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Porites coral response to an oceanographic and human impact gradient in the Line Islands

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Abstract

Coral bleaching caused by heat stress (warm water) will arguably be the greatest driver of coral reef loss in the coming decades. Understanding how corals have adapted to distinct oceanographic regimes on multiple scales can provide insight into future tolerance and persistence, information critical to directed intervention or targeted protections. The northern Line Islands span a gradient in oceanographic regimes across latitudes, with seawater becoming warmer, fresher, more oligotrophic, and more saturated with aragonite away from the equator. The combination of this regional gradient and island-scale (local) conditions was used as a natural experiment against which to test how massive *Porites* corals respond to these background conditions and episodic heat stress. We found that coral condition, represented by a metric combining tissue thickness, lipids, and calcification, was similar at almost all islands, though there were differences in how corals allocate resources among these biological parameters. Corals at Teraina, the most densely inhabited island, showed evidence for reduced calcification, potentially associated with human impacts and/or outflow of freshwater from the island. In contrast, *Porites* corals at Palmyra, a wildlife reserve, exhibited unexpectedly high tissue-condition metrics for its latitude, suggesting an additional food source, possibly plankton-rich lagoonal outflow. We did not find a strong relationship between human habitation and the response of *Porites* corals to recent heat stress. However, differences in coral calcification rates and energy stores between observed values and those expected based solely on the regional oceanographic gradient, suggests local effects have indirect impacts on these corals.

Increased coral bleaching caused by warming waters has been identified as the most important global-scale threat to coral reefs worldwide (Brainard et al. 2011; Pandolfi et al. 2011; Pandolfi 2015; Hughes et al. 2017*a,b*). Despite the poor outlook for corals exposed to ever-increasing heat stress, evidence is accumulating that coral heat tolerance is affected by local background conditions, including nutrient inputs, sedimentation, and thermal variability (Castillo and Helmuth 2005; Middlebrook et al. 2008; Carilli et al. 2009, 2010, 2012; Wooldridge 2009; Guest et al. 2012; Fabricius et al. 2013; Mellin et al. 2016; Wooldridge et al. 2017). Some of these studies suggest that managing local stressors might benefit corals by increasing their resistance to or recovery from bleaching. Local management strategies include reducing land-based pollution (e.g., sewage; Banner 1974; Wear

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and Vega Thurber 2015), creating Marine Protected Areas that typically protect fish and other harvested organisms from collection, benefitting the rest of the ecosystem (Fernandes et al. 2005; McClanahan et al. 2006; although also see Cox et al. 2017), and direct human intervention such as assisted evolution (van Oppen et al. 2015).

Scleractinian corals obtain most of their nutrition via photosynthesis of intracellular symbiotic dinoflagellates (*Symbiodinium* spp.) and other endosymbionts that make up the coral holobiont. Corals can also feed heterotrophically on zooplankton, particulates, and dissolved organic matter (Houlbreque and Ferrier-Pagès 2009). Energy obtained from these sources is allocated to tissue growth and lipid storage, skeletal growth, reproduction, and maintenance (i.e., recovery from injury; Ward 1995*a,b*; Anthony et al. 2002; Grottoli et al. 2006; Hughes et al. 2010; Leuzinger et al. 2012). Oceanographic variability is likely to drive large-scale patterns of energy allocation in corals (e.g., Lough and Barnes 2000), but there is evidence that resource allocation also shifts in response to local stress such as sedimentation (e.g., less energy is devoted to lipid storage and more to maintain tissue growth; Anthony et al. 2002). Here, we use samples from *Porites* corals growing in the northern Line Islands to examine the relationship between local and regional drivers of coral condition, as defined by skeletal growth rates and tissue energy content.

The primary local human impacts on coral reefs adjacent to inhabited islands in the northern Line Islands are fishing and sewage inputs (Sandin et al. 2008; Carilli and Walsh 2012). Both of these stressors can increase nutrient availability (Carilli and Walsh 2012). Enhanced nutrients exceeding natural conditions appear to reduce coral bleaching thresholds (Vega Thurber et al. 2014), potentially by increasing algal endosymbiont densities (Wooldridge et al. 2017) or by increasing the thermal susceptibility of algal thykaloid membranes through altered lipid compositions (Wiedenmann et al. 2013). With respect to competitors of corals, increased macroalgae due to elevated nutrients or reduced herbivory caused by fishing might also lead to direct negative effects on corals through chemical poisoning (Rasher and Hay 2010), or indirect effects by feeding microbes that may cause coral disease (Smith et al. 2006). Sewage pollution can have direct negative impacts by introducing pathogens (Sutherland et al. 2010) and pharmaceuticals (Singh et al. 2010), as well as indirect effects via nutrient loading (Wear and Vega Thurber 2015).

The northern Line Islands offer a natural experiment to test the hypothesis that background environmental conditions (regional and local-scale) influence susceptibility of corals to bleaching when they experience episodic heat stress events associated with climate change. At a regional scale, upwelling increases along a north-to-south gradient that encompasses all six islands. As such, surface temperature and precipitation decreases, interannual temperature variability increases, nutrient availability increases, and the aragonite saturation state of seawater decreases along this gradient (Fig. 1; Table 1). Local conditions differ among islands as well. Two of the islands are uninhabited (Kingman Reef and Jarvis Island) and one island has only a small research station (Palmyra Atoll). All three of these islands are unfished. The other three islands, Teraina, Tabuaeran, and Kiritimati, are part of the Republic of Kiribati, are inhabited and fished, and experience low levels of dispersed untreated sewage, but no other significant runoff from land (there is virtually no industry or agriculture and little development; Sandin et al. 2008; Carilli et al. 2012). We used coral calcification rates and tissue energy content to explore how this gradient of regionally- and locally-distinct environmental regimes affected coral condition and response to past episodic heat stress events.

