

Paleoceanography and Paleoclimatology

RESEARCH ARTICLE

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Key Points:

- Coral Sr/Ca is a robust paleothermometer across both temporal and spatial scales in the Red Sea
- Multicoral, multisite mean annual and bulk Sr/Ca-mean SST calibrations are robust and applicable to fossil colonies
- Mean annual temperature drives calibration slope differences in the Red Sea and likely accounts for nearly 30% of variability across the Indo-Pacific

Supporting Information:

- Supporting Information S1
- Data Set S1

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Spatial and Temporal Robustness of Sr/Ca-SST Calibrations in Red Sea Corals: Evidence for Influence of Mean Annual Temperature on Calibration Slopes

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Abstract Sr/Ca ratios recorded in the aragonite skeleton of massive coral colonies are commonly used to reconstruct seasonal- to centennial-scale variability in sea surface temperature (SST). While the Sr/Ca paleothermometer is robust in individual colonies, Sr/Ca-SST relationships between colonies vary, leading to questions regarding the utility of the proxy. We present biweekly-resolution calibrations of Sr/Ca from five Porites spp. corals to satellite SST across 10° of latitude in the Red Sea to evaluate the Sr/Ca proxy across both spatial and temporal scales. SST is significantly correlated with coral Sr/Ca at each site, accounting for 69–84% of Sr/Ca variability ($P \ll 0.01$). Intercolony variability in Sr/Ca-SST sensitivities reveals a latitudinal trend, where calibration slopes become shallower with increasing mean annual temperature. Mean annual temperature is strongly correlated with the biweekly-resolution calibration slopes across five Red Sea sites $(r^2 = 0.88, P = 0.05)$, while also correlating significantly to Sr/Ca-SST slopes for 33 Porites corals from across the entire Indo-Pacific region ($r^2 = 0.26$, P < 0.01). Although interannual summer, winter, and mean annual calibrations for individual Red Sea colonies are inconsistently robust, combined multicoral calibrations are significant at summer ($r^2 = 0.53$, $P \ll 0.01$), winter ($r^2 = 0.62$, $P \ll 0.01$), and mean annual time scales $(r^2 = 0.79, P \ll 0.01)$. Our multicoral, multisite study indicates that the Sr/Ca paleothermometer is accurate across both temporal and spatial scales in the Red Sea and also potentially explains for the first time variability in Sr/Ca-SST calibration slopes across the Indo-Pacific region. Our study provides strong evidence supporting the robustness of the coral Sr/Ca proxy for examining seasonal to multicentury variability in global climate phenomena.

1. Introduction

As the impact of anthropogenic climate change evolves, understanding past climate variability is essential to constraining future variability. Relatively short instrumental climate records, however, limit our knowledge of long-term changes in natural systems (Abram et al., 2016). Temperature observations often extend only to the 19th century, with reliable observations in some tropical regions only available from the mid-20th century (Giese & Ray, 2011; Smith et al., 2008). Paleoclimate archives overcome the limitations of instrumental records by recording climate variability over past centuries and beyond (Gagan et al., 2000; Grottoli, 2001; Jones et al., 2009; Lough, 2004).

Massive coral colonies provide multicentury climate records at subannual resolution due to their annual density banding and high linear extension rates (Corrège, 2006; Grottoli, 2001; Grottoli & Eakin, 2007). As corals grow, chemicals are incorporated into their skeletons based on the physical conditions of the surrounding seawater (Gagan et al., 2000). The Sr/Ca ratio in coral aragonite, for example, inversely correlates to variability in sea surface temperature (SST) at the time of deposition (Smith et al., 1979). To reconstruct SST, coral Sr/Ca measured from the uppermost skeleton in living corals is ideally calibrated to local in situ or gridded SST data (Beck et al., 1992; Corrège, 2006). The calibration is then applied down core to reconstruct SST variability for decades to centuries. Some studies have previously applied calibrations utilizing local SST across colonies to reconstruct seasonal to interdecadal Sr/Ca-SST anomalies (e.g., Felis et al., 2004, 2012). However, colonyspecific calibrations are necessary to reconstruct absolute SSTs, making the accuracy of calibrations crucial (e.g., DeLong et al., 2014; Linsley et al., 2000). Many studies have demonstrated that Sr/Ca is a robust paleothermometer (e.g., Alibert & McCulloch, 1997; Beck et al., 1992; Bolton et al., 2014; Calvo et al., 2007; Corrège et al., 2000; DeLong et al., 2007, 2011, 2012; Fallon et al., 2003; Gagan et al., 1998; Heiss et al., 1997; Hendy et al., 2002; Linsley et al., 2000, 2004; Marshall & McCulloch, 2001; Pfeiffer et al., 2009; Quinn & Sampson, 2002; Quinn et al., 2006; Ramos et al., 2017; Stephans et al., 2004; Sagar et al., 2016; Wu et al., 2013, 2014), although caution must be used during sampling to avoid nontemperature artifacts. Cold-temperature biases in the Sr/Ca temperature proxy can result when sampling massive corals with large corallites (e.g., *Orbicella faveolata* and *Diploria strigosa*) along different skeletal structures, including the columella and corallite walls (Giry et al., 2010; Smith et al., 2006). Massive corals with smaller corallites (e.g., *Porites lobata/lutea*) instead show cold-temperature biases in Sr/Ca when sampling corallites found in the "valleys" of the fan-like structure (Alibert & McCulloch, 1997; Cohen & Hart, 1997), and warm temperature biases when sampling corallites that extend at an angle to the slab surface (DeLong et al., 2007, 2013). Careful sampling is thus necessary to accurately reconstruct SST using the coral Sr/Ca, and indeed any, proxy.

Even with proper sampling techniques, Sr/Ca variability across colonies, both between and within different genera, requires further careful calibration. It has long been established that there are significant intergeneric differences in Sr/Ca-SST sensitivities (e.g., de Villiers et al., 1994; Weber, 1973). To avoid potential discrepancies, previous work has focused on single genus calibrations, primarily reconstructing SST using Porites corals in the Indo-Pacific (Alibert & McCulloch, 1997; Beck et al., 1992; Bolton et al., 2014; Corrège et al., 2000; Heiss et al., 1997; Linsley et al., 2004; Wu et al., 2014) and Diploria and Siderastrea corals in the Atlantic (DeLong et al., 2011, 2014; Giry et al., 2012; Goodkin et al., 2005, 2007; Hetzinger et al., 2006, 2010). However, even within a single genus, mean Sr/Ca can differ spatially in the modern ocean (Corrège, 2006) due to variability in the Sr/Ca ratio in seawater, influenced by oceanographic processes such as upwelling and coastal runoff (de Villiers et al., 1994; Shen et al., 1996; Sun et al., 2005). The difference in mean Sr/Ca becomes even more pronounced during glacial periods, owing to the erosion of aragonite on exposed continental shelves (Stoll & Schrag, 1998). Additionally, offsets in mean Sr/Ca ratios between modern coral colonies from vital and local effects can influence mean SST reconstructions from fossil corals (Felis et al., 2004, 2012, 2014; Giry et al., 2012; Linsley et al., 2006). With such spatial and intercolony disparities, Sr/Ca must be carefully compared to SST for each location in order to reconstruct absolute SST, as generalized calibrations that incorporate data influenced by different oceanographic conditions may result in inaccurate SST estimates when applied to individual records (Alpert et al., 2016).

