

Record of Little Ice Age sea surface temperatures at Bermuda using a growth-dependent calibration of coral Sr/Ca

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[1] Strontium to calcium ratios (Sr/Ca) are reported for a massive brain coral *Diploria labyrinthiformis* collected from the south shore of Bermuda and are strongly correlated with both sea surface temperature (SST) and mean annual skeletal growth rate. High Sr/Ca ratios correspond with cold SSTs and slow skeletal growth rate and vice versa. We provide a quantitative calibration of Sr/Ca to extension rate and SST along the axis of maximum growth and derive a growth-dependent Sr/Ca–SST calibration equation to reconstruct western subtropical North Atlantic SSTs for the past 223 years. When the influence of growth rate is excluded from the calibration, Sr/Ca ratios yield SSTs that are too cold during cool anomalies and too warm during warm anomalies. Toward the end of the Little Ice Age (~1850), SST changes derived using a calibration that is not growth-dependent are exaggerated by a factor of 2 relative to those from the growth-corrected model that yields SSTs ~1.5°C cooler than today. Our results indicate that incorporation of growth rate effects into coral Sr/Ca calibrations may improve the accuracy of SSTs derived from living and fossil corals.

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1. Introduction

[2] Accurate estimates of past SSTs, not captured in short instrumental records, are key to understanding long-term variability in Earth's climate system. One method of SST reconstruction is based on the inverse correlation between the Sr/Ca content of reef coral skeleton and ocean temperature [Smith *et al.*, 1979]. With this technique, Sr/Ca–SST calibrations derived from living corals are applied to ancient specimens to reconstruct SST [Beck *et al.*, 1992; Corregge *et al.*, 2004; Guilderson *et al.*, 1994; McCulloch *et al.*, 1999]. With high accretion rates, longevity, and skeletal annual growth bands, corals can potentially provide seasonally resolved, precisely dated records of SST spanning several centuries. Despite this potential, Sr/Ca–derived SSTs from ancient corals are often several degrees cooler than those derived from other marine proxies [Lea *et al.*, 2000; Pelejero *et al.*, 1999; Rosenthal *et al.*, 2003] and their accuracy has been questioned [Crowley, 2000].

[3] There are several indications that growth or calcification rate may influence the Sr/Ca ratio of coral skeleton.

Across coral taxa, faster growing species have lower Sr/Ca ratios than slow growing species [Corregge *et al.*, 2004; Weber, 1973]. Within a single species, fast growing colonies often have lower Sr/Ca ratios than slow growing colonies or slower growing parts within a colony [Alibert and McCulloch, 1997; Cohen and Hart, 2004; deVilliers *et al.*, 1995]. Corals whose calcification rates are enhanced by symbiont photosynthesis have lower Sr/Ca ratios than conspecifics without symbionts [Cohen *et al.*, 2002]. Culture studies demonstrate that differences in ion transport rates during calcification lead to reduced Sr uptake relative to Ca during periods of rapid calcification and vice versa [Cohen and McConnaughey, 2003; Ferrier-Pages *et al.*, 2002; Ip and Krishnaveni, 1991]. Hypotheses regarding the mechanisms by which growth may influence coral Sr/Ca ratios include sampling artifacts linked to slow growth, convoluted skeletal architecture [Cohen *et al.*, 2004; Swart *et al.*, 2002], and kinetic effects [deVilliers *et al.*, 1994]. To date, effects related to calcification or growth rates have been examined between colonies of the same species [deVilliers *et al.*, 1995], between fast and slow growing axes of the same colony [deVilliers *et al.*, 1994] and between different times in the life of a coral polyp [Alibert and McCulloch, 1997].

[4] Here we present data that demonstrate the impact of variability in skeletal extension rates on the accuracy of Sr/Ca–based SST reconstructed along a single, fast growing axis of a massive brain coral, *Diploria labyrinthiformis*.

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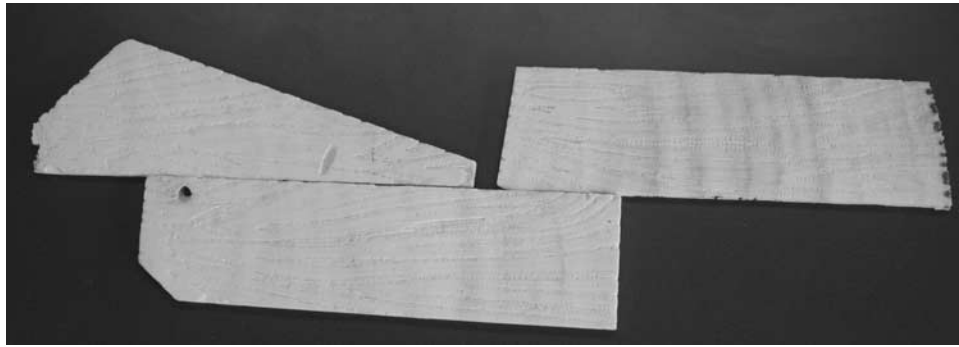


Figure 1. Three 5- to 10-mm-thick slabs were sliced from the ~1-m-long coral to capture the major growth axis through time. Slabs were cut in an overlapping fashion to ensure proper age model development and consecutive sampling of the entire record.