Materials

Oceanographic setting

The northern Line Islands span approximately 6.75° of latitude along a southeast to northwest strike, beginning with Jarvis Island (0.37°S, 160.00°W) and ending with Kingman Reef (6.39°N, 162.42°W). The islands straddle the transition between the westward-flowing South Equatorial Current and the eastward-flowing North Equatorial Counter Current (Sverdrup 1947). Equatorial upwelling of cool, more nutrient rich, and lower pH water most strongly affects Jarvis Island, followed by Kiritimati (2.03°N), and is weak at Tabuaeran (3.84°N). Teraina (4.70°N), Palmyra (5.87°N), and Kingman Reef are successively affected by warmer, lower nutrient, and higher pH Counter Current waters (Table 1; Wyrtki 1981). Kingman, Palmyra, and Jarvis are unfished and unpopulated, while Teraina, Tabuaeran, and Kiritimati each host human populations of several thousand individuals. A physical metric that combines sea surface temperature (SST), nitrate, and aragonite saturation state data from the literature (Table 1) is highly correlated with absolute latitude ($F_{1,4} = 230$, adjusted $R^2 = 0.98$, $p = 0.0001$); all of these variables are correlated to latitude and one another. Thus, we used absolute latitude as a proxy for the relevant changes in oceanography across the island chain to test for influences on coral calcification and tissue condition.

Coral core collection and growth rate analysis

Cores of coral skeleton approximately 5-cm in diameter were collected vertically to capture the maximum growth axis in each colony, using a hand-held pneumatic drill powered by a ship-board air compressor, or a hydraulic drill powered by a ship-board hydraulic engine. Most cores used in this manuscript were collected in October 2010 and November 2010, rinsed in freshwater and air dried, and left intact. These cores were scanned whole by computed tomography (CT) to reveal density banding at Woods Hole Oceanographic Institution in January 2011 following methods in

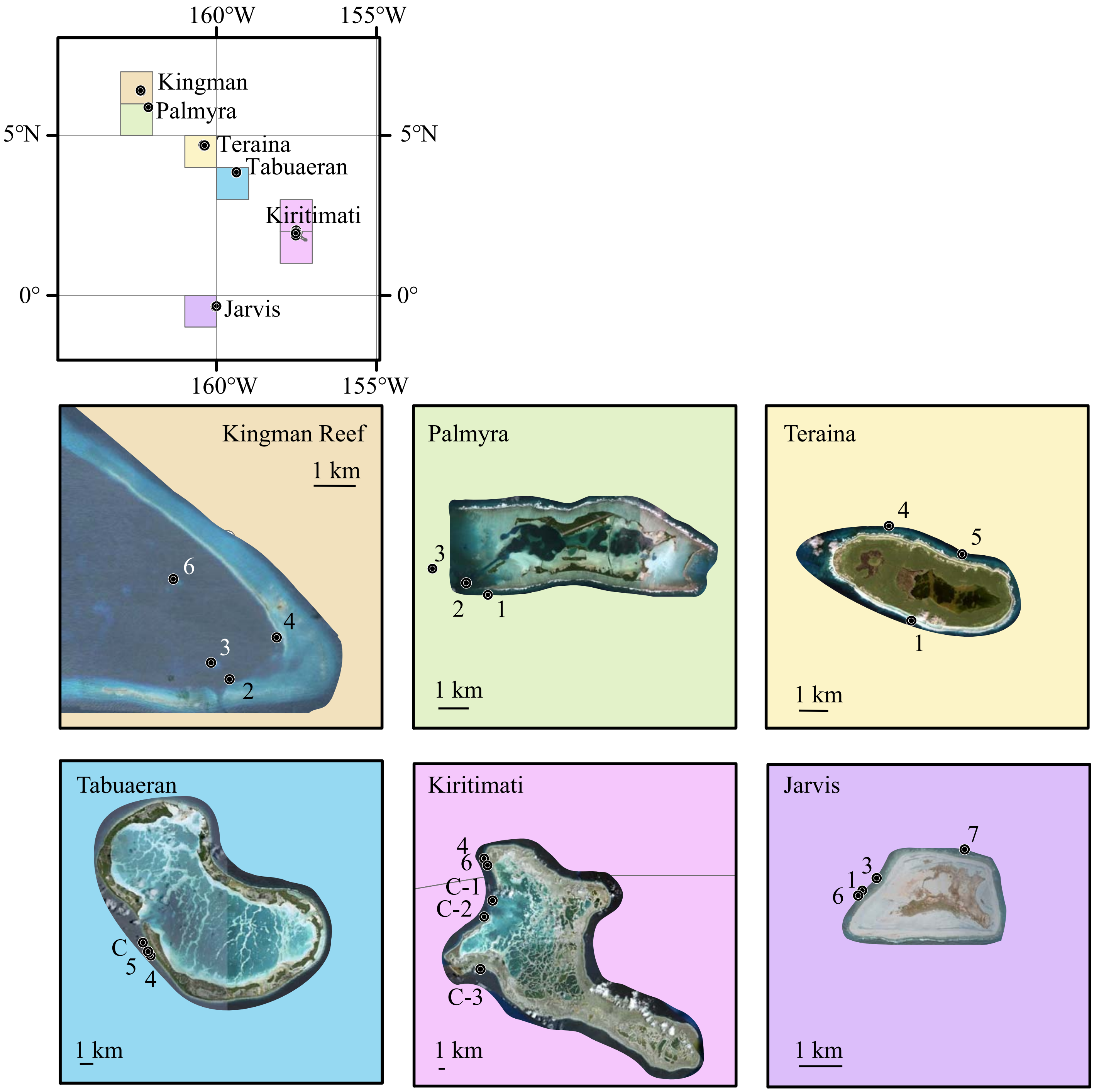

Fig. 1. Maps of northern Line Islands and each studied island with Google Earth imagery overlaid and sites denoted with black and white circles. Site numbers correspond to names in Table 2; sites denoted with "C" indicate cores collected on earlier expeditions by K. Cobb. Background colors on upper location map match lower maps.

Cantin et al. (2010), including the use of solid hydroxyapatite density standards to calibrate CT imagery for density analysis. Additional cores from Tabuaeran and Kiritimati were collected on other expeditions by R. Dunbar and K. Cobb (Table 2); a slab was removed from the middle of each of these cores with a saw and X-rayed to reveal density banding by R. Dunbar and K. Cobb, respectively. Density, and therefore calcification, was not measured for these X-rayed slabs, because the X-rays did not include standards of known density.

Table 1. Physical oceanographic variables across the northern Line Islands.

