Calcification trends in long-lived corals across the Indo-Pacific during the industrial era

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Abstract

Skeletal cores from massive, long-lived coral colonies provide a unique approach to investigating the chronic effects of climate change on coral calcification across decadal to centennial timescales. Here, we show an overall decline in calcification rates during the industrial era, broadly consistent with other studies, based on 148 skeletal cores from ten reef locations throughout the Indo-Pacific. However, these declines are region-specific, modulated by the opposing influences of density and linear extension (the product of which equals calcification), and superimposed on multi-decadal oscillations. The main drivers of declines in calcification were recent marine heatwaves that induced reductions in linear extension, rather than decreasing skeletal density. Our findings contrast with some regional studies that show growth declines beginning only in recent decades, which in some cases may be the most recent troughs of multi-decadal oscillations in calcification.

Introduction

Coral calcification—the formation of $CaCO_3$ skeletons from seawater constituents—underpins the creation of geologic reef structures and their capacity to keep pace with rising sea levels. Existing only within a narrow range of environmental conditions[1], reef-building corals are thought to be highly sensitive to climate change, although current understanding of their calcification sensitivity comes primarily from acute exposures in laboratory experiments[2]. Ecologically, the complex three-dimensional structures created by corals harbor immense biodiversity, while economically, these coastal environments support tourism and fishing industries and protect shoreline communities by dampening incoming waves[3]. Despite the immense human dependence on corals, anthropogenic carbon emissions pose threats to the survival of corals and maintenance of reef structures via increased sea surface temperature (SST) and CO_2-driven ocean acidification. Massive, reef-building (hermatypic) corals record changes in their ambient environment—and their physiological responses to those changes—within their skeletons in two parameters[4]: upward growth ("extension"; length per unit time) and skeletal density (mass per unit volume)[5]. Short term laboratory experiments are commonly used to investigate the sensitivity of coral calcification to temperature and acidification[2,6], but these experiments do not accurately simulate the pace of climate change in the surface ocean over decades to centuries. Rather, the only way to reconstruct climate impacts on reef-building coral colonies prior to the 21st century is by extracting information from long-lived skeletal cores.

Coral growth reconstructions have been conducted on a regional basis at several locations throughout the tropics, including across Australia[7–9], Southeast Asia[10], remote Pacific islands and atolls[11], the South China Sea[12–14], and the western Atlantic[15–19]. However, these studies have reported differing patterns over time: declining growth rates[7,8,20], stable growth rates over time[9], and even initial increases in calcification with rising SST[12,21,22]. In addition, differences in methodology have limited the reproducibility of some results[23], especially when compounded with low replication (<10 cores in some cases[20,24]) and inaccuracies in accounting for the complex three-dimensional geometry of skeletal growth[20,25]. These methodological issues and overall lack of consensus regarding regional calcification trends limit our understanding of the long-term, chronic impacts of climate change on coral growth across the tropics.

Here, we present the most comprehensive multi-regional reconstruction of coral growth to date, with cores from across the Indo-Pacific. We use advanced, state-of-the-art software to accurately identify and measure coral growth rates in three dimensions (3D) to capture even subtle changes in skeletal extension and density since the start of the industrial era. Our novel core collection includes 148 *Porites* spp. skeletal cores from ten locations spanning 40 degrees of latitude and nearly 120 degrees of longitude, including the Coral Sea off the coast of Australia, the Great Barrier Reef (GBR), the Red Sea, South China Sea, Taiwan, Hawai‘i, and the Solomon Islands (Fig. 1; Supplemental Table S1). Three-dimensionally scanned computed tomography (CT) images were used to identify annual density bands, and using CoralCT[26], we measured linear extension in 3D to capture the complex geometry of coral growth (Supplemental Fig. S1). We modeled growth parameters (linear extension, skeletal density, and calcification), separately, as functions of several factors including time, mean annual SST, max annual SST, and atmospheric CO_2 (Supplemental Table S3). Along with these environmental conditions, we also examined the impacts of reef proximity to human population centers using the human “gravity” metric[27] (Supplemental Tables S2 and S4). Models incorporated various combinations of core- or location-specific intercepts and slopes, and were constructed both with and without periodic components and autocorrelation structures. The rationale behind testing if periodic components improved model fit includes (i) many skeletal growth records contain decadal+ variability, (ii) linear trends do not capture this variability and can be biased depending on the phase at the ends of time series, and (iii) while we did test temperature as a model predictor, coral responses can be lagged and of lower frequency than climate drivers, so periodic components enable a model fit to approximate decadal+ variability in growth even if there is not a strong correlation to an environmental parameter on a year-by-year basis.

