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REPORT

Skeletal records of community-level bleaching in *Porites* corals from Palau

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Abstract Tropical Pacific sea surface temperature is projected to rise an additional 2–3 °C by the end of this century, driving an increase in the frequency and intensity of coral bleaching. With significant global coral reef cover already lost due to bleaching-induced mortality, efforts are underway to identify thermally tolerant coral communities that might survive projected warming. Massive, long-lived corals accrete skeletal bands of anomalously high density in response to episodes of thermal stress. These "stress bands" are potentially valuable proxies for thermal tolerance, but to date their application to questions of community bleaching history has been limited. Ecological surveys recorded bleaching of coral communities across the Palau archipelago during the 1998 and 2010 warm events. Between 2011 and 2015, we extracted skeletal cores from living *Porites* colonies at 10 sites spanning barrier reef and lagoon environments and quantified the proportion of stress bands present in each population during bleaching years. Across Palau, the prevalence of stress bands tracked the severity of thermal stress, with more stress bands occurring in 1998 (degree heating weeks = 13.57 °C-week) than during the less severe 2010 event (degree heating weeks = 4.86 °C-week). Stress band prevalence also varied by reef type, as more corals on the exposed barrier reef formed stress bands than did corals from sheltered lagoon environments. Comparison of *Porites* stress band prevalence with bleaching survey data revealed a strong correlation between percent community bleaching and the proportion of colonies with stress bands in each year. Conversely, annual calcification rates did not decline consistently during bleaching years nor did annually resolved calcification histories always track interannual variability in temperature. Our data suggest that stress bands in massive corals contain valuable information about spatial and temporal trends in coral reef bleaching and can aid in conservation efforts to identify temperature-tolerant coral reef communities.

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Introduction

The tropical oceans that sustain coral reef ecosystems have warmed on average 0.09 °C per decade from 1950 to 2011, a trend that is expected to continue over the course of this century (Lough 2012). An increase in sea surface temperature (SST) just 1 °C above climatological summer SST can trigger the breakdown of the coral host–zooxanthellae symbiosis, resulting in coral bleaching and, if prolonged, to mortality (Hoegh-Guldberg 1999; Jones et al. 2006). More than 16% of global coral reef cover has been lost in the last two decades due to bleaching-induced mortality (Wilkinson 2008). If model projections of future rates of SST rise

are realized, most tropical reef ecosystems could experience severe bleaching every year by 2055 with insufficient time for recovery (van Hooidonk et al. 2014).

These projections raise concerns about the ability of coral reef ecosystems to survive through the twenty-first century. Nevertheless, thermal thresholds of corals vary by genera, habitat, and depth, and thus, considerable efforts are underway to exploit this natural variability, identify thermally tolerant reef communities, and prioritize their protection with the goal to maximize their chances of surviving future warming (West and Salm 2003; Baker et al. 2008; van Woesik et al. 2012). Identification of thermally tolerant reef communities is challenging, however, because it requires in situ monitoring over extensive areas during bleaching events. Observations spanning multiple bleaching events are considered most valuable in the forecasting of future thermal tolerance (West and Salm 2003; Obura 2005; Baker et al. 2008). Yet, despite multiple mass bleaching events in the last 30 yrs, few comprehensive ecological datasets exist that report spatial patterns in coral reef bleaching within a single reef system. Even fewer span multiple events (Glynn et al. 2001; Berkelmans et al. 2004; Obura 2005; Gilmour et al. 2013).

Previous studies have reported the presence of discrete, anomalously high-density bands in the skeletons of massive reef-building corals (Druffel and Linick 1978; Hudson 1978; Scoffin et al. 1992; Dodge et al. 1993; Smithers and Woodroffe 2001; Mendes and Woodley 2002; Hendy et al. 2003; Carilli et al. 2009, 2010; Cantin et al. 2010; Cantin and Lough 2014; Mallela et al. 2015). These high-density regions, termed "stress bands," are considered to reflect episodes of sublethal thermal stress (and possibly bleaching) from which the colony later recovered. Prominent stress bands in coral skeletal cores have been documented in several species (e.g., *Orbicella* spp., *Colpophyllia natans*, and *Porites* spp.) and on coral reefs in the Caribbean, Pacific, and Indian Oceans (Hudson 1978; Carilli et al. 2010; Cantin and Lough 2014; Mallela et al. 2015). Most evidence suggests that stress bands form in response to warmer than average temperatures (Hendy et al. 2003; Cantin et al. 2010; Carilli et al. 2010, 2012; Cantin and Lough 2014; Mallela et al. 2015), with anomalously low-density bands attributed to periods of cold water stress (Lough and Cooper 2011). Thus, the presence of skeletal stress bands can serve as an archive of thermal stress responses to historical, high-temperature events in the absence of extensive observational data. However, to date, the interpretation of coral stress bands has remained largely qualitative and restricted to the scale of individual coral colonies.