Island	SST*	Ω_{arag}[†]	Ω_{arag}[‡]	Ω_{arag}[§]	Nitrate[‡]	Nitrate[‖]	Nitrate[¶]	Physical metric[#]
Kingman	28.08	3.8	3.42	3.37	2.5	1	0.722	0.31
Palmyra	28.10	3.76	3.45	3.40	3.1	1.75	0.633	0.28
Teraina	28.14	3.68	—	—	—	—	1.4	0.67
Tabuaeran	28.02	3.63	—	—	—	2.51	2.275	1.10
Kiritimati	27.93	3.54	—	—	—	3.61	3.296	1.61
Jarvis	27.93	3.57	3.29	2.89	8	—	4.209	2.04

[*] HadISST 1961–1990 average (°C), Rayner et al. (2003).

[†] Freeman et al. (2012).

[‡] DeCarlo et al. (2015).

[§] Price et al. (2012).

[‖] Sandin et al. (2008).

[¶] Boyer et al. (2013).

[#] Physical metric = normalized SST* – normalized Ω_{arag}[†] + normalized nitrate[¶].

Table 2. Number of coral skeletal cores and tissue samples collected from each site, along with site details. Individual core numbers for samples collected by K. Cobb and R. Dunbar are included in parentheses.

Site number	Habitat	Cores	Tissue samples	Latitude (N)	Longitude (W)
KING2	Lagoon patch reef	3	3	6.386	162.356
KING3	Lagoon patch reef	3	0	6.390	162.360
KING4	Lagoon back reef	2	1	6.395	162.346
KING6	Lagoon patch reef	2	2	6.407	162.368
PAL1	Fore-reef	1	2	5.867	162.108
PAL2	Lagoon back reef	4	2	5.870	162.115
PAL3	Lagoon back reef	1	1	5.875	162.125
PAL-Cobb (P3, P5)	—	2	0	—	—
TER1	Fore-reef	1	4	4.671	160.383
TER4	Fore-reef	1	0	4.702	160.392
TER5	Fore-reef	1	1	4.693	160.367
TAB4	Fore-reef	2	1	3.836	159.358
TAB5	Fore-reef	2	1	3.839	159.360
TAB-Dunbar (5a, 5b, 6a, 7)	—	4	0	—	—
TAB-Cobb	Fore-reef	1	0	3.845	159.363
KIR4	Fore-reef	4	3	2.026	157.497
KIR6	Fore-reef	1	1	2.015	157.492
KIR-Cobb1 (Kir_Cobb_97, X12–5e)	Fore-reef	2	0	1.960	157.484
KIR-Cobb2 (X12–2, X12–3a, b)	Fore-reef	3	0	1.935	157.497
KIR-Cobb3 (X12–6)	Fore-reef	1	0	1.853	157.503
JAR1	Fore-reef	1	2	−0.372	160.011
JAR3	Fore-reef	2	1	−0.369	160.008
JAR6	Fore-reef	1	1	−0.372	160.012
JAR7	Fore-reef	1	1	−0.363	159.991

Coral annual extension rates were analyzed from X-rays using extension/luminance mode in CoralXDS (Helmle et al. 2002). Coral growth rates (annual extension, density, and calcification) from CT scans were analyzed using Osirix software following methods in Carilli et al. (2012), which included using the “Maximum Intensity Projection” mode in Osirix. These CT scan collection and analysis methods were used in previous work (Cantin et al. 2010; Carilli et al. 2012) because they produced reasonable density and calcification estimates that fit with expected density values from the literature for *Porites* corals. However, subsequent work on other coral species showed that these methods do not work well for other coral genera, potentially because of differences in the CT scan pixel : corallite size ratio and the importance of porosity in corals that contributes to the overall bulk density of the skeleton. DeCarlo et al. (2015), in contrast, used standards made from known-density coral samples and "Mean Projection" mode to analyze CT scans. When Mean Projection mode was used on the CT scans collected here that were scanned with hydroxyapatite standards (which contain no pore spaces), resulting densities were approximately 50% of those measured for *Porites* using other methods. This projection mode was thus deemed unacceptable for these CT scans. CT scan analysis is time consuming and expensive, so instead of repeating the original scans, we tested the accuracy of density values for the CT scanned Line Islands corals (using hydroxyapatite density standards and Maximum Intensity Projection mode), using buoyant weight methods as in Bucher et al. (1998) on subsamples cut from several coral cores. We found that the CT scan methodology we used overestimated density by approximately 12%; thus, all density measurements were adjusted by dividing by 1.12; resulting densities thus matched the buoyant-weight density estimates within measurement error. Calcification was calculated using adjusted densities.

To capture recent *Porites* calcification rates from each island, we chose to compute the average of calcification from 2008 and 2009, the most recent two complete years contained in cores collected in 2010. Because the topmost annual band was not fully complete, this year was excluded. In addition, the lengths (timespans) of the cores differed significantly, so computing and comparing long-term growth rates for each core/island would be inappropriate as these long-term calculations could be artificially affected by trends or extreme events not captured equivalently in all cores.

Annual growth rates from Line Islands massive *Porites* sp. cores were not strongly correlated to one another within individual islands through time. This may have resulted from unresolved dating errors, but attempts to identify misdated bands using standard techniques including use of the computer program *COFECHA*, skeleton plots, and close inspection of X-rays and CT scans did not reveal problem bands. To verify the annual nature of banding in northern Line Islands corals, top sections from two cores from Jarvis Island and one core from Tabuaeran were cut into slabs and cleaned with an ultrasonic probe. Small amounts of coral powder were sampled using a milling machine along the maximum growth axis every 0.5 mm, and every other sample was analyzed for Sr/Ca. These Sr/Ca records were matched to SST records using Analyseries and visually compared to density bands (Supporting Information Fig. S1), verifying that visually identified bands were annual. Master growth rate chronologies are often constructed by averaging standardized growth rates from multiple organisms at a given site. However, the low coherence in coral growth rate records within islands makes the construction of master chronologies inappropriate (Fritts 1976) and thus individual growth rate records are presented here (Fig. 2).

Incidences of stress banding (where skeletal extension rates are reduced and density is increased) and partial mortality (where part of the colony dies, and is usually later overgrown by remaining living polyps) were identified visually in CT scans and verified with visual inspection of cores (Supporting Information Fig. S2).