With no universal calibration, studies commonly utilize individual colony-specific and local intraspecies calibrations applied downcore or to locally collected fossil corals. Published slopes for subannual resolution calibrations range from -0.04 to -0.08 mmol mol⁻¹ °C⁻¹ for Porites corals, with average slopes of -0.06 mmol mol⁻¹ °C⁻¹ (Corrège, 2006). Although Gagan et al. (2000) determined that the slopes were overall similar, shallower slopes of -0.042 mmol mol⁻¹ °C⁻¹ (±0.001; ordinary least squares [OLS]; Sagar et al., 2016), and -0.054 mmol mol⁻¹ °C⁻¹ (±0.002; OLS; Bolton et al., 2014) are statistically different from steeper slopes of $-0.068 \text{ mmol mol}^{-1} \circ \text{C}^{-1}$ (±0.002; OLS; Ramos et al., 2017), $-0.063 \text{ mmol mol}^{-1} \circ \text{C}^{-1}$ (±0.005; OLS; Wu et al., 2014), and −0.0593 mmol mol⁻¹ °C⁻¹ (±0.0006; OLS; Marshall & McCulloch, 2001). Previous studies have attributed these differences to numerous factors, including biological or kinetic processes (e.g., Allison & Finch, 2004; Gagan et al., 2012), spatial differences in seawater Sr/Ca (de Villiers, 1999; de Villiers et al., 1994; Shen et al., 1996), interlaboratory offsets (Hathorne et al., 2013), and methodological differences (DeLong et al., 2010). For example, DeLong et al. (2010) suggest that continuous milling of the coral skeleton (e.g., DeLong et al., 2010; Quinn et al., 1996) may reduce climate signal variability due to time averaging, in contrast with drilling discrete amounts of coral skeleton at defined increments (e.g., Felis et al., 2004; Linsley et al., 2000). Varying sampling resolutions present further potential for error in resolving climate signals, where lower-resolution (e.g., bimonthly) records may result in decreased variability compared with higher resolution monthly or submonthly records (DeLong et al., 2010). Furthermore, uncertainty in age assignment can increase if inflection points of the Sr/Ca record are not included as tie points (in addition to the maxima and minima) when aligning the record with instrumental SST (DeLong et al., 2014). Thus, factors ranging from varying methodologies to oceanographic and biological differences may influence discrepancies in the sensitivity of Sr/Ca to SST observed in subannual resolution single colony calibrations.



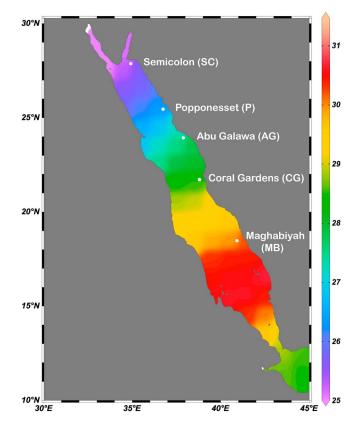


Figure 1. Map of Red Sea study sites. Drill cores from massive Porites *spp*. coral colonies were collected along a north-south transect on the eastern edge of the Red Sea (white circles) between 2008 and 2010. The sites span roughly 10° of latitude. The coloring indicates mean annual sea surface temperature in °C from 1986 to 2010.

Additional differences between Sr/Ca-SST sensitivities can occur when comparing calibrations that do not similarly account for bio-smoothing effects. In order to reconstruct low-frequency variability in mean SST, Gagan et al. (2012) argue that seasonally resolved calibrations must be rescaled to account for bio-smoothing of the records during the formation of the calcium carbonate skeleton in the tissue layer. This rescaling results in Sr/Ca-SST sensitivities ranging between -0.08 and -0.09 mmol mol⁻¹ °C⁻¹, which is much steeper than the average sensitivity of -0.06 mmol mol⁻¹ °C⁻¹ reported by Corrège (2006). One approach to overcome potential bio-smoothing effects is to compare bulk Sr/Ca to mean SST across sites experiencing variable average temperatures (Gagan et al., 2012). The calibration of mean Sr/Ca to mean SST for sites across the southwestern Pacific Ocean (DeLong et al., 2010) reveals a sensitivity of -0.089 mmol mol⁻¹ °C⁻¹, which is within the range of rescaled calibration slopes, but much steeper than calibrations that do not account for bio-smoothing effects. This regional "core-top" calibration exemplifies the importance of examining the influence of mean temperature on the Sr/Ca proxy regionally. However, no study has yet evaluated the influence of mean annual SST on individual-colony Sr/Ca-SST slopes, which can vary significantly across scales from reefs to ocean basins. The Red Sea, oriented on a north-south axis over roughly 15° of latitude, provides a distinct region optimal for examining both the strength of the Sr/Ca proxy across temporal and spatial scales, as well as the contribution of mean annual SST to variability in Sr/Ca-SST sensitivities.

In this paper, we present Sr/Ca-SST calibrations from five *Porites* corals in the Red Sea to examine the temporal and spatial coherency of the Sr/Ca paleothermometer. Through individual and multiple-coral calibrations, we find that Sr/Ca is a robust proxy for SST at both biweekly and interannual time scales, across nearly 10° of latitude in the Red Sea. We also examine the influence of mean annual temperature on

calibration slope variability in the Red Sea and the entire Indo-Pacific region. Our study emphasizes the strength of Sr/Ca as a paleothermometer and may further constrain the factors that drive spatial differences in calibrations throughout the Indo-Pacific region.