Growth rate changes of up to factors of 2–3 are associated with anomalously warm and cool Sr/Ca–derived SSTs, compared to recorded temperatures. A Sr/Ca–SST calibration that takes growth rate into account shows improved agreement with instrumental SST, and an application of the growth-corrected model yields late Little Ice Age (LIA), ~1850 AD, SSTs 1.5°C cooler than they are today. In contrast, SSTs derived from Sr/Ca while excluding growth rate effects were up to 3.0°C cooler than today.

2. Methods

2.1. Study Site

[5] In May 2000, an ~230-year-old massive brain coral colony was sampled live off John Smith’s Bay (JSB) on the southeastern edge of the Bermuda platform at 16-m depth. On Bermuda, growth rates of *Diploria labyrinthiformis* range from 2 to 6 mm/yr [Cohen *et al.*, 2004; Dodge and Thomson, 1974; Logan and Tomascik, 1991; Logan *et al.*, 1994], compared to 8 mm/yr and up to 20 mm/yr in more widely used species such as *Porites* [Alibert and McCulloch, 1997; Hughen *et al.*, 1999; Mitsuguchi *et al.*, 1996; Shen *et al.*, 1996]. *Diploria spp.* inhabit a wide range of water temperatures and are found in both the tropical and subtropical Atlantic. While *Diploria spp.* have not often been widely used for paleoclimate reconstruction [Cardinal *et al.*, 2001; Cohen *et al.*, 2004; Kuhnert *et al.*, 2002] the long life spans and large geographic distribution indicate its promise as a tool for long paleoclimate records.

[6] The south terrace of Bermuda was chosen because of its exposure to open ocean waters and proximity to hydrostation S located 30 km to the southeast. SST from 0- to 16-m depth has been recorded at hydrostation S biweekly since 1954. Over that time, monthly averaged SST ranged from 18.0° to 28.9°C with annual averages between 22.4° and 24.3°C. For the calibration period of this study (1976–1997), mean annual SST ranged from 22.8° to 23.5°C with a seasonal range of 18.3° to 28.9°C. The SST record is incomplete over different intervals including 2 or more months of missing data in the years 1978–1980, 1986 and 1989.

2.2. Subsampling and Analysis of Coral

[7] Three 5- to 10-mm-thick slabs were cut from the maximum growth axis of the coral using a diamond blade

rock saw (Figure 1). The slabs were cleaned in an ultrasonic bath with deionized H₂O 3 times for 10 min and dried in an oven at 50°C. X-radiographs were performed at Falmouth (Massachusetts) Hospital with machine settings of 50 kV and 1.6 mAs, a film focus distance of 1 m and an exposure time of 0.2 s.

[8] All samples were drilled from the solid thecal wall (the septotheca) that separates the calyx from the ambulacrum [Cohen *et al.*, 2004]. We targeted the theca to ensure that ample material could be extracted for analysis and to diminish the potential for diagenetic alteration or secondary aragonite precipitation due to the isolation of the center of the wall from skeletal pore spaces filled with seawater. In situ staining studies suggest that extension rates on the theca are higher in the summer (June through September) than they are in the winter [Cohen *et al.*, 2004].

[9] Annual extension rates, calculated from the distance between successive high-density bands in the X-radiograph, indicate an average growth rate of 3.8 mm/yr. From 1976 to 1997, the thecal wall was sampled at 0.33 mm (approximately monthly resolution) with a drill press and micrometer-controlled stage. Approximately 200 µg of powder was collected for each Sr/Ca analysis. The years 1775–1997 were sampled biennially, using a diamond blade band saw. To generate the biennial record, samples were cut between every second high- low-density band interface, and the theca was isolated by grinding away the calyx with a hand-held Dremel tool. Thecal samples (~0.9 g) representing the full 2 years growth were cleaned in an ultrasonic bath with deionized H₂O 3 times for 10 min, and dissolved in 1N HNO₃ for analysis.

[10] Sr and Ca were measured using Inductively Coupled Plasma–Atomic Emission Spectrometry (ICP–AES) applying solution standards to correct for drift and matrix effects related to interference from varying Ca concentrations [Schrug, 1999]. The samples, blanks, and external standard (a homogenized, powdered *Porites* coral) were prepared simultaneously. Repeat measurements on the coral external standard over 12 months showed reproducibility ($n = 96$, standard deviation = 0.02 mmol/mol).

[11] The age model was constructed from density banding visible in the X-radiographs and refined by tuning Sr/Ca to monthly averaged SSTs at inflection points. While this lessens the independence of the Sr/Ca–SST relationship,

