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Modeling intra-annual variation in coral extension rate using multiproxy geochemical records from Pacific corals

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Abstract: The relationship between coral growth and environmental parameters is not straightforward, and few studies have explored intra-annual changes in extension rate. Variations in the magnitude and timing of intra-annual extension could be influenced by various environmental parameters such as sea surface temperature (SST), light and nutrient availability, turbidity or salinity stress, as well as by inter-annual climate variations such as the El Niño-Southern Oscillation (ENSO). In this study we use SST proxy data from *Porites spp.* corals to model intra-annual growth using an iterative numerical model comparing growth and temperature sine functions to measured Sr/Ca data to find the best combination of intra-annual variation in both variables. This approach converts sampling distance within cores into time, providing a framework that allows us to quantify how extension rate varies both within and between years. The model was applied to coral records spanning both the tropical Pacific (Australia to the Galapagos) and the past 400 years (Little Ice Age to present). To validate model results, modern coral data are compared with observational temperature and ENSO records. In this project, we focused on testing the idea that intra-annual SST is a dominant control on the timing of intra-annual coral extension. Results indicate that maximum coral extension in the West Pacific typically occurs during the periods of warmest SST, and in the East Pacific dominantly in periods of cooler SST. These records also indicate that multiple exogenous factors influence skeletal extension in these dynamic equatorial settings, particularly in the context of ENSO. Growth recovered from these records offers a picture of how extension rate and environment interact in the Equatorial Pacific. This modeling approach has the potential to improve seasonally resolved coral records of climate, and for understanding the relationship between coral calcification and climate change by comparing changes in intra-annual extension patterns over time.

Modeling intra-annual variation in coral extension rate using multiproxy geochemical records from
Pacific corals

By

Jessica (Jessie) McCraw,
B.S. University of Arizona, 2018

Thesis

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Sciences

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1 Introduction

Corals are charismatic and well-studied organisms, but as marine environments change due to anthropogenic climate warming, the habitat and health of coral reefs are increasingly jeopardized. Developing a deeper understanding of the environmental variables to which coral growth is most sensitive will serve to help them in the future. Useful information in this context is instrumental climate data tied to records of coral skeletal growth to study the response of corals to specific environmental changes over the year. In addition, records of past conditions archived in the skeletons of corals offer significant insight into the history of Earth's climate system. Interpretation of these data is more accurate if constraints can be placed on when during the year the corals grow their skeletons. In both cases then, knowledge of intra-annual variation in coral growth is a key piece of information. However, seasonal changes in coral growth rate are infrequently studied in comparison to interannual records, despite their relevance to both climate reconstruction and coral (paleo)biology. The lack of high-resolution geochemical proxy data from corals, and the difficulty in studying their intra-annual growth metrics, as well as the reef sensitivity to changes in climate, have made the interpretation of seasonal growth difficult. A seasonal perspective of growth and climate allows us to make more specific and well-informed statements about climate variability in the past and help inform us of where Earth's climate might be heading and what these key organism's ecological responses to that change might be.

Here, we examine sub-annual variation in extension rate using high-resolution geochemical data from coral skeletons as a paleotemperature proxy in combination with a numerical model that reconstructs intra-annual patterns in the timing of calcification from accretionary biogenic records (Judd et al., 2018). Variation in extension rate within individual years of growth can then be compared with sea surface temperature (SST) data to determine specifically how temperature and related variables affect coral growth. The objective of this study is to validate the application of this model to the useful climate

archives of corals, model patterns of intra-annual extension rates, and determine what the potential seasonal environmental parameters are that control intra-annual growth. This project focuses dominantly on the potential for intra-annual SST to control intra-annual coral extension. The model is validated with modern coral and instrumental records from the Great Barrier Reef (GBR) in Australia and the northern Galapagos Islands (Figure 1), including modern/historical records of the El Niño-Southern Oscillation (ENSO), and then applied to a subfossil record from the central Galapagos Islands.

2 Background

2.1 *Metrics of Coral Growth*

Physiological variations in calcification rates reflect other environmental signals affecting corals (Lough and Barnes, 1997). Correlative growth increment analysis has become the gold standard for tree-ring studies to describe the relationship between environmental and biological/ecological variables. These model organisms bear a strong resemblance to the growth increments in a wide variety of marine species, including massive corals. By constraining a chronology with the known year of sample collection and counting annual bands back in time using the guidance of the thickness of annual growth bands, brightness of density band x-rays, luminosity data, and inter-annual isotope or trace element signatures, coral records and the archives of climate contained therein can be correlated across space and time (DeLong et al., 2014).

Intra-colony variability in extension rates has been well documented when cores are sampled from different positions within the colony (Lough and Barnes, 2000; Lough and Cooper, 2011) and rates can vary significantly due to the direction of accretion in the vertical direction towards light (i.e. extension rates are lower on the sides of coral heads as opposed to the surface parallel with the ocean surface). There are also age effects wherein younger corals extend less in younger years than older corals (Lough, 2008). Inter-colony variability within local reefs can have high variability as a function of the depth of the coral,

subjection to additional stressors such as wave action, sand abrasion, and position within the reef framework (Felis et al., 2003; Al-Rousan, 2012; Lough and Cooper, 2011).

Both intra-colony and inter-colony examinations of the variability of climate signals preserved in coral skeletons show that there can be large and unexplainable differences, up to 2°C difference in the context of temperature reconstructions from geochemical proxies (DeLong et al., 2007; Sayani et al., 2019). As these studies come from cores taken from the same coral head, and from corals within or across a small region, such as one atoll, the distinctions cannot be attributed to responses to climate that all corals experience so must be explained by vital effects. Even in tank growth, climate-controlled studies, corals showed inter- and intra-colony variability in Sr/Ca and $\delta^{18}\text{O}$, likely as a function of varying skeletal growth rates and biological effects (Suzuki et al., 2005; Felis et al., 2003). The variability in vital effects within such small areas should be the focus of additional study. In contrast, many corals from the same reef or atoll show remarkable agreement between environmental proxies between cores (Stephans et al., 2004; DeLong et al., 2007). Additionally, when cross-dating coral cores using methodologies taken from dendrochronology, by correlating conspicuous annual bands and using additional constraints from both the geochemical and physiological/morphological parameters, these “stacked” records demonstrate very high reproducibility that shows that both intra- and inter-colony corals are recording the same signal and responding to the same environmental variations (DeLong et al., 2007; Sayani et al., 2019; Stephans et al., 2004). Where replication is available, cross-dating coral growth bands can provide annually resolved, environmentally sensitive chronologies (Black et al., 2019; Carilli et al., 2010; DeLong et al., 2014; DeLong et al., 2007).

2.1.1 Density bands

Total skeletal calcification in corals consists of trade-offs in both linear extension and skeletal density. Corals secrete a high-density band and a low-density band that together comprise one year of

coral growth (Knutson et al., 1972), but the exact environmental triggers for the seasonal change in skeletal density within bands are somewhat unclear. In-depth studies of controls on the timing of the changes in the density band formation are limited by the annual resolution of density bands, and the estimates of linear extension rate from this are solely derived from the linear thickness of annual density band pairs (Wellington and Glynn, 1983). Density bands can appear faint or irregular in some species of coral, *Porites* spp. in particular, or in certain localities (Glynn and Wellington, 1983), making some corals more difficult than others to examine for high resolution or seasonal calcification measurements. Lough and Barnes (1990) determined from a survey of tropical Pacific corals that most low-density bands form in cold SST and high density bands in the summer; the exceptions were mostly *Porites* spp. (such as a study of Red Sea *Porites* corals suggesting that high density bands form in the winter with low SST and low light intensity (Klein and Loya, 1991)). The Red Sea is an atypical location for corals (Loya & Slobodkin, 1971), which mostly grow in the Caribbean and equatorial Indo-Pacific coral triangle, the Red Sea thus representing the northern latitudinal extreme for coral communities.

The contradictions in timing of density band formation between these northern *Porites* and others is described by a review on coral density banding by Highsmith (1979) and suggests that the controls on the timing of density band formation may vary along a latitudinal gradient (Highsmith, 1979). The author described an “equatorial” group, which demonstrate high-density bands forming during periods of high SST (and less concretely, low light availability) and the opposite for the low-density bands (Macintyre & Smith, 1974; Weber et al., 1975b). A “transitional” group is comprised of locations in the south Pacific where high density bands form during periods of warm SST, but form at least partially during the coldest months of the year and when solar radiation is low or moderate but rising rapidly. The pattern common to all southern transitional localities seems to be that low density bands form during periods in which light and temperature are both declining. The author also described a “high latitude” group, in which high

density bands form during periods of probable low light availability and low SST, and low-density bands form during periods of high light availability and high SST (such as in Klein and Loya, 1991). These studies together suggest that the dominant factor affecting density is external and related to climate and environment, but perhaps not dominantly controlled by SST.

Changes in calcification rate and the timing of density band formation have been shown to correlate with seasonal changes in light intensity as a function of cloud cover for corals in the Panamanian Eastern Pacific (Wellington and Glynn, 1983), Hawaii (Schneider and Smith, 1982) and the Indian Ocean (Smith, 1981). In most studies, light intensity is measured from clouds via precipitation, visual cloud assessments or total days of sunlight (Buddemeier and Kinzie, 1975 in Hawaii; Buddemeier, 1974 on Christmas Island; Didge and Thompson, 1974 in Bermuda).

Upwelling sites in the eastern Pacific have high nutrient productivity and typically variable intra-annual SST. Comparisons of growth metrics between upwelling and non-upwelling sites suggest that there is an increase in calcification rate at the upwelling site, concurrent with the low-density band formation at low SST, high productivity and high light availability (Wellington and Glynn, 1983). Results of their study suggest that light and nutrients are important contributors to the timing of the seasonal change in density banding, more so than SST (Wellington and Glynn, 1983).

2.1.2 *Linear Extension*

Extension rate is the dominant driver of total skeletal calcification in massive *Porites* spp., accounting for up to ~70% of total skeletal calcification (Barnes and Lough, 1993). Linear extension is also of greater importance and ecological significance than density because of the relevance to acquisition of substratum, competition with other corals for overgrowth/shading, and resistance to predation or burial (Highsmith, 1979). Extension rate has historically been measured as the linear thickness of annual density bands, and as such there are fewer examples of studies of environmental drivers of extension rate

variability in the literature. Linear extension has been shown to vary as a function of sea surface temperature and total solar irradiance, decreasing with increasing latitude (Wellington, 1996; Lough and Barnes, 2000; Smith et al., 2007; Storz and Gischler, 2011). Increases in SST of $\sim 1^\circ\text{C}$ correspond to increases in calcification rate of 3-5% (Lough and Barnes, 2000; Bessat and Buigues, 2001). A study of eastern Pacific *Pavona* corals showed that maximum calcification tends to occur between 23.7° and 28.5°C , and that extreme highs over 30°C and lows less than 18°C impede calcification (Wellington and Glynn, 1983). Higher extension rates in the summer are due in part to warmer SST, but also to increased solar irradiance (Lough and Barnes, 1992; Grigg, 2006). Many studies have shown a positive correlation between SST and coral extension rate in *Porites* and *Pavona* spp. from measured band thicknesses (Glynn et al., 1979; Dunbar et al., 1994). This is substantiated by a demonstrated weak inverse correlation between annual $\delta^{18}\text{O}$ and extension rate (Dunbar et al., 1994). Research has shown disruption of extension at low SST (such as at Galapagos, i.e. Dunbar et al., 1994), as well as anomalous high-density bands or growth cessations under warm thermal stress.

Another environmental factor potentially driving coral growth is light availability. At Curacao, growth rates correlate with light intensity determined by cloud cover rather than by day length (Bak, 1974). The relationship between SST, irradiance, and extension is complicated however, as shown by a study of Galapagos corals where most of the annual extension occurred during the warm season but total calcification rates were higher in a cool upwelling site (Wellington and Glynn, 1983). Galapagos *Porites* spp. living in cooler water with seasonal upwelling appear to exhibit higher linear extension rates than those in climatically stable environments with low levels of SST variability (Wellington and Glynn, 1983). Productivity in upwelling zones may contribute to the increased thickness of the low-density bands and thus the increased extension rate as compared to non-upwelling sites. *Pavona* in the Galapagos benefit from the reduced Equatorial Undercurrent (EUC) upwelling as a result of El Niño events (and the reduced

cloud cover and increased light), because the sustained upwelling of 17°-18° C water can cause low thermal stress and reduce the extension rate (Glynn and Wellington, 1983). Extension rate is suggested to not be dependent on zooxanthellate photosynthesis, but total calcification rate is (Barnes and Crossland, 1980). Extension rates decline with depth because of reduced light availability for photosynthesis for the zooxanthellae (Highsmith, 1979).

2.2 Coral growth as a record of the environment: ENSO and anthropogenic warming

With the understanding that coral growth is dominantly controlled by seasonal variations in SST and irradiance, the effects of both sustained thermal stress and anomalous thermal events on coral extension require further study. Numerous studies have found an increase in extension with increasing SST (see Section 2.1.2 above), but coral extension rate plateaus at a species-specific upper temperature threshold (Lough and Cooper, 2011). Long records of coral growth using spectral analysis have found peaks in extension variability coincident with the ENSO scale of ~4-7 years, with conflicting results about the effects of ENSO thermal anomalies on extension (Evangelista, 2007). A conceptual energy budget suggests that a stressed coral would have a higher respiration rate and significantly reduce its energy investment in tissue growth (Edmunds and Davies, 1986), in agreement with studies that found reductions in extension following thermal anomalies such as ENSO and bleaching events (Glynn, 1994; Suzuki et al., 2003; Lough and Cooper, 2011; Hetzinger et al., 2016; Zamani et al., 2016). Thermal stress from ENSO can lead to nondeposition, or anomalously weak high-density stress bands (Glynn, Wellington & Birkland, 1979). Contradictory studies suggest that a positive thermal anomaly in SST (reconstructed from coral SST geochemical proxies) leads to increased extension, particularly in the context of ENSO (Bessat and Buigues 2001; Evangelista et al. 2007). Reed et al. (2019) find no consistent coral growth anomalies in response to regional ENSO events, though extension rate was calculated on annual time scales, and thus is likely less sensitive to sub-annual ENSO anomalies, underestimating calcification anomalies. Whether or not warm temperature anomalies result in faster extension is likely species- and

latitude-dependent in terms of controls on the thermal threshold for growth. Therefore, studies of extension over long time spans can provide insights about how particular populations are likely to respond to future warming and which are most vulnerable.