Here we combine coral skeletal records with in situ observational data to investigate the relationship between stress bands and community bleaching. SST on Palau has increased by ~ 0.7 °C since 1970, consistent with the global trend (Osborne et al. 2013). Superimposed on this warming have been multiple periods of high temperature associated with phases of the El Niño Southern Oscillation (ENSO). Approximately 6–10 months after the peak ENSO, sustained elevated SSTs in the western Pacific led to moderate to high levels of bleaching on Palau reefs (Bruno et al. 2001; van Woesik et al. 2012). The availability of bleaching data collected on Palau during both events enables us to quantitatively connect colony-scale stress markers with community-level bleaching. We address four main questions regarding the potential use of coral skeletal records as proxies for community-level bleaching. First, we asked whether stress band prevalence could be used to reconstruct past bleaching events within the coral community. Second, we tested whether evidence of bleaching or stress in one bleaching event predisposed a colony to stress in a subsequent event. Third, we tracked spatial and temporal variability in stress band prevalence and used stress band data to interpret spatial and temporal patterns in bleaching on Palau. Finally, we assessed the sensitivity of annual calcification rates to thermal stress during specific bleaching years and over the longer-term rise in temperature. Our findings explore the potential of coral skeletal records to reconstruct the spatial and temporal patterns in thermal stress responses of coral communities over multiple high-temperature events.

Methods

Sea surface temperature

Monthly satellite SST and SST anomaly records (January 1990 to December 2013) at 0.25 °C resolution were acquired from the National Oceanic and Atmospheric Administration (NOAA) optimum interpolated sea surface temperature (OI-SST) database (downloaded from http://coastwatch.pfeg.noaa.gov) for Palau (centered at 7.250°N, 134.375°E) and analyzed as netCDF files in MATLAB (version 2013a). Data for 1 June to 30 November of 1998 and 2010 were extracted to calculate SST anomalies experienced by Palau reefs during the warmest months (SST anomalies >1 °C) of both events. OI-SST anomalies are calculated relative to a 30-yr climatological mean (1971–2000). In addition, degree heating weeks (DHW) were calculated following the standard NOAA procedure to measure accumulated thermal stress during each bleaching period (Gleeson and Strong 1995).

Coral skeletal core collection

We collected 101 skeletal cores from massive *Porites* coral colonies at ten reef sites representing two major reef

environments, barrier reef and lagoon, the latter including fringing reefs around the uplifted karst Rock Islands (Electronic Supplementary Materials, ESM, Table S1). The two environments are broadly distinguishable in both physical (flow, temperature, and light regimes) and chemical (carbon system parameters, salinity) characteristics with generally higher flow, light, pH, and salinity and lower SST on the barrier reefs (Shamberger et al. 2014; Barkley et al. 2015).

Skeletal cores (20–40 cm in length) were collected in April 2011, September 2011, April 2012, August 2014, and January 2015 vertically from live coral colonies at 1–6 m depth using pneumatic drills with 3.8-cm-diameter diamond drill bits (ESM Table S1). Core holes were filled with cement plugs hammered flush with the colony surface and sealed with underwater epoxy. Visual inspections of colonies 6–12 months after coring revealed significant overgrowth of plugs and no long-term impacts to the corals. Coral cores were oven-dried and scanned with a Siemens Volume Zoom Helical Computerized Tomography (CT) Scanner at Woods Hole Oceanographic Institution. 3-D CT scans of coral cores were analyzed using OsiriX freeware to visualize the 3-D image (Cantin et al. 2010; Crook et al. 2013) and an automated MATLAB code to quantify skeletal growth parameters and stress banding (DeCarlo and Cohen 2016).

Stress bands

Coral cores that included growth records prior to 1998 were assessed for the presence of high-density stress bands associated with elevated temperatures in 1998 ($n = 86$), and all cores were examined for stress bands in 2010. A stress band was defined as a region of the coral core >1 mm in height and extending the entire width of the core where density values exceeded two standard deviations of the whole-core density mean (Fig. 1). We defined a minimum band thickness in order to filter out smaller-scale density variability and high-density noise. A value of 1 mm for this thickness threshold was selected based on the average linear extension rates of Palau *Porites* corals (0.88 cm yr^{-1}, interquartile range = 0.35 cm yr^{-1}), where 1 mm represents, on average, approximately 10% of overall annual linear extension. High-density anomalies of this width therefore represent significant perturbations in growth. Density thresholds were set based on standard deviations from mean values in order to account for significant differences in density means and variability between individuals. Density values were normally distributed within coral cores, and values greater than two standard deviations were defined as the threshold for a stress band. This threshold was selected to aid in the identification of only the most anomalously high-density

areas (i.e., areas with densities greater than approximately 95% of all values) while also minimizing the probability of type II errors in coral cores where stress bands exist, but high-density values are slightly less extreme. Stress bands were identified as occurring within a particular year (specifically, 1998 and 2010) based on annual patterns of density banding, in which successive low-density bands were counted down from the top of the core and subsequently dated based on the known date of collection. Although a small number of coral skeletal cores had occasional high-density regions in additional years, we did not consistently detect stress bands corresponding to years other than 1998 and 2010.