Coral tissue analyses

Coral tissue thickness was measured by first sectioning a portion of each core parallel to the growth axis, then making and averaging between 5 and 8 digital caliper measurements of the tissue depth. Coral tissue samples approximately 1-cm in diameter were collected with a hammer and chisel from live colonies and stored in plastic canisters filled with seawater until dives were completed. Note that tissue samples for lipid extractions were not collected from all coral heads that were cored, and at some locations, additional tissue samples were collected from other coral heads that were not cored. Upon return to the ship, samples were wrapped in aluminum foil and frozen in a −20°C freezer. Samples were transported to Scripps Institution of Oceanography in liquid-nitrogen charged dewars and kept in a −20°C freezer until they were processed. Lipids were extracted using a modified Bligh and Dyer (1959) method and lipid classes were analyzed with thin layer chromatography-flame ionization detection (Iatroscan MK5, Iatron Industries) described in Carilli et al. (2012). Lipid content was normalized to tissue content (as ash-free dry weight). The following lipid metrics were used to examine coral energy stores: energetic lipids (wax esters and triacylglycerol, sometimes referred to as "storage" or "energy" lipids); structural lipids (sterols and phospholipids); free fatty acids; and total lipids.

Heat stress metrics

Accumulated thermal stress has been strongly linked to the incidence and severity of coral bleaching (Eakin et al. 2010). SST for the study locations was acquired from the NOAA Pathfinder v5.0 dataset (0.0439°, daily resolution) for the period 1985–2009 and composited to weekly resolution. Remaining data gaps, due to clouds or poor-quality retrievals, were filled by temporal and spatial interpolation following the method of Heron et al. (2010). To extend these timeseries through the year 2010, NOAA's near real-time 11 km SST data (February 2009–December 2010) were concatenated, using the overlap period to bias-adjust the latter dataset to match the former (Pollock et al. 2014). The measure of thermal stress, degree heating weeks (DHWs), was calculated using the NOAA Coral Reef Watch methodology (Liu et al. 2014). As thermal stress events in these locations span the change from 1 yr to the next (i.e., through December and January), annual maximum DHW values were calculated from July to June, with the value attributed to the former year. Because corals are adapted to historical thermal conditions (Donner 2011; Carilli et al. 2012), we scaled the annual maximum DHW experienced at each island to a percentage

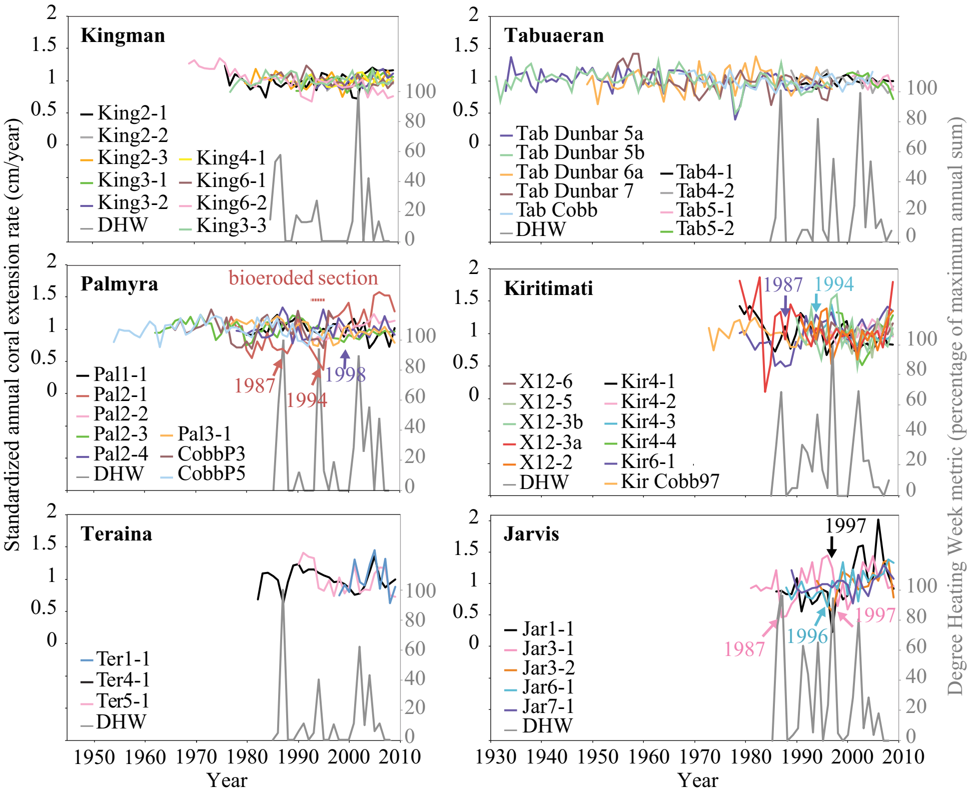

Fig. 2. Standardized extension rates of all coral cores analyzed at each island (colored lines), along with a relative DHW metric (gray). Partial mortality scars observed in cores are denoted with arrows colored to match the cores that contained these scars, and the best estimate for the year in which the mortality occurred is included.

of the long-term (1985–2009) maximum DHW at that island (Fig. 2).

Statistical treatments

Because coral tissue thickness and coral lipid concentrations were not measured from the same population of coral colonies (Table 2), we calculated the mean and standard deviation of coral lipid stores from the product of 10,000 bootstrapped samples of the tissue thickness and 10,000 bootstrapped samples of lipid variables (lipid mass per unit of tissue mass for each lipid class) at each island (Fig. 3, Supporting Information Fig. S3). The influence of the dependent variable *absolute latitude* on the explanatory variables *calcification* (the average calcification rate from the years 2008 and 2009, which were the most recent complete 2 yr from each core and occurred in all cores collected in 2010), *total lipid stores* (calculated as the product of tissue thickness and total lipid concentration), *energetic lipid stores* (calculated as the product of tissue thickness and energetic lipids [wax esters and triacylglycerol]), *structural lipid stores* (calculated as the product of tissue thickness and structural lipids [sterols and phospholipids]), and *free fatty acid stores* (calculated as the product of tissue thickness and free fatty acids) was assessed using linear models (function *lm* in R, Fig. 3, Supporting Information Fig. S3). The influence of the dependent variable *absolute latitude* on the lipid class explanatory variables *total lipids*, *energetic lipids*, *structural lipids*, and *free fatty acids* were also assessed on their own (without taking into account tissue thickness) using linear models (*lm*) in R.