2.3 *El Niño-Southern Oscillation (ENSO) across the Pacific*

2.3.1 *Northern Australia and the GBR*

In Northern Australia, ENSO manifests primarily through precipitation anomalies and minor SST anomalies. In ENSO-neutral years, precipitation over the GBR peaks in February with river output to the coastal reefs peaking in March (Reed et al. 2019). The weakening of the trade winds results in the development of an El Niño event, which changes circulation patterns across the equator, resulting in reduced precipitation and river discharge over the GBR. Leading up to an El Niño, July-Nov. demonstrate anomalously cool SST. El Niño peaks in December in the GBR, and SSTs immediately afterward are high and continue to be so through the following austral winter. The opposite of this SST pattern is true for La Niña, though SST anomalies associated with La Niña tend to be less strong than those of El Niño. The strengthening of neutral convection patterns in a La Niña results in higher precipitation and increases the number of tropical storms, increasing seasonal river output to the GBR. The very minor SST anomalies associated with ENSO likely do not cause significant changes in the timing of maximum coral extension rates. Rather, the precipitation anomalies associated with ENSO may contribute to salinity and turbidity stress due to river output to nearshore corals, leading to altered timing of extension rates. Due to the small SST fluctuations in the Northern GBR as a function of ENSO, previous work (Reed et al. 2019) has shown that luminescence and $\delta^{18}\text{O}$ analyses tracking precipitation anomalies are a better proxy for identifying ENSO events. Density was anomalously high during El Niño (when there was low precipitation) and low during La Niña (with increased precipitation), but extension did not inversely covary with these density anomalies (Reed et al., 2019). Density changes in El Niño years could be weak

stress bands, but without the high resolution in extension rate anomalies, we likely underestimate calcification anomalies in response to ENSO.

2.3.2 *Eastern Pacific and the Galapagos Islands*

In the Eastern Tropical Pacific, ENSO manifests as dramatic intra-annual SST anomalies, and the Galapagos Islands are often considered to be located at the epicenter of ENSO activity. ENSO-neutral years have a warm and wet season (Jan.-May) and a cool, dry season (Jun.-Dec.); this seasonality is a function of the position of the Intertropical Convergence Zone (ITCZ) affecting atmospheric convection patterns. Weakening of the trade winds leads to El Niño events, which result in reduced convection, reduced upwelling of the EUC and the deepening of the thermocline, causing strong positive SST anomalies particularly during the cool season (Kessler 2006). The increase in precipitation during El Niño leads to increased cloud cover and reduced light during the otherwise cool and dry season (Trueman & D'Ozouville 2010). La Niña results in particularly arid conditions driven by reduced SST, increased trade winds and increased subsidence (Trueman & D'Ozouville 2010).

Pavona spp. corals in the Galapagos have been shown to benefit from the reduced EUC upwelling as a result of El Niño events because the sustained upwelling of 17-18° C water can cause low thermal stress and reduce the extension rate (Glynn and Wellington, 1983). However, it has also been shown that the increased productivity associated with upwelling zones may lead to increases in annual extension rates, as compared with non-upwelling localities or periods of reduced upwelling (Wellington and Glynn, 1983) such that neutral or La Niña years have higher extension rates. Thermal stress from ENSO (positive anomalies under El Niño conditions, or cold anomalies from La Niña) can lead to nondeposition, or anomalous weak high-density stress bands, and low extension rates (Glynn et al., 1979). Galapagos corals are not generally subject to high volumes of river output, so precipitation anomalies associated with ENSO likely play only a minor role in their effects on the timing of maximum extension. The seasonal

change in light intensity associated with increased cloud cover has been shown to correspond to changes in overall calcification rate and the timing of density band formation (Wellington and Glynn, 1983; Schneider and Smith, 1982; Smith, 1981), which as ENSO affects precipitation patterns and thus cloud cover, could affect the timing of extension via variability in light intensity.

3 Materials and Methods

3.1 *The Growth Model*

We use the numerical model of Judd et al. (2018) to investigate intra-annual variation in coral extension as related to temperature. Input requires serially sampled temperature proxy data, in this case Sr/Ca measurements of coral subsamples, and their associated depth (distance) within the coral core. The chronology of coral bands, in calendar years, is determined based on Sr/Ca minima (recording local annual SST maxima), substantiated by the annual growth bands in the coral, and additionally constrained by the radiometric age-dating (e.g., U/Th dating) and time of collection of the coral. The model assumes that intra-annual SST variation at the site of calcification is sinusoidal and that variation in extension can be approximated by a clipped and skewed sinusoid. Best-fit temperature and growth sinusoids for each year of extension are determined by fixing the periodicity of each curve to 365 days, assigning a date (Julian day) to the annual maximum temperature value (minimum Sr/Ca measurement), and iteratively varying the other parameters to generate sinusoids that best reproduce the observed geochemical data. This approach converts sample depth within the core into the time domain (Judd et al. 2018). Model runs span each year of the core for the entire record of sampled coral extension, resulting in a time series of yearly growth profiles measured in daily modeled extension rate. The growth model relies on an assumption of sinusoidal variation in annual temperature (Judd et al., 2018), so the local climatology must be validated using instrumental or gridded satellite SST data for each study area (section 3.4 below).

3.2 *Assessment of Growth Patterns*

The model output is an extension rate in millimeters/day throughout each year of a given record. We use these to construct an average annual growth profile, describing both the amount and timing of

changes in extension rate throughout the year. Extension rate is normalized to the total annual extension such that each day can be measured in percent of annual extension, thus making patterns of intra-annual growth comparable among years and coral records. A constant normalized daily extension rate throughout the year would be 0.0027% of annual extension per day. The month of maximum growth (MMG) within every modeled year of each record is extracted and used to examine changes in the timing of maximum extension rate over the duration of the record. Estimates of annual linear extension derived from the sampled distance between each adjacent pair of Sr/Ca minima (SST maxima) are compared with inferences of annual extension rate from the model to evaluate its ability to reproduce observed distances.

We identified the length of the growing period using changes in the inflection of modeled extension rate sines. Using first differences between each day of intra-annual modeled coral extension rate sine curves, the calendar day of the year in which extension rates begin increasing from one point to the next marks the day of the start of the growing period, while the point where modeled extension rates begin to decrease monotonically from one day to the next marks the end of the growing period. The total length of the growing period is the total number of days of the year in which daily extension rates are increasing. The rest of the year are days in which extension is either decreasing or daily extension rate is modeled as a growth cessation.

To characterize the mean annual extension profiles for each record, we subtracted the minimum from the maximum daily extension rate to yield the annual range in extension rate and calculated the mean annual extension rate from these averaged growth profiles for each record. All these metrics were computed over the entirety of each coral record and also over subsets of the coral records partitioned by ENSO phase (see Section 3.3 below).

3.3 Assessment of ENSO phase

We evaluated the seasonal SST pattern of ENSO years, as defined by the Oceanographic Niño Index (ONI) defined over the Niño 3.4 region (Figure 1). Years in which December-January-February (DJF)

thermal anomalies of $\pm 0.5^\circ\text{C}$ above the climatological mean were classified as El Niño, La Niña, or “neutral state” calendar years, as per conventional NOAA and coral climatology practices. Niño 3.4 was chosen because it exhibits the initial dynamic thermal anomalies associated with the beginning of an ENSO event as it migrates across the Equatorial Pacific. This allows us to categorize ENSO year for both the West Pacific and the East Pacific as a function of the timing of the main anomaly. Years of coral records are partitioned by ENSO phase using the ONI from NOAA which has records and classifications of ENSO events dating back to the early 20th century. Using this index, we categorized years of coral extension as either El Niño, La Niña, or neutral events.

3.4 Coral records and site climatology

3.4.1 Great Barrier Reef, Northern Australia

For the purpose of model validation, we first examine published Sr/Ca SST proxy records from two short, modern cores (NOM and CLK) from 2 colonies of *Porites* from the Great Barrier Reef off the coast of Northern Australia (Figure 1; Reed et al. 2019). CLK is located further north than NOM, and closer to land (4 km offshore) compared to NOM (15 km offshore), and both corals were collected from similar water depths of 2-5 m (Reed et al. 2019). The GBR records come from a relatively climatically consistent region in terms of SST variability (Figure 2) and span from 1991-2007 (NOM) and 1993-2007 (CLK), recent enough to employ good satellite-based coverage for examination of SST patterns, making them appropriate records to test the growth model on corals. Daily optimum interpolation sea surface temperature (OISST) data from near the site of coral collection (11.75-12.25°N, 143.25-143.5°E) describe annual SST variability at this site.

3.4.2 Wolf Island, Northern Galapagos Archipelago

A long, modern (1940-2010) coral Sr/Ca record (referred to as W3 in this study, Jimenez et al. 2018) from Shark Bay on the northeastern side of Wolf Island in the northern Galapagos serves as another model validation site where, in this case, corals experience strong interannual SST variability due to

ENSO anomalies. This record is both old enough and long enough to provide clear evidence of anthropogenic SST warming (Jimenez et al. 2018) and affords the opportunity to explore the response of coral extension rates to both episodic and long-term climate change. Daily OISST data taken from 1.25-1.75°N, 91.5-92° W describe annual variation in SST.

3.4.3 *Urvina Bay, Isabella Island, Central Galapagos Archipelago*

To explore the ability of the growth model to quantify intra-annual extension in subfossil corals, we examined a record of Sr/Ca ratios from a core from an uplifted reef of *Porites lobata* from Urvina Bay in the central platform of the Galapagos. This site was chosen due to its unique climatology, where seasonal upwelling of cold water from the Equatorial Undercurrent (EUC) drives associated shifts in winter SST (Kessler 2006). Isabella is 2-3°C colder than the other islands in the archipelago, so has sparser corals than the others. In addition, as above at Wolf Island, the site is strongly affected by ENSO SST anomalies. U/Th radiometric dating give an age of the coral record of ~1571-1626 CE, during the Little Ice Age, an interval during which Northern Hemisphere temperatures were low yet little is known about conditions in the equatorial Pacific (Rustic et al. 2015; Hendy et al. 2002). Modern daily OISST (0.25-0.75°S, 91-91.5°W) from Urvina Bay show the modern annual distribution of SST at this site (Figure 2).

4 Results

4.1 Test of Sinusoidality of OISST Variability from Coral Localities

When a best fit sine function is applied to the OISST data in the GBR, the mean R^2 value for the entire 1982-2018 record is 0.89, suggesting regularly sinusoidal annual variation in temperature at this site (Figure 2). Maximum SSTs occur in December-January, and minimum SSTs in July-August. Little deviation from this sinusoidal pattern occurs during either ENSO phase, suggesting minimal impacts of ENSO dynamics on the sinusoidal distribution of temperatures in the GBR. Our examination of Optimum Interpolated Sea Surface Temperature (OISST) since 1982 show that ENSO-neutral years have the most seasonal annual SST, and El Niño phase years have the least sinusoidal distribution (Figure 2). El Niño

increases both the mean annual maximum and minimum SST from the neutral state, and La Niña phases remain similar to neutral years in the annual SST distribution. The GBR has the highest SST sinusoidality of all examined sites in this study (Figure 2).

Daily OISST data from Wolf Island show sinusoidal annual SST variation (Figure 2). The R^2 of a best fit sine function fit to the measured data is 0.537 for the entire (1982-2019) OISST record, confirming that overall the Northern Galapagos region has more irregular annual temperature variability than the GBR. When we examine the OISST record as a function of ENSO phases, El Niño years have the best fit to a sine function with an R^2 of 0.63, followed by La Niña years ($R^2=0.496$), while neutral years SST's have the poorest sine fit ($R^2=0.481$).

Daily OISST from Urvina Bay demonstrates annual SST variability that is more sinusoidal than Wolf Island, but less so than the GBR (Figure 2). The R^2 of best fit sine functions approximating daily temperature measurements for this record is 0.718. During El Niño years $R^2=0.774$, neutral years $R^2=0.664$ and for La Niña years $R^2=0.717$. Residuals of the difference between best fit sine values and SST measurements were close to zero during the entire year, supporting the conclusion that sinusoidality is a function of climate variability (Appendix, Figure A1).

Our examination of OISST data for the Northern Galapagos (Wolf Island) and the Central Galapagos (Isabella Island) demonstrate remarkably less sinusoidal annual SST variation than the GBR (Figure 2), wherein El Niño phases of ENSO have the most sinusoidal distribution of annual SST, followed by La Niña years, with neutral years having the least sinusoidality in SST variation. The lack of consistent sinusoidal variability in SST in the Galapagos could be due to confounding factors regarding the equatorial position of the archipelago with respect to solar radiation peaking twice a year (Appendix; figures A2-A3) and the lag in SST following insolation, combined with the seasonal upwelling of cold water. UB is likely more sinusoidal than Wolf because of the relatively consistent seasonal timing of the

upwelling of the EUC in the central portion of the archipelago, driving most of the seasonal pattern in SST variation.

4.2 Variations in *inter-* and *intra-*annual extension rates

4.2.1 Western Pacific coral growth: The Great Barrier Reef

The two coral cores from the GBR (NOM and CLK) show sinusoidal variation in annual extension, with the peak in extension rate occurring in December/January, coinciding with maximum SST at this site (Figure 3). Extension rate is not constant throughout the year, with periods of low extension corresponding to winter SST in the GBR. Mean modeled annual extension rate for the entirety of the NOM and CLK records is 13.6 mm/year and 14.8 mm/year, respectively (Table 4).

The correlation between SST and extension of all years in the NOM coral record is strong, both overall and in each ENSO phase (Table 1, Figure 3). In the average NOM record, the length of the growing period is 211 days, with a difference of 0.12% of annual extension rate per day between the fastest and the slowest extension rates during the average year (Table 2). The length of the growing season and amplitude of the growth profile differ when parsed out by ENSO phase. During El Niño years, the length of the growing season is 199 days, with an amplitude of 0.15% of annual extension per day. During neutral years, the length of the growing season is 183 days, with an amplitude of 0.05% of annual extension per day. During La Niña years, the length of the growing season is 227 days, with an amplitude of 0.20% of annual extension per day (Table 2). The month of maximum growth (MMG) for the entire NOM record is March. When separated by ENSO phase, the MMG is driven strongly by low number of years (small n) and a peak of March MMG's occurring during La Niña years (Figure 4). NOM has fairly constant extension throughout the year, with no years in which growth ceases (Figure 5). The growing season (where extension rate is monotonically increasing) begins consistently in early July and ends (extension rate is decreasing) in January-February, regardless of ENSO phase (Table 3).

For the CLK record, the correlation between all years of modeled extension and SST is $R^2=0.972$, El Niño $R^2=0.966$, neutral years $R^2=0.960$, and for La Niña years $R^2=0.945$, suggesting extension is correlated with SST in this coral (Table 1; Figure 3). The length of the growing period for the entire length of the CLK record is 142 days, with an amplitude of 0.31% of annual extension per day. During El Niño years, the length of the growing season is 145 days, with an amplitude of 0.33% of annual extension per day (Table 2). During neutral years, the length of the growing season is 125 days, with an amplitude of 0.21% of annual extension per day. During La Niña years, the length of the growing season is 148 days, with an amplitude of 0.37% of annual extension per day (Table 2). The MMG for CLK is December. During El Niño years, the MMG occurs dominantly in November, in neutral years it occurs in February and December, and in La Niña years it dominantly occurs in December (Figure 4). Patterns of annual extension in the CLK record are highly seasonal and less constant throughout the year, with a number of years demonstrating growth cessations in mid-September (Figure 5), shortly after the annual SST minima. The growing season begins mid-August-early September and ends by mid-January (Table 3).

4.2.2 *Eastern Pacific Coral Growth: Wolf Island, Northern Galapagos*

The bottom portion of the Wolf coral, W3B, grew from 1941-1983, until the coral bleached and died during the 1982-1983 El Niño event. Following regrowth, the upper portion of the Wolf coral record spans from 1987 to 2009 (collection year). The two components of the N. Galapagos coral record demonstrate stark differences in extension, with each other and with the GBR corals. Mean modeled annual extension rate for the entirety of the W3B and W3T records is 11.5 mm/year and 13.3 mm/year respectively (Table 4).