The percentage of *Porites* corals with stress bands was compared with community bleaching data for each reef site collected during the 1998 and 2010 high-temperature events. Bleaching data from 1998 were collected at nine reef sites in November 1998 using a point-intercept technique with three replicate 20-m transect surveys per site conducted at 3–5 m depth (Bruno et al. 2001). A subset of six of these nine sites was used to compare bleaching data to stress band records based on proximity to our core collection sites. Data from 2010 were collected at 80 randomly assigned reef sites in July and August 2010 with three replicate 30-m transect surveys conducted at 2–5 m depth (van Woesik et al. 2012). A subset of 31 of these sites was included in this study. Because in situ bleaching data were collected at randomized locations, the spatial matches between sites with bleaching data and sites with coral cores were not always exact. Therefore, for each coral core collection site, we averaged bleaching data from the two or three sites that both fell within a 10 km radius of each core site and that represented the same environment type to calculate a community bleaching estimate. Bleaching information about specific coral colonies from which we collected cores was not available.

Coral calcification histories

Annual calcification rates were calculated as the product of annual linear extension and density following the automated procedure described in DeCarlo et al. (2015), which traces density variations along individual corallites identified within the entire 3-D core. Extension rates (upward linear growth) were measured between the successive low-density bands of annual high–low-density couplets. Annual density banding was clearly represented in all cores, with low-density bands formed at the beginning of each year (c. February) and high-density bands accreted toward the mid- to late months of the year (c. September). Band identifications were verified using cross-dating, a dendrochronology technique in which shared years of lower growth rates are identified and matched across core records (Fritts 1976;

Fig. 1 Example CT scans showing stress bands (*red arrows*) in *Porites* skeletal cores in relation to annual high–low-density bands, which provide the chronology (every 5 yr indicated in *yellow*). **a**, **b** Accreted stress bands in 1998 but not 2010; **c**, **d** accreted stress bands in 2010 but not 1998. Date of collection is indicated at the *top of each core*. CT scan images are displayed in negative: Areas of high density (such as stress bands) appear *white* and areas of lower density appear *black*
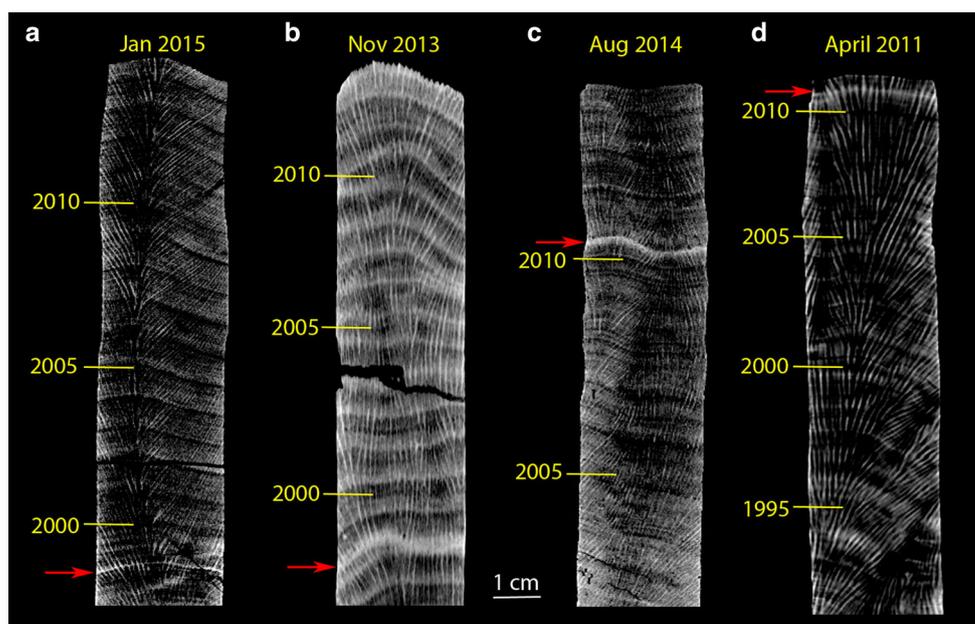
Yamaguchi 1991). Annual skeletal densities were calculated from CT scan intensities converted to calcium carbonate density values using nine coral standards (0.81–1.54 g cm^{-3}), where independent measurements of weight and volume for each standard were used to derive a linear relationship between CT scan intensity values (in Hounsfield units) and calcium carbonate density (in g cm^{-3}) (DeCarlo et al. 2015).

Statistical analysis

All statistical analyses were conducted in R (version 3.0.1). We evaluated the effect of year, reef type (lagoon or barrier), and their interaction in the presence of high-density stress bands in *Porites* coral cores. Stress band proportion data calculated for each individual reef site met criteria for normality and homoscedasticity, and were evaluated with two-way ANOVAs with post hoc Tukey honest significant difference (HSD) tests. Stress band proportions were compared to site and event-specific bleaching data with generalized linear models. To evaluate coral calcification records, linear mixed effects models were constructed using the *nlme* package (Pinherio et al. 2012) following the statistical procedures outlined in De'ath et al. (2009) and Castillo et al. (2011, 2012). In our mixed effects models, coral cores were considered to be random effects, and individual slopes and intercepts were fit to each core record to account for repeated, nonrandom measurements on the same colonies through time, controlling for the fact that coral colonies often have very different underlying calcification rates. In addition, residual correlation structures

were included to account for the temporal autocorrelation present in the calcification time series. We constructed models to evaluate the relationship between annual coral calcification rates and (1) year, (2) reef type, (3) growth after 1998 and 2010, and (4) annual SST anomaly. The year predicator was centered in 2001 to improve model fit, and calcification rates after the two major bleaching events were coded as binary variables for post-1998 (1998–2000) and post-2010 (2010–2012). Models were scored and selected by minimizing the Akaike information criterion (AIC).