Results and Discussion

Our analysis reveals that *Porites* coral calcification has, overall, significantly declined in the Indo-Pacific over recent decades to centuries despite high interannual and decadal variability. Calcification, the product of linear extension and skeletal density, is ultimately the most important growth parameter in terms of the construction of $CaCO_3$ building blocks that form reef structures. We first tested, but ultimately eliminated, models containing environmental conditions and the "gravity" metric as they did not produce the best fits to the data (Supplemental Tables S3 and S4). Rather, in a model with all cores, calcification was best described by a model with a periodic component of 21 years, with core-specific temporal trends and y-intercepts reflecting inherent growth variability between individual coral colonies (Supplemental Table S5). A model fit to all cores had a significant negative calcification trend ($p < 0.001$), while in a model with core-specific trends, 17.6% (26/148) of cores had a significant negative calcification trend compared to only 2.7% (4/148) with a significant positive trend (Table 1). Further analysis revealed four reef locations where calcification declined significantly (Fig. 2): central Red Sea ($p < 0.001$), southern Red Sea ($p < 0.001$), Lizard Island GBR ($p = 0.0056$), and Dongsha Atoll ($p < 0.001$). Cores from all other locations showed a nonsignificant decline in calcification, with the exception of the Solomon Islands and Yonge Reef (GBR), which experienced nonsignificant positive calcification trends (Table 1). These regional differences could arise from human impacts or exposure to different oceanographic or climatic regimes. However, the human "gravity" metric did not improve performance (*i.e.*, growth trends were not modulated by local human impacts). The greatest calcification declines were observed in the Red Sea, the surface of which has warmed more rapidly than much of the rest of the ocean, especially in recent decades[28]. Conversely, Lizard Island and Yonge reef are located only 20 km apart yet showed opposing long-term calcification trends.

The prominence of linear extension versus skeletal density as the main driver of the calcification declines was also regionally variable. For example, the significant negative trend in calcification at Dongsha Atoll in the South China Sea was due to the significant negative trend in skeletal density. Conversely, calcification at Lizard Island in the GBR and both Red Sea locations was regulated by the significant negative trends in linear extension despite the significant positive trend in skeletal density ($p < 0.001$) in the southern Red Sea. This inverse relation between density and extension was not unique to the southern Red Sea, as we found a weak but significant ($r = 0.18$, $p < 0.001$) inverse relationship in extension and density anomalies across our entire dataset (Fig. 3a), a finding which is broadly consistent with previous studies[29]. The models fit to data pooled across all locations showed multi-decadal oscillations in skeletal density and extension of nearly opposite phase (Fig. 3b), a pattern that was also found in specific regions including Dongsha Atoll, Yonge Reef, and the southern Red Sea (Supplemental Figs. S4-5).

We performed similar analyses on linear extension and skeletal density separately to diagnose which aspect of calcification drove the observed long-term declines. Linear extension across our full 204-year time series was best explained by a model with a periodic component of 21 years and core-specific intercepts and slopes. More than twice as many individual cores showed a significant decline in linear extension (21/148 or 14.2%) than a significant increase (8/148 or 5.4%). As with calcification, we found that in a pooled model fit with a single slope, linear extension significantly declined over time ($p < 0.001$). Superimposed on extension trends were multi-decadal oscillations (Fig. 3b). To place the strength of these oscillations in context, the magnitude of extension decline over the past century (0.068 cm yr^{-1}) was similar to the amplitude of the 21-year oscillation in the model fit (0.065 cm yr^{-1}) (Fig. 3b). Significant regional declines were apparent in linear extension datasets in both Red Sea locations and at Lizard Island, GBR across the entire time series (but with a nonsignificant positive trend from 1950 onward) (Table S1).