The correlation between SST and extension of all years in the W3B coral record is $R^2=0.228$, for El Niño years $R^2=0.448$, neutral years $R^2=0.678$, and for La Niña years the relationship between SST and

extension is not statistically significant. Overall this record of extension is poorly correlated with SST except for during neutral ENSO phases (Table 1, Figure 3). In the average W3B record, the length of the growing period is 198 days, with a difference of 0.13% of daily percent of annual extension between the fastest extension rate and the lowest extension rates (Table 2). When parsed out by ENSO phase, the length of the growing season does not vary significantly, while the difference between annual range of extension rates varies substantially. During El Niño years, the length of the growing season is 206 days, with an amplitude of 0.13% of annual extension per day. During neutral years, the length of the growing season is 191 days, with an amplitude of 0.09% of annual extension per day. During La Niña years, the length of the growing season is 195 days, with an amplitude of 0.3% of annual extension per day (Table 2). The month of maximum growth (MMG) for the entire W3B record is July and September. When MMG is examined by ENSO phase, El Niño years show MMG to occur dominantly in June and September. For neutral years, MMG most commonly occurs in September, and for La Niña years MMG occurs most often in July (Figure 4). Nearly 50% of W3B years demonstrate some form of intra-annual growth cessation (Figure 5). The growing season begins fairly consistently in January regardless of ENSO phase and can end anywhere from late June-late August (Table 3).

The upper portion of the Wolf coral record (W3T) differs from the lower (W3B) record. Within the W3T record, the correlation between all years of modeled extension and SST is $R^2=0.321$, El Niño $R^2=0.132$, neutral years have an insignificant correlation, and for La Niña years $R^2=0.709$, suggesting an inconsistent relationship between extension and SST that varies strongly between ENSO phases in this record (Table 1, Figure 3). The mean length of the growing period for the entire length of the W3T record is 177 days, with a range of 0.28% of annual extension per day. During El Niño years, the length of the growing season is 190 days, with an amplitude of 0.27% of annual extension per day (Table 2). During neutral years, the length of the growing season is 178 days, with an amplitude of 0.42% of annual

extension per day. During La Niña years, the average length of the growing season is 205 days, with an amplitude of 0.34% of annual extension per day (Table 2). The month of maximum growth is November - December, driven by MMG occurring most often in December in El Niño years. In neutral years, MMG is most coming to occur in November and January, and in La Niña years in September and November (Figure 4). Patterns of annual extension in the W3T record are highly seasonal with nearly half of the years in this record including seasonal growth cessations, while some years demonstrate a pattern of more constant extension throughout the year (Figure 5). The growing season can begin anywhere from mid-March to late June and ends sometime between early October and late December (Table 2).

4.2.3 *Eastern Pacific Coral Growth with Seasonal Upwelling: Urvina Bay, Central Galapagos*

The fossil coral from Urvina Bay exhibits broadly sinusoidal extension over the course of a year, almost directly out of phase with daily OISST measured for Isla Isabella ($R^2=0.694$, figure 3). Due to a lack of historical records of ENSO reconstruction, this fossil record cannot be parsed out according to ENSO phase directly, and as such we compare the entire mean extension profile to the different phases of ENSO SST. The correlation between the fossil extension rate and modern OISST for El Niño years is 0.695, for neutral years is 0.551, and is highest when compared with La Niña years with an $R^2=0.724$ (Table 1). The growing season for the mean extension profile is ~162 days long, beginning in early May and ending in mid-Oct. and the range of max and min growth is 0.16% of annual extension per day (Table 2). The peak in growth, occurring approximately in August (Figure 4), and corresponds to cool/cold temperatures in the central Galapagos. There are some modeled years of extension (~4 years) that are dramatically seasonal with most of the extension constrained to a few cool months of the year, while ~15 years are very low, constant growth rate throughout the year. However, most years of the UB record are relatively seasonal and inversely correlated with the trends in local OISST. The model approximates mean annual extension rate to be ~15.1 mm/year.

5 Discussion and Interpretation

5.1 Drivers of intra-annual extension

The primary environmental correlate of extension is not consistent across sites in the Equatorial Pacific. Previous research demonstrates that SST and/or light availability play important roles in determining the time of maximum extension, but our study suggests a more complex relationship, potentially including additional drivers.

5.1.1 Sea Surface temperature

The relationship between SST and intra-annual extension rate differs between the Great Barrier Reef and the Eastern Pacific Galapagos sites. Extension rate in the GBR exhibits a generally positive relationship with SST, while in the Galapagos, SST and extension are inversely related. In the GBR, extension rate tends to peak during periods of warm but not maximum SST (Figure 4), suggesting that max SST may exceed the thermal threshold for accretion but that warm temperatures nonetheless foster faster extension rates up to a point. These model results demonstrate support for theories of increasing extension rate with increased SST (Wellington, 1996; Lough and Barnes, 2000; Smith et al., 2007), with maximum extension generally occurring around 29°C, up to the maximum SST near 30°C, the upper thermal threshold for coral accretion (Done 2011). However, our GBR results contradict the timing of formation of high-density bands in the summer for the GBR (Reed et al. 2019; Lough and Barnes 2000), as the hypothesis of coral skeletal calcification would suggest that times of high-density accretion are periods of low extension rates. The relationship between the timing of density band formation and intra-annual extension rate is not as straightforward or consistent as suggested by prior works. The higher seasonality of extension at CLK as compared to NOM could derive from its closer proximity to land and to river output.

In the Northern Galapagos during ENSO neutral phases, intra-annual extension rate is antiphase with SST. Generally, within the W3B record of neutral years, peaks in extension rate occur dominantly in

September, ~1-2 months after the periods of lowest SST for this locality (Figure 4). This is counter to the hypothesis that skeletal extension peaks during SST maxima (Wellington et al. 1996; Lough and Barnes, 2000; Smith et al., 2007). It is possible that summer temperatures in the Galapagos are near the upper threshold of accretion for this coral. During neutral years, the correlation between SST and inter-annual extension rate is not statistically significant, suggesting that coral extension is neither in nor out of phase with intra-annual SST variability. Because the lower thermal stress threshold for corals is ~18°C (Done 2011), the minimum SST at this site of ~24.5°C could be ideal for maximum accretion for corals in this environment.

The mean annual extension profiles from UB demonstrate the same antiphase relationship between SST and extension rates seen in the W3 records, and in this case the inverse correlation is stronger (Table 1). This sub-fossil record cannot be parsed by ENSO years. However, when the mean extension profile for the entire UB record is compared with the mean SST signatures of different ENSO phases, we find that ENSO-neutral years show the weakest inverse relationships with SST of any ENSO phase. Maximum extension appears to occur when SST is ~23°C. Previous studies of Galapagos *Pavona spp.* coral extension rates indicate that maximum extension occurs on average between mid-January and mid-July (the warm and cooling seasons, Wellington and Glynn 1983). The model results of intra-annual extension suggest that maximum extension in the Galapagos tends to occur between August and January during ENSO neutral years, when SST is coolest and/or warming from winter within the annual temperature cycle.

5.1.2 Light availability

Results from the Galapagos support prevailing theories describing a positive relationship between light availability and extension rate (Glynn and Wellington, 1983), and that coral extension is negatively correlated with cloud cover (Goreau, 1959; Bak, 1974; Glynn, 1977). This relationship between light

availability and coral growth predicts that in the dry season, with colder SSTs, coral extension should be higher than during the wet season with warm SST and increased cloud cover, consistent with our observations from the preceding section. Modeled extension in Galapagos corals suggests that light availability is a more important driver of extension than are high SSTs. In contrast, in the GBR extension rate peaks at the same time as maximum precipitation in the region, when light intensity would be at its seasonal minimum due to cloud cover.

Solar insolation at the top of the atmosphere varies as a function of latitude throughout the year (Appendix figures A2-A3), but radiation and energy from the sun as it reaches the coral would additionally be a function of the amount of light penetrating through the atmosphere. This is often a function of cloud cover, which can vary both seasonally within the year, and inter-annually during variable climate states that shift circulation and precipitation patterns. To consider the role of light availability in driving intra-annual extension rate, we must consider the function of cloud cover as a distillation of the total radiative flux at Earth's surface. In the Galapagos, peak insolation occurs at the equinoxes, on days 83 and 261 of the calendar year, March and September, the warmest and coldest SST at this site respectively, ~6 months apart. In the GBR, insolation peaks on day 50 and day 294, in February and October respectively, during and ~3 months prior to peak SST at this location. In the GBR, maximum extension generally coincides with or immediately follows maximum solar insolation, despite this also being the rainiest (and hence presumably cloudiest) season of the year. In the Galapagos, maximum extension coincides with the second equinox in September, and thus despite SST being at the annual low, peak extension is coincident with a peak in insolation. The correlations between maximum extension rate and annual solar insolation at the top of the atmosphere as a function of latitude is contradictory to the proposed idea that coral growth is better correlated with light availability as a function

of cloud cover as opposed to insolation (Glynn, Wellington & Wells, 1983), but supports the theory that light availability is more important for coral extension than warm SST.

To examine this issue more thoroughly, there are a number of datasets and models with regional and local cloud coverage data, that contain information regarding the cloud cover, thickness of clouds, water vapor content, etc. (Zhang et al., 1995; Karlsson et al., 2013) that would allow a more in-depth comparison of the relationship between seasonal cloud cover and intra-annual variation in extension rate. Utilizing the various satellite measurements of clouds across the globe would provide increased high-resolution data with which to correlate radiation at the surface and when maximum extension occurs at these sites.

5.1.3 *Role of seasonal nutrient influx*

Maximum extension rate coincides with peak nutrient availability in both localities. In the GBR, rainfall and maximum river discharge bring nutrients to the nearshore corals in March, while in the Galapagos seasonal upwelling brings cold, nutrient-rich water to the surface in September. Upwelling of the EUC in the Galapagos also coincides with the time of higher light availability that fosters zooxanthellate photosynthesis.

While conceptual energy models suggest that hermatypic corals can acquire up to 90% of their energy purely from the products of zooxanthellate photosynthesis (Falkowski, 1984), the fact that nutrient availability coincides with maximum extension in both coral localities would suggest that nutrient availability may play a larger role the timing of intra-annual extension rate in *Porites* corals than previous work would suggest.

5.1.4 *Role of timing of reproduction cycles*

GBR *Porites spp.* typically spawn between November and January, during the warmest months of the year (Pichon et al., 2011). Gametes develop over 3-4 months (beginning July-October), with the most

rapid development occurring in the final 2 weeks preceding spawning (Pichon et al., 2011). While this might suggest that metabolic energy is directed away from skeletal extension to focus on reproduction, conceptual energy models of corals indicate that only ~1% of total metabolic energy is dedicated to reproduction (Edmunds & Davies, 1986). Our results similarly demonstrate maximum skeletal extension coincident with reproduction in the GBR.

Coral reproduction for Eastern Pacific *Porites spp.* is generally confined to the warmer months of the year (Pichon et al., 2011). While gamete development and spawning are occurring, there are few to no months in which maximum extension occurs simultaneously. The reproduction period in *Porites spp.* is linked to the beginning of water temperature rise (Klein & Loya, 1991), and thus is not diverting much energy from skeletal growth during reproduction in the GBR specifically. This supports the conclusion that coral extension in the GBR is dominantly controlled by extrinsic environmental factors that vary seasonally, and that intrinsic biological factors appear to play a very minor role in the intra-annual timing of accretion. In the Galapagos, reproduction may be more energetically balanced with skeletal extension where reproduction is confined to the warm months, such that exogenous factors drive extension in the Eastern Pacific.

5.2 *Effects of ENSO on inter-annual growth patterns*

In the GBR, La Niña extends the length of the growing season by about a month, beginning earlier than in neutral years. This could be due to the marginally cooler SST reducing thermal stress during the warmest months, or potentially from the increased precipitation and river discharge during La Niña phases of ENSO leading to marginally higher amounts of nutrients being distributed to the reefs. El Niño and La Niña both correlate with an increase in seasonality of intra-annual extension rates. El Niño reduces precipitation from ENSO-neutral years over Australia, thus reducing discharge from February to April and reducing any turbidity or salinity stress through the remainder of the warm period. This appears to result in an earlier peak in extension rate (MMG) in the shoreward corals. Precipitation rates begin to sharply

increase around November in the GBR, with the growing season ending within a few months of the precipitation increase.

In the Galapagos, El Niño years appear to increase the length of the growing season from neutral years in both W3 records. The response of Galapagos corals to thermal stress during ENSO could suggest that both warm and cold thermal anomalies inhibit extension, and that perhaps it is the rate of departure from mean SST that causes the stress, rather than the magnitude of the anomaly. This finding is consistent with previous studies that demonstrated a similar response to thermal stress (Glynn 1994; Suzuki et al. 2003; Lough and Cooper 2011; Hetzinger et al. 2016; Zamani et al. 2016). El Niño, with more precipitation and cloud cover and hence reduced light availability during the cool season, could attenuate the intra-annual range of extension rates that we see in the W3 records as compared to La Niña years.

La Niña years exhibit the highest intra-annual range in extension rate. In W3T, because the strongest inverse correlation between extension rate and SST occurs during La Niña years, as well as an extension of the growing season by nearly a month compared to ENSO neutral years, the increase in seasonality of extension during La Niña years could be due to the cooler SST anomalies (although the relationship between SST and annual extension is not statistically significant during La Niña years in W3B) or the increased upwelling during the cold season bringing more nutrients. W3T extension is much more seasonal than W3B, consisting of strong seasonal peaks in extension rate and seasonal cessations/reductions in extension. Additionally, with the more arid conditions during La Niña, precipitation and cloud cover decrease, allowing for increased light availability during La Niña years. La Niña years also result in a shifting of the growing season to begin and end earlier in both W3 records, although it lasts for a comparable length of the year as other ENSO phases. This shift could also correspond with the increased nutrient upwelling from the EUC and the beginning of the dry season occurring earlier in the year than in neutral years.

Because the subfossil Urvina Bay record extends beyond the reach of historical ENSO records, we are unable to parse this record out as a function of ENSO phase to examine how growth profiles for different years correlate with their respective ENSO phase SST, and can only examine the correlation between mean SST in UB with the mean intra-annual extension profile. We see that the higher sinusoidality of La Niña SST results in the strongest relationship between annual extension profiles and SST, followed closely by El Niño years, reflecting the same pattern we see in the Wolf corals in this subfossil record. This suggests that the cooler SST anomalies, reduced cloud cover, or increased nutrients from upwelling associated with La Niña produce a stronger sinusoidal pattern of intra-annual extension rate that correlates best with the very sinusoidal SST of La Niña years. While El Niño years are warm and sinusoidal, the SST extremes occurring with the summer anomalies are possibly reducing the strength of the relationship between temperatures and intra-annual extension due to high thermal anomalies, increased precipitation or reduced nutrients from upwelling.