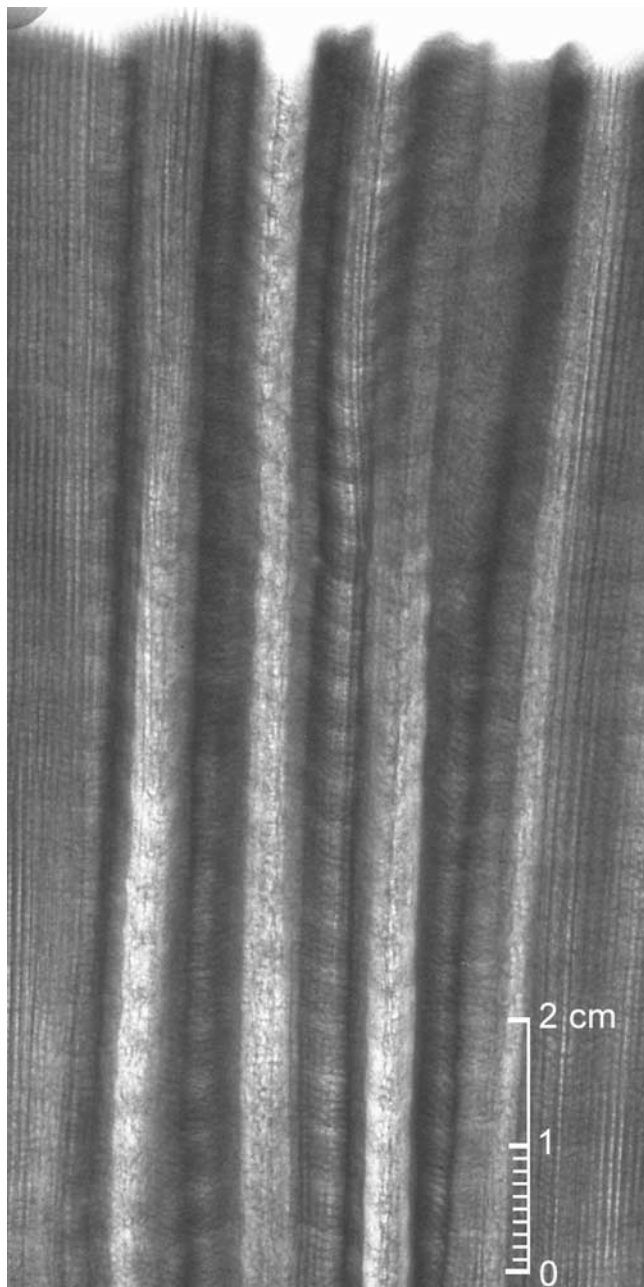


Figure 2. X-radiograph positive image of the first 97 mm of the top slab. X rays show clear annual banding made up of one low-density and one high-density band.

maximum and minimum values rather than median values at the inflection points drive the correlation of Sr/Ca to SST. The Sr/Ca data were resampled by linear interpolation at even monthly intervals equivalent to SST data.

[12] Reported annual growth (extension) rates for the high-resolution record (approximately monthly sampling) were calculated from the distance between two successive Januarys in each annual cycle as defined by the Sr/Ca-derived age model. Growth rates for the biennial record were determined using X-radiographs (Figure 2) as follows; the distance between every other high- low-density band

interface was measured and divided in two to calculate the average growth per year over the 2 years sampled.

3. Results

3.1. Reproducibility of the Sr/Ca Record Within the Colony

[13] As this *Diploria* colony grew, the position of the maximum growth axis changed relative to the center of the dome (Figure 1). Therefore it was difficult for the entire length of the coral to be sampled along one planar growth transect, mandating that sampling transects change between the theca from along the slabs. Parallel transects were drilled for the periods 1979–1986 and 1989–1992. A strong relationship exists between the multiple tracts ($r^2 = 0.83$, $p = 0$, slope = 1.04, intercept = -0.000705), demonstrating the reproducibility of the Sr/Ca signal between parallel sample transects.

3.2. Monthly Resolution Calibration

[14] A linear regression of monthly resolved Sr/Ca ratios to SST yields the following correlation (Figure 3a):

$$\text{Sr/Ca} = 10.1 (\pm 0.04) - 0.0358 (\pm 0.0018) * \text{SST}$$

$$(2\sigma, 95\% \text{ conf.}, r^2 = 0.86, p \ll 0.0001, \text{stdr} = 1.2^\circ\text{C})$$

(1)

where stdr is the standard deviation of the residual. These results are consistent with previous studies of slow to moderately slow growing corals, including a colony of *Diploria* from Bermuda [Cardinal *et al.*, 2001], *Montastrea* from Florida [Swart *et al.*, 2002], and *Diploastrea* from Fiji [Bagnato *et al.*, 2004]. On the basis of results from Cohen *et al.* [2004] using microbeam measurements, our sampling resolution may dampen the full range of Sr/Ca variability over the annual cycle. Owing to this smoothing, the monthly calibration cannot be used to reconstruct interannual variability as the dampened slope would return overestimated changes in SST. For this reason, calibrations using interannual variability were derived.

3.3. Interannual Calibrations

[15] To derive the Sr/Ca–SST calibrations based on interannual variability, 4-month summer (JJAS), 4-month winter (DJFM), and mean annual averages were calculated. Examination of the monthly Sr/Ca calibration (Figure 3a) indicates that summertime Sr/Ca reflects SST from 1977 to 1986 differently than from 1987 to 1997, while the wintertime signal continues to capture interannual SST variability. This can be seen clearly when the data are averaged for summer (Figure 3b) and winter (Figure 3c) periods. Coincident with the change in the summer time Sr/Ca–SST relationship is a decrease in the mean annual extension rate from above average to below average for the calibration period (Figures 3b, 3c, and 3d). Average annual SSTs derived from coral Sr/Ca are essentially a combination of the summer and winter signals and also diverge from instrumental data at the same time as the decrease in mean annual extension rate (Figure 3d). Average summer Sr/Ca