Previous field, laboratory, and modeling studies have suggested that density is the growth parameter most impacted by ocean acidification[30–32]. However, our results show that skeletal density remained more stable than extension during the industrial era (Fig. 3b; Supplemental Figs. S2-3). For instance, 18.9% (28/148) and 10.8% (16/148) of the individual cores displayed significant negative and positive trends in density, respectively, when fit by a model across the entire time series with core-specific slopes and intercepts and a periodic component of 17 years (Table 1). Examining density results by reef location revealed significant negative trends in three of the ten locations: Coral Sea ($p < 0.001$), Dongsha Atoll ($p < 0.001$), and Xiaoliuqiu ($p = 0.0334$), while a significant positive trend was found for the southern Red Sea ($p < 0.001$). Across the entire dataset, though, the overall decline in skeletal density was 1.7×10^{-4} g cm^{-3} yr^{-1}, whereas the decline in extension was 6.8×10^{-4} cm yr^{-2}. Given that calcification is the product of density and extension, the discrepancy in the magnitude of decline indicates that density contributed only 20% to the declining calcification observed in our study (Fig. 3b).

Our cores from the Great Barrier Reef and Coral Sea also provided an opportunity to evaluate the continuation of trends identified in previous studies. De'ath *et al.*[7] reported declining calcification over an approximately 15-year period (1990–2005) on the Great Barrier Reef based on 189 cores. They reported an initial increase in calcification (1900 to 1930) followed by steady growth until 1990, and then a sharp decline in linear extension and calcification after 1990, suggesting that a "tipping point" for coral growth had been reached. Our cores from the northern Great Barrier Reef and offshore in the Coral Sea were collected in 2017, providing an additional 12 years of growth to determine if the declining trend continued, albeit at a smaller number of sites than the original study. To facilitate comparison of our study to that of De'ath *et al.*[7], we reexamined our linear extension dataset post-1990. The GBR and adjacent Coral Sea location were among the least sensitive regions (*i.e.*, shallowest trends) across both the entire 204-year time series, as well as from 1990 onward. A negative trend in linear extension ($p = 0.031$, which would be non-significant when applying a Bonferroni correction) was identified at Lizard Island across the entire time series, but a non-significant positive trend was found when examining this same location post-1990 (Table 1). A similar (but opposite) phenomenon was found in the Coral Sea: a nonsignificant positive trend across the entire time series followed by a nonsignificant negative trend in the post-

1990 subset. Yonge Reef had non-significant positive trends during both time periods (full dataset and post-1990). Similarly, only Lizard Island had a significant negative calcification trend over the full 204-year time series ($p = 0.0056$), and no significant trend in calcification post-1990 (Table 1). The inconsistency in the trends from our study suggest that massive *Porites* corals on the Great Barrier Reef, at least at our coring sites, may not have crossed a climate-driven tipping point in calcification.

In some cases, differences between our findings and previous works may be due to multi-decadal variability. Our best-fitting models for each growth parameter all included periodic components ranging from 12 to 34 years. The substantial amplitude (Figs. 2-3) of these periodic components in our models points to real cycles in growth amidst larger interannual variability. The origin of these cycles could be related to El Niño Southern Oscillation (ENSO), the Pacific Decadal Oscillation (PDO), the related Interdecadal Pacific Oscillation (IPO)[33], or low-frequency coral responses to these or other climate cycles. These naturally-occurring fluctuations in the atmosphere and ocean impact temperature, precipitation, cloud cover, and ocean circulation. Most pronounced are anomalies in SST and changes in currents in the Pacific Ocean basin associated with the 2–7 year periodicity of ENSO. However, because corals in our study displayed longer period oscillations than ENSO—and some authors have argued that the IPO and PDO largely represent "reddened" or lower-frequency versions of ENSO[33,34]—we compared our observed coral-growth oscillations to the IPO index (Fig. 4; see Supplemental Fig. S6 for comparison to PDO). Despite being of similar periodicity, our observed growth oscillations did not align well with the IPO throughout much of the 20th century. However, we found some consistency between various reef locations in recent years (Fig. 4). In particular, troughs in the merged-location model fits for both the extension and calcification datasets generally correspond with two major El Niño events (and thus positive IPO anomalies) in 1997/1998 and 2015/2016 (Fig. 4). Additionally, we found that maximum annual SST improved model performance, but only in the post-1950 extension rate dataset (Supplemental Table S2). The periodic components in our models may broadly capture low-frequency or extended coral responses to acute thermal stress, even if the models predict smoother sinusoidal patterns than the observed time series. In other words, the general correspondence of troughs in growth rates with recent large El Niño events does not mean calcification declines precede El Niño, but rather that strong El Niño events may be contributing—potentially alongside other factors—to temporary growth declines that lead to troughs in the model fits.