During the LIA (1400-1700 C.E.), surface temperature reconstructions suggest that thermal anomalies over the Niño 3 region in the equatorial Pacific could be $\sim 0.5^{\circ}\text{C}$ cooler than a 1961-1990 mean climatological relative baseline temperature (Mann et al., 2009), with a statistically significant negative anomaly of $0.3\text{-}0.5^{\circ}\text{C}$ over the Galapagos. If LIA SST followed the same patterns of cooling as seen in the reconstructed LIA surface temperatures relative to the modern Galapagos SST, this cooler tropical Pacific could have a thermal effect on the UB coral record growing at that time. When considering the role of SST driving intra-annual variability in Galapagos coral extension rate, we observed that thermal anomalies in the Eastern Pacific may be so extreme that the W3 corals grow during the cooler months of the year to avoid the transient extrema of summer SST. The inverse correlation between modern SST and timing of extension is stronger in the UB record, suggesting that if the relationship is entirely (or mostly) driven by SST variability, that the cooler mean state during the LIA

would be additionally beneficial to contribute to maximum extension during the winter months of the year.

5.3 *Potential additional factors*

The complex results of the Galapagos coral growth record, particularly W3B, highlight the need for a more comprehensive study of other Eastern Pacific environmental parameters that could be affecting intra-annual coral extension. There could be a number of reasons to explain the complexity of the extension record. A 2016 study of Caribbean corals proposed that after a bleaching event, coral colonies may acquire different species of photosymbionts than they possessed prior to the bleaching (Hetzinger et al. 2016). While the repercussions of a new group of zooxanthellae are unclear, these studies suggest that these new symbionts create a different growth signature in the coral skeleton, namely a large shift in mean $\delta^{18}\text{O}$ values from the coral. The bleaching associated with the 1982 El Niño could explain the differences between the records of intra-annual extension rate in the older and younger portions of this coral head.

Ultra-fine bands within the larger density band pairs, called dissepiments, have been correlated with the lunar cycle (DeCarlo & Cohen, 2017). Dissepiments thus provide a potential opportunity to evaluate coral linear extension on sub-monthly timescales. The spacing of dissepiments has been shown to exhibit seasonality; for example, in a *Porites* coral from Taiwan, the spacing between dissepiments is narrower within high-density bands (warm season) than within the low-density band (cool season), independently suggesting that extension is slower in the summer than in the winter (DeCarlo and Cohen 2017). Unfortunately, dissepiments are not ideal for long reconstructions of extension variation because they are not easily detectable in all corals. However, when dissepiments are available for examination, researchers should explore these for independent confirmation of modeled patterns in intra-annual extension rate.

Additional geochemical climate proxies from concurrent analyses in coral cores provide opportunities for diverse exploration of intra-annual variation in environmental parameters in future

studies. For example, Ba/Ca and $\delta^{13}\text{C}$ could be used as tracers of variation in upwelling and primary production (Felis & Patzold, 1998; Gonnea et al., 2017; LaVigne et al., 2016; Lea, Shen & Boyle, 1989; LaVigne et al., 2011). $\delta^{13}\text{C}$ may also allow for studies of the role of reproduction in metabolic contributions to extension (Gagan, 1994; Grottoli, 2002). Other researchers have suggested that $\delta^{13}\text{C}$ may serve as a proxy for cloud cover as a function of light availability for zooxanthellate photosynthetic contributions to the metabolic carbon available for skeletal accretion (Heikoop et al., 2000, Omata et al., 2008; Brenner et al., 2017; Horta-Puga & Carriquiry, 2012). $\delta^{18}\text{O}$ provides the opportunity to explore the potential for variable freshwater influences of precipitation on coral extension. For fossil corals, for which climate data aren't readily available, the multiproxy data may provide additional avenues with which to study the oceanographic drivers of intra-annual extension.

The GBR corals presented in this study have concurrent high-resolution measurements of skeletal density. As total coral growth consists of the interplay between extension and density, a side-by-side examination of these growth metrics would allow for a more robust interpretation and understanding of the relationship between growth and the environment and energy trade-offs occurring in coral growth around the world. The study by Reed et al. (2019) also presents high resolution luminosity data demonstrating the intra-annual influence of river discharge of nutrients into the nearshore reefs. An in-depth examination of these concurrent proxies may help further elucidate the primary drivers of intra-annual extension rates in the GBR.

While the focus of this study was originally to examine the relationship between SST variability and intra-annual extension rate, it has nonetheless provided a perfunctory overview of additional factors that could be contributing to variability in intra-annual extension rate in corals. A more in-depth study on factors in the climatologically ideal setting of the GBR would help to elucidate many of the potential influences briefly touched on in this study. Focusing model development and application in the GBR, with

high resolution recent SST, nearby precipitation and river discharge data, resources for examining cloud cover as it seasonally filters solar radiation throughout the year, would allow for robust understanding of the fundamental environmental drivers of coral extension rate in this highly seasonal locality. Utilizing these modern coral records which overlap temporally and are relatively close in proximity, in conjunction with the environmental data mentioned above, would allow for validation of the model and begin to more thoroughly answer the question as to which environmental parameter is the most significant driver of extension rate. These published coral records, in conjunction with published, concurrent, high-resolution density and luminosity data alongside the SST proxy data, will allow for a holistic examination of the intra-annual drivers of total coral calcification, and pave the way for application of the model to other corals.

5.4 *Model performance & future applications*

The growth model was most successful at accurately simulating coral extension rates from the GBR, with NOM exhibiting the narrowest 1σ error envelopes around the modeled intra-annual extension rate (Table 3, Figure 3). This is likely due to the regular sinusoidal variation in SST in the Northern GBR. The success of model fit is reduced with the CLK record from the GBR, likely due to the more complex relationships between coral extension, precipitation, and local SST. The model fit is similar across all corals (Appendix, Figure A4) except NOM, with R^2 between 0.72 and 0.79 (Table 3). This suggests that the SST variability in the Galapagos is accurately reflected in the geochemical data collected from those corals, and that we are able to accurately model intra-annual extension variability. The high level of interannual variability in the Galapagos corals modeled extension (seen in the wide 1σ envelopes in Figure 3) reminds us of the complex and dynamic environment in different sites.

The first-order assumption that annual SST follows a sinusoidal pattern works well for many geographic sites. When the local climate deviates from this pattern, a new characterization of the annual cycle is needed to properly inform the model and recover growth patterns. Such years can either be

modeled separately with different constraints on the model parameters or omitted from the model output. This has a benefit for paleoenvironmental proxy records when instrumental data are not available with which to calibrate the model. Years that are modeled to have highly anomalous extension patterns could actually be indicators of periods of anomalous climate that invalidated the sinusoidal function of the model, providing a tool with which to identify events such as ENSO in fossil or subfossil coral records. The reduced consistency of the Galapagos coral extension reconstruction may thus be a consequence of violating model assumptions.

The validation of the model in modern records establishes an intriguing perspective from which to investigate records of intra-annual extension in fossil corals. If the spatial relationships between climate and extension hold true, application of this model could help researchers to understand variation in both intra-annual extension and climate through time. Understanding the limitations of the background climatology for different modern coral environments in combination with model performance in the present will make this approach more useful to the coral research community both today and in the past. The ability to reconstruct extension patterns allows us to evaluate the health and performance of corals that grew in different periods of Earth's climate history, for example before the Industrial Revolution. The model allows researchers to examine variation in intra-annual extension and study how corals respond to perturbations on an intra- and inter-annual basis.

The potential relevance of this approach stresses the importance of making raw geochemical data publicly available for use in studies of intra-annual and seasonal variation. A more complete understanding of the seasonality of coral extension will make interpretation of paleoclimate data inferred from corals more accurate.

6 Conclusions

The model reproduces intra-annual coral extension data relatively well, as demonstrated by the high R^2 values modeling the goodness of fit between modeled Sr/Ca values and observed sample values

(Appendix, Figure A4, Table 3). Mean annual extension is captured well with the prescribed metrics, as the fit between observed extension and modeled extension is a perfect correlation (Table 4).

In the GBR, the NOM record demonstrates less seasonal intra-annual extension with peaks in extension occurring in association with warm temperatures and elevated precipitation, river discharge and cloud cover, as well as near the timing of maximum solar insolation in the region. In the CLK record, the increased proximity to river output tells a more dynamic story of the influence of precipitation runoff and the effects of ENSO on Australian precipitation patterns driving high seasonality in coral extension. CLK exhibits much more seasonal growth, with extension again peaking near the time of SST maxima. Low extension rates verging on growth cessations coincide with SST minima. Effects of ENSO in the GBR primarily manifest through changes in precipitation patterns and their associated effects on terrestrial processes, while SST changes are minor. This suggests that the corals are not sensitive to the $\sim 1\text{-}2^\circ\text{C}$ changes in temperature but could be affected by terrestrial influences such as turbidity, freshwater, and sediment/nutrient loading from seasonal fluvial sources on ENSO scales.

The contrast between coral extension in the GBR and the Galapagos reflects the variability of the Eastern Tropical Pacific. In the Galapagos, extension typically peaks during SST minima, likely due to a combination of light availability from maximum insolation and reduced cloud cover associated with low precipitation, and influx of nutrients from upwelling. Extension can be fairly constant or very seasonal, and the effects of ENSO are very dynamic and not consistent through time or space in the Galapagos. This may suggest that Galapagos corals are particularly stressed by the environmental temperature fluctuations, and the $\sim 1\text{-}2^\circ\text{C}$ change during average ENSO events is more impactful. When the correlation between SST and extension is highly variable, it provides the opportunity to examine other oceanographic or endogenous factors that may be driving variations in intra-annual extension rate in corals across the Pacific.

Strong differences in the timing of reproduction in the GBR and the Galapagos relative to extension suggest that the metabolic role of reproduction in corals is relatively minor and not a major contributor to the timing of skeletal extension.

This subfossil Urvina Bay record provides the first seasonal paleo-perspective of extension rate reconstructions from this model and could ultimately provide a tool with which to identify anomalous climate events from coral geochemistry and growth patterns. It also provides a unique application of this model with respect to evaluating coral response to long term changes in climate in a comparison of pre- and post- industrial era coral records of extension in highly dynamic environments. This work provides the baseline for studies of modern intra-annual coral extension rates in well understood environments and illustrates some of the complexities and potential research directions for other coral environments in space and time.

7 Tables

7.1 Table 1: Annual Extension Profiles Correlated with Annual SST

Coral	Mean (R ²)	Nino (R ²)	Nada (R ²)	Nina (R ²)
NOM	0.937	0.917	0.868	0.926
CLK	0.972	0.966	0.96	0.945
W3B	0.228	0.448	0.678	NS
W3T	0.321	0.132	NS	0.709
UB	0.694	0.695	0.551	0.724

R² values for the linear regression between mean annual extension profiles and annual OISST variation, for the entire length of the coral record and parsed out by ENSO phase. NS= not statistically significant at the p=0.05 level.

7.2 Table 2: Growing Season Information

Coral	Locality	Mean Range of annual growth (%)	Days in growing season	Growth Season <u>Start</u> day	MMG	Growth Season <u>End</u> day
NOM- All Years (n=17)	GBR	0.13	211	190 - Early July	March	38 -Early Feb
NOM Niño (n=6)	GBR	0.15	199	193- Early July	N/A	29-Late Jan
NOM neutral (n=6)	GBR	0.05	183	194- Early July	N/A	14 -Mid Jan
NOM Niña (n=5)	GBR	0.20	227	187- Early July	March	51-Late Feb
CLK-All Years (n=15)	GBR	0.31	142	235- Late Aug	December	14-Mid Jan
CLK Nino (n=5) (shortened record)	GBR	0.33 (0.33)	145 (159)	234 - Late Aug (230)	November	16-Mid Jan (26)
CLK Nada (n=5)	GBR	0.21	125	248 - Early Sept	Dec./March	10- Early Jan
CLK Nina (n=5) (shortened record)	GBR	0.37 (0.34)	148 (167)	229- Mid Aug (212)	December	14 - Mid Jan (16)
W3B-All Years (n=43)	Galapagos, Wolf	0.13	198	4-Early Jan	July/Sept.	211-Late July

W3B Nino (n=15)	Galapagos, Wolf	0.13	206	21 -Late Jan	June/Sept.	237-Late Aug
W3B Nada (n=18)	Galapagos, Wolf	0.09	191	5-Early Jan	Sept.	230-Late Aug
W3B Nina (n=10)	Galapagos, Wolf	0.33	195	344-Mid Dec	July	176-Late June
W3T-All Years (n=23)	Galapagos, Wolf	0.28	177	141- Late May	Nov./Dec.	317 -Mid Nov
W3T Nino (n=8)	Galapagos, Wolf	0.27	190	151- Late May	December	340 -Early Dec
W3T Nada (n=7)	Galapagos, Wolf	0.42	178	179- Late June	Nov./Jan.	356-Late Dec
W3T Nina (n=8)	Galapagos, Wolf	0.34	205	71-Mid March	Sept./Nov.	275-Early Oct
UB (n=43)	Galapagos, Urvina Bay	0.16	162	125- Early May	August	286 -Mid Oct

Various calculations regarding different metrics of growth for each coral record, parsed out by ENSO phase. The range of annual growth is calculated by the maximum and minimum extension rate values for each mean growth profile for each ENSO phase. This metric is normalized to annual growth and is presented in percent of annual growth per day. The length of the growing season is presented in number of days in which coral extension rate is monotonically increasing. The start of the growing season is presented as Julian day, approximated to a month in the year. This is the day in which extension rates begin to increase.

7.3 Table 3: Goodness of Fit Results for Coral Growth Models

Coral record	Mean R ² for record
NOM	0.89
CLK/CLK Shortened	0.77/0.79
W3B	0.72
W3T	0.74
UB	0.77

The linear regression R² fit value for Sr/Ca observed sample values and Sr/Ca modeled values. CLK shortened refers to having the years 2005 and younger removed from the record due to anomalously low extension rates as reported in Reed et al. 2019.

7.4 Table 4: Modeled Extension Rate vs. Measured Annual Linear Extension Rate

Coral Record	Measured Mean Annual Linear Extension (mm/year)	Modeled Mean Annual Extension (mm/year)	Correlation Between Measured and Modeled Annual Extension (R ²)
NOM	14.5	13.6	0.988

CLK	15.7	14.8	1
W3B	12.4	11.5	0.996
W3T	14.3	13.3	0.998

Measured annual extension rates from literature in which coral record was published (NOM and CLK) or calculated based on sampling distance between Sr/Ca minima (thermal maxima) for the length of the coral record.