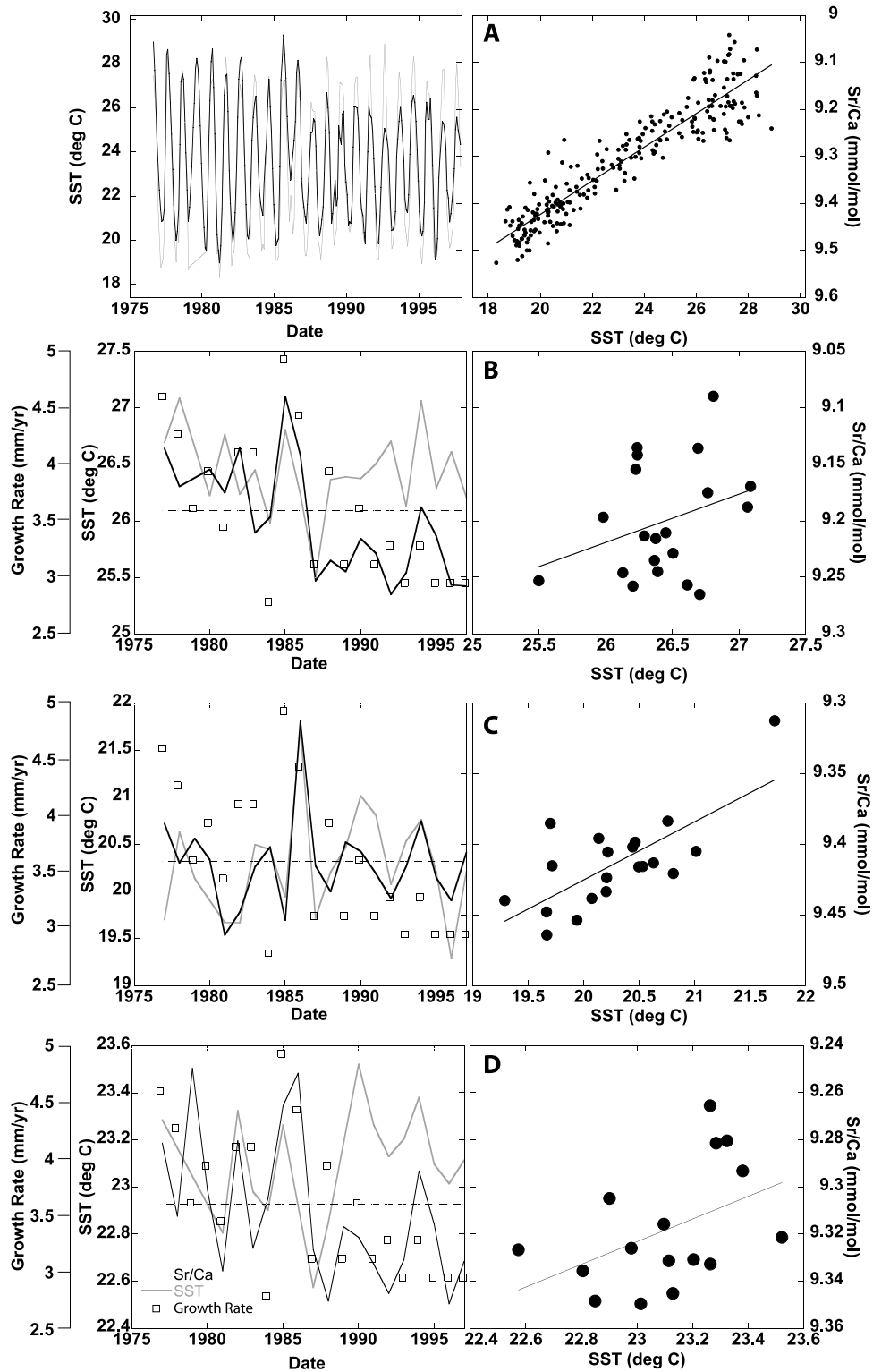


Figure 3. Coral Sr/Ca (solid line) and hydrostation S sea surface temperature (SST) (shaded line) plotted versus year and correlated using linear regression. Calibration results for (a) monthly ($r^2 = 0.86$, $p \ll 0.0001$), (b) summer (June, July, August, September (JJAS)) ($r^2 = 0.10$, $p = 0.17$), (c) winter (December, January, February, March (DJFM)) ($r^2 = 0.51$, $p = 0.0004$), and (d) mean annual ($r^2 = 0.21$, $p = 0.077$) resolved data. Mean annual coral growth rates (squares) and average growth (dashed line) are shown for the calibration period. Size of circles represents 2σ analytical error.