To test whether the co-occurrence of partial mortality events or stress banding between corals could be explained by random chance, we performed a chi-squared test. To test whether the occurrence of partial mortality events or stress banding differed significantly between islands, we performed Mann-Whitney *U*-tests using *wilcox.test* in R on time series that consisted of the total number of partial mortality events or stress bands for each year at each island.

Overall coral condition was assessed using a metric calculated by summing the standardized product of total lipids and tissue thickness with average 2008/2009 calcification at each island.

Results

Porites coral calcification (the product of extension and density) is mostly driven by changes in extension rate rather than density (average $R = 0.79$ for extension, 0.51 for density here, and also see Carilli et al. 2009 and Lough and Barnes 2000); however, for some individual coral heads (KING2

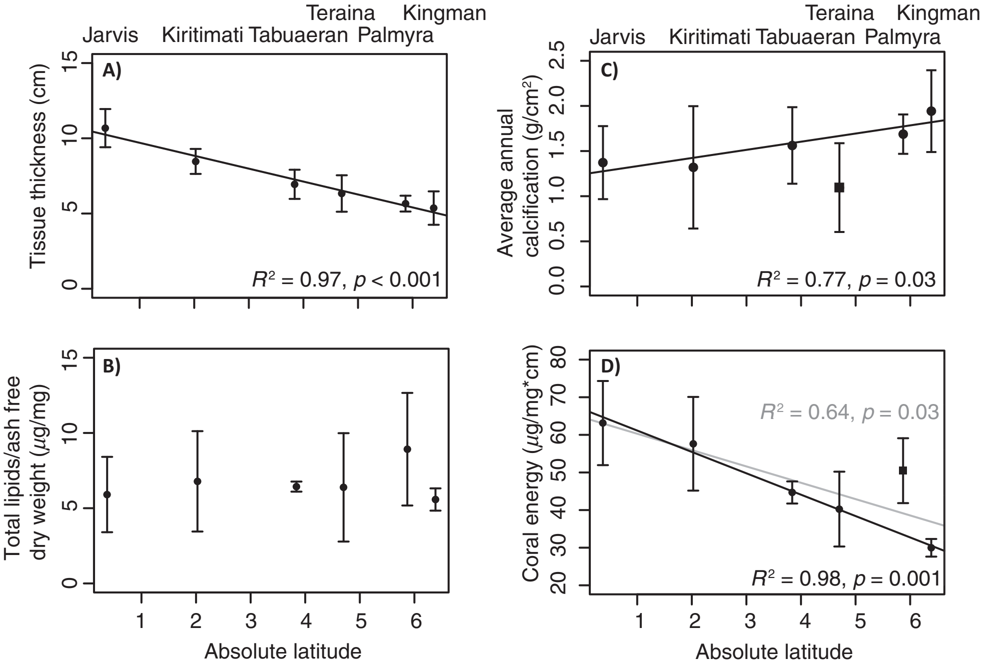

Fig. 3. (**A**) Tissue thickness in cm (black circles), (**B**) total μg of lipid per milligram of tissue (black circles), (**C**) mean 2008/2009 calcification, (black circles and square) and (**D**) coral lipid energy content vs. absolute latitude (black circles and square). Error bars are one standard deviation. Significant linear models from Table 4 are included. In (**C**) and (**D**), Teraina and Palmyra (squares), respectively, were excluded from the linear regressions shown in black.

core3, KING4 core1, TAB4 core1, KIR4 core1), density changes drove calcification. Skeletal growth was not well correlated among coral heads, as reflected by poor series intercorrelation values (< 0.4) calculated using the program COFECHA (Grissino-Mayer 2001) for all growth metrics at all islands. Reflecting this, coral skeletal growth rates responded differently to changes in water temperatures; there were no significant differences in the numbers of corals that responded to heat stress events by reducing skeletal growth rates compared to increasing growth rates at any island (Fisher's exact test, $p > 0.05$). Similarly, there were no consistent patterns within islands for correlations between growth and heat stress metrics for individual coral cores.

A total of nine partial mortality scars were identified from seven different cores: Jarvis3-1 (1987, 1997), Kiritimati6-1 (1987), Palmyra2-1 (1986/1987, 1994), Kiritimati6-1 (1994), Jarvis6-1 (1996/1997), Jarvis1-1 (1997), Palmyra2-4 (1998). Relatively strong heat stress accumulated in 1987/1988 and 1997/1998 in the northern Line Islands (Fig. 2). In contrast, obvious stress bands indicating prior bleaching events (Cantin and Lough 2014) were infrequent, and were only clearly identified in the core with partial mortality in 1987 at Jarvis, in 1997 in one core with partial mortality and two additional cores without partial mortality at Jarvis, and one core in 2009 at Palmyra (Pal2–1, which had partial mortality in 1986/1987 and 1994 but not in 1998 or 2009; Fig. 2). The results from our chi-square test indicate that the occurrence of partial mortality events was not random ($\chi^2 = 203.1$, 1 degree of freedom, $\chi^2_{\text{critical}} = 10.83$ at $p = 0.001$). The results from the Mann-Whitney *U*-test indicate that the rate of occurrence of partial mortality and/or stress banding was significantly higher at Jarvis than Kingman, Tabuaeran ($p < 0.05$), and possibly Teraina ($p = 0.09$), that it was significantly higher at Kiritimati than Tabuaeran ($p < 0.05$), and that it was possibly higher at Palmyra than Tabuaeran ($p = 0.09$, Table 3).

Metrics of coral health including tissue thickness (Fig. 3A), lipid content (Fig. 3B), and calcification (Fig. 3C) were compared across islands and oceanographic gradients, represented by absolute latitude. In addition to oceanographically-driven responses, these analyses identified island-specific outliers in a number of these metrics. From Kingman to Jarvis, with decreasing latitude, tissue thickness increased and mean annual calcification rate decreased, with unexpectedly low calcification at Teraina (Fig. 3A,C; Table 4). Latitude did not explain significant variability in any lipid concentration metric normalized to ash free dry weight of tissue, without taking into account tissue thickness (Fig. 3B).

Excluding Palmyra, latitude explained 98% of variability in the coral energy content metric calculated using total lipids in the northern Line Islands ($F_{1,3} = 264.7$, $p < 0.001$, Fig. 3D, Table 4). Palmyra had higher tissue energy content than would be expected based on latitude, which was driven by higher lipid concentrations (tissue thickness was not exceptional). The higher total lipid stores at Palmyra were driven by higher energetic lipid concentrations rather than

Table 3. Results from Mann-Whitney *U*-tests using the *wilcox.test* package in R to test for significant differences in partial mortality and stress band occurrence between all pairs of islands. The first number shown is the *U* statistic, and the second is the *p*-value. Islands with partial mortality events are in bold, as are results from island pairs that are significantly different. Tests were not applicable (NA) when both islands had neither stress bands nor partial mortality events.