8 Figures

8.1 Figure 1: Site map

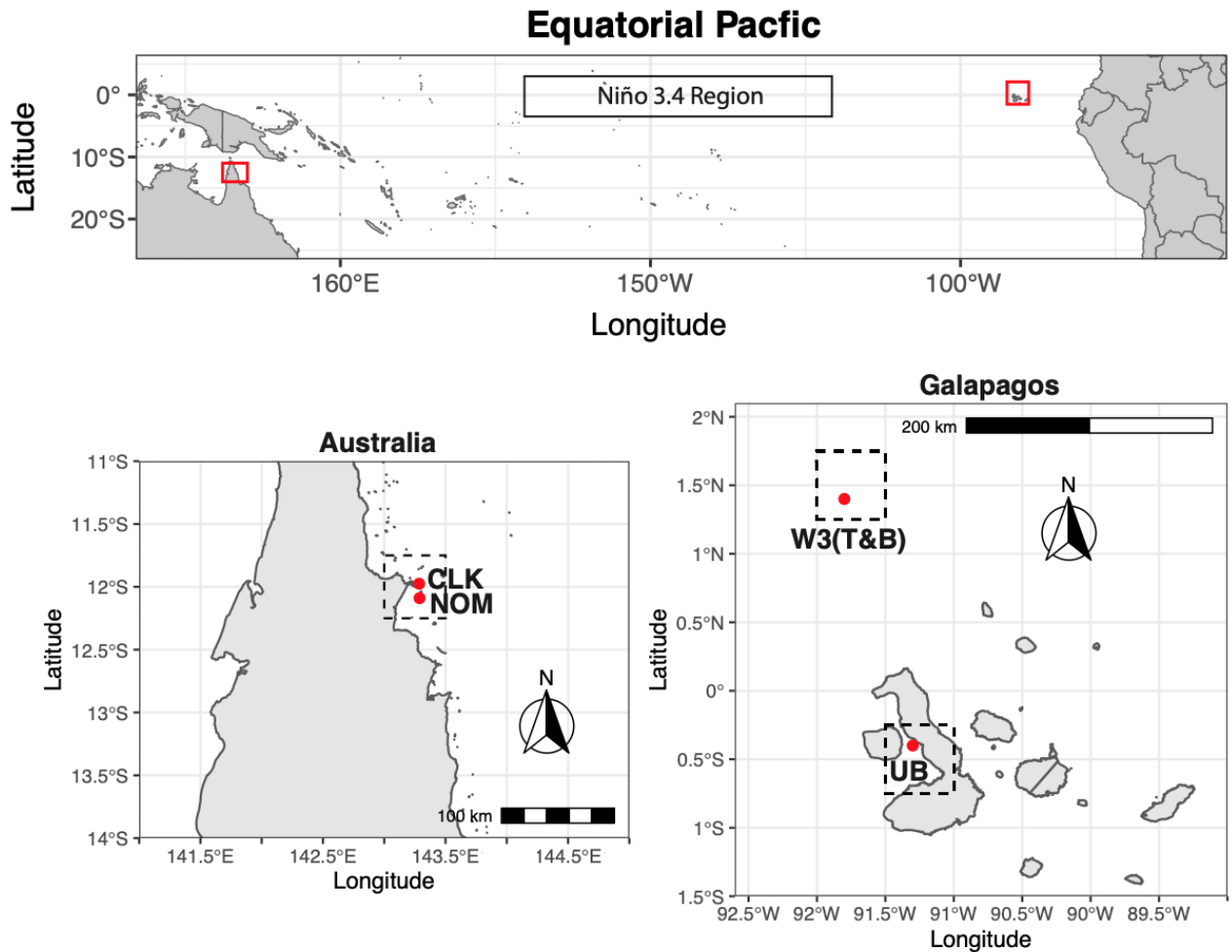


Figure 1. Sites of collection of original coral cores. (a) The relative locations of the Great Barrier Reef and Galapagos sites (red boxes) as well as the Niño 3.4 region. (b) NOM and CLK were collected from the Great Barrier Reef off the northern coast of Australia. Dashed lined boxes delineate the grid cell from which daily OISST data were sourced for the GBR (11.75-12.25° S, 143-143.5°E). (c) Coral Wolf3 (W3) was cored near Isla Wolf in the northern Galapagos. The fossil coral came from Urvina Bay (UB) near Isla Isabella in the central Galapagos platform. Dashed box indicates the grid from which daily OISST data were sourced for the Galapagos (W3: 1.25-1.75°N, 91.5-92°W, UB: 0.25-0.75°S, 91-91.5°W).

8.2 Figure 2: Annual Site Climatology

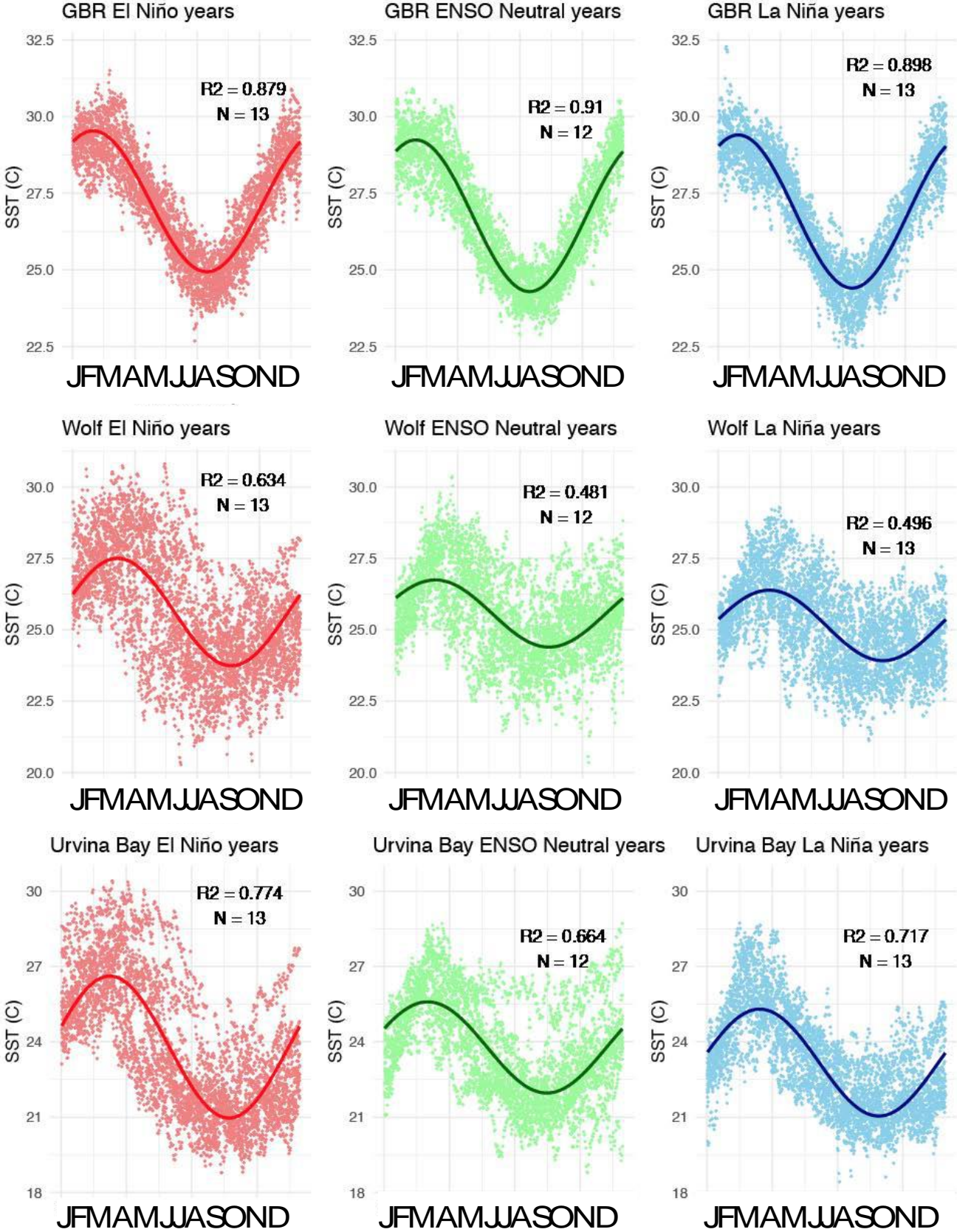


Figure 2. The climatology for each site of coral collection. Light colored points represent daily OISST record data for the GBR, and Wolf Island and Urvina Bay in the Galapagos. Each year of measured SST was first classified by ENSO phase (El Niño=red, Neutral=green, La Niña=blue) and was then fit with a best fit sine function. The mean of these best fit sines is plotted for each site and ENSO phase as the respective darker colored line. R^2 values represent the overall linear model fit between each best fit sine function and its respective year of SST data. N values indicate the number of years from the total SST record belonging to each class of ENSO phase. The OISST records were examined over the years 1982-2019.

8.3 Figure 3: Intra-annual coral growth profiles

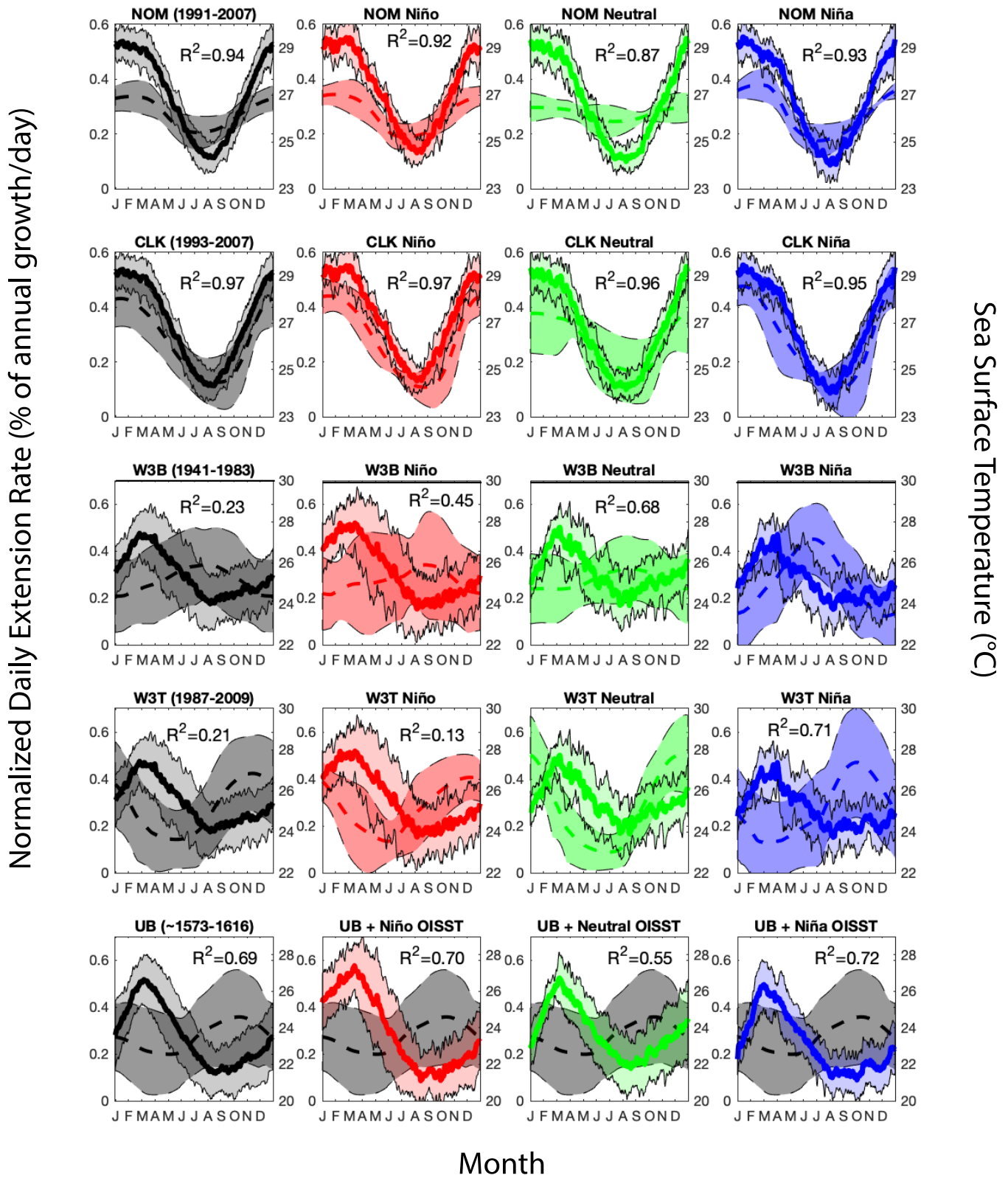


Figure 3: Plotted in each panel is the mean modeled extension rate growth profile, normalized to % of annual growth per day, over a year. The first column in black is the mean extension rate (dashed line) for the entire duration of each coral record, plotted alongside the mean annual SST for that site (solid line). The second column, in red, is the mean extension rate (dashed line) for the years of coral growth classified as El Niño years, alongside the mean annual SST for El Niño years within that SST record. The third column, in green, is the same as column 2 with respect to the variables plotted and their respective line types, with the ENSO-Neutral years selected. In column 4 is plotted the same coral growth profile for the mean of the La Niña years, alongside the SST curve for the La Niña years of the SST record. Reported R^2 values reflect the fit of a linear model between the mean coral growth rate and mean SST record plotted for each panel (reported if significant at $p < 0.05$ level) as a function of the respective ENSO phase.

8.4 Figure 4: Timing of intra-annual growth (MMG)

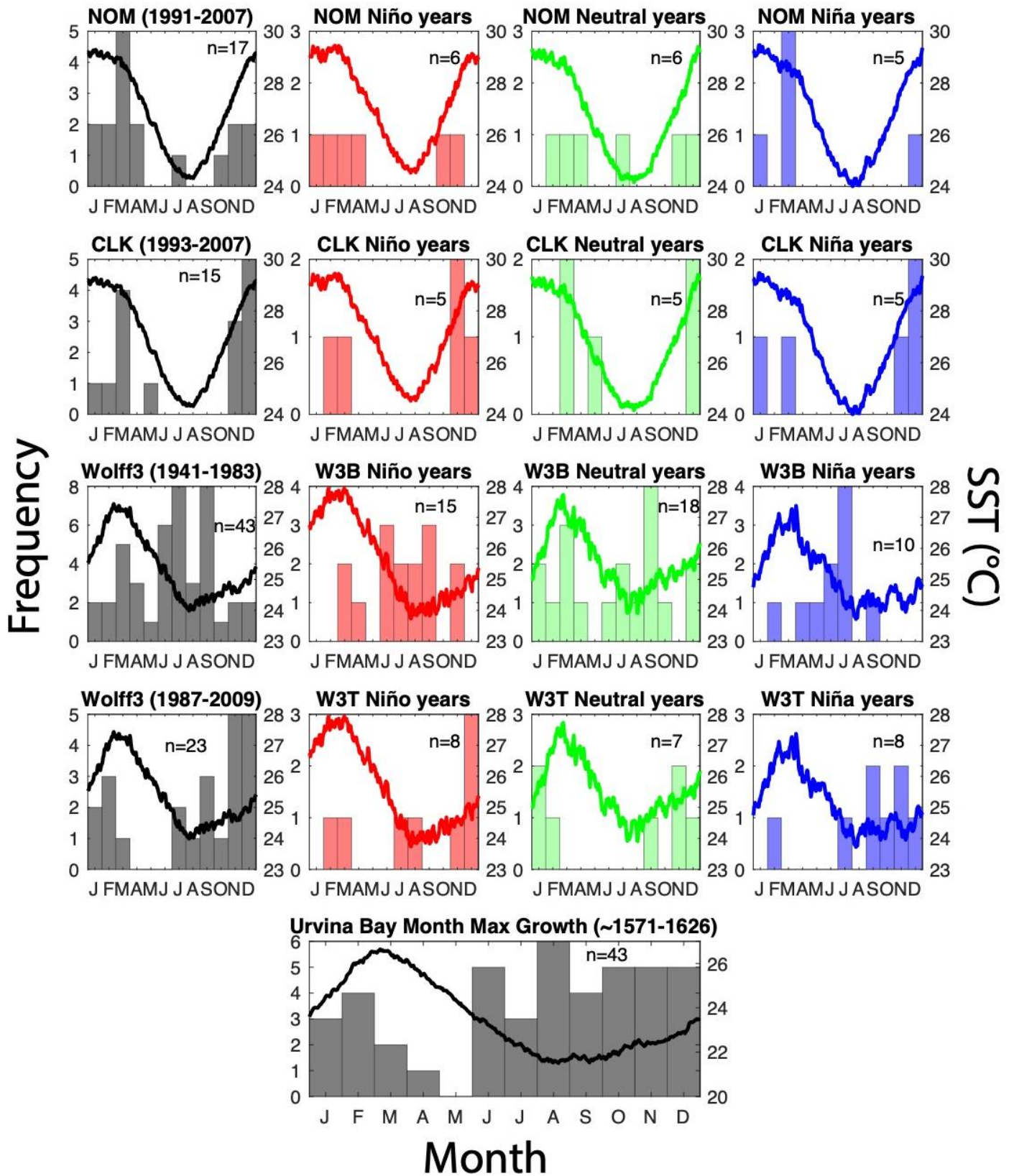


Figure 4. Each panel illustrates a histogram of the distribution of the Month of Maximum Growth (MMG, left y axis) for each coral record at different sites as a function of ENSO phase. Each panel also contains the mean SST curve each locality (in °C, right y axis), separated by SST of each ENSO phase. The first column in gray/black illustrates the distribution of the MMG for every year of the coral record. N values reference the number of years of coral growth ascribed to each histogram throughout the figure. The following columns demonstrate the breakdown of distribution of MMG's according to how each year of coral growth is classified within the ENSO framework: Red=El Niño, Green=Neutral, Blue=La Niña years. The fossil coral record from Urvina Bay cannot be identified according to ENSO type, and so shows the distribution of MMG's for the entirety of the record.