2. Methods

2.1. Study Sites

Between 2008 and 2010, five living *P. lutea* coral colonies (3–5 m depths) were drilled along a north-south transect of the Red Sea using an underwater hydraulic drill (Semicolon [SC]: 27.98°N, 34.81°E; Popponesset [P]: 25.58°N, 36.55°E; Abu Galawa [AG]: 23.75°N, 37.97°E; Coral Gardens [CG]: 21.78 N, 38.83°E; Maghabiyah [MB]: 18.27°N, 40.74°E; Figure 1). Spanning roughly 10° of latitude, the sites vary in average annual ranges of SST. The northernmost SC has an SST range of 22.0 °C to 29.7 °C, while southernmost MB ranges from 26.5 °C to 32.3 °C (see section 2.3 for information of the satellite-derived SST product used). Mean annual temperatures are 25.4 °C (SC), 26.9 °C (P), 27.8 °C (AG), 28.4 °C (CG), and 29.8 °C (MB) for the calibration period of each coral record (see section 2.2).

2.2. Coral Sampling and Analysis

Cores were split parallel to the maximum growth axis and cut into 1-cm-thick slabs at the Woods Hole Oceanographic Institution. Prior to sampling and analysis, the slabs were cleaned in an ultrasonic bath of deionized water and dried at 50 °C overnight. X-radiographs were taken using 65 kV, 2 mAs, and a focal distance of 30 cm to visualize the density banding and identify the major growth axis for sampling (see Figure S1 in the supporting information). Subsamples were drilled at 0.5-mm (approximately biweekly) resolution along a continuous path using a manual drill press with a 1-mm diameter drill bit. Samples were drilled to

a depth of ~1 mm, controlled by fixing the allowable range of motion of the drill press. The resulting records span 5 (MB), 24 (SC, AG, and CG), and 25 (P) years. From each drilled sample ~250 μ g of coral powder was used for Sr/Ca analysis.

Samples were dissolved in 2 mL of 1 N HNO₃⁻ overnight and analyzed to determine the Sr/Ca ratios using an Inductively Coupled Plasma-Atomic Emission Spectrometer at Woods Hole Oceanographic Institution. Solution standards were used to correct for drift and matrix effects due to varying Ca concentrations (Schrag, 1999). To determine the Sr/Ca precision, an in-house coral standard of homogenized powder from an Indonesian *P. lobata* was repeatedly analyzed, yielding a relative standard deviation of 0.31% (1 σ ; *n* = 453). Accuracy of Sr/Ca was verified against certified coral powder standard JCp-1 (Hathorne et al., 2013), providing an in-house coral standard value of 8.8279 ± 0.0091 mmol mol⁻¹ (1 σ ; *n* = 124 pairs).

2.3. Satellite SST Data

Satellite SST data at 4-km resolution from Advanced Very High Resolution Radiometer (AVHRR) Pathfinder version 5.2 from the U.S. National Oceanographic Data Center and Group for High Resolution Sea Surface Temperature (http://pathfinder.nodc.noaa.gov) were used to calibrate the Sr/Ca records. The Pathfinder version 5.2 data are updated from the 5.0 and 5.1 versions described in Casey et al. (2010). The gridded SSTs were spatially interpolated to obtain biweekly SST records at the GPS coordinates for each site, as listed in section 2.1. The AVHRR SST data also contain relative quality scores for each data point, calculated using a series of tests (Kilpatrick et al., 2001). A quality value of 0 is the lowest quality, while a value of 7 indicates the highest quality data. The National Oceanographic Data Center recommends using data with quality scores between a minimum of 4 and 7. For our study, low-quality data with a score less than 5 for each record were removed. Removing low-quality data resulted in some short gaps in the SC and P time series (SC: 1995, 2002; P: 2001, 2002).

2.4. Age Model Development and Calibration

Subannual age models for the Sr/Ca records were developed with the AVHRR SST product using Analyseries version 2.0 software (Paillard et al., 1996). Minima, maxima, and inflection points of the Sr/Ca seasonal cycle were tied respectively to SST maxima, minima, and inflection points each year. Sr/Ca values were then resampled at biweekly resolution using linear interpolation to match the AVHRR SST product. Calibrations of paired Sr/Ca and SST were performed using reduced major axis (RMA) linear regressions at biweekly and interannual time scales. RMA regression differs from the commonly employed ordinary least squares (OLS) regression by assuming error in both the dependent and independent variables. For this reason, we employ RMA regressions throughout our study, in addition to OLS regressions that are included to facilitate comparison to published work. For both regression techniques, the SC and P calibrations do not include years where there was insufficient high-quality SST data to calibrate the Sr/Ca proxy (see section 2.3). Interannual winter- and summer-averaged calibrations were calculated using the coldest 1 and warmest 2.5 consecutive months each year, respectively, based on the satellite SST data. The difference in the temporal length of the summer and winter averages is due to the asymmetrical structure of SST seasonality in the Red Sea. Regionally, coldest temperatures occur rapidly, while higher summer temperatures extend over a more sustained period.

2.5. Calculation of Extension Rates

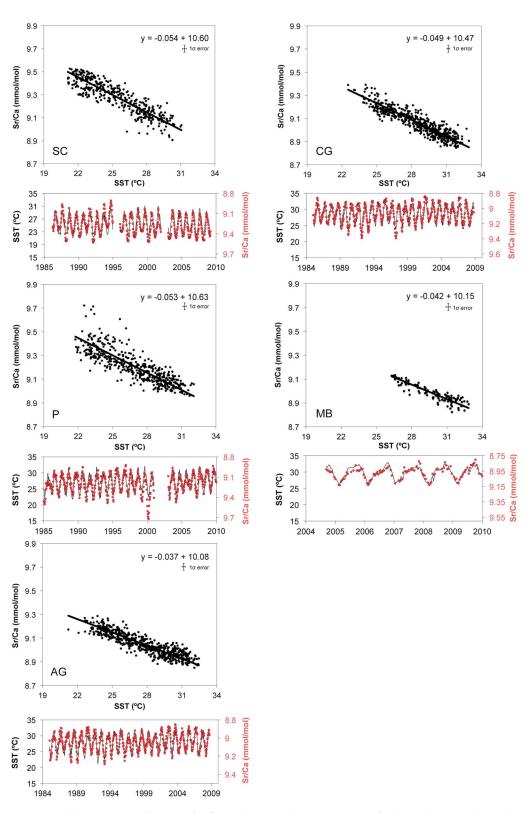
The annual extension rate of each coral was calculated from the distance between Sr/Ca maxima for consecutive years. The calculated extension rates were then regressed against winter, summer, and mean annual Sr/Ca for each coral to determine whether growth rate significantly influences coral Sr/Ca in the Red Sea corals.