Results

Satellite SST records show that temperatures in Palau have increased significantly over the period 1990–2013 by 0.03 °C yr^{-1} (generalized linear model, $p < 0.001$). In addition to long-term warming, Palau's reefs experienced ENSO-driven elevated temperature anomalies in mid- to late 1998 and 2010 (Fig. 2a). During the 1998 bleaching event (1 June to 30 November 1998), Palau reefs experienced mean ± SD SST anomalies of 1.02 °C ± 0.46 °C and maximum DHW = 13.57 °C-week (Fig. 2b). Over the same 6-month period in 2010, mean SST anomalies reached 0.90 °C ± 0.26 °C with maximum DHW = 4.82 °C-week. The spatial resolution of OI-SST data was not high enough to confidently distinguish SST anomalies and DHW between Palau's barrier and lagoon reef environments.

Stress bands were identified in lagoon and barrier *Porites* skeletal cores during both 1998 and 2010 high-
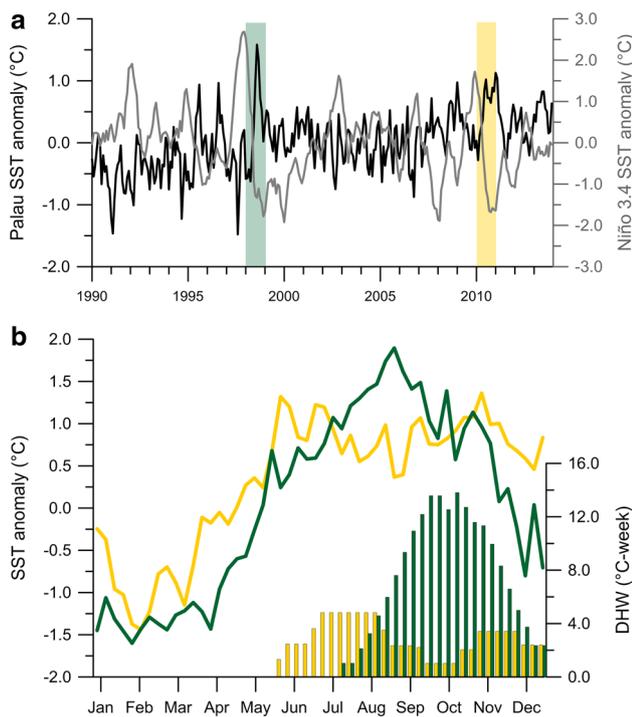
Fig. 2 **a** Monthly sea surface temperature (SST) anomalies on Palau (*black*) versus Niño 3.4 (*gray*) from 1990 to 2013. **b** Weekly SST anomalies and degree heating weeks (DHW) corresponding to *shaded areas* within **a** for 1998 (*green*) and 2010 (*yellow*)

temperature events (Fig. 3; Table S1). Stress band prevalence varied significantly by year (two-way ANOVA, $F_{1,16} = 38.03$, $p < 0.001$), as the occurrence of stress bands across all reefs was greater in 1998 than in 2010, which was a less severe thermal stress event (Tukey HSD, $p < 0.001$). We found no effect of multiple bleaching events on the occurrence of stress bands, as only 10% of all corals analyzed had a stress band during both events, and corals with a stress band in 1998 were no more likely to have a stress band in 2010 than were those with no evidence of stress during the 1998 event (odds ratio = 2.1, 95% confidence interval = 0.7, 6.1). Stress band prevalence also varied significantly by reef type (two-way ANOVA, $F_{1,16} = 14.57$, $p = 0.001$), with more corals on the barrier reefs showing stress responses than corals on the lagoon reefs. In 1998, stress band prevalence was greater on barrier reefs (50–67%) than inshore reefs (18–50%; Tukey HSD, $p = 0.002$). However, in 2010, stress band presence was more evenly distributed across reefs (10–30%), and there was no significant difference across reef types (Tukey HSD, $p = 0.79$). The percentage of coral cores with a stress band and the observed extent of community-scale bleaching that same year were significantly correlated ($n = 15$, $r = 0.96$, $p < 0.001$). In addition, *Porites* stress band prevalence was a strong predictor of benthic community bleaching across reef sites over two

bleaching events (Fig. 4; generalized linear model, slope = 0.89, SE = 0.07, $p < 0.001$).

Periods of anomalously high SST did not consistently result in declines in annual calcification (Fig. 5a; ESM Table S2). Significantly reduced site-averaged calcification rates during or post-1998 were detected at only one site on the western (leeward) barrier reef (Siaes) and one inshore Rock Islands site (Mecherchar) and during or post-2010 at one inshore Rock Islands site (Risong). Calcification rates at all other sites were maintained after these periods of thermal stress, even in coral assemblages with a high prevalence of skeletal stress markers during both bleaching events.

