes TP, Anderson KD, Connolly SR, Heron SF, Kerry JT, Lough JM, Baird AH, Baum JK, Berumen ML, Bridge TC, Claar DC (2018) Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. *Science* 359(80):80–83
- Hughes TP, Kerry JT, Álvarez-Noriega M, Álvarez-Romero JG, Anderson KD, Baird AH, Babcock RC, Beger M, Bellwood DR, Berkelmans R, Bridge TC, Butler IR, Byrne M, Cantin NE, Comeau S, Connolly SR, Cumming GS, Dalton SJ, Diaz-Pulido G, Eakin CM, Figueira WF, Gilmour JP, Harrison HB, Heron SF, Hoey AS, Hobbs J-PA, Hoogenboom MO, Kennedy EV, Kuo C, Lough JM, Lowe RJ, Liu G, McCulloch MT, Malcolm HA, McWilliam MJ, Pandolfi JM, Pears RJ, Pratchett MS, Schoepf V, Simpson T, Skirving WJ, Sommer B, Torda G, Wachenfeld DR, Willis BL, Wilson SK (2017) Global warming and recurrent mass bleaching of corals. *Nature* 543:373–377
- IPCC AR5 (2014) Climate Change 2014: Synthesis Report
- Kessler WS, Kleeman R (2000) Rectification of the Madden-Julian Oscillation into the ENSO cycle. *J Clim* 13:3560–3575
- Liu G, Strong AE, Skirving WJ, Arzayus F (2006) Overview of NOAA Coral Reef Watch Program's Near-Real-Time Satellite Global Coral Bleaching Monitoring Activities. *Proc 10th Int Coral Reef Symp* 1783–1793
- Logan CA, Dunne JP, Eakin CM, Donner SD (2014) Incorporating adaptive responses into future projections of coral bleaching. *Glob Chang Biol* 20:125–139
- Lough JM, Anderson KD, Hughes TP (2018) Increasing thermal stress for tropical coral reefs: 1871–2017. *Sci Rep* 1–8
- Mallela J, Hetzinger S, Halfar J (2015) Thermal stress markers in *Colpophyllia natans* provide an archive of site-specific bleaching events. *Coral Reefs* 35:181–186
- Mangubhai S, Rotjan R, de Villiers S, Braun C, Carilli J, Cavin J, Cohen A, Coker D, Cook C, Drenkard L, Gawne P, Harper S, Koethen J, Lasley R, Nand Y, Payet S, Rivera H, Sandin S, Kiareti A, Thorold S, Young CC, Zgliczynski B (2015) Phoenix Islands Protected Area 2015 Expedition Report
- Mantel N, Haenszel W (1959) Issue Cover 22(4), April 1959 < Previous Next > Statistical Aspects of the Analysis of Data From Retrospective Studies of Disease. *J Natl Cancer Inst* 22:719–748
- Matson EG (2011) Core Plugs. *Encycl Mod Coral Reefs* 294–296
- Maynard JA, Anthony KRN, Marshall PA, Masiri I (2008) Major bleaching events can lead to increased thermal tolerance in corals. *Mar Biol* 155:173–182
- McClanahan TR, Ateweberhan M, Muhando C, Maina J, Mohammed SM (2007) Climate change and spatio-temporal variation in seawater temperature effects on coral bleaching and mortality in East Africa. *Ecol Monogr* 77:503–525
- Obura D, Mangubhai S (2011) Coral mortality associated with thermal fluctuations in the Phoenix Islands, 2002–2005. *Coral Reefs* 30:607–619
- Oliver TA, Palumbi SR (2011) Do fluctuating temperature environments elevate coral thermal tolerance? *Coral Reefs* 30:429–440
- Pandolfi JM, Connolly SR, Marshall DJ, Cohen AL (2011) Projecting Coral Reef Futures Under Global Warming and Ocean Acidification. *Science* 333(80):418–422
- Pratchett M, Munday P, Wilson S, Graham N, Cinner J, Bellwood D, Jones G, Polunin N, McClanahan T (2008) Effects Of Climate-Induced Coral Bleaching On Coral-Reef Fishes - Ecological And Economic Consequences
- Reynolds RW, Rayner NA, Smith TM, Stokes DC, Wang W (2002) An Improved In Situ and Satellite SST Analysis for Climate. *J Clim* 15:1609–1625
- Rodrigues LJ, Grottoli AG (2006) Calcification rate and the stable carbon, oxygen, and nitrogen isotopes in the skeleton, host tissue, and zooxanthellae of bleached and recovering Hawaiian corals. *Geochim Cosmochim Acta* 70:2781–2789
- Rowan R, Knowlton N, Baker A, Jara J (1997) Landscape ecology of algal symbionts creates variation in episodes of coral bleaching. *Nature* 388:265–269
- Safaie A, Silbiger NJ, McClanahan TR, Pawlak G, Barshis DJ, Hench JL, Rogers JS, Williams GJ, Davis KA (2018) High frequency temperature variability reduces the risk of coral bleaching. *Nat Commun* 9:1–12
- Smithers SG, Woodroffe CD (2001) Coral microatolls and 20th century sea level in the eastern Indian Ocean. *Earth Planet Sci Lett* 191:173–184
- Trenberth KE (1997) The Definition of El Niño. *Am Meteorol Soc*
- Vargas-Ángel B, Looney EE, Vetter OJ, Coccagna EF (2011) Severe, widespread El Niño-associated coral bleaching in the US Phoenix Islands. *Bull Mar Sci* 87:623–638
- Wilkinson C (2008) Status of Coral Reefs of the World: Executive Summary. *Glob Coral Reef Monit Netw* 5–28
- Van Woesik R, Houk P, Isechal AL, Idechong JW, Victor S, Golbuu Y (2012) Climate-change refugia in the sheltered bays of Palau: Analogs of future reefs. *Ecol Evol* 2:2474–2484

- Van Woesik R, Sakai K, Ganase A, Loya Y (2011) Revisiting the winners and the losers a decade after coral bleaching. *Mar Ecol Prog Ser* 434:67–76
- Wooldridge SA (2009) Water quality and coral bleaching thresholds: Formalising the linkage for the inshore reefs of the Great Barrier Reef, Australia. *Mar Pollut Bull* 58:745–751

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