3. Results

3.1. Individual Biweekly Calibrations

Coral Sr/Ca at SC, P, AG, CG, and MB in the Red Sea all show seasonal cycles that inversely correspond to AVHRR SST (Figure 2). Highest SSTs occur on average from July and August (SC, P, AG, and CG) or September and October (MB), while coldest SSTs occur in February and March in all corals. RMA linear regressions of biweekly Sr/Ca to AVHRR SST reveal significant relationships at all sites (Figure 2 and Table 1),





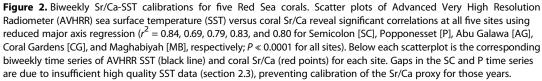


Table 1 Sr/Ca-SST Calibrations Using Red Sea Porites Corals								
Coral site	т	1σ _m	b	1σ _b	r ²	n	Р	
Eilat (Felis et al., 2004)	-0.0597	0.005	10.78	0.12	0.78	NA	NA	
Semicolon (SC)	-0.054	0.001	10.60	0.03	0.84	387	«0.00	
Popponesset (P)	-0.053	0.001	10.63	0.04	0.69	461	«0.00	
Abu Galawa (AG)	-0.037	0.001	10.08	0.02	0.79	566	«0.00	
Coral Gardens (CG)	-0.049	0.001	10.47	0.03	0.83	552	«0.00	
Maghabiyah (MB)	-0.042	0.002	10.15	0.05	0.80	114	«0.00	

Note. Calibrations as follows: Sr/Ca (mmol mol⁻¹) = $b + m * SST(^{\circ}C)$. $1\sigma_m$ is the 1σ error of the slope, $1\sigma_b$ is the 1σ error of the *y*-intercept, r^2 is the square of the correlation coefficient, *n* is the number of data points used in the regression, and *P* is the *P* value of the regression. For sites from our study, calibrations were performed using reduced major axis (RMA) regression. The Felis et al. (2004) calibration was performed using ordinary least squares (OLS) regression.

although some individual calibration slopes differ (Table 1). Notably, northernmost SC has the steepest calibration slope and is within error of a previously published calibration slope for Eilat in the Gulf of Aqaba, northern Red Sea (Felis et al., 2004; OLS regression). The Red Sea calibration slopes are overall shallower than most published, seasonally resolved, *Porites* Sr/Ca-SST calibrations (e.g., Corrège, 2006, and references therein; Bolton et al., 2014; DeLong et al., 2007; Nurhati et al., 2011; Ramos et al., 2017; Wu et al., 2013, 2014; Zinke et al., 2014), although with the exception of AG, all are within the range of reported values. The dampened slopes in the Red Sea may be due to a flattened Sr/Ca-SST relationship at maximum temperatures. To investigate further, we calculated interannual Sr/Ca-SST calibrations at each of the five sites for mean winter, summer, and annual SSTs.

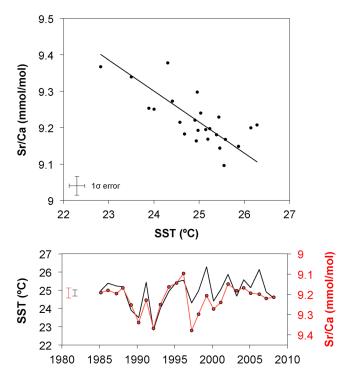


Figure 3. Example of an interannual winter-average Sr/Ca-sea surface temperature (SST) calibration for Coral Gardens (CG). (top) Scatterplot of Advanced Very High Resolution Radiometer (AVHRR) SST versus CG Sr/Ca for 1-month winter averages. Reduced major axis regression (black line) reveals a significant relationship ($r^2 = 0.53$, $P \ll 0.0001$) for the calibration period 1985–2009. (bottom) Time series of AVHRR SST (black line) and CG coral Sr/Ca (red line and points) for the coldest 1 month each year. The error bars represent 1 σ error.

3.2. Individual Interannual Calibrations

Reduced major axis linear regressions of winter Sr/Ca to winter AVHRR SST reveal significant relationships for SC, AG, CG, and MB (Table S1 in the supporting information). Results for CG are shown as an example in Figure 3. No winter relationship was found for P, likely due to the high Sr/Ca values in the winters of 1999 and 2000. These years are near the bottom of the first slab (1A), where the skeletal structure appears to be more disorganized (see Figure S1). The lack of coherent corallite structure may contribute to the augmented Sr/Ca values, similar to the cold temperature biases observed by DeLong et al. (2013) when sampling disorganized coral slab sections. RMA linear regressions of mean annual Sr/Ca to AVHRR SST are significant for SC, P, AG, and CG (Table S2). No relationship was found for MB, likely due to the limited temporal period of the calibration caused by alteration of the aragonite skeleton down core. Additionally, a significant summer interannual relationship was only found at P ($r^2 = 0.31$, P = 0.01). Average extension rates for SC, P, AG, CG, and MB are 0.90 (± 0.23), 1.1 (±0.32), 1.3 (±0.15), 1.4 (±0.16), and 1.5 (\pm 0.06) cm yr⁻¹, respectively. Coral Sr/Ca was not significantly correlated with average annual extension rates for winter, summer, or mean annual time scales at any site. The lack of consistent sensitivity of Sr/Ca to SST at interannual time scales is likely due to the relatively small signal in seasonally averaged data, compared to the full range of biweekly resolution calibrations. We therefore investigate whether using multiple corals to increase the range of temperature variability can increase the significance and strength of the calibrations.

3.3. Multicoral Calibrations

Reduced major axis regression of biweekly Sr/Ca and SST for all sites together results in a significant relationship with an intermediate slope (Figure 4):



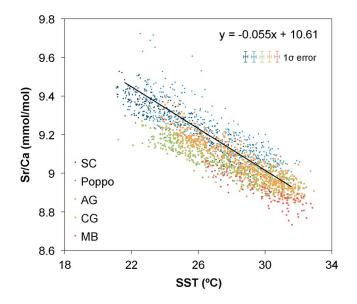


Figure 4. Combined multicoral biweekly Sr/Ca-sea surface temperature (SST) calibration. Sr/Ca versus Advanced Very High Resolution Radiometer SST data are plotted for each site: Semicolon (SC, dark blue), Popponesset (P; light blue), Abu Galawa (AG, green), Coral Gardens (CG, orange), and Maghabiyah (MB, red). Reduced major axis regression through all points combined (black line) reveals a significant, biweekly-resolution calibration ($r^2 = 0.72$, $P \ll 0.0001$).

$$Sr/Ca = 10.61 (\pm 0.02) - 0.055 (\pm 0.001)^* SST (1\sigma, r^2 = 0.72, P << 0.0001, n = 1,829)$$
(1)

Multicoral combined winter and summer interannual calibrations also show significant relationships (Figure 5 and Table 2). In each case, the combined correlations are stronger than the individual-coral calibrations, likely due to the extended temperature ranges reducing the amount of noise relative to signal. The combined calibrations reveal steeper slopes compared to the biweekly-resolution regressions and are more similar to the majority of previously published slopes, which average 0.06 mmol mol⁻¹ °C⁻¹ (Corrège, 2006). The combined winter calibration yields the steepest slope (-0.083 mmol mol⁻¹ °C⁻¹), while the combined summer calibration has a shallower slope of -0.068 mmol mol⁻¹ °C⁻¹. To facilitate comparison with the majority of published studies, we also calculate slopes using OLS rather than RMA regressions. This again reveals slightly steeper relationships for colder temperatures than for warm, with winter and summer slopes of -0.065 and -0.049 mmol mol⁻¹ °C⁻¹, respectively (Figure S2 and Table S3).