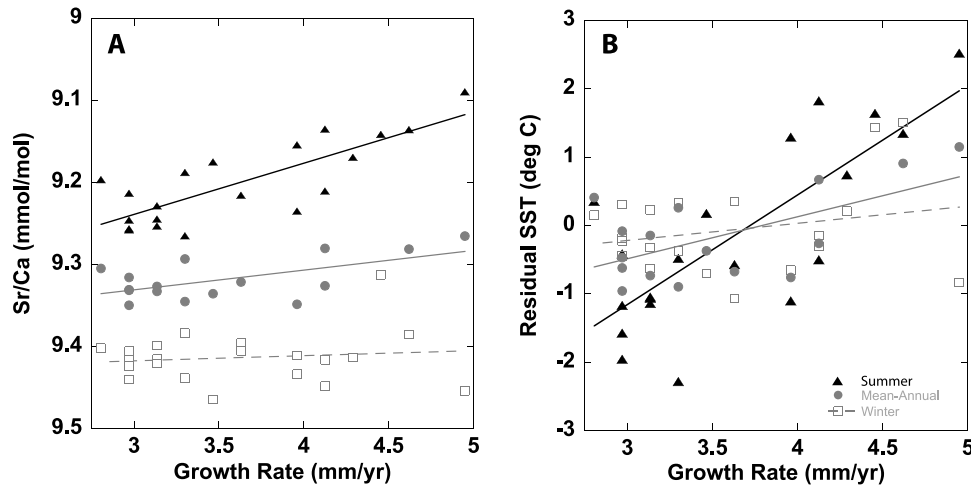


Figure 4. Mean annual growth rate compared to Sr/Ca and Sr/Ca–based SST residuals. (a) Sr/Ca to growth rate correlations for summer (JJAS) (triangles) ($r^2 = 0.64$, $p < 0.0001$), mean annual (circles) ($r^2 = 0.36$, $p = 0.014$), and winter (DJFM) (squares) ($r^2 = 0.01$, $p = 0.61$) resolved data. (b) Residual SST to growth rate correlations for summer ($r^2 = 0.59$, $p < 0.0001$), mean annual ($r^2 = 0.36$, $p = 0.013$), and winter ($r^2 = 0.06$, $p = 0.31$) resolved data. Residuals are calculated by converting monthly Sr/Ca to SST and then subtracting from instrumental SST.

shows no relationship to SST when correlated over the entire 1977–1997 calibration interval ($r^2 = 0.10$, $p = 0.17$) (Figure 3b), and the mean annual record shows a poor correlation ($r^2 = 0.21$, $p = 0.077$) (Figure 3d). Average winter Sr/Ca does not show any discrepancy affiliated with growth rate (Figure 3c), and a winter linear least squares regression to SST shows a significant relationship:

$$\text{Sr/Ca} = 10.3 (\pm 0.4) - 0.0412 (\pm 0.0191) * \text{SST}$$

$$(2\sigma, 95\% \text{ conf.}, r^2 = 0.51, p = 0.0004, \text{stdr} = 0.54^\circ\text{C})$$

(2)

The winter correlation r^2 value is diminished in comparison with the monthly calibration, because of the lower signal-to-noise ratio (winter SST range = $19^\circ\text{--}22^\circ\text{C}$, annual SST range = $18^\circ\text{--}29^\circ\text{C}$).

[16] Examination of the relationship between Sr/Ca and growth reveals that summer Sr/Ca correlates more strongly to annual skeletal extension rate ($r^2 = 0.64$, $p < 0.0001$) (Figure 4a) than to SST ($r^2 = 0.10$, $p = 0.17$). Mean annual Sr/Ca correlates relatively equally to growth rate ($r^2 = 0.36$, $p = 0.014$) and SST ($r^2 = 0.21$, $p = 0.077$), whereas winter Sr/Ca shows no relationship to growth rate ($r^2 = 0.01$, $p = 0.61$) (Figure 4a) and a strong relationship to SST ($r^2 = 0.51$, $p = 0.0004$). The impact of growth rate on summer, winter, and mean annual Sr/Ca–SST calibrations is further investigated by correlating growth rate with SST residuals (calculated by subtracting instrumental SST from reconstructed monthly SST). Summer SST residuals are strongly correlated with growth rate ($r^2 = 0.59$, $p < 0.0001$), but no significant relationship is observed between growth rate and winter SST residuals ($r^2 = 0.06$, $p = 0.31$) (Figure 4b). Mean annual SST residuals show a correlation with growth rate ($r^2 = 0.37$, $p = 0.013$) that is better than the winter residual Sr/Ca regression

but not as good as the summer residual Sr/Ca regression (Figure 4b). Thus averaging over the annual cycle does not eliminate the impact of growth rate on Sr/Ca signals, implying that a growth-corrected model must be employed to examine interannual variability.

[17] In the mean annual Sr/Ca regression, mean annual Sr/Ca was linearly regressed on mean annual SST by the preceding equation (Figure 3d):

$$\text{Sr/Ca} = m * \text{SST} + b \quad (3)$$

This regression produced the following result:

$$\text{Sr/Ca} = 10.4 (\pm 1.2) - 0.0481 (\pm 0.0503) * \text{SST}$$

$$(2\sigma, 95\% \text{ conf.}, r^2 = 0.21, p = 0.0766, \text{stdr} = 0.46^\circ\text{C})$$

(4)

In the growth-corrected mean annual model, the slope (m) of the mean annual Sr/Ca–SST relationship (equation (3)) is hypothesized to change as a linear function of growth rate where

$$m = n * (\text{growth rate}) + c \quad (5)$$

and growth rate is the 3-year averaged linear extension rate. The net regressed equation is

$$\text{Sr/Ca} = c * (\text{SST}) + n * (\text{growth rate}) * (\text{SST}) + b \quad (6)$$

For the purposes of the growth-corrected model, growth rates were averaged over 3-year periods, providing a more conservative estimate of the continuous calcification rates