Despite the overall correspondence of recent El Niño events with temporary coral growth reductions across the Indo-Pacific, regional variations exist both in terms of sensitivity and correspondence with longer-term growth trends. For example, even though calcification troughs aligned with recent El Niño events at both GBR locations, these cores lack consistent long-term calcification declines. Conversely, El Niño-driven growth declines at both Red Sea locations appear strong enough to contribute to long-term declines, consistent with a previous report[20]. The inclusion of multi-decadal variability in statistical models may also help explain differences among studies in the apparent existence of growth declines over only recent decades. Had multi-decadal variability not been accounted for, statistical models could indicate an apparent trend in short reconstructions and, potentially, apparent declines at the end of the time series. For example, in our dataset, mean annual temperature had a significant effect ($p < 0.001$) on extension rate in a post-1950 analysis without a periodic component; however, when a periodic component was added, temperature became a nonsignificant factor. Thus, these apparent declines in recent years at some locations may not necessarily represent a trend or a "tipping point," but rather one part of a fluctuation that is likely to swing back in the other direction over decadal timescales. However, if the magnitude of high-temperature anomalies continues to increase as El Niño events are superimposed onto greenhouse gas-driven warming, more and more regions may shift into declining coral calcification trends.

Our Indo-Pacific-wide collection of cores, spanning up to 204 years and including 6,336 total annual growth measurements, paints a unique picture of the sensitivity of corals to the chronic effects of climate change. Recently, a systematic review of laboratory experiments indicated future pH and temperature changes would lead to declines in coral calcification[2], and while our data seem to support this prediction globally, our results suggest these declines are region-specific and strongly modulated by multi-decadal variability. The drivers of the regional variability in long-term trends remains enigmatic, necessitating continued efforts in compiling growth rate time series from more cores across the tropics to increase the sample size and variance across human-disturbance and environmental gradients. We find that in at least a few cases, such as on the Great Barrier Reef, corals appear more tolerant of ocean warming and acidification than expected from laboratory experiments, potentially due to longer-term acclimation in the wild than can be adequately simulated with acute stressors in the lab. Other coral taxa present within the reef community may be less tolerant of environmental change than the massive-morphology and "stress-tolerant" life history strategy[35] of long-lived *Porites* colonies, so it is possible that Indo-Pacific reefs will experience a shift in their overall species composition favoring these massive and relatively slow-growing *Porites* colonies. *Porites* may therefore become an increasingly important contributor to reef formation. Yet, our findings show that even the stress-tolerant strategy of *Porites* is reaching its limits across the Indo-Pacific during recent El Niño events. As global warming accelerates[36] and today's ENSO-driven heat extremes become commonplace, *Porites* acclimation is unlikely to keep pace. Our results suggest that this will lead to Indo-Pacific-wide declines in *Porites* calcification. Novel approaches to measuring coral growth rates over time from repeated 3D photogrammetry will be essential for extending these findings to the broad array of coral growth morphologies[37,38].

Methods

1. Core collection

Porites coral cores were collected from June 2013 through July 2022 via pneumatic drills between 0.5 to 20-meter depths from the reef flat to the fore reef environments. Cores were then CT scanned with either a Siemens Volume Zoom Spiral CT scanner at Woods Hole Oceanographic Institution[25], a Skyscan 1176 Bruker-microCT scanner[39] at Harry Perkins Institute of Medical Research, General Electric BrightSpeed CT scanners[40] at King Abdullah University of Science and Technology (KAUST) and Adventist Health Castle in Kailua, Hawaiʻi, or the Philips Ingenuity CT scanner at Taiwan Instrument Research Institute depending on collection site location. In all cases, density was calibrated against coral skeleton cylinders of known mass/volume following DeCarlo *et al.*[25]. While the various CT scanners generate different resolution images, there is no effect on measured growth parameters because extension measurements are based on distance, which is calibrated for each scanner, and density is based on our external calibration.