Trajectories in annual calcification from 1990 to 2013 varied across reef environments and between reef sites, with variations in the change in calcification rates over time generally corresponding with distance inshore from the open ocean (Fig. 5, ESM Table S2 & S3). Overall barrier reef coral calcification rates declined by 0.009 ± 0.003 g cm^{-2} yr^{-1} (mean $\pm$ SE; $p = 0.003$, 95% confidence interval: -0.014, -0.003) from 1990 to 2013. Within the barrier reef environment, calcification rates from two forereef sites (Short Drop Off and Siaes) decreased significantly, while there was no change in calcification at two sites on the reef crest (Ngerdiluches and Uchelbeluu) or a patch reef slightly inshore (Ngerchelong). The growth rates of barrier corals also corresponded significantly to variability in SST anomalies, with calcification rates declining 0.090 ± 0.032 g cm^{-2} yr^{-1} with increases in SST (mean $\pm$ SE; $p = 0.006$, 95% confidence interval: -0.154, -0.025; ESM Table S4).

There was no overall temporal trend in calcification rates of corals in lagoon reefs or a significant relationship between lagoon growth rates and SST from 1990 to 2013. However, within the lagoon reef environment, trends also varied across sites: Calcification rates decreased significantly at the two more exposed Rock Island reefs (PICRC and Taoch), but increased significantly over the same period at the three highly sheltered reefs (Mecherchar, Nikko Bay, and Risong). At all lagoon reef sites, the observed changes in calcification over time were relatively small (ranging from -0.019 to 0.007 g cm^{-2} yr^{-1}) and were less than <5% of measured annual calcification rates.

Calcification data also revealed significant differences in growth rates between reef types. On average, growth rates of barrier reef corals (1990–2013 mean $\pm$ SD = 1.31 ± 0.42 g cm^{-2} yr^{-1}) were greater than corals from lagoon reefs (0.85 ± 0.23 g cm^{-2} yr^{-1}) ($p < 0.001$). This difference between barrier and reef interior was driven in large part by the high calcification rates of corals on the western (leeward) barrier reef (1.39 ± 0.39 g cm^{-2} yr^{-1}), which were significantly greater than those on the eastern (windward) barrier (1.15 ± 0.43 g cm^{-2} yr^{-1}; $p = 0.019$).
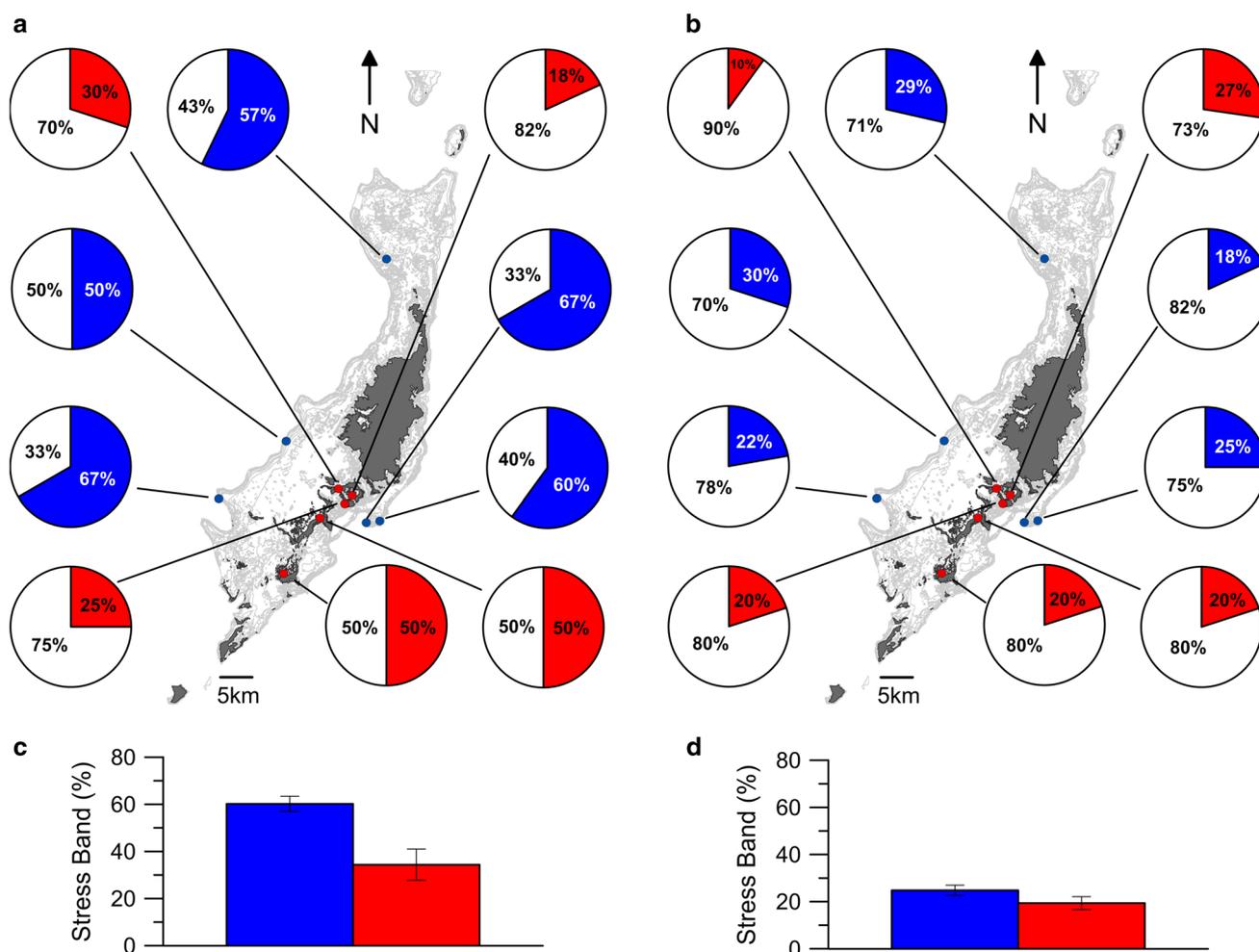
Fig. 3 Map of Palau reef and study sites: *Dark gray* indicates land and *light gray* indicates reef. **a**, **b** *Pie charts* show the distribution of *Porites* stress band prevalence corresponding with elevated temperatures in **a** 1998 and **b** 2010. *Colored slices* represent percent of coral cores with a stress band on either barrier (*blue*) or lagoon (*red*) reefs, compared with percent of corals with no stress bands (*white*). **c**, **d** Average percent (±SE) of coral population from each reef type with stress bands during the **c** 1998 and **d** 2010 events