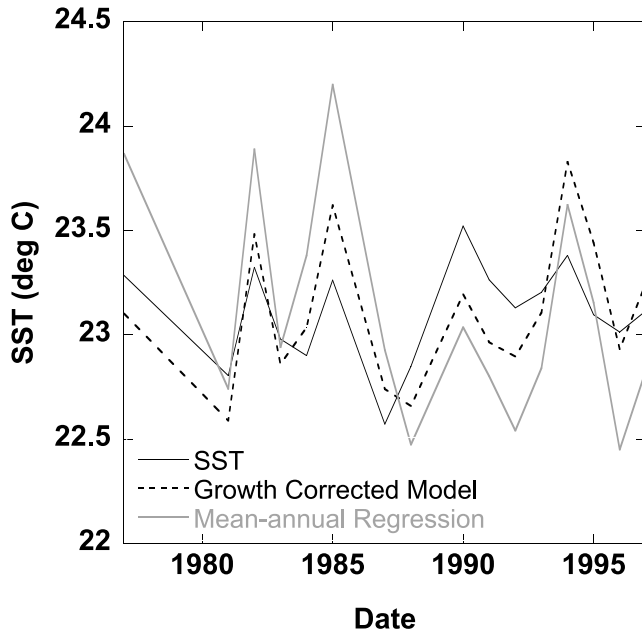


Figure 5. Mean annual instrumental SST from hydrostation S (solid line) compared to reconstructed mean annual SST using the mean annual Sr/Ca–SST regression (shaded line) and growth-corrected model (dashed line). The growth-corrected model has a stronger fit to the instrumental records ($r^2 = 0.49$, $p = 0.0026$ compared to $r^2 = 0.21$, $p = 0.077$ for the nonmean annual Sr/Ca–SST regression).

that occurred as the aragonite was formed by both extension and infilling for the time represented by sampling methods. The linear least squares multiple regression returns the following equation:

$$\begin{aligned} \text{Sr/Ca} = & -0.0529 (\pm 0.0334) * (\text{SST}) \\ & -0.00170 (\pm 0.00078) * (\text{growth rate}) * (\text{SST}) \\ & + 10.7 (\pm 0.8) \end{aligned}$$

(2σ , 95% conf., $r^2 = 0.68$, $p_c = 0.0074$,
 $p_n = 0.00078$, $\text{stdr} = 0.24^\circ\text{C}$) (7)

where p_c is the significance on slope c from equation (6) and p_n is the significance on slope n from equation (6). The inclusion of this additional relationship into the growth-corrected model leads to a significant improvement in fit ($r^2 = 0.68$, $p_c = 0.0074$, $p_n = 0.00078$) compared to the mean annual Sr/Ca–SST regression ($r^2 = 0.21$, $p = 0.077$). While the variance of the two fits are not comparable because of the change in the number of variables, mean annual Sr/Ca values over the calibration period were converted to SST using the mean annual Sr/Ca–SST regression and the growth-corrected model to demonstrate the improved accuracy in reconstructing SST. SSTs reconstructed with the growth-corrected model agree more closely with instrumental data ($r^2 = 0.49$, $p = 0.0026$) than those with the mean annual Sr/Ca–SST regression ($r^2 = 0.21$, $p = 0.077$) (Figure 5). This improvement is exemplified by a decrease in the variance of the residual

where the standard deviation equals 0.46°C in the Sr/Ca–SST regression compared to 0.24°C in the growth-corrected model (Figure 5).

3.4. Application of Calibration Regressions

[18] In order to examine the potential effects of the different calibrations on paleotemperature reconstructions, the monthly, mean annual Sr/Ca–SST regression and growth-corrected mean annual model were used to quantify SST from the 223-year biennially sampled Sr/Ca record. Reconstructed SST shows distinct cooling during the LIA, with an abrupt temperature drop in the 1840s and a gradual warming culminating in the 1960s. However, the amplitude of these changes varies significantly depending on which calibration is applied.

[19] The reconstruction based on the monthly calibration shows that biennial SST changed nearly 5°C from 1960 to the end of the LIA in the late 1840s, 2.5 times the change found using the growth-corrected mean annual model (Figure 6). The use of a monthly resolved calibration which does not capture the full amplitude of the seasonal cycle clearly influences the magnitude of interannual SST change calculated back through time. The biennial record does not necessarily capture the exact same months in each sample through time which may lead to some seasonal biases. However, this effect is diminished by looking at 2-year periods and is likely not large enough to account for the changes in temperature seen in this record.

[20] The mean annual extension rate of the coral is shown to covary with the Sr/Ca record over the length of the

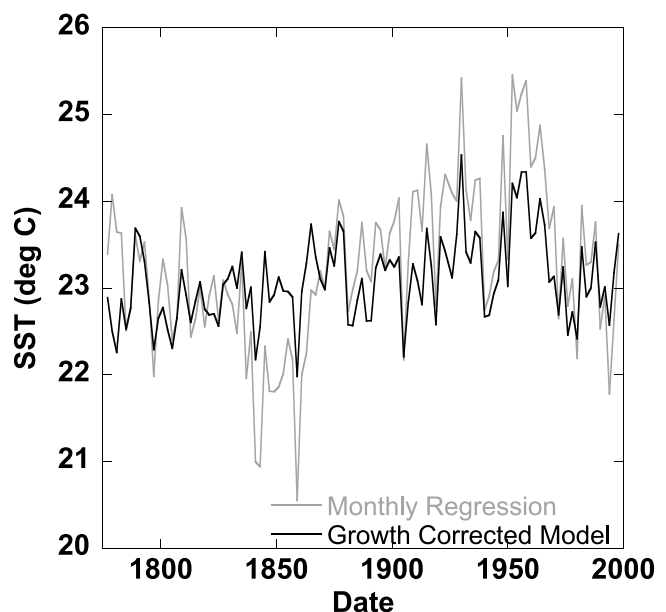


Figure 6. Biennial-resolution SST reconstructed to 1780. SST was reconstructed using the growth-corrected mean annual model (solid line) and the monthly regression (shaded line). By exaggerating both maximums and minimums, the monthly regression shows an SST change 2.5 times greater than the growth-corrected mean annual model reconstruction.