Islands	Kingman	**Palmyra**	Teraina	Tabuaeran	**Kiritimati**
Palmyra	1189, 0.23	—	—	—	—
Teraina	NA	756, 0.323	—	—	—
Tabuaeran	NA	2133, 0.09	NA	—	—
Kiritimati	841, 0.15	1090, 0.97	574, 0.24	**1620, 0.045**	—
Jarvis	**656, 0.038**	854, 0.39	448, 0.09	**1264, 0.004**	596, 0.41

Table 4. Results from linear models of explanatory variable *absolute latitude* on response variables *calcification*, *total lipid stores*, *energetic lipid stores*, *structural lipid stores*, and *free fatty acid stores*. Lipid stores were estimated by bootstrapping the product of tissue thickness and lipid metrics. Linear models were fit with data from all islands as well as with certain islands excluded (as outliers) when various metrics appeared to deviate from expected results based on the metrics at other islands. Models were assessed based on *p*-values for slope of the linear models and *F*; the best-fit models for each dependent variable (i.e., with all islands or a subset of islands only) are highlighted in bold. Corresponding figures that include these comparisons and models are noted; nonsignificant linear models ($p \geq 0.05$) not shown in figures are marked with *.

Model	*F*	df	Adjusted R^2	*p*-value for slope	Figure
Tissue thickness ~ Latitude	**141.3**	1,4	**0.97**	**0.0003**	**3A**
Total lipid ~ Latitude	0.37	1,4	−0.14	0.575	3B*
Calcification ~ Latitude	1.82	1,4	0.14	0.25	3C*
Calcification ~ Latitude without Teraina	**14.51**	1,3	**0.77**	**0.032**	**3C**
Total lipid * tissue thickness ~ Latitude	10.05	1,4	0.64	0.03	3D
Total lipid * tissue thickness ~ Latitude without Palmyra	**254.7**	1,3	**0.98**	**0.0005**	**3D**
Energetic lipid * tissue thickness ~ Latitude	0.89	1,4	−0.02	0.4	S3A*
Energetic lipid * tissue thickness ~ Latitude without Palmyra	**8.79**	1,3	**0.66**	**0.06**	**S3A**
Energetic lipid * tissue thickness intercept only without Kingman	0.001	1,3	−0.33	0.973	S3A*
Structural lipid * tissue thickness ~ Latitude	32.34	1,4	0.86	0.005	S3B
Structural lipid * tissue thickness ~ Latitude without Teraina	**47.66**	1,3	**0.92**	**0.006**	**S3B**
FFA lipid * tissue thickness ~ Latitude	0.029	1,4	−0.24	0.89	S3C*
FFA lipid * tissue thickness ~ Latitude uninhabited only	9.79	1,1	0.81	0.2	S3C*
FFA lipid * tissue thickness ~ Latitude without Jarvis	**10.93**	1,3	**0.71**	**0.046**	**S2C**

structural lipids or free fatty acids, suggesting corals there had unusually high stores of energy available relative to expectations based on latitude (Supporting Information Fig. S3A). While all islands had similar total lipid concentrations (Fig. 3B), lipid class profiles differed among islands (Supporting Information Fig. S3). Excluding Palmyra, energetic lipid content decreased with increasing latitude ($F_{1,3} = 8.79$, adjusted $R^2 = 0.66$, $p = 0.06$; Table 4). Structural lipid stores also decreased at all islands with increasing latitude ($F_{1,4} = 32.34$, adjusted $R^2 = 0.86$, $p = 0.005$); when Teraina was excluded from the linear model, this relationship strengthened ($F_{1,3} = 47.66$, adjusted $R^2 = 0.92$, $p = 0.006$), suggesting Teraina had lower structural lipid stores than would be expected based on latitudinally-associated oceanographic drivers. Free fatty acid stores increased with increasing absolute latitude, excluding Jarvis, which had much higher than expected free fatty acid stores (Supporting Information Fig. S3C, $F_{1,3} = 10.93$, adjusted $R^2 = 0.71$, $p = 0.046$).

Calcification was also correlated with latitude when Teraina was excluded; absolute latitude explained 77% of this variability (Fig. 3C; $F_{1,3} = 14.51$, $p = 0.032$). Calcification rates at Teraina were lower than expected based on latitude, and when that data point was included, latitude did not significantly explain calcification. Note that other years were tested (for calcification) and resulted in similar outcomes, but the 2008/2009 choice of dates was chosen to maximize the sample size.

Because of the latitudinally-correlated tradeoff between calcification and tissue energy reserves, overall coral condition taking into account both of these factors was indistinguishable at all islands except Teraina, which had a lower coral condition metric than the other islands (Fig. 4).

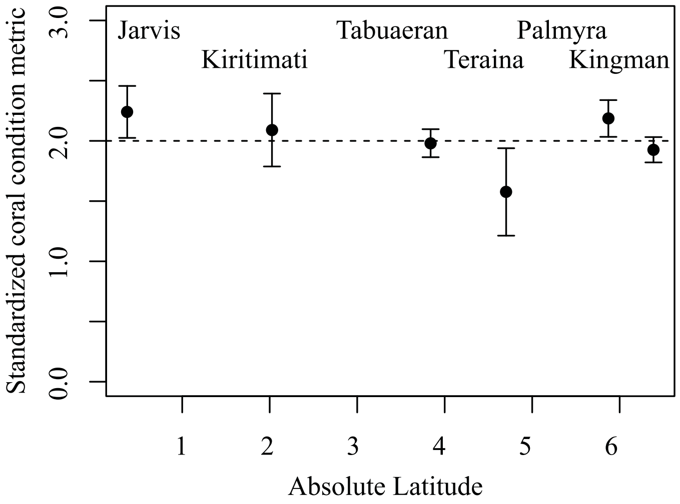

Fig. 4. Average overall *Porites* coral condition metric for each island. Error bars are standard errors. The dashed line represents the average value for this overall condition metric.