8.5 Figure 5: Coral growth rate through time: inter- and intra-annual trends

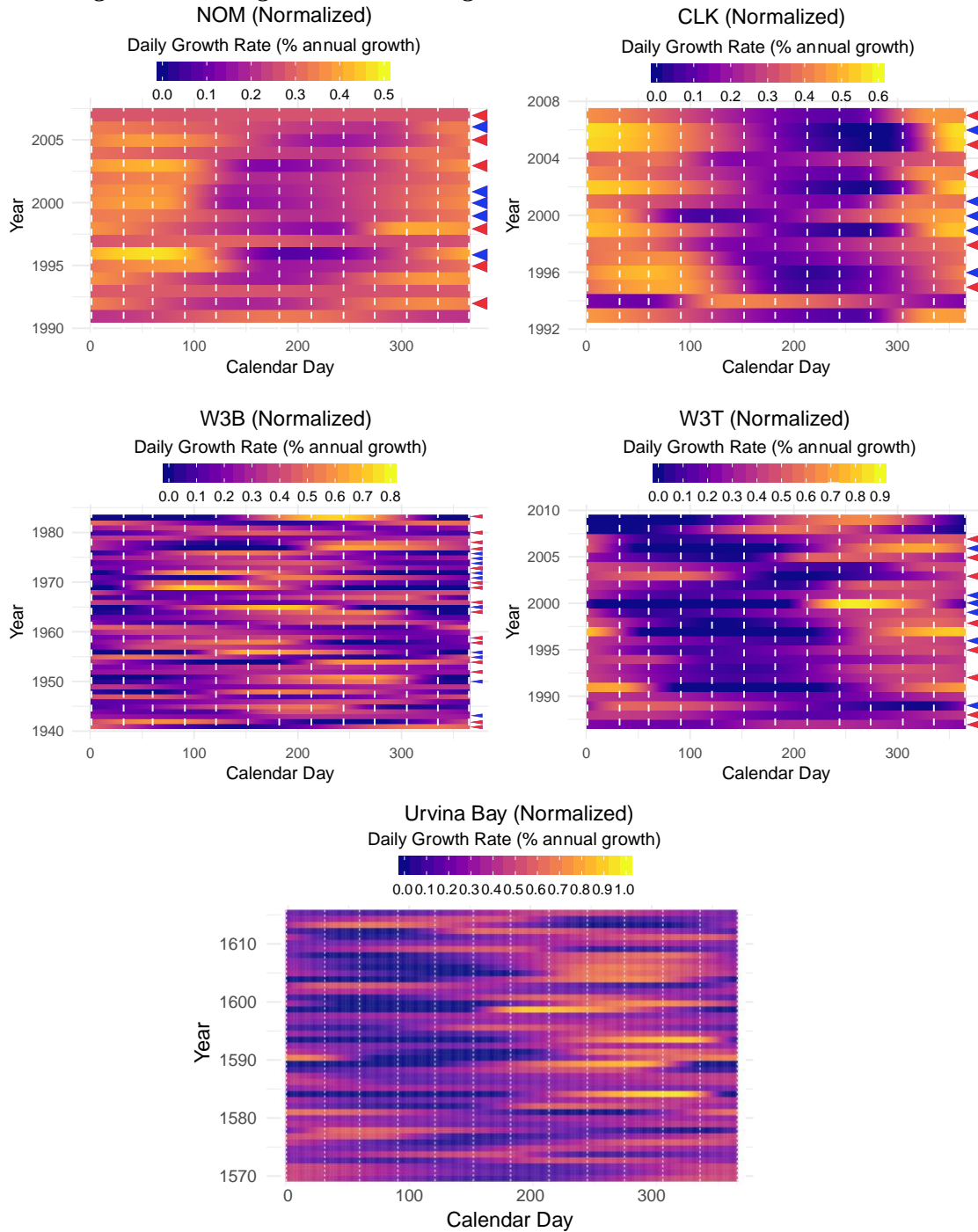
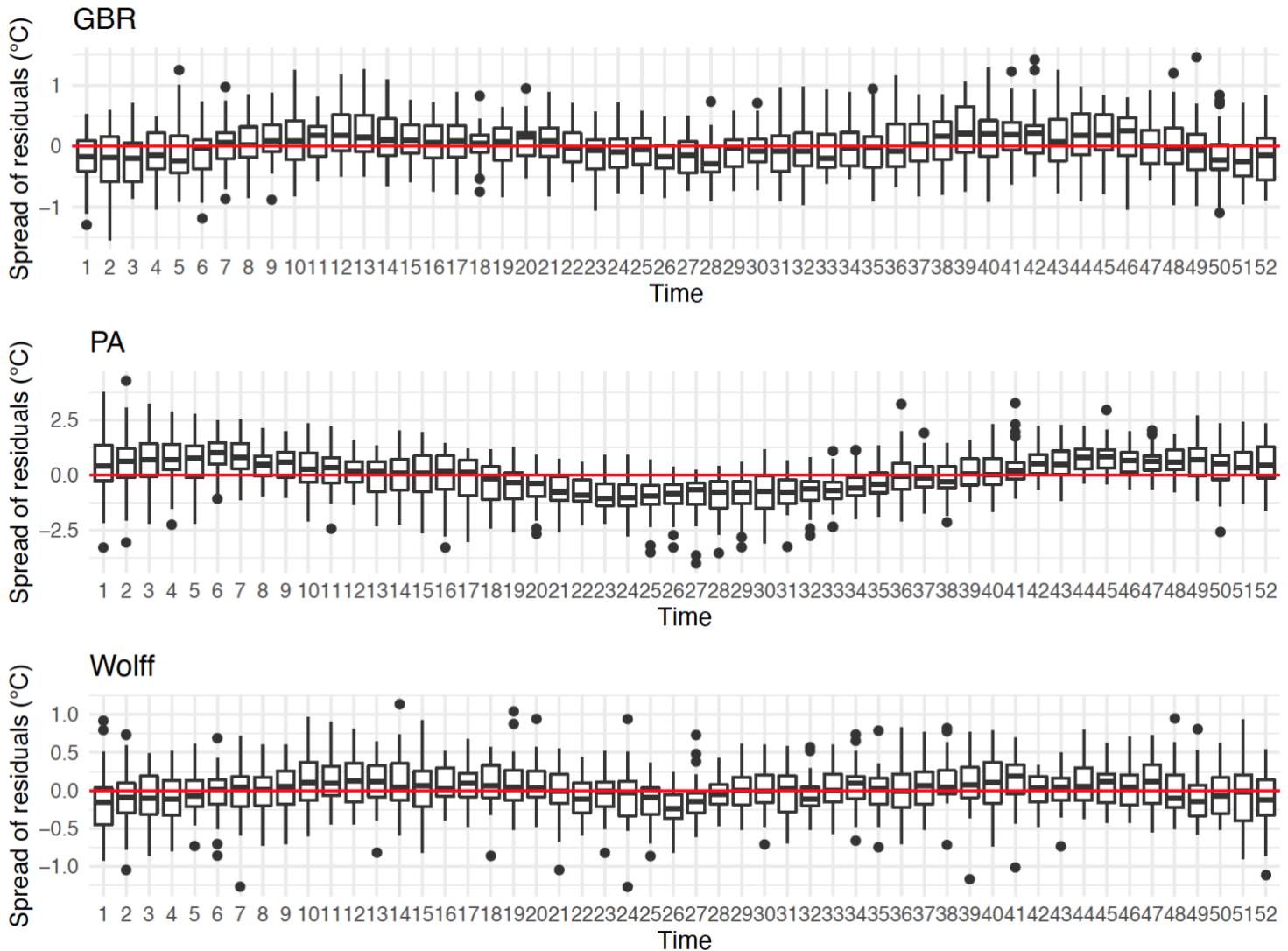


Figure 5. Heat maps allow for visualization of daily growth rate inter- and intra-annually. Daily growth rate is normalized and presented as percent of total annual growth. Each year has 365 modeled growth rate values for the length of the coral record. Color bars are scaled to maximize contrast in extension rate for each site. The white dashed lines denote the boundaries between months of the year. Each horizontal line of colored data represents one calendar year of coral growth. Red and blue triangles represent El Niño and La Niña years respectively.

9 Appendix

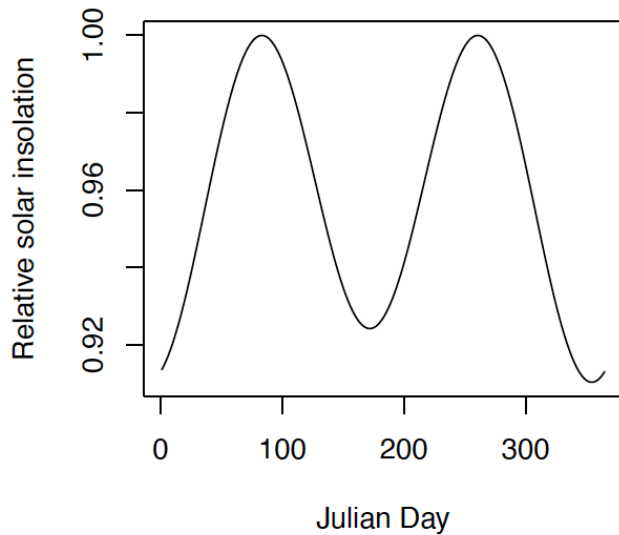
9.1 Appendix Figure A1



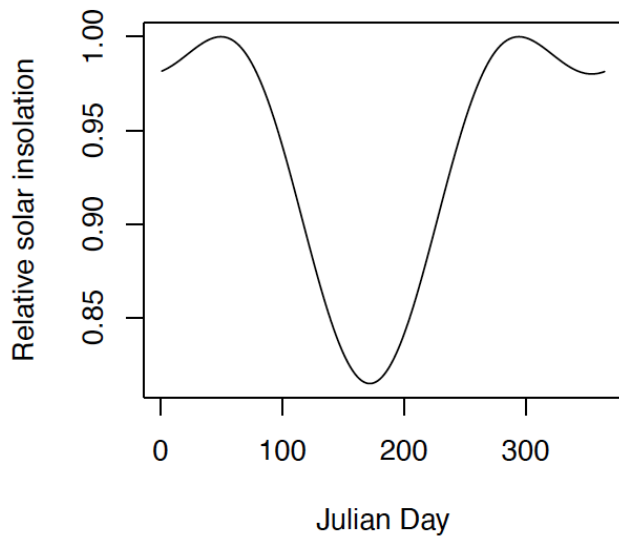
Residuals (in °C) from the correlation of observed and modeled sinusoid climate data by each site. Whisker plots show the distribution of residuals grouped by week of the year (black bar = median, top/bottom of box = 1σ , reach of whiskers = 2σ , points = outliers beyond 2σ), red line indicates zero. Note that there is a non-random secular trend in the residuals, which indicates that the sinusoidal temperature fit may be systematically underestimating measured SST extremes at all sites. Residuals from the GBR site tend to be closest to 0 (the red line passes through all the boxes), which reflects the increased sinusoidality of that site compared to the others. PA references Puerto Ayora instrumental SST data from the Charles Darwin Research Station, the only instrumental logger in the Galapagos. The GBR and Wolff data come from the OISST grid cells denoted in Figure 2.