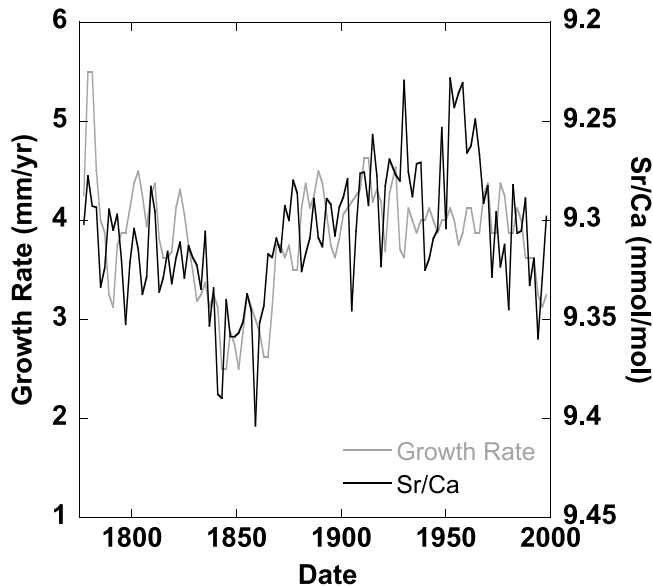


Figure 7. Biennially average mean annual extension (growth) rate (shaded line) and Sr/Ca (solid line) from 1780 to 1997. Extension rate and Sr/Ca have the same large-scale variability patterns over the entire 200-year period ($r^2 = 0.32$, $p \ll 0.0001$).

biennial record, supporting the initial observation that both growth and SST may influence the Sr/Ca record (Figure 7). The highest mean annual Sr/Ca values seen in the mid-to-late 1800s are also the periods of slowest growth. Use of the mean annual Sr/Ca–SST regression yields an SST change of 3.5°C from the 1960s to the 1840s, whereas the growth-corrected model shows a change of only 2°C over this same period (Figure 8).

3.5. Temperature Trends at Bermuda

[21] The biennially growth-corrected reconstruction agrees with both hydrostation S and other long coral records from this site. Hydrostation S shows a nearly 2°C cooling from the late 1950s to the late 1960s, simultaneous with the cooling in this record. In coral growth rate records from Bermuda [Patzold and Wefer, 1992], growth rate is correlated to SST and shows a $>2^\circ\text{C}$ temperature change from approximately the late 1800s to the 1950s consistent with the growth-corrected biennial Sr/Ca record over the same period. A coral $\delta^{18}\text{O}$ record from Bermuda shows a similar trend, with an abrupt cooling around 1840 followed by a slow warming coming out of the end of the Little Ice Age [Draschba et al., 2000].

[22] LIA temperature changes at Bermuda have also been investigated using $\delta^{18}\text{O}$ of foraminifera [Keigwin, 1996] and the alkenone unsaturation index, U_{37}^k [Ohkouchi et al., 2002; Sachs and Lehman, 1999]. Unfortunately, foraminiferal $\delta^{18}\text{O}$ is influenced both by temperature and the $\delta^{18}\text{O}$ of water, which is a function of salinity. Keigwin [1996] addressed this problem by assuming that the modern salinity and temperature relationship remained constant back in time, and reconstructed an SST change in the Sargasso Sea back to the middle of the LIA of $1^\circ\text{--}2^\circ\text{C}$. The unsaturation index of alkenones provides an SST proxy

that is unaffected by water chemistry [Sikes and Sicre, 2002] and has been used to reconstruct abrupt shifts in SST at this location [Sachs and Lehman, 1999]. However, U_{37}^k reconstructions of LIA SSTs are much larger ($4^\circ\text{--}6^\circ\text{C}$) than suggested by foraminiferal $\delta^{18}\text{O}$, and compound specific ^{14}C dating of these alkenones shows they are susceptible to resuspension and long distance transport [Ohkouchi et al., 2002], rendering U_{37}^k LIA reconstructions at this location suspect. Our growth-corrected calibration also provides an SST reconstruction not influenced by salinity, yielding late LIA cooling of 1.5°C . Overall, our data show that application of a Sr/Ca–SST calibration that takes growth rate variations into account yields coral-based SSTs in good agreement with the instrumental record (Figure 5) and with foraminiferal $\delta^{18}\text{O}$ SST estimates [Keigwin, 1996].

4. Discussion

[23] While our data support previous observations of growth-related impacts on coral Sr/Ca, the underlying mechanism, a sampling artifact [Swart et al., 2002], a growth regime [Cohen et al., 2004], or a kinetic effect [deVilliers et al., 1994], is not clear. Microscale analyses of *Diploria labyrinthiformis* reveal that the amplitude of the annual Sr/Ca cycle is greater than that derived by these sampling techniques [Cohen et al., 2004]. Bulk sampling of insufficient resolution smoothes the record as previously suggested [Swart et al., 2002], even though in this study relative winter variability is accurately captured. Examination of the high- and low-density bands in the coral X rays and duration of summer and winter in the Sr/Ca seasonal cycle shows that winter skeletal extension is consistent from