2. Band Identification

Annual extension was measured from successive pairs of high- and low-density bands (Fig. S1) using CoralCT, a purpose-built program designed to analyze CT scans of coral skeletal cores[26]. The three-dimensionally scanned images of the coral skeletons were displayed in two dimensions as slabs cut digitally along the vertical growth axis to visualize the annual banding patterns. Within each slab, annual density bands were identified at multiple locations across the width and down the length of the slab. CoralCT then traces simulated corallites (the skeletal tubes constructed by each coral polyp) perpendicular to the identified growth bands in three dimensions to measure the annual extension, or upward growth of the coral, as well as the annual density of the bands[26].

3. Cross-dating and quality control

Following growth band measurements of all coral cores, the Dendrochronology Program Library in R (dplR) package was used to cross-date the cores in order to evaluate correlations among the growth rate time series. Developed for dendrochronology, the dplR package assesses variability in ring-width, or linear extension in our case, then quantifies any common signals in growth rate variations[41]. Cores that lack this signal may indicate an error in the way the growth bands were identified, and these cores were reassessed with particular focus on any “marker years” that are consistently high- or low-growth years among correlated cores. Cross-dating was mainly used to reduce the uncertainty in defining the first calendar year of each core because density bands do not necessarily represent January-December and depending on the collection month, there can be observer interpretation of which calendar year should be assigned to the top-most band[26]. An adjustment of one calendar year to the first band was made if it met the following criteria: (i) the change was plausible based on the appearance of the top of the core and the collection month, (ii) the assigned year was not later than the collection year, and (iii) the interseries correlation was improved. The interseries correlation is the correlation between an individual core's detrended times series and the "master chronology", which is the mean of the detrended time series from all cores being considered (*i.e.*, per reef location). We used pre-whitening in the dplR toolbox, meaning that the interseries correlation represents year-to-year variability across time series, but low-frequency (multiple-year periodicity) is removed while calculating interseries correlations. Therefore, interseries correlations indicate the high-frequency (year-to-year) correlation across growth time series, but do not capture low-frequency (multi-annual) variability common among cores. In other words, interseries correlations are a tool to help ensure time series alignment, but are not a representation of the total common signal in a set of cores. Supplemental Table S2 shows the final interseries correlations for all reef locations.

As part of this process, we also excluded cores for which we were not entirely confident in the banding pattern. Initially, we attempted to interpret and measure growth parameters on all cores. During the crossdating step, which involves revisiting the image analysis of each core, we made a final assessment of whether there was reasonable confidence in the banding pattern for each core, and excluded cores for which there were multiple instances of ambiguity in whether density variations represented annual bands (*i.e.*, overcounting due to sub-annual density variations or undercounting due to weak banding patterns). The interseries correlations from crossdating contributed to identifying cores to focus on during this step, in that a low correlation to the master chronology suggests possible miscounting of bands. However, we did not exclude cores merely for a low correlation to the master chronology, but rather based on confidence in the ability to measure growth parameters accurately. A total of 19 cores were excluded based on unclear banding. Final numbers of replicates per reef location were as follows: Coral Sea (*n* = 28), Dongsha Atoll, South China Sea (*n* = 15), Green Island, Taiwan (*n* = 8), Lizard Island, Great Barrier Reef (*n* = 15), Oahu, Hawai‘i (*n* = 10), central Red Sea (*n* = 17), southern Red Sea (*n* = 40), Solomon Islands (*n* = 3), Xiaoliuqiu, Taiwan (*n* = 2); Yonge Reef, Great Barrier Reef (*n* = 10).