Similar to the winter and summer interannual calibrations, a multicoral combined mean annual RMA calibration is also significant (Figure 5 and Table 2) and is stronger than the individual-coral mean annual calibrations. The combined mean annual calibration reveals an intermediate slope of -0.074 mmol mol⁻¹ °C⁻¹ when compared to the combined

summer and winter interannual calibrations. OLS regression of the combined mean annual calibration also reveals a significant relationship, where the slope ($-0.063 \text{ mmol mol}^{-1} \text{ °C}^{-1}$) is similar to that of the winter interannual calibration (Figure S2 and Table S3). With both RMA and OLS regression, the combined mean annual calibration slope is steeper than those of the biweekly resolution regressions (Tables 1 and S4), though

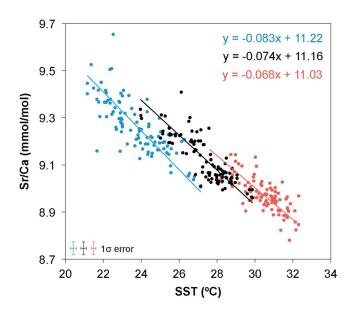


Figure 5. Combined multicoral interannual Sr/Ca-sea surface temperature (SST) calibrations. Reduced major axis regressions of Advanced Very High Resolution Radiometer SST and Sr/Ca for 1-month winter (blue), mean annual (black), and 2.5-month summer (red) data for the five sites combined reveal significant relationships ($r^2 = 0.62$, 0.73, and 0.53, respectively; $P \ll 0.0001$ for all). The winter calibration has the steepest slope, and the summer slope is the shallowest (-0.083 and -0.068 mmol mol⁻¹ °C⁻¹, respectively).

not as steep as the mean annual slope reported in Felis et al. (2009; $-0.140 \text{ mmol mol}^{-1} \text{ °C}^{-1}$). While Felis et al. invoked calcification and coral physiology to explain the steeper mean annual slope compared to their seasonal calibration, our moderate mean annual Sr/Ca sensitivity does not imply the influence of vital effects.

Mean annual AVHRR SST, averaged over the entire calibration period for each coral, was additionally regressed using RMA regression against mean Sr/Ca across all sites to perform a bulk or "core-top" Sr/Ca-SST calibration. This calibration (not shown) reveals a robust relationship ($r^2 = 0.92$, P = 0.01) with a slope (-0.081 mmol mol⁻¹ °C⁻¹) similar to that of the winter interannual calibration.

3.4. Calibration Slopes Versus Mean Annual Temperature

Calibration slopes from both OLS and RMA regression become shallower with decreasing latitude in the Red Sea (Tables 1 and S4). Mean annual AVHRR SST was regressed against the individual Sr/Ca-SST RMA calibration slopes for the Red Sea corals to assess the influence of mean annual temperature on the decreasing sensitivity of the Sr/Ca proxy. This regression reveals a positive correlation, where the relationship is significant with AG removed as an outlier ($r^2 = 0.86$, P = 0.07; Table 3 and Figure 6a). Performing the regression using OLS calibration slopes allows for the inclusion of Eilat (Felis et al., 2004) and does not change the trend of decreased slope with increased mean annual temperature. In fact, the relationship is significant with and without AG ($r^2 = 0.67$ and 0.88, respectively; P < 0.05 for both;

Combined Sr/Ca-SST Calibrations Using Red Sea Porites Corals								
Calibration	т	1σ _m	b	1σ _b	r ²	n	Р	
Combined winter	-0.083	0.006	11.22	0.13	0.62	97	«0.0001	
Combined summer	-0.068	0.005	11.03	0.15	0.53	98	«0.0001	
Combined mean annual	-0.074	0.004	11.16	0.11	0.73	97	«0.0001	

Note. Calibrations as follows: Sr/Ca (mmol mol⁻¹) = $b + m^*$ SST (°C). $1\sigma_m$ is the 1σ error of the slope, $1\sigma_b$ is the 1σ error of the y-intercept, r^2 is the square of the correlation coefficient, n is the number of data points used in the regression, and P is the P value of the regression. Regressions performed using reduced major axis (RMA) regression.

Table 3 and Figure 6b). This mean annual temperature influence is likely not impacted by the variable growth rates between the northern and southern Red Sea, as no significant relationship was found between average growth rates and biweekly calibration slope across the five Red Sea sites, with or without the AG site.

To assess the influence of mean annual temperature on calibration slopes across the entire Indo-Pacific region, we compiled data from all studies using Porites spp. corals and OLS regression where we could determine (1) the mean annual SST using the same SST record used to derive the calibration, (2) a weekly to bimonthly resolution calibration where SST accounted for at least 50% of variability in Sr/Ca, and (3) a calibration slope that the paper determined was robust enough to reconstruct SST at their site (see Table 4 for a complete list of included studies). In instances where local or in situ SST data were used, we calculated mean annual SST at the coral site using 1° × 1° Integrated Global Ocean Services System SST (http://iridl.ldeo.columbia.edu/SOURCES/.IGOSS/.nmc/.Reyn_SmithOlv2/), as this product is most commonly employed for calibrations. Mean annual SST is significantly correlated with the individual Sr/Ca-SST slopes from the Red Sea sites and the published studies ($r^2 = 0.26 P = 0.003$), revealing a similar slope compared to the Red Sea regional relationship (Table 3 and Figure 6c).

Mean annual temperature is also significantly inversely correlated with SST seasonality for sites across the Red Sea (including Eilat) with and without the AG outlier ($r^2 = 0.67$ and 0.79, respectively, P < 0.05 for both; Figure S3). Similarly, sites across the Indo-Pacific (Table 4) also reveal a decrease in the SST range with increasing mean annual temperature ($r^2 = 0.28$, P = 0.002; Figure S3).