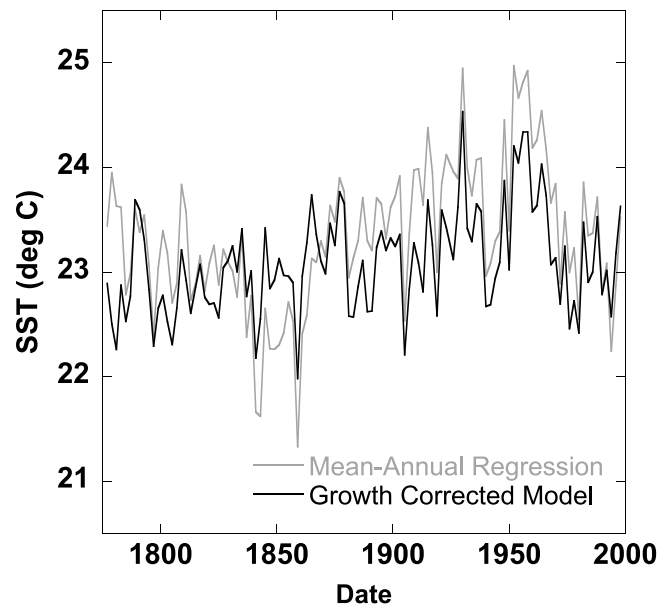


Figure 8. Biennial-resolution SST reconstructed to 1780. SST reconstructed using the growth-corrected model (solid line), as shown in Figure 4, compared to SST, reconstructed using the mean annual Sr/Ca–SST regression (shaded line). The mean annual Sr/Ca–SST regression exaggerates SST changes from maximum to minimum by a factor of 2.

year to year, compared to more variable summer extension. This could lead to a consistent attenuation of the record during sampling of winter skeleton but variable attenuation of summer skeleton, creating the observed growth impact on the summer record but not the winter. *Swart et al.* [2002] show similar results in a 2-year calibration study in which one summer peak has an average growth rate (during the peak) of >8 mm/yr and Sr/Ca values that match the SST maximum, but the second and third summers with lower summer growth rates (<7 mm/yr and <6 mm/yr during the peak) have Sr/Ca values that do not reflect the same magnitude summertime SST. These data clearly support an influence of growth rate on the summer Sr/Ca–SST relationship. Similarly, in studies by *deVilliers et al.* [1994] and *Alibert and McCulloch* [1997], Sr/Ca values associated with relatively slow growth and calcification rates are elevated relative to those from high growth rate and calcification rate intervals. However, in both studies, the records with slower growth or calcification rates appear offset rather than dampened, inconsistent with bulk-sample smoothing as the sole mechanism.

[24] Another hypothesis for the impact of growth on coral Sr/Ca is that different growth mechanisms employed by this coral in the summer and winter may influence the Sr/Ca signal. *Cohen et al.* [2004] proposed that skeleton accreted during the summer is overlain by skeleton accreted during the following winter, dampening the summer peak in reconstructed SSTs. Thus the extent of dampening may differ from year to year depending on whether summer extension is slow or fast and the ratio of summer to winter skeleton is shifted.

[25] Coral culture studies indicate that uptake of Sr relative to Ca might increase at low calcification rates, increasing the Sr/Ca ratio of the skeleton [*Ferrier-Pages et al.*, 2002; *Ip and Krishnaveni*, 1991] which implies the existence of a kinetic effect. Potential evidence supporting a combined growth regime and kinetic effect is seen in the need to average extension rates over 3 years to fully capture the growth effect in our study. Because in-filling may occur within the skeleton for several years, aragonite laid down in the same location will reflect different calcification rates. By averaging the extension rates (effectively a measure of calcification through time) over 3 years, a better estimate of the average calcification rate over the period of skeletal accretion is achieved and allows for the development of the growth-corrected model. Further study of Sr/Ca measurements in conjunction with specific calcification rates could further elucidate the viability of this hypothesis. Independ-

ent of the mechanism by which coral growth rate affects Sr/Ca, our data show that changes in growth rate along the axis of maximum growth may cause large excursions in Sr/Ca that do not accurately reflect the SSTs experienced by the coral.

5. Conclusions

[26] The use of a monthly resolved Sr/Ca–SST calibration to reconstruct biennial temperature records appears to cause exaggeration of decadal SST variability over the end of the LIA by a factor of 2.5. This demonstrates the importance of using calibrations that are appropriate to the desired resolution of temperature reconstructions to prevent such amplification of signals, especially if the full seasonal range of Sr/Ca variability is not captured by bulk sampling techniques. However, the mean annual Sr/Ca–SST regression also exaggerates SST variability by as much as a factor of 2, demonstrating that growth rate variability can also amplify variations in the Sr/Ca reconstructions of temperature. While growth effects are more often referenced for slower growing species such as *Diploria*, the more commonly studied genera *Porites* show that interannual growth rates between colonies and within single sampling transects, can vary by factors of 2–2.8 [*Alibert and McCulloch*, 1997; *Hughen et al.*, 1999; *Mitsuguchi et al.*, 1996; *Shen et al.*, 1996], comparable to the range observed here. It is possible that the influence of growth rate effects on Sr/Ca–SST calibrations could explain previous coral-based SST reconstructions back in time showing larger SST changes [*Beck et al.*, 1997; *Correge et al.*, 2004; *Guilderson et al.*, 1994; *McCulloch et al.*, 1996] than seen with other proxies [*Lea et al.*, 2000; *Pelejero et al.*, 1999; *Rosenthal et al.*, 2003; *Rühlemann et al.*, 1999]. The quantitative incorporation of growth rate information into coral Sr/Ca reconstructions could improve the thermometer and result in more accurate estimates of past SST changes and should therefore be considered when undertaking site and species specific calibrations where growth rate data are available.

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