4. Statistical analyses

After cross-dating, 148 *Porites* cores were deemed suitable for statistical analysis. We initially conducted three versions of the statistical analyses: (1) linear extension across the entire time series, (2) linear extension from 1950 onward, and (3) density across the entire time series. These analyses were conducted in RStudio version 2023.09.1+494 following methods modified from Castillo *et al.*[16]. A series of linear models were created to test for temporal trends of *Porites* coral growth parameters, as well as relationships between growth parameters and several environmental factors. Specifically, linear extension and density were modeled as functions of SST (annual mean and max) and atmospheric carbon dioxide (CO_2) (Supplemental Tables S3-4). Temperature data were obtained from the HadISST dataset. CO_2 data were obtained from the Scripps CO_2 program, which combines direct measurements on Mauna Loa (from 1958 onwards) and ice-core data from 1815 to 1957. We recognize that coral reefs can have distinct pH environments from the surrounding open ocean and that they do not necessarily track atmospheric CO_2, especially on sub-annual timescales. Nevertheless, there are not sufficient *in situ* data from all reef locations, especially going back multiple decades, and atmospheric CO_2 should impose similar acidification trends across these reefs even if they have different mean pH and substantial diurnal to seasonality variability superimposed on the long-term trend. We did not explicitly test the effect of depth for two reasons. First, only nine cores, all from the Coral Sea, were collected deeper than 10 meters, leaving a narrow test bed of depths to evaluate. Second, while depth is well known to affect mean growth rates, there is little evidence that it affects variability across our sampling range. Our models included core-specific y-intercepts, so differences in mean growth rates do not contribute to any of the conclusions regarding growth rate trends. Additionally, initial models that did include depth as a factor modulating growth rate trends did not produce significant effects of depth, so subsequent models excluded depth as a factor.

Location-specific annual average and maximum SST time series were used in various models for each reef location, while a single annual CO_2 time series was assigned across all locations. To test the effects of direct human impact on coral growth, some models included a site-specific “gravity” value, which is a metric that relates population size of nearby communities inversely with travel time to coral reefs[27]. Acting as a continuous variable, gravity values correlate positively with human impact (Supplemental Table S2). We used Akaike information criterion (AIC) for model selection because it quantifies the model fit to the data while penalizing for additional explanatory variables that by definition can only improve the model correlation to the data. Thus, AIC helps to prevent overfitting via the inclusion of variables with near-negligible model improvement. The absolute value of AIC is generally not meaningful, but rather differences in AIC among models applied to the same dataset indicate the best model as the lowest AIC value. However, differences in AIC of less than 2 are generally considered not to be a meaningful difference in model performance. Each growth parameter (extension, density, calcification) was modeled separately. Following Castillo *et al.*[16], we considered six approaches to modeling cores and reef locations: (1)

all data share a common slope and intercept, (2) slopes and intercepts vary by reef location, (3) intercepts vary by individual core while slopes vary by reef location, (4) both slopes and intercepts vary by individual core, (5) a singular slope applies to the entire dataset but intercepts vary by individual core, and (6) no slope ($m = 0$) but intercepts vary by individual core.

The first set of linear models examined coral growth as a function of time and several environmental conditions (mean annual SST, maximum annual SST, detrended SST, and atmospheric CO_2) with location-specific slopes and core-specific intercepts. In other words, all cores from one location would have the same slope for each growth parameter, but each core would have its own intercept (to account for differences in mean growth rate). Here, slope means the sensitivity to an explanatory variable, whether it be time or an environmental factor that varies with time. Model parameters and AIC values can be found in Supplemental Table S3. Time and atmospheric CO_2 were highly correlated ($r > 0.9$), which precluded us from definitively separating time and CO_2 in our analysis. We continued with time as the explanatory variable, noting that CO_2-driven ocean acidification is a potential mechanism for the temporal trends observed here. Both extension and density across the entire 204-year time series were best fit by time, but this was not the case for the post-1950 subset of the extension data, in which annual mean or maximum SST improved model performance (relative to a model with only a linear trend over time).

These same models were then repeated, but including gravity as a modulating factor of slopes (Supplemental Table S4). In other words, reef locations with greater gravity values could have steeper or shallower slopes than locations with lesser gravity values. Overall, the inclusion of the gravity factor did not improve AIC values and the models achieved nearly the same rankings as in the set of models without gravity: that is, extension and density across the full dataset were best fit to just time, and the inclusion of annual temperatures improved the post-1950 extension model fit.