4. Discussion

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Table 2

Significant biweekly-resolution Sr/Ca-SST calibrations from six corals suggest that Sr/Ca is a robust paleothermometer throughout the Red Sea. In each case, the calibration is strong, where changes in SST account for 69 to 84% of the coral Sr/Ca variability ($r^2 = 0.69$, 0.79, 0.80, 0.83, and 0.84), similar to a calibration from Eilat in the northern Red Sea, where SST accounted for 78% of Sr/Ca variability (Felis et al., 2004). Our study confirms that the Sr/Ca proxy is robust across spatial scales that extend over much of the Red Sea basin.

While the biweekly calibrations are consistently strong, the sensitivity of Sr/Ca to SST is overall significantly different between sites, revealing a latitudinal trend. Sites in the northern Red Sea exhibit steeper calibration

Coral sites	т	1σ _m	b	1σ _b	r ²	n	Р
RMA							
Red Sea, all sites	0.003	0.002	-0.13	0.05	0.43	5	0.23
Red Sea, no AG	0.003	0.001	-0.12	0.02	0.86	4	0.07
OLS							
Red Sea, all sites (incl. Eilat ^a)	0.003	0.001	-0.14	0.03	0.67	6	0.05
Red Sea, no AG	0.003	0.001	-0.13	0.02	0.87	5	0.02
Red Sea and published studies ^b	0.003	0.001	-0.13	0.02	0.26	33	0.003

Note. Calibrations follow biweekly Sr/Ca-SST calibration slope = $b + m^a$ SST (°C). $1\sigma_m$ is the 1σ error of the slope, $1\sigma_b$ is the 1 σ error of the y-intercept, r^2 is the square of the correlation coefficient, n is the number of data points used in the regression, and *P* is the *P* value of the regression. ^aEilat site from northern Red Sea (Felis et al., 2004).

^bSee Table 4 for all studies included in this calculation.



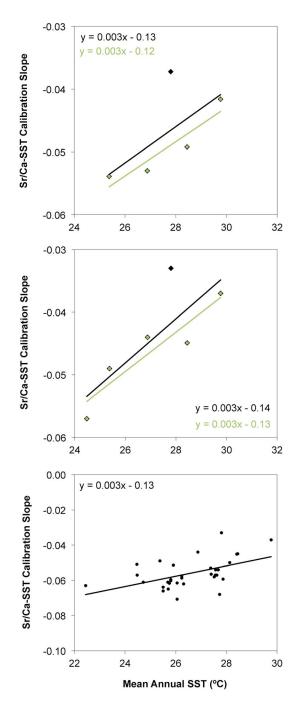


Figure 6. Mean annual sea surface temperature (SST) versus Sr/Ca-SST calibration slope. (top) Sr/Ca-SST reduced major axis calibration slopes plotted against mean annual Advanced Very High Resolution Radiometer SST for each Red Sea site in this study. Regressions of all five sites (black) and all sites except Abu Galawa (AG, green) reveal similar slopes and a significant relationship when the AG site is removed ($r^2 = 0.43$ and 0.86; P = 0.23 and 0.07, respectively). (middle) Sr/Ca-SST ordinary least squares calibration slopes plotted against mean annual AVHRR SST for each Red Sea site. Regressions of all six sites (black, includes Eilat from Felis et al., 2004) and all sites except AG (green) reveal similar slopes and significant relationships ($r^2 = 0.67$ and 0.87; $P \le 0.05$ for both). (bottom) Sr/Ca-SST calibration slopes plotted against mean annual SST for this study together with published calibrations (further information found in Table 4). A regression for all corals combined reveals a significant relationship ($r^2 = 0.26$, P = 0.003), with a similar slope compared to the Red Sea only.

slopes, with the northernmost coral (SC) showing a Sr/Ca-SST sensitivity of $-0.054 \text{ mmol mol}^{-1} \circ \text{C}^{-1}$ (RMA) and $-0.049 \text{ mmol mol}^{-1} \circ \text{C}^{-1}$ (OLS), similar to the observed bimonthly relationship at Eilat (-0.0597; Felis et al., 2004). With decreasing latitude, the RMA and OLS biweekly calibration slopes become successively shallower (with the exception of AG), with calibration slopes for the southernmost coral (MB) of $-0.042 \text{ mmol mol}^{-1} \circ \text{C}^{-1}$ (RMA) and $-0.037 \text{ mmol mol}^{-1} \circ \text{C}^{-1}$ (OLS). Notably, SC, CG, and MB are statistically different with both RMA and OLS regression, showing a significant difference between the northern, central, and southern Red Sea. Eilat (Felis et al., 2004) further supports this trend, as it is statistically distinct from all other sites when comparing OLS regression slopes.

Although biological influences on coral skeletal chemistry, or "vital effects," may influence intercolony calibration differences (e.g., Alpert et al., 2016; Cahyarini et al., 2009; de Villiers et al., 1994, 1995; Pfeiffer et al., 2009), it is unlikely that such vital effects are solely responsible for slope discrepancies across the Red Sea. For example, past studies have documented the inconsistent nature of vital effects, showing that the impacts can vary between colonies of the same species in the same location (e.g., de Villiers et al., 1994; Saenger et al., 2008). Though the exact mechanisms remain unclear, these vital effects are likely related to colony-specific differences in coral metabolism, calcification, and extension rates, impacting skeletal Sr/Ca uptake (Alibert & McCulloch, 1997; Cahyarini et al., 2009; de Villiers et al., 1994; Saenger et al., 2008). Coral calcification and extension rates are further influenced by a variety of environmental parameters, including light and nutrient availability, and water turbidity (e.g., de Villiers et al., 1994; Lough et al., 1999; Lough & Cooper, 2011; Tomascik, 1990). The complex relationships between vital effects and coral Sr/Ca suggest that these influences are unlikely to drive coherent spatial variability across the Red Sea, instead suggesting that other, environmental factors may play a role.