9.2 Appendix Figure A2-A3

Daily insolation at 1 degree North

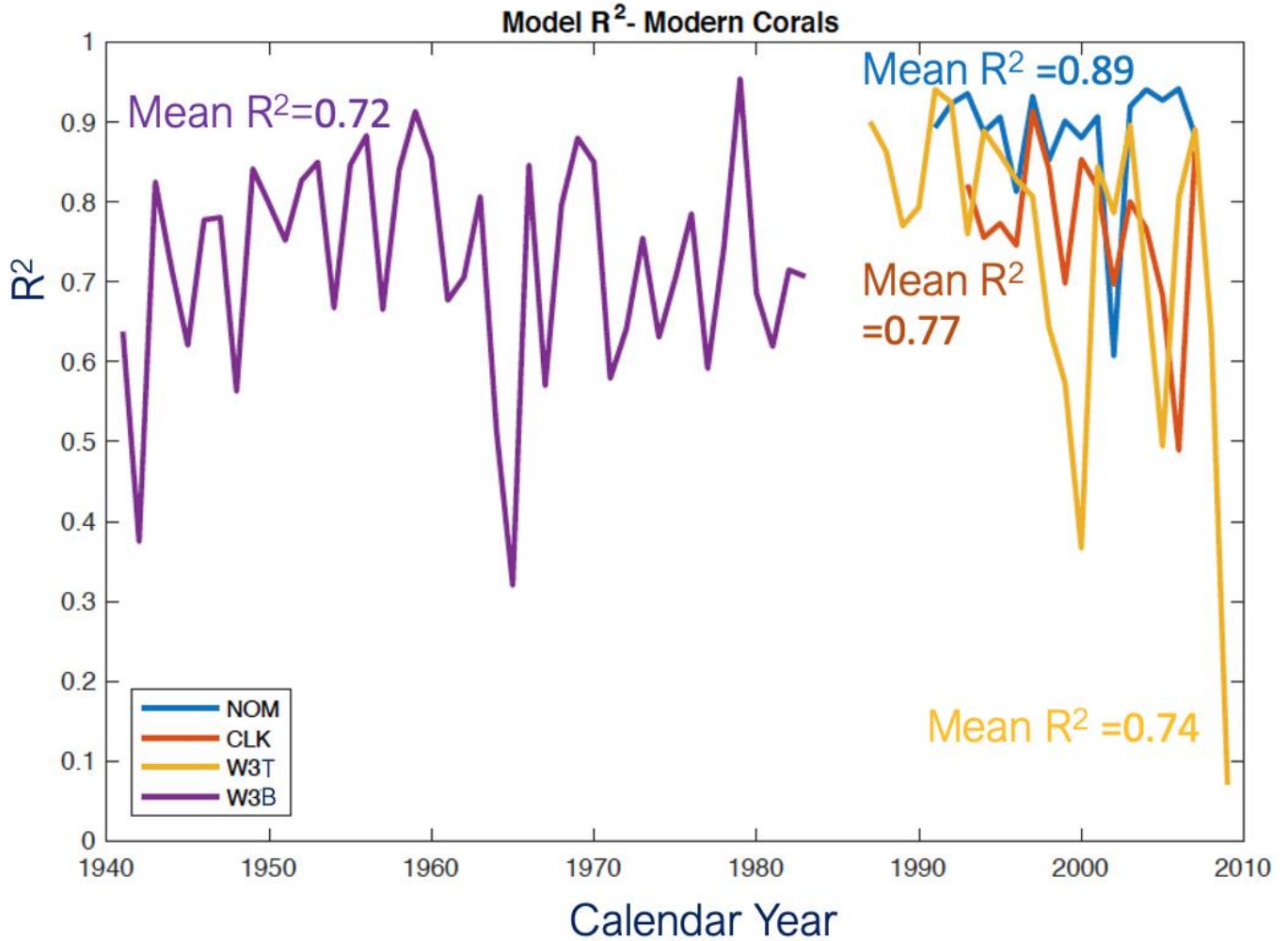


Daily insolation at 12 degrees South



Relative solar insolation for 1°N and 12°S, roughly the latitudes of the Wolf Island and GBR sites, respectively. Relative solar insolation is defined geometrically based on the formula $I = \cos(\text{lat} - \text{declination})$, where solar declination is defined by $\text{declination} = 23.45 \cos((2\pi(t-172))/365)$, where t is the Julian day. On the y axis, 1 refers to the local maximum annual solar insolation; therefore, the relative numbers are not comparable across localities and only refer to within-site variability. In the tropics (between 23.45°N or S), local solar insolation peaks twice per year, while only peaking once outside of the tropics. For the Wolf sites, insolation peaks on days 83 and 261, while in the GBR sites insolation peaks on days 50 and 294. Furthermore, there is more variability as latitude increases, which may contribute to inter-regionally seasonal differences in coral growth.

9.3 Appendix Figure A4



A graphic representation of the correlation between measured Sr/Ca values that were input to the model, and output modeled Sr/Ca values for each year of modeled coral growth, color coded by record. Mean R² values for the entire record are labelled on the plot in the same color as the plotted values.

10 References

- Al-Rousan, S. (2012). Skeletal extension rate of the reef building coral *Porites* species from Aqaba and their environmental variables. *Natural Science*, 04(09), 731-739.
- Bak, R. P. M. (1974). Available light and other factors influencing growth of stony corals through the year in Curacao. Caraibisch Marien-Biologisch Instituut.
- Barnes, D. J., and J. M. Lough. 1993: On the nature and causes of density banding in massive coral skeletons. *Journal of Experimental Marine Biology and Ecology* 167:91–108.
- Barnes, D. J., & Crossland, C. J. (1980). Diurnal and seasonal variations in the growth of a staghorn coral measured by time-lapse photography. *Limnology and Oceanography*, 25(6), 1113–1117.
- Bessat, F., and D. Buigues. 2001: Two centuries of variation in coral growth in a massive *Porites* colony from Moorea (French Polynesia): A response of ocean-atmosphere variability from south central Pacific. *Palaeogeography, Palaeoclimatology, Palaeoecology* 175:381–392.
- Black, B. A., Andersson, C. G., Butler, P. L., Carrol, M. L., DeLong, K. J., Reynolds, D. R., Witbaard, R. U. (2019). The revolution of crossdating in marine palaeoecology and palaeoclimatology. *Biology Letters*, 15(1).
- Brenner, L. D., Linsley, B. K., & Dunbar, R. B. (2017). Examining the utility of coral Ba/Ca as a proxy for river discharge and hydroclimate variability at Coiba Island, Gulf of Chirquí, Panamá. *Marine pollution bulletin*, 118(1-2), 48-56
- Buddemeier, R. W., Smith, S. V., & Kinzie, R. A. (1975). Holocene windward reef-flat history, Enewetak Atoll. *Geological Society of America Bulletin*, 86(11), 1581.
- Buddemeier, R. W., Maragos, J. E., & Knutson, D. W. (1974). Radiographic studies of reef coral exoskeletons: Rates and patterns of coral growth. *Journal of Experimental Marine Biology and Ecology*, 14(2), 179-199.
- Buddemeier RW, Kinzie III RA (1976) Coral growth. *Oceanogr Mar. Biol* 14:183-225
- Buddemeier RW (1974) Environmental controls over annual and lunar monthly cycles in hermatypic coral calcification. *Proc 2nd Int Coral Reef Symp* 2:259-267
- Carilli JE, Norris RD, Black B, Walsh SM, McField M. 2010 Century-scale records of coral growth rates indicate that local stressors reduce coral thermal tolerance threshold. *Global Change Biol.* **16**, 1247-1257.
- Chakraborty, S., R. Ramesh, and J. M. Lough. 2000: Effect of intraband variability on stable isotope and density time series obtained from banded corals. *Proceedings of the Indian Academy of Science* 109:145–151.
- DeCarlo, T. M., and A. L. Cohen. 2017: Dissepiments, density bands and signatures of thermal stress in *Porites* skeletons. *Coral Reefs* 36:749–761.

- DeLong, K. L., T. M. Quinn, and F. W. Taylor (2007), Reconstructing twentieth-century sea surface temperature variability in the southwest Pacific: A replication study using multiple coral Sr/Ca records from New Caledonia, *Paleoceanography*, 22, PA4212
- DeLong, K. L., Flannery, J. A., Maupin, C. R., Poore, R. Z., & Quinn, T. M. (2011). A coral Sr/Ca calibration and replication study of two massive corals from the Gulf of Mexico. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 307(1-4), 117-128.
- DeLong KL, Flannery JA, Poore RZ, Quinn TM, Maupin CR, Lin K, Shen CC. (2014) A reconstruction of sea surface temperature variability in the southeastern Gulf of Mexico from 1734 to 2008 CE using cross-dated Sr/Ca records from the coral *Siderastrea siderea*. *Paleoceanography* **29**, 403-422.
- Dodge, R. E., Aller, R. C., & Thomson, J. (1974). Coral growth related to resuspension of bottom sediments. *Nature*, 247(5442), 574–577.
- Done T. (2011) Corals: Environmental Controls on Growth. In: Hopley D. (eds) *Encyclopedia of Modern Coral Reefs*. Encyclopedia of Earth Sciences Series. Springer, Dordrecht.
- Edmunds, P. J., and P. S. Davies. 1986: An energy budget for *Porites porites* (Scleractinia). *Marine Biology: International Journal on Life in Oceans and Coastal Waters* 92:339–347.
- Evangelista, H., D. Godiva, A. Sifeddine, Z. M. A. N. Leão, N. R. Rigozo, B. Segal, T. Ambrizzi, M. Kampel, R. K. P. Kikuchi, and F. Le Cornec. 2007: Evidences linking ENSO and coral growth in the Southwestern-South Atlantic. *Climate Dynamics* 29:869–880.
- Falkowski, P., Dubinsky, Z., Muscatine, L., & Porter, J. (1984). Light and the Bioenergetics of a Symbiotic Coral. *BioScience*, 34(11), 705-709.
- Felis, T., Pätzold, J., Loya, Y., & Wefer, G. (1998). Vertical water mass mixing and plankton blooms recorded in skeletal stable carbon isotopes of a Red Sea coral. *Journal of Geophysical Research: Oceans*, 103(C13), 30731-30739.
- Felis, T., Patzold, J., & Loya, Y. (2003). Mean oxygen-isotope signatures in *Porites* spp. corals: Inter-colony variability and correction for extension-rate effects. *Coral Reefs*, 22(4), 328-336. doi:10.1007/s00338-003-0324-3
- Gagan, M. K., Chivas, A. R., & Isdale, P. J. (1994). High-resolution isotopic records from corals using ocean temperature and mass-spawning chronometers. *Earth and Planetary Science Letters*, 121(3), 549-558.
- Glynn, P. W. 1994: State of coral reefs in the Galápagos Islands: Natural vs anthropogenic impacts. *Marine Pollution Bulletin* 29:131–140.
- Glynn, P.W. 1983: *Corals and Coral reefs of the Galapagos Islands*. University of California Press

- Glynn, P. W., Wellington, G. M., & Birkeland, C. (1979). Coral reef growth in the Galapagos: limitation by sea urchins. *Science*, 203(4375), 47–49.
- Glynn, P. W., & PW, G. (1977). Coral growth in upwelling and nonupwelling areas off the Pacific coast of Panama.
- Gonneea, M. E., Cohen, A. L., DeCarlo, T. M., & Charette, M. A. (2017). Relationship between water and aragonite barium concentrations in aquaria reared juvenile corals. *Geochimica et Cosmochimica Acta*, 209, 123-134.
- Goreau, T. F. (1959). The physiology of skeleton formation in corals. I. A method for measuring the rate of calcium deposition by corals under different conditions. *The Biological Bulletin*, 116(1), 59–75.
- Grigg, R. W. 2006: Depth limit for reef building corals in the Au'au Channel, S.E. Hawaii. *Coral Reefs* 25:77–84.
- Grottoli, A. G. (1999). Variability of stable isotopes and maximum linear extension in reef-coral skeletons at kaneohe bay, hawaii. *Marine Biology*, 135(3), 437-449.
- Heikoop, J. M., Dunn, J. J., Risk, M. J., Schwarcz, H. P., McConnaughey, T. A., & Sandeman, I. M. (2000). Separation of kinetic and metabolic isotope effects in carbon-13 records preserved in reef coral skeletons. *Geochimica et Cosmochimica Acta*, 64(6), 975-987.
- Hendy, E. J., Gagan, M. K., Alibert, C. A., McCulloch, M. T., Lough, J. M., & Isdale, P. J. (2002). Abrupt decrease in tropical Pacific sea surface salinity at end of Little Ice Age. *Science*, 295(5559), 1511–1514.
- Hetzinger, S., M. Pfeiffer, W. C. Dullo, J. Zinke, and D. Garbe-Schönberg. 2016: A change in coral extension rates and stable isotopes after El Niño-induced coral bleaching and regional stress events. *Scientific Reports* 6:1–10.
- Highsmith, Raymond C. "Coral Growth Rates and Environmental Control of Density Banding." *Journal of Experimental Marine Biology and Ecology*, vol. 37, no. 2, 1979, pp. 105-125.
- Horta-Puga, G., & Carriquiry, J. D. (2012). Coral Ba/Ca molar ratios as a proxy of precipitation in the northern Yucatan Peninsula, Mexico. *Applied geochemistry*, 27(8), 1579-1586.
- Jimenez, G., J. E. Cole, D. M. Thompson, and A. W. Tudhope. 2018: Northern Galápagos Corals Reveal Twentieth Century Warming in the Eastern Tropical Pacific. *Geophysical Research Letters* 45:1981–1988.
- Judd, E. J., B. H. Wilkinson, and L. C. Ivany. 2018: The life and time of clams: Derivation of intra-annual growth rates from high-resolution oxygen isotope profiles. *Palaeogeography, Palaeoclimatology, Palaeoecology* 490:70–83.
- Karlsson, K.G., Riihela, A., Müller, R., Meirink, J.F., Sedlar, J., Stengel, M., Lockhoff, M., Trentmann, J.,

- Kaspar, F., Hollmann, R. and Wolters, E., 2013. CLARA-A1: a cloud, albedo, and radiation dataset from 28 yr of global AVHRR data. *Atmospheric Chemistry and Physics*, 13(10), pp.5351-5367.
- Kessler, W. S. (2006). The circulation of the eastern tropical Pacific: A review. *Progress in Oceanography*, 69(2-4), 181-217.
- Klein, R., and Y. Loya. 1991: Skeletal growth and density patterns of two *Porites* corals from the Gulf of Eilat, Red Sea. *Marine Ecology Progress Series* 77:253-259.
- Knutson, D., Buddemeier, R., & Smith, S. (1972). Coral Chronometers: Seasonal Growth Bands in Reef Corals. *Science*, 177(4045), 270-272.
- LaVigne, M., Grottoli, A. G., Palardy, J. E., & Sherrell, R. M. (2016). Multi-colony calibrations of coral Ba/Ca with a contemporaneous in situ seawater barium record. *Geochimica et Cosmochimica Acta*, 179, 203-216.
- LaVigne, M., Hill, T. M., Spero, H. J., & Guilderson, T. P. (2011). Bamboo coral Ba/Ca: calibration of a new deep ocean refractory nutrient proxy. *Earth and Planetary Science Letters*, 312(3-4), 506-515.
- Lea, D. W., Shen, G. T., & Boyle, E. A. (1989). Coralline barium records temporal variability in equatorial Pacific upwelling. *Nature*, 340(6232), 373-376.
- Lough, J.M. 2008: Coral calcification from skeletal records revisited. *Marine Ecology Progress Series* Vol. 373: 257-264
- Lough, J. M., and D. J. Barnes. 1992: Comparisons of skeletal density variations in *Porites* from the central Great Barrier Reef. *Journal of Experimental Marine Biology and Ecology* 155:1-25.
- Lough, J. M., & Barnes, D. J. (1997). Several centuries of variation in skeletal extension, density and calcification in massive *Porites* colonies from the Great Barrier Reef: A proxy for seawater temperature and a background of variability against which to identify unnatural change. *Journal of Experimental Marine Biology and Ecology*, 211(1), 29-67. doi:10.1016/s0022-0981(96)02710-4
- Lough, J.M., and D.J. Barnes. 2000: Environmental controls on growth of the massive coral *Porites*. *Journal of Experimental Marine Biology and Ecology* 245:225-243.
- Lough, J. M., and T. F. Cooper. 2011: Earth-Science Reviews New insights from coral growth band studies in an era of rapid environmental change. *Earth Science Reviews* 108:170-184.
- Loya, Y., and L. B. Slobodkin (1971). "The coral reefs of Eilat (Gulf of Eilat, Red Sea). *Symp Zool Soc London*, no 28." 117-139.
- Macintyre, I.G., Smith, S.V. (1974) X-Radiographic studies of skeletal development in coral colonies. *Proceedings of the Second International Coral Reef Symposium*. Vol. 2.