Discussion

As the oceans warm and episodes of coral reef bleaching become more frequent, identifying and protecting coral reef communities with high thermal thresholds and rapid recovery after bleaching becomes an increasingly attractive and viable strategy to maximize survival of coral reefs under global climate change. Yet, the identification of temperature-tolerant reefs on a large scale remains a challenging task despite the occurrence of multiple mass bleaching events in the last few decades; reef environments are often environmentally and compositionally heterogeneous, and the logistical and financial constraints associated with intensive on-site monitoring are exacerbated in remote areas. For this reason, massive, long-lived coral colonies that have experienced and survived those events and recorded their responses in their skeletons may serve as

valuable sources of information in the absence of, or in addition to, in situ survey data.

Our results reveal a high level of agreement between *Porites* coral stress band prevalence and observed community bleaching levels across two distinct high-temperature events on Palau. Prevalence of stress bands was within one standard error of mean observed bleaching during the two events for ten coral reef sites representing two distinct types of reef environments and community assemblages. While we do not know how the presence of stress bands in a *Porites* skeleton reflects the timing and extent of bleaching at the scale of the coral colony, this suggests that *Porites* skeletal stress markers may quantitatively estimate levels of community-scale bleaching regardless of levels of individual colony bleaching. The strong relationship between stress bands in *Porites* corals that survived repeat bleaching events and the average extent of community
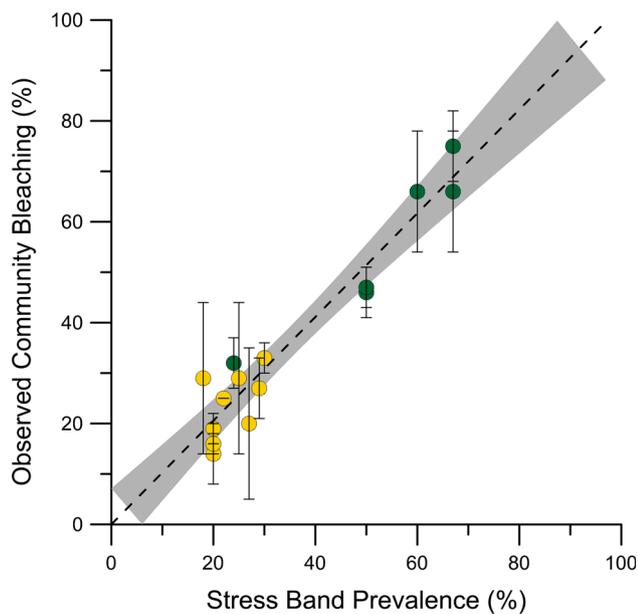
Fig. 4 Percent of *Porites* coral skeletal cores forming a stress band during the 1998 (*green*) and 2010 (*yellow*) thermal anomalies plotted against the mean (±SE) percent community bleaching observed from each reef during the same event (1998 data from Bruno et al. (2001) and 2010 data from van Woesik et al. (2012)). Data are plotted with a line of best fit with a 95% confidence interval (*shaded gray*)

bleaching observed here may exist because *Porites* is a moderately to highly temperature-tolerant genus (van Woesik et al. 2011; Guest et al. 2012). Under this hypothesis, evidence of sublethal stress preserved within skeletons of *Porites* colonies would be indicative of bleaching of less tolerant species within the broader coral community.