Mean annual SST likely contributes to intercolony Sr/Ca-SST calibration differences in the Red Sea. Across the Red Sea, variability in mean annual temperature accounts for 86% of the variability in RMA calibration slopes, once the AG site has been removed. Although including AG produces an overall insignificant relationship, in both cases, we nevertheless find a consistent change in calibration slopes of 0.003 mmol mol⁻¹ °C⁻¹. We find a similar result when examining the influence of mean annual SST on OLS calibration slopes, where mean annual temperature accounts for 87% of the variability, once the AG site is removed. For the OLS regression, including AG produces a significant, but slightly weaker relationship that also has a consistent change in slope of 0.003 mmol mol⁻¹ for each °C of mean annual temperature change. It is important to note that the calibration slope from Felis et al. (2004) was included for both OLS comparisons, suggesting that the mean annual temperature influence is likely coherent across the Red Sea and is not limited to the sites from our study. The influence of mean annual temperature in the Red Sea may be related to the significant reduction of SST seasonality with increasing mean temperature. The Red Sea seasonal temperature range decreases from 7.9 °C at Eilat (Felis et al., 2004) to 5.7 °C at MB, coinciding with the decrease in calibration slopes from north to south. With increasing mean



Table 4

Published Studies With Porites spp. Sr/Ca-SST Calibrations

Reference	т	Mean annual SST	Seasonal SST range	Location	SST product
Alibert & McCulloch (1997)	-0.062	26.06	5.04	GBR, Australia	Local (Integrated Global Ocean Services System SST, IGOSS)
Bolton et al. (2014)	-0.057	27.56	4.54	Vietnam	HadISST
Bolton et al. (2014)	-0.054	27.57	4.54	Vietnam	HadISST
Calvo et al. (2007)	-0.045	28.41	2.82	Coral Sea, Australia	HadISST
Fallon et al. (1999)	-0.063	22.44	10.32	Shikoku Island, Japan	Local (IGOSS)
Fallon et al. (2003)	-0.060	25.80	5.50	GBR, Australia	Local/IGOSS
Fallon et al. (2003)	-0.057	27.40	4.60	GBR, Australia	Local/IGOSS
Fallon et al. (2003)	-0.071	26.06	5.04	GBR, Australia	Local/IGOSS
Fallon et al. (2003)	-0.060	25.80	5.50	GBR, Australia	Local/IGOSS
Felis et al. (2004)	-0.057	24.48	7.89	Eilat, Red Sea	Local (IGOSS)
Felis et al. (2009)	-0.051	24.47	8.28	Ogasawara, Japan	Local (IGOSS)
Felis et al. (2012)	-0.057	27.62	2.72	Tahiti	Local (IGOSS)
Gagan et al. (1998)	-0.062	25.75	5.08	GBR, Australia	IGOSS
Gagan et al. (1998)	-0.066	25.50	5.05	GBR, Australia	IGOSS
Gagan et al. (1998)	-0.064	25.50	5.03	GBR, Australia	IGOSS
Heiss et al. (1997)	-0.061	25.69	4.92	Réunion	Local (IGOSS)
Linsley et al. (2000) ^a	-0.065	25.70	5.32	Raratonga	IGOSS
Linsley et al. (2004)	-0.053	27.38	3.31	Fiji	IGOSS
Marshall and McCulloch (2001)	-0.059	27.87	3.07	Christmas Island	IGOSS
Marshall and McCulloch (2002)	-0.058	26.24	5.00	GBR, Australia	Local (IGOSS)
Marshall and McCulloch (2002)	-0.059	26.24	5.00	GBR, Australia	Local (IGOSS)
Quinn and Sampson (2002)	-0.061	24.72	4.51	New Caledonia	GISST
Ramos et al. (2017)	-0.068	27.73	6.48	Palaui, Philippines	IGOSS
Shen et al. (1996)	-0.051	25.90	5.79	Taiwan	Local (IGOSS)
Wei et al. (2000)	-0.054	27.68	4.22	South China Sea	Local (IGOSS)
Wu et al. (2013)	-0.062	26.31	3.96	Tonga	IGOSS
Wu et al. (2013)	-0.058	27.52	4.18	Fiji	IGOSS
Zinke et al. (2004)	-0.050	28.13	1.57	Madagascar	IGOSS

Note. Sr/Ca-SST calibrations included in Figure 6 and Table 3. Calibrations as follows: Sr/Ca (mmol mol⁻¹) = $b + m * SST(^{\circ}C)$. For all studies, calibrations were performed using ordinary least squares (OLS) regression. ^aCorrected in Linsley et al. (2004).

temperatures resulting in reduced variability in SST seasonality, a greater noise to signal ratio likely obscures the SST signal and leads to the dampened sensitivity of the coral proxy.

Importantly, the influence of mean annual temperature on calibration slopes and SST seasonality continues to be significant when combining studies that utilize different data and analytical techniques across the entire Indo-Pacific region. The compiled studies use varying temperature products, including GISST (1° grid), HadISST (1° grid; replaced GISST), and Integrated Global Ocean Services System SST (1° grid), while also using different analytical technology, including ICP-OES (Bolton et al., 2014; Linsley et al., 2000, 2004; Ramos et al., 2017; Wu et al., 2013; Zinke et al., 2004), SF-ICP-MS (Quinn & Sampson, 2002), LA-ICP-MS (Fallon et al., 1999, 2003; Felis et al., 2012), ICP-MS (Felis et al., 2004, 2009), and ID-TIMS (Alibert & McCulloch, 1997; Calvo et al., 2007; Gagan et al., 1998; Heiss et al., 1997; Marshall & McCulloch, 2001, 2002; Shen et al., 1996; Wei et al., 2000). These studies further differ in their temporal resolution (fortnightly to bimonthly), use differing drilling techniques (continuous and discrete sampling), and use a variable number of tie points to develop the age models (2-6 per year). Yet even with large differences in the methodology, sites from the Indian Ocean, Red Sea, South China Sea, and Pacific Ocean collectively show a similar influence of mean annual temperature on Sr/Ca-SST calibration slopes and SST seasonality. The consistency of the relationship across differing studies and ocean basins suggests that the average water temperatures at which the corals grow may more universally and coherently contribute to variability in the Sr/Ca-SST relationship than individual coral vital effects (e.g., Allison & Finch, 2004; Gagan et al., 2012), differences in Sr/Ca of the seawater (de Villiers, 1999; de Villiers et al., 1994; Shen et al., 1996), interlaboratory offsets (Hathorne et al., 2013), or differing methodologies (DeLong et al., 2010). However, the influence of mean SST on Sr/Ca-SST sensitivities and the seasonal temperature range may not be limited to intercolony differences, but may also extend to intracolony discrepancies.