- Mann, M. E., Zhang, Z., Rutherford, S., Bradley, R. S., Hughes, M. K., Shindell, D., Ni, F. (2009). Global Signatures and Dynamical Origins of the Little Ice Age and Medieval Climate Anomaly. *Science*, 326(5957), 1256-1260. doi:10.1126/science.1177303
- Omata, T., Suzuki, A., Sato, T., Minoshima, K., Nomaru, E., Murakami, A., ... & Maruyama, T. (2008). Effect of photosynthetic light dosage on carbon isotope composition in the coral skeleton: Long-term culture of *Porites* spp. *Journal of Geophysical Research: Biogeosciences*, 113(G2).
- Patzold, J. P. 1984: Growth Rhythms Recorded in Stable Isotopes and Density Bands in the Reef Coral *Porites lobata* (Cebu , Philippines). *Coral Reefs*:87–90.
- Pichon M. (2011) *Porites*. In: Hopley D. (eds) *Encyclopedia of Modern Coral Reefs*. *Encyclopedia of Earth Sciences Series*. Springer, Dordrecht.
- Razak, T. B., G. Roff, J. M. Lough, D. Prayudi, N. E. Cantin, and P. J. Mumby. 2019: Long-term growth trends of massive *Porites* corals across a latitudinal gradient in the Indo-Pacific. *Marine Ecology Progress Series* 626:69–82.
- Reed, E. V., J. E. Cole, J. M. Lough, D. Thompson, and N. E. Cantin. 2019: Linking climate variability and growth in coral skeletal records from the Great Barrier Reef. *Coral Reefs* 38:29–43.
- Rustic, G. T., Koutavas, A., Marchitto, T. M., & Linsley, B. K. (2015). Dynamical excitation of the tropical Pacific Ocean and ENSO variability by Little Ice Age cooling. *Science*, 350(6267), 1537–1541.
- Sayani, H. R., Cobb, K. M., DeLong, K., Hitt, N. T., & Druffel, E. R. M. (2019). Intercolony $\delta^{18}\text{O}$ and Sr/Ca variability among *Porites* spp. corals at Palmyra Atoll: Toward more robust coral-based estimates of climate. *Geochemistry, Geophysics, Geosystems*, 20, 5270–5284.
- Schneider RC, Smith SV (1982) Skeletal Sr content and density in *Porites* spp. in relation to environmental factors. *Mar Biol* 66:121-131
- Smith, L. W., D. Barshis, and C. Birkeland. 2007: Phenotypic plasticity for skeletal growth, density and calcification of *Porites lobata* in response to habitat type. *Coral Reefs* 26:559–567.
- Smith, S. V. (1981). The Houtman Abrolhos islands: Carbon metabolism of coral reefs at high latitude. *Limnology and Oceanography*, 26(4), 612-621.
- Stephans, C. L., T. M. Quinn, F. W. Taylor, and T. Correge (2004), Assessing the reproducibility of coral-based climate records, *Geophys. Res. Lett.* , 31, L18210
- Stimson JS (1978) Mode and timing of reproduction in some common hermatypic reef corals at Hawaii and Enewetak. *Mar Biol* 48:173-184
- Storz, D., and E. Gischler. 2011: Coral extension rates in the NW Indian Ocean I: Reconstruction of 20th century SST variability and monsoon current strength. *Geo-Marine Letters* 31:141–154.

- Suzuki, A., M. K. Gagan, K. Fabricius, P. J. Isdale, I. Yukino, and H. Kawahata. 2003: Skeletal isotope microprofiles of growth perturbations in *Porites* corals during the 1997-1998 mass bleaching event. *Coral Reefs* 22:357–369.
- Suzuki, A., Hibino, K., Iwase, A., & Kawahata, H. (2005). Intercolony variability of skeletal oxygen and carbon isotope signatures of cultured *Porites* corals: Temperature-controlled experiments. *Geochimica et Cosmochimica Acta*, 69(18), 4453–4462. <https://doi.org/10.1016/j.gca.2005.05.018>
- Trueman, M., & d'Ozouville, N. (2010). Characterizing the Galapagos terrestrial climate in the face of global climate change. *Galapagos Research*, 67, 26–37.
- Weber JN, White EW, Weber PH (1975b) Correlation of density banding in reef coral skeletons with environmental parameters: the basis for interpretation of chronological records preserved in the coralla of corals. *Paleobiology* 1:137-149
- Wellington, G. M., and P. W. Glynn. 1983: Environmental influences on skeletal banding in eastern pacific (Panama) corals.
- Wellington, G. M., R. B. Dunbar, and G. Merlen. 1996: Calibration of stable oxygen isotope signatures in Galapagos Corals. *Paleoceanography* 11:467–480.
- Zamani, N. P., A. Arman, and Lalang. 2016: The Growth Rate of Coral *Porites Lutea* Relating to the El Niño Phenomena at Tunda Island, Banten Bay, Indonesia. *Procedia Environmental Sciences* 33:505–511.
- Zhang, Y.C., Rossow, W.B. and Lacis, A.A., 1995. Calculation of surface and top of atmosphere radiative fluxes from physical quantities based on ISCCP data sets: 1. Method and sensitivity to input data uncertainties. *Journal of Geophysical Research: Atmospheres*, 100(D1), pp.1149-1165.

11 Curriculum Vitae

Jessie McCraw
Tuscaloosa, AL

Education

- 01/2021 University of Alabama, Tuscaloosa, Alabama
PhD Student and Graduate Council Fellow, Department of Geological Sciences
Advisor: Dr. Tom Tobin
- 08/2018–12/2020 Syracuse University, Syracuse, New York
M.S. Student and Syracuse University Fellow, Department of Earth Sciences
Advisor: Dr. Linda Ivany
- 08/2014–05/2018 University of Arizona, Tucson, Arizona
B.S., Geosciences, Emphasis in Earth Systems, Department of Geosciences
Minor in Ecology and Evolutionary Biology
Cum Laude and Honors

Research Interests

I am interested in Marine Paleobiology, Paleoecology, Invertebrate Paleontology, and Geochemistry. My research questions ultimately center around the relationship between the geochemistry of the shells of extinct cephalopods and their paleoenvironment and paleobiology.

Research Experience

- 2021-Present PhD Student, Paleobiology Laboratory, University of Alabama, under the supervision of Dr. Tom Tobin
- 2018-2020 M.S. Student, Paleobiology Laboratory, Syracuse University, under the supervision of Dr. Linda Ivany
- 2017– 2018 Research Assistant, Paleoclimate Laboratory, University of Arizona, worked under the supervision of Dr. Julia Cole
 - Honors Senior Thesis Student
 - NSF REU, *Reconciling divergent histories of Eastern Pacific climate with new coral data from Galápagos (Ecuador)*, Advised by P.I. Julia Cole
- 2015 – 2017 Laboratory Assistant, Radiogenic Isotope Laboratory, University of Arizona, worked under the supervision of Dr. Mihai Ducea
- 2014-2015 Volunteer Researcher, Arizona LazerChron Laboratory, University of Arizona, worked under the supervision of Dr. George Gehrels

Publications and Presentations

- Papers** **McCraw J.**, Judd, E., Cole, J., Vetter, L., Ivany, L., Tudhope, A., Edwards, L.R
Intra-annual timing of coral extension using multiproxy geochemical Pacific coral records
In Prep

Oral Presentations **McCraw, J.**, Judd, E., Cole, J., Vetter, L., Ivany, L., Tudhope, A., Edwards, L.R.

Talk: Intra-annual variation in coral extension rate using multiproxy geochemical records from Pacific corals

McCraw M.S. Thesis Defense, Syracuse, NY, December 2020.

McCraw, J., Judd, E., Cole, J., Vetter, L., Ivany, L., Jimenez, G., Tudhope, A., Edwards, L.R.

Talk: A multiproxy investigation of fossil coral growth rate and paleoclimate in the Galapagos during the Little Ice Age

Presented at 2019 WAGGS Graduate Student Research Seminar, Syracuse, NY, 19 April 2019.

Poster Presentations

McCraw, J. J.E. Cole, L. Vetter

Talk: History of ENSO in the 16th Century using fossil coral geochemistry *Presented at 2018 University of Arizona GeoDaze Research Symposium, Tucson, AZ, 13 April 2018.*

McCraw, J., Judd, E., Cole, J., Vetter, L., Ivany, L., Jimenez, G., Tudhope, A., Edwards, L.R. A multivariate record of Eastern Equatorial Pacific paleoclimate from a fossil Galapagos Coral

Poster, presented at 2019 Central New York Earth Science Student Symposium, Syracuse NY

McCraw, J., Cole, J., Vetter, L., Cheung, A., Jimenez, G., Tudhope, A., and Edwards, L.R. A multivariate record of eastern Pacific climate from a fossil Galápagos coral, CE 1571-1626

Poster, presented at 2018 Fall Meeting of GSA in Indianapolis, IN

McCraw, J., Profeta, L.R., Ducea, M., and Gehrels, G. Depth Proxies For Hadean to Paleoproterozoic Felsic Rock Forming Processes as Revealed by LA/YB Coupled With U-PB Dating of Jack Hills Zircons

Poster, presented at 2016 Fall Meeting of GSA in Denver, CO

McCraw, J., Profeta, L.R., Ducea, M., and Gehrels, G. Granitoid Forming Processes in the Hadean From Trace Elements in Jack Hills Zircons

Poster, presented at 2016 Graduate and Professional Student Council Conference at University of Arizona

McCraw, J., Gehrels, G., and Kapp, J. Detrital Zircon Ages and the Implied Geohistory of Quartzite from the Aracuaí Orogen of Eastern Brazil

Poster, presented at 2015 Honors First Year Project Showcase

McCraw, J., Gehrels, G., Mazzone, P., DeWitt, and K., Fleming, E. Igneous and Detrital Zircon Ages and the Implied Geohistory of Rock Slabs from Brazil

Poster, presented at 2015 Geodaze Symposium at University of Arizona

McCraw, J., Gehrels, G., Arias, J., DePauli, A., Fallon, S., Kolodij N., and Nelson, J. Zircon Ages from the Jack Hills Quartzite, Western Australia

Poster, presented at 2015 Doug Shakel Poster Event, Arizona Geological Society and Arizona State University

McCraw, J., Gehrels, G., Arias, J., DePauli, A., Fallon, S., Kolodij N., and

Nelson, J. Zircon Ages from Conglomerate of the Jack Hills Quartzite, Western Australia

Poster, presented at 2015 Geodaze Symposium at University of Arizona

Technical Skills

Scientific	Familiar with U-Pb geochronology and coral paleoclimate SST methods. Proficient with ICP-OES, Quadrupole, Nu, and Element LA-ICP-MS, SEM, TIMS, Micromill, and acid dissolution, distillation, and titration.
Technology	Experience with MATLAB programming, R programming, L ^A T _E X document preparation, and standard office programs.

Research Funding

2018	Graduate Student Organization Travel Grant, <i>A multivariate record of EEP paleoclimate from a fossil Galapagos coral</i> , Syracuse University, Support to travel to GSA annual meeting
2017	Honors College Legacy Undergraduate Thesis Research Grant, <i>History of El Nino in the Galapagos in the Past Millennium Using Coral Geochemistry</i> , University of Arizona Honors College
2017	George H. Davis Undergraduate Thesis Research Grant, <i>History of El Nino in the Galapagos in the Past Millennium Using Coral Geochemistry</i> , Department of Geosciences, University of Arizona
2017	Honors College Legacy, Conference Travel and Professional Development Grant, <i>Coral Geochemistry</i> , Support to travel to GSA annual meeting
2016	Honors College Legacy, Conference Travel and Professional Development Grant, <i>Jack Hills Quartzite</i> , Support to travel to GSA annual meeting to present

Awards

2021-2022	Graduate Council Fellowship, University of Alabama, Tuscaloosa, Alabama
2018-2019	University Graduate Research Fellow, Syracuse University, New York
2018	Top 10 Finalist, Honors Thesis Elevator Pitch Competition, University of Arizona Honors College
2018	Best Undergraduate Presentation and Talk Award, Department of Geosciences, GeoDaze Research Symposium, University of Arizona
2018	Excellence in Undergraduate Research Award, Department of Geosciences, University of Arizona
2014-2018	Arizona Excellence Scholarship
2014- 2018	Department of Geosciences Tuition Grant
2017	Tucson Gem and Mineral Society Scholarship
2017	American Institute of Professional Geologists Scholarship
2015	Best in Category Winner, Honors First Year Research Project Symposium, University of Arizona Honors College
2015	Best in Showcase Winner, Honors First Year Research Project Symposium, University of Arizona Honors College

Professional Development

2020	Attended Geological Society of America virtual annual meeting, online
2020	Alan Alda Science Communication Workshop, Syracuse University, New York

2019-2020	Graduate Student Organization (GSO) Senator, Student Life Committee, Syracuse University, New York
2019	Attended Geological Society of America annual meeting, Phoenix, AZ
2018	Attended Geological Society of America annual meeting, Indianapolis, IN
2017	Paleontological Society Short Course: <i>Biogeochemical Approaches in Paleobiology and Paleoecology</i> , GSA Annual Meeting in Seattle, WA
2016-2017	University Recognized Professional Development Experience, 100 Percent Engagement Recognition, designed and implemented an intensive professional outreach program
2016	Attended Geological Society of America annual meeting, Denver, CO

Teaching Experience

Fall 2020	Volunteers in the Parks, Resource Education, <i>Badlands National Park</i>
Summer 2020	Geologists in the Parks Internship, Natural Resource Interpreter, <i>Badlands National Park</i>
Spring 2020	Graduate TA, EAR 210: <i>History of Earth and Life</i> , Syracuse University
Fall 2019	Graduate TA, EAR 104: <i>Earth Sciences Laboratory</i> , Syracuse University
2016-2019	Guest Lecturer, <i>Paleontology, Mineralogy, Being a Geologist</i> , Invited speaker at K-12 Schools and Museums (10 lectures total)
Spring 2018	Undergraduate TA, Geos 412 Lab and Field Excursion: <i>Introduction to Oceanography</i> , University of Arizona, Requested TA
Spring 2017	Undergraduate TA, Geos 255 Lab: <i>Historical Geology</i> , University of Arizona, Requested TA
Fall 2016	Undergraduate TA, Geos 302 Lab: <i>Principles of Sedimentology and Stratigraphy</i> , University of Arizona, Requested TA
Spring 2016	Undergraduate TA, Geos 255 Lab: <i>Historical Geology</i> , University of Arizona
Fall 2015	Undergraduate TA, Geos 251 Lab: <i>Physical Geology</i> University of Arizona, Requested TA

Outreach

Fall 2020	Chasing Coral Screening and Panel Discussion, Department of Sustainability and Department of Earth and Environmental Sciences, Syracuse University
2020	GIP Internship, Natural Resource Interpretation, Badlands National Park
2020	Skype a Scientist digital outreach class(es), Paleontology, with grade school students in Bangalore, India and Louisiana homeschool students
2018-Present	Volunteer educator: Geology, Paleontology, Climate, and Women in STEM events. Museum of Science and Technology, Syracuse, NY
2018-2019	Frontiers of Science Coordinator, Syracuse University
2014-2018	Society of Earth Science Students, Outreach Coordinator 2015-2016, President 2016-2018
2016-2017	100 Percent Engagement Coordinator/STEMcat, service project working with STEM Clubs at the University of Arizona and the Pima County Libraries
2016-2018	Tau Beta Sigma band service sorority, Omega Chapter, University of Arizona

Treasurer 1 term
College of Science Ambassador

2015-2018

Field Experience

2020 Paleontology Resource Management and Education, Badlands National Park,
South Dakota

2019: 3 weeks Field assistant, fossil collection from eastern Kansas, Pennsylvanian-Permian

2017: 4 weeks University of Arizona Geology Field Camp
Western Cordillera: Arizona, Utah, Wyoming, Nevada, California
Structural Mapping and Stratigraphy