While *Porites* stress band data provide an approximation of community responses to temperature in Palau, future work should evaluate the broad applicability of this proxy to other reef systems with different community compositions. In our study area, stress band prevalence accurately reflected community-level bleaching across a variety of reef environments and community compositions. However, in other reef systems, it is possible that *Porites* stress band prevalence could underestimate bleaching levels if communities are dominated by coral genera with relatively low thermal tolerances or overestimate bleaching sensitivity in communities with an abundance of very thermally tolerant species. Another aspect that requires evaluation is the possibility of reduced thermal tolerance during the lifetime of a single colony, for which there is some evidence from experimental data (Schoepf et al. 2015). We do not find strong evidence for this in our coral cores, as we found that accreting a stress band during the 1998 bleaching event did not change the odds that an individual coral would form a stress band during the 2010 event. This suggests that

thermal thresholds of coral colonies that were stressed by the 1998 warming did not decline or that colonies had already recovered by the time the 2010 warm event occurred.

Despite these potential caveats, our results suggest that stress bands in massive long-lived corals contain critical information about spatial and temporal variability in bleaching sensitivity within and across reef assemblages. We propose that it is possible to develop skeletal stress markers in *Porites* and other long-lived massive species to retroactively document spatial and temporal variability in coral reef bleaching in the absence of extensive visual surveys. Where survey data are available, application of this index in combination with other ecological metrics, such as coral cover or diversity, would strengthen assessments of reef-scale thermal sensitivities and assist in the identification of reef assemblages with particularly high resistance to temperature stress.

Our study revealed differences in thermal tolerance across Palau's reefs. In 1998, the prevalence of stress bands was significantly higher in corals collected from barrier reef environments than in those collected inshore, a result supported by anecdotal evidence from sheltered lagoon sites (Fabricius et al. 2004; Penland et al. 2004). Observational bleaching data collected in November 1998 found no overall influence of reef type on bleaching extent, but did record significant differences in bleaching between the individual reef sites considered in this study (Bruno et al. 2001). This inconsistency between the survey data and the stress band result may relate to the exact sites surveyed or the timing of the survey, which occurred several weeks after peak temperature anomalies. In 2010, when SST anomalies and DHW were less severe than 1998, we observed fewer skeletal stress markers in *Porites* corals across our study sites. While not statistically significant, corals from barrier reef sites again showed generally higher occurrence of stress bands than those on the inshore reefs. This observation is consistent with monitoring data collected from July to August 2010 (van Woesik et al. 2012), implying that inshore corals displayed persistently higher thermal tolerance than barrier reef corals on Palau through two bleaching events.

The differences in stress band prevalence between barrier and inshore sites, which we interpret as reflecting differences in bleaching extent, could relate to a number of localized environmental or physiological factors. For example, Palau's lagoon reefs are highly turbid and heavily shaded by the surrounding Rock Islands, factors which may alleviate stress from excess temperature or irradiance during bleaching events (West and Salm 2003; Golbuu et al. 2007; Cacciapaglia and van Woesik 2015). Alternatively, temperatures on Palau barrier reefs are cooler than the temperatures experienced by lagoon reefs (ESM Fig. S1),
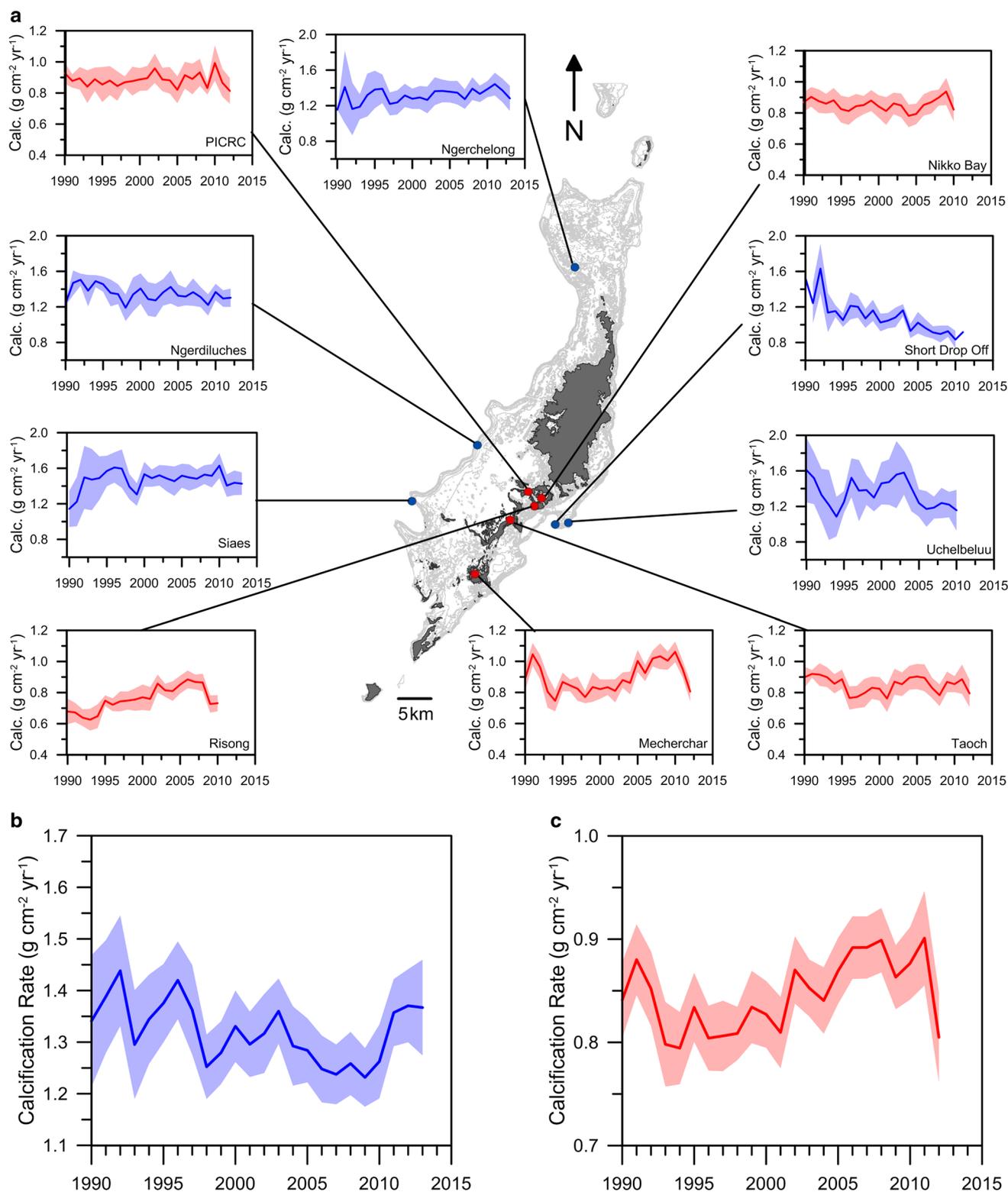
Fig. 5 **a** Annual calcification histories for corals from ten reef sites representing lagoon (*red*) and barrier (*blue*) reef environments, and mean annual calcification rates for corals from **b** barrier and **c** lagoon reefs. Calcification time series are presented as master chronologies for each reef site, created by averaging the yearly growth records from individual cores. *Shaded regions* are one standard error of the annual mean calcification rate. Trends in coral core records through time were analyzed using linear mixed effects models, which fit random slopes and intercepts to each individual core time series (ESM Tables S2 and S3, Figure S2)