Differences between average winter and summer SST may explain varying Sr/Ca-SST sensitivities between the two seasons in each coral. At biweekly resolution, the Sr/Ca-SST calibrations are shallower than previously reported seasonal calibrations (e.g., Corrège, 2006, and references therein; Bolton et al., 2014; DeLong et al., 2007; Ramos et al., 2017; Wu et al., 2013, 2014), potentially due to reduced sensitivity of the Sr/Ca proxy at the warmest temperatures in the Red Sea. The inconsistent strength and significance of individual winter- and summer-season interannual calibrations prevent comparisons of the seasonal slopes within any single coral. However, the multicoral winter and summer interannual calibrations reveal a significant difference between winter (-0.083 mmol mol⁻¹ °C⁻¹) and summer (-0.068 mmol mol⁻¹ °C⁻¹) slopes (RMA; Table 2). Seasonal differences are also apparent when OLS regressions are used, resulting in winter and summer slopes of -0.065 and -0.049 mmol mol⁻¹ °C⁻¹, respectively (Figure S2 and Table S3). The shift toward shallower slopes from the winter to summer calibrations could be related to augmented summer-averaged SSTs, similar to the influence of mean annual temperature on subannual calibration slopes. For example, the significant reduction of SST seasonality with mean annual temperature suggests the possibility that higher average SSTs during summer may drive the overall reduced summer temperature range (4.7 °C) compared to winter (6.0 °C). The smaller range of summer SST likely increases the noise to signal ratio and contributes to the dampened Sr/Ca-SST relationship. Because only a few studies have reported both interannual summer and winter (or wet and dry monsoon season) Sr/Ca-SST calibrations (Bolton et al., 2014; Goodkin et al., 2005; Ramos et al., 2017), it is unclear whether seasonal slope differences within individual corals are limited to the Red Sea. However, the influence of mean annual temperature on biweekly calibration slopes observed here suggests a possible influence of season-averaged SST on calibration sensitivities within corals throughout the Red Sea and, potentially, the Indo-Pacific region.

Although Red Sea winter and summer calibration slopes might be explained by season-averaged SST, it is difficult to constrain these relationships quantitatively, limiting our ability to recommend using these multicoral interannual calibrations downcore. In contrast, the multicoral combined biweekly calibration presented here guantifies the Sr/Ca-SST relationship across a larger temperature range than individual corals, and for this reason may be useful in reconstructing absolute SST from fossil corals where no colony-specific calibration is available. However, recent observations of an attenuated Sr/Ca-SST relationship due to bio-smoothing in the tissue layer have raised concerns about the utility of seasonally resolved calibrations to resolve decadal to millennial SST variability (Gagan et al., 2012). Gagan et al. instead suggest rescaling the Sr/Ca-SST relationship based on a slope of -0.084 mmol mol⁻¹ °C⁻¹. Notably, Gagan et al. mention that DeLong et al. (2010) avoided the need to rescale their Sr/Ca-SST relationship by calibrating bulk (mean) coral Sr/Ca to mean SST across sites experiencing a 5 °C range of mean temperature. In comparing our own multisite interannual calibrations, we find that both the winter and mean annual RMA calibrations have slopes (-0.083 and -0.074 mmol mol⁻¹ °C⁻¹, respectively) similar to the 0.08 to 0.09-mmol mol⁻¹ °C⁻¹ range proposed by Gagan et al. (2012) necessary for reconstructing mean SST at low frequencies. Furthermore, our own bulk coral Sr/Ca-SST RMA calibration slope (-0.081 mmol mol⁻¹ °C⁻¹) is similar to the slope determined by DeLong et al. (2010; -0.089 mmol mol⁻¹ °C⁻¹) and the rescaled slope of Gagan et al. (2012), suggesting that our combined mean annual and bulk Sr/Ca-SST calibrations may both be useful in reconstructing mean SST from fossil corals.

Fossil coral temperature reconstructions have previously required the application of modern calibrations from nearby colonies to fossil colonies (e.g., Beck et al., 1992, 1997; Corrège et al., 2000; Gagan et al., 1998; Kilbourne et al., 2004). This is not ideal, however, as nearby colonies may not have identical Sr/Ca-SST relationships or mean Sr/Ca values, particularly if vital effects or local environmental conditions differently influence the corals (Alpert et al., 2016; Cahyarini et al., 2009; Pfeiffer et al., 2009; Saenger et al., 2008). Studies that apply a modern, subannually resolved Sr/Ca-SST calibration to a fossil colony are consequently best able to reconstruct seasonal SST variability rather than mean SST or absolute temperatures (e.g., Felis et al., 2012). The combined mean annual and bulk Sr/Ca-SST calibrations derived from the Red Sea coral sites may therefore improve paleotemperature estimations from fossil corals, though we do not recommend applying the multicoral calibration when a colony-specific calibration is available, that is, for modern coral colonies. Rather, the multicoral calibrations from the Red Sea provide important insight into variability in the Sr/Ca paleothermometer that is difficult to examine with individual calibrations, particularly at summer and winter interannual time scales. These combined calibrations not only demonstrate the strength of the Sr/Ca proxy but also highlight key variability that may help explain observed Sr/Ca-SST slope differences across the Indo-Pacific region.



5. Conclusions

Sr/Ca-SST calibrations from five *Porites* corals across the Red Sea allow evaluation of the temporal and spatial coherency of the Sr/Ca paleothermometer. Coral Sr/Ca across the five sites is a robust proxy for SST, where SST accounts for up to 84% of Sr/Ca variability in the individual biweekly calibrations. Combining all biweekly data into a single calibration reveals a similarly strong relationship that may be useful in reconstructing absolute SSTs. Performing a multisite bulk (mean) coral Sr/Ca calibration to mean SST reveals a steeper calibration slope that is applicable to fossil colonies where the modern temperature influence cannot be quantified. At interannual time scales, limited SST variability at individual sites hinders the Sr/Ca-SST calibrations capture greater SST variability and yield significant calibrations for separate winter and summer seasons, as well as mean annual averages. Thus, Sr/Ca is a reliable paleothermometer across both temporal and spatial scales in the Red Sea, allowing for accurate multicentury SST reconstructions.

Though individually robust, the biweekly Red Sea calibrations reveal intercolony slope differences, where Sr/Ca-SST sensitivities shallow with decreasing latitude. Mean annual SST appears to drive most of the differences in slope across the Red Sea, likely accounting for nearly 30% of intercolony slope variability in studies throughout the Indo-Pacific region. By quantifying the influence of mean annual temperature on calibration slope, we demonstrate that there may be systematic environmental factors that contribute to differences in Sr/Ca-SST calibrations. Ultimately, such information may be used to refine the Sr/Ca proxy and improve confidence in spatial SST reconstructions at the largest, ocean basin scales.

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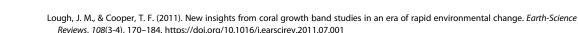
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