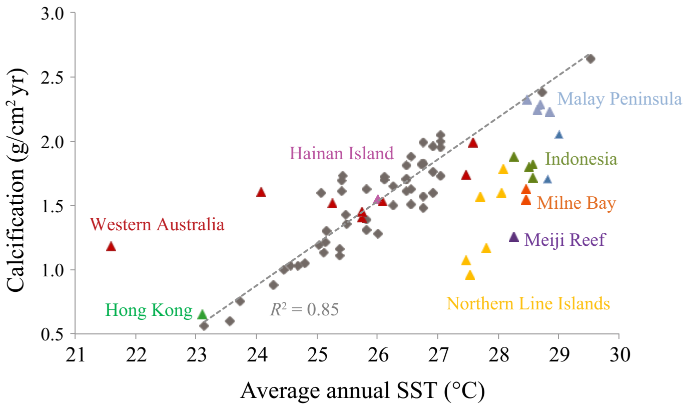

Fig. 5. Average annual *Porites* coral calcification is well correlated with average annual temperature in many locations worldwide (gray and colored symbols that fall on the linear fit to these data points; modified from Lough et al. 2014). However, local differences in other physical parameters may drive observed differences from expected values (colored points that fall away from the gray dashed best-fit line). Data from this study are in yellow.

Discussion

Physical attributes associated with latitude drive most of the variability in *Porites* coral calcification rates and tissue energy content in the northern Line Islands. However, certain island-scale conditions (e.g., military alteration at Palmyra and a freshwater lake at Teraina) appear to also influence coral health metrics. We first discuss our coral calcification records, including evidence for past bleaching events in our cores, and then discuss our coral tissue energy store results.

Coral calcification generally increases with water temperature to a local optimum (Fig. 5), until further increases in temperature cause bleaching and reduced calcification or even mortality (Fig. 2). Lack of synchronicity in coral skeletal growth rates from colonies sourced from the same sites and islands suggests that individual corals sampled here responded differently to the same reef-scale environmental conditions (Fig. 2). Potentially, these corals each experienced micro-scale physical variability that drives individual skeletal growth rates at these islands. Alternatively, other colony-specific factors such as the burden of bioeroders (e.g., Shima et al. 2010), fish bites (e.g., Bruckner et al. 2000), competition with macroalgae (e.g., Lirman 2001), coral gender (Cabral-Tena et al. 2013; Carricart-Ganivet et al. 2013), or genotype overprinted any common signal in coral skeletal growth rates driven by common environmental factors such as SST.

The within-reef variability observed among coral colonies inhabiting a single island underscores the importance of collecting a large sample size when studying time series of coral skeletal growth rates. By doing so, shared environmentally-driven signals can be discerned through the noise of individual variation. In dendrochronology, the strength of this common signal is often calculated as the expressed population signal (EPS; Cook and Kairiukstis 1989). Wigley et al. (1984) suggested that a minimum EPS of 0.85 is "acceptable," in terms of sufficiently capturing the common environmental signals driving growth rates. The highest EPS from the Line Islands cores collected in 2010 was 0.65 for both calcification at Kingman and extension at Kiritimati, indicating that additional samples would be needed from these sites to interpret year-to-year variability in growth rates at these islands. Carilli et al. (2010) previously found that 10 cores are a reasonable sample size for growth rate reconstructions from *Orbicella* (formerly *Montastraea*) *faveolata* from Belize and Honduras, generally achieving EPS values >0.85. However, even with 10 cores from Kingman reef, we were unable to capture the common environmental signal in growth rates of *Porites* spp. corals from the Line Islands, possibly because of relatively low sensitivity (year-to-year variability) at that island, and/or higher genotypic variability in *Porites* (Baums et al. 2012). Due to limited time at each island, as well as the limited availability of suitable corals, all other islands had even smaller sample sizes collected in 2010. The records from these cores were supplemented with extension-rate data from additional cores collected by R. Dunbar and K. Cobb. However, even still, series intercorrelations and EPS values remained low, suggesting that at these islands larger sample sizes would be needed to construct robust annually-resolved coral growth rate master chronologies. These findings also highlight the importance of making available archived core material, datasets, and/or imagery of cores to the wider research community to enable studies incorporating large sample sizes to overcome these challenges.

Despite low coherence in year-to-year variability in growth rates within each island, certain growth patterns emerge from the core data. For instance, the partial mortality scars and stress banding in 1987/1988 at inhabited Kiritimati, and uninhabited Palmyra and Jarvis; in 1994 at Kiritimati and Palmyra and 1996/1997 at Jarvis; and in 1998 and 2009 Palmyra were all likely caused by prior bleaching events. No evidence of *Porites* bleaching was found in cores from inhabited Tabuaeran or Teraina, nor uninhabited Kingman Reef. Jarvis and Kiritimati experience the most extreme year-to-year SST variability driven by El Niño events (Donner 2011; Heron et al. 2016; Fig. 2), but warm water events associated with El Niño also influence the islands up through Palmyra, albeit to a lesser extent, as revealed by coral geochemical records (Cobb et al. 2003; Nurhati et al. 2009).

Coral bleaching observations from the central Pacific are relatively sparse, and these core-based records enhance understanding of the historical record of bleaching in the northern Line Islands. Bleaching affecting approximately 25–30% of corals was observed in 1998 at Kiritimati (K. Cobb pers. obs.; Nurhati et al. 2009), and mortality that occurred between successive surveys of the US Line Islands suggested bleaching in the mid-late 1990s had occurred. Bleaching in the 1990s was observed at Kingman, although the extent and species affected were not described (Maragos et al. 2008). Benthic surveys completed at Kingman Reef in 2010 suggested a recent mortality event, possibly bleaching, that targeted *Acropora* branching corals at site 6 (Fig. 1). Indeed, U/Th dates from 3 of 9 standing-dead *Acropora* colonies fell in the mid-late 1990s (J. Pandolfi and J.-X. Zhao unpubl. data). Thus, the core-based observations suggesting bleaching of *Porites* corals in the past several decades at Palmyra, Kiritimati, and Jarvis, but not at Kingman, Teraina and Tabuaeran adds substantially to the previously sparse bleaching observations, but other more susceptible species may have bleached at those islands during periods not recorded in our *Porites* cores.