and experimental evidence suggests that corals living in chronically warm environments may be better able to survive elevated temperatures than individuals acclimatized to cooler conditions (Castillo and Helmuth 2005; Middlebrook et al. 2008). Furthermore, some coral genera within the Rock Islands have also been shown to host more thermally tolerant clade D symbionts. However, because *Porites* corals in Palau appear to consistently harbor clade C symbionts even within the very warm lagoon, variation in symbiont type cannot necessarily explain the variations in temperature sensitivity that we observe even within *Porites* corals (Fabricius et al. 2004).

There is strong evidence that coral calcification is sensitive to temperature. Studies that have examined both skeletal stress markers and calcification rates post-stress have generally, but not always, found marked calcification declines after the presence of stress bands (Mendes and Woodley 2002; Carilli et al. 2009, 2010; Cantin and Lough 2014; Mallela et al. 2015). In Palau, we did not consistently detect large changes in annually resolved calcification rates following periods of known bleaching, even in corals forming stress bands during bleaching years. This might imply a high level of resilience in the Palau *Porites* corals, with colonies recovering very quickly after the bleaching event.

Over longer time scales, Palau barrier reef corals exhibited overall small, but significant declines in calcification rates, although there was considerable variability in calcification trends across individual reef sites within the barrier environment. This observation is consistent with multiple studies that have reported marked decreases in coral growth over the past few decades, including data from the Great Barrier Reef (Cooper et al. 2008; De'ath et al. 2009), Red Sea (Cantin et al. 2010), Belize (Castillo et al. 2011), Andaman Sea (Tanzil et al. 2009), the Thai–Malay Peninsula (Tanzil et al. 2013), and Panama (Manzello 2010). On many of these reefs, declining trends in growth have been linked to increasing SST, suggesting that ocean warming may have already produced temperatures that surpass the thermal thresholds of many reef-building corals worldwide. However, the same overall declines in calcification over time were not observed in Palau's inshore corals. Our results are consistent with those from Belize, where calcification declines were observed in exposed, forereef communities relative to more sheltered inshore reef environments (Castillo et al. 2011, 2012). One explanation for this pattern is that thermal tolerances of inshore corals are higher than barrier reef corals. Alternatively, the distinct calcification trajectories between the barrier and inshore reefs may reflect differential changes in other environmental parameters such as light or pH. If declines in calcification of *Porites* on the barrier reef are causally linked to thermal stress or the result of some other

driver, they may be indicative of a common underlying level of stress experienced across the reef community. For example, concurrent with declining *Porites* calcification rates has been a >50% decline in coral cover on Palau barrier reefs since 1992 (Golbuu et al. 2007). Significant decreases in the skeletal growth of *Porites* and other major reef-building genera may reduce rates of overall reef accretion and ultimately compromise the structural integrity of reef habitats (De'ath et al. 2009).

As ocean temperatures continue to rise over the next few decades, monitoring, tracking, and evaluating coral reef temperature sensitivities will become increasingly important if we are to project coral reef trajectories under climate change and to protect coral reef communities that have the highest thermal tolerances. Coral skeletal records may be invaluable tools in these efforts. As such, it is vital that we continue to fine-tune our understanding of coral skeletal stress markers across coral species and reef assemblages so that we may better apply the historical insight that they provide into coral conservation efforts over the next century.

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