Because time appeared to be the overarching explanatory variable amongst the growth parameters, we created a new set of linear models exploring the impacts of time on coral growth (Supplemental Table S5), with the six possible ways of treating slopes and intercepts by location and core. In addition to the three datasets we used previously (extension across the entire time series, density across the entire time series, and extension post-1950), we added an additional subset of the extension data (1990 onward) to assess recent trends in linear extension and to compare with the results of De'ath *et al.* (2009). Following this, we removed the models with (1) a common intercept and slope, and (2) with slopes and intercepts varying by reef location, as neither were found to best fit the datasets. We continued with the remaining four models.

Next, we tested whether the addition of autocorrelation structures and periodic components improved fits in generalized least squares (GLS) models (Supplementary Table S6). Autocorrelation means that each datapoint is not independent of its neighbors, and if so, the effective number of degrees of freedom would be reduced. Autocorrelation was apparent on short (1-year) and longer (17–22-year) timescales based on partial autocorrelation plots. To address the multidecadal cyclicity, we added a periodic component to each model through an iterative process of running the model with sines and cosines of various periods (*i.e.*, 10 years, 11 years, etc.), and then we chose the period (T) with the lowest AIC. Additionally, we fit each the models with an Autoregressive Moving Average (ARMA) component to address any remaining shorter-term (*i.e.*, year-to-year) autocorrelation in the datasets. The addition of both the periodic component and first-order autocorrelation structure improved the model fit. For these analyses, we also created models analyzing calcification (the product of extension and density). No periodic component was included when modeling the extension dataset from 1990 onward due to the short timeframe, so it is not included in Supplemental Table S6.

Table 1 summarizes the significance of trends across a range of models. The best models (lowest AIC) for both extension and density included core-specific intercepts and core-specific trends (Supplemental Table S6). For these models, we report the number of cores that had significant (based on $p < 0.05$) positive and negative trends (Table 1). While models that included location-specific trends had higher AICs, the results of significant trends per location are easier to interpret than core-specific trends, and thus are also reported in Table 1. Finally, single trends fit to all cores provides a broadbrush view of whether each growth parameter overall increased or decreased over time (Table 1), even though the model fits were not as good as trends specific to cores or location (Supplemental Table S6). We also tested an additional subset of our linear extension dataset (1990-2017 in the Great Barrier Reef region) for comparison to De'ath *et al.*[7] (Table 1).

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Table 1. *Temporal trends from final models in all five time periods / datasets examined. The first set of models show location-specific slopes, with + and – indicating the sign of the growth parameter trend and the significance of the trend ($p < 0.05$ is bolded). Next are core-specific models, which are summarized as the number of cores (out of 148) with significant positive or negative growth parameter trends. Finally, the last row shows the results of a single model fit to all cores and the sign (+ or -) of the growth parameter trend and its significance are shown.*

Figure 1. Map of coral core collection sites. *Panel* ***a*** *shows the global distribution of sites and all other panels show regions. Colored symbols indicate core collection sites. Land and submerged shallow reefs are in black and* n *values represent the number of cross-dated cores in the final dataset.*

Figure 2. Coral calcification rates ($g\ cm^{-2}\ yr^{-1}$) over time by reef location. *Each panel represents a different reef location and is colored by region as defined in Figure 1. Thin black lines show individual core time series. Colored curves show model fits with 95% confidence intervals of the curves shown by shading.*

Figure 3. Relationship between linear extension and skeletal density anomalies. a, *skeletal density anomalies and linear extension anomalies for all cores. The black line shows a reduced major axis regression fit between these parameters and the gray shading shows 95% confidence interval of the fit.* ***b****, model fits with both monotonic trends and 21-yr periodic components applied to the full datasets (all 148 cores) for linear extension (grey) and density (black).*

Figure 4. Annual extension rate model fits plotted against the Interdecadal Pacific Oscillation (IPO) index. *Model fits for each of the ten reef locations are plotted in colors corresponding to Figure 1, with the global model fit plotted in black. The IPO index is plotted as red and blue shading, which represent positive and negative index values, respectively. Both the annual (unfiltered) and 13-yr low-pass filtered versions of the IPO*[33] *are displayed. Two major El Niño events are highlighted (1997 and 2015) and approximately correspond with the two most recent troughs in the global extension and calcification model fits.*