The evidence that bleaching has been worse at Palmyra than Teraina and Tabuaeran is surprising, given its thermal history. The frequency of severe thermal stress (DHW $\geq$ 8°C-weeks) at reef locations around each island decreases with increasing latitude, from 23% of years at Jarvis to 4% of years at Kingman (Heron et al. 2016). As Teraina and Tabuaeran are to the south of Palmyra, they should be more strongly affected by El Niño warming and should experience more extreme heat stress (Figs. 1, 2; Heron et al. 2016). The cores with partial mortality and stress banding from Palmyra were collected near the channel entrance on the western terrace, where mild bleaching was observed in 2009 (Williams et al. 2010) and where coral mortality was observed in 1998 (Maragos et al. 2008). It is therefore possible that bleaching there is localized and exacerbated on the western terrace of Palmyra beyond regional water temperature changes by particularly warm and/or turbid water exiting the militarily-altered lagoon (Williams et al. 2010; Gardner et al. 2011).

The observation that Kiritimati and Jarvis have historically experienced the most thermal bleaching events in the northern Line Islands is supported by observations during the 2015–2016 El Niño event. Kiritimati and Jarvis experienced almost complete bleaching-induced coral mortality (on the order of 80% and 95%, respectively), due to heat stress during the 2015–2016 El Niño (K. Cobb and J. Baum pers. obs.; B. Vargas-Angel pers. obs., respectively; Eakin et al. 2016). While Palmyra experienced some bleaching, it was comparatively mild (S. Sandin and J. Smith pers. obs.). No reports of bleaching at Tabuaeran or Teraina from this event were received by the Kiribati Fisheries department (A. Tekiau pers. comm.). We have no records of bleaching conditions at Kingman Reef during this most recent El Niño event.

The lack of evidence for prior bleaching in *Porites* at inhabited Tabuaeran and Teraina could be an artifact of low sample sizes. For instance, Hendy et al. (2003) calculated that with three coral cores, there would be a 40% chance of capturing a bleaching event that affected 30% of corals. The small core sample size here was caused by low availability of suitable *Porites* corals from which to collect cores. In 2010, we conducted manta tows over several kilometers of reef at both islands and only found a small number of massive *Porites* corals at both islands; the colonies that we did find were generally small and in some cases flatter than the typical hemispherical shape expected of *Porites lobata* and *P. lutea*. In contrast, Kingman Reef is dominated by extremely large massive *Porites* colonies, so we were able to collect 10 long cores from that island without difficulty. The lack of evidence for prior bleaching in these 10 cores suggests that *Porites* corals have not historically bleached strongly at Kingman Reef. It is possible that *Porites* at Teraina and Tabuaeran, which have historically experienced lower heat stress than the most equatorial islands, Kiritimati and Jarvis (Fig. 2), have therefore not historically experienced major bleaching events. An alternative hypothesis is that there are relatively few *Porites* corals on Teraina and Tabuaeran because past bleaching events led to mortality of colonies. This scenario seems unlikely because the reefs at those islands are dominated by *Pocillopora* and *Montipora* (both islands) and *Acropora* (Tabuaeran) corals, which tend to be more susceptible to bleaching, but also faster growing, than *Porites* corals (Marshall and Baird 2000).

Our observations also provide context to interpret the observed latitudinal variability of *Porites* tissue energy stores. Corals at lower latitudes had equivalent lipid content but thicker tissues relative to corals at higher latitudes, and therefore had more total energy available for respiration and survival through bleaching events (Rodrigues and Grottoli 2007). Corals closer to the equator might build up tissue and lipid stores to increase survivorship when starved during bleaching events (Rodrigues and Grottoli 2007; Anthony et al. 2009). Thus, in contrast to Barnes and Lough (1992, 1999), who showed that chronic stress may lead to thinner coral tissues, in the northern Line Islands and in other environments that experience episodic stress, thicker tissues appear to be a potential way that corals have adapted to more episodically stressful conditions to enhance survival (e.g., Anthony et al. 2009).

The potential for heterotrophy (i.e., the availability of alternative nutritional sources) also appears to have influenced bleaching impact in this region. Because upwelling is greater near the equator, nutrients, primary productivity, and zooplankton abundance are typically higher (King et al. 1957; Roman et al. 2002), enhancing the potential for coral heterotrophy and associated energy stores (Palardy et al. 2008) compared with corals at latitudes away from the equator. Lagoon outflow at Palmyra could similarly boost coral heterotrophy, either due to enhanced feeding on particulates like suspended sediment (Anthony 1999; Williams et al. 2011), or increased zooplankton (e.g., Le Borgne et al. 1989). While Kingman Reef and Tabuaeran also have lagoons, Kingman is almost completely open and therefore likely oligotrophic (e.g., Le Borgne et al. 1997). The Tabuaeran lagoon has high productivity (Gordon et al. 1970), however, lagoonal outflow is unlikely to contribute extensively to coral feeding outside the lagoon due to long residence times (~ 11 months). Furthermore, the small volume of lagoon water that is flushed rushes out of the major pass as a diurnal tidal jet (3–5 knots), possibly delivering plankton to deeper water that is beyond the reach of fringing corals (Gallagher et al. 1970). The core-based records of bleaching support this interpretation. Cores from Jarvis, Kiritimati, and Palmyra indicate that bleaching events occurred in the past, yet the samples were collected from live corals that had clearly survived these events. In contrast, live corals sampled from the other islands show no evidence for past bleaching events, suggesting that those corals have not experienced heat stress of the same magnitude and thus have had no need to adaptively allocate more energy to tissue storage than skeletal growth. The potential for lagoon productivity to serve as a source of nutrition for corals both inside and outside lagoons is an important focus for future research.

Both regional-scale and local-scale oceanography appear to drive coral tissue energy content via food availability. Average coral calcification rates are also being driven largely by regional-scale oceanography in the northern Line Islands, with strong correlation to latitude. Calcification is driven nonlinearly by water temperature and may also be affected by aragonite saturation state; thus, as waters warm and become more acidic with climate change, calcification is expected to decrease (Evenhuis et al. 2015). Average coral calcification rates and energy content at a given location may be predictable based on oceanographic variables, and thus deviance from expectations could suggest changes in average coral condition that is local in nature (Figs. 4, 5). The data presented here suggest that corals at certain locations are better suited to survive stress events, and that both coral calcification rates and tissue energy stores provide useful information about coral condition.

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Conflict of Interest

None declared.

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