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Growth rates, stable oxygen isotopes (δ^{18}O), and strontium (Sr/Ca) composition in two species of Pacific sclerosponges (*Acanthocheatetes wellsi* and *Astrosclera willeyana*) with δ^{18}O calibration and application to paleoceanography

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[1] The isotopic and elemental composition of sclerosponge skeletons is used to reconstruct paleoceanographic records. Yet few studies have systematically examined the natural variability in sclerosponge skeletal δ^{18}O, growth, and Sr/Ca, and how that may influence the interpretation of sclerosponge proxy records. Here, we analyzed short records in seven specimens of *Acanthocheatetes wellsi* (high-Mg calcite, 21 mol% Mg) from Palau, four *A. wellsi* (high-Mg calcite, 21 mol% Mg) from Saipan, and three *Astrosclera willeyana* (aragonite) sclerosponges from Saipan, as well as one long record in an *A. wellsi* specimen from Palau spanning 1945–2001.5. In Saipan, species-specific and mineralogical effects appear to have a negligible effect on sclerosponge δ^{18}O, facilitating the direct comparison of δ^{18}O records between species at a given location. At both sites, *A. wellsi* δ^{18}O and growth rates were sensitive to environmental conditions, but Sr/Ca was not sensitive to the same conditions. High-resolution δ^{18}O analyses confirmed this finding as both *A. wellsi* and *A. willeyana* deposited their skeleton in accordance with the trends in isotopic equilibrium with seawater, though with a 0.27‰ offset in the case of *A. willeyana*. In the high-Mg-calcite species *A. wellsi*, Mg may be interfering with Sr incorporation into the skeleton. On multidecadal timescales, *A. wellsi* sclerosponge δ^{18}O in Palau tracked the Southern Oscillation Index variability post-1977, but not pre-1977, coincident with the switch in the Pacific Decadal Oscillation (PDO) at ~1976. This suggests that water mass circulation in the region is influenced by El Niño— Southern Oscillation variability during positive PDO phases, but not during negative ones.

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1. Introduction

[2] Sclerosponges, slow-growing reef organisms that deposit a calcium carbonate exoskeleton in sequential layers over time, are found throughout the tropics across a 1000 m depth range and can live for centuries [e.g., *Böhm et al.*, 1996; *Druffel and Benavides*, 1986; *Swart et al.*, 1998]. Increasingly, the isotopic and elemental compositions of their skeletons are being used to reconstruct tropical paleoceanographic records. The ratio of stable oxygen isotopes (δ^{18}O) in sclerosponge skeletons appears to track the δ^{18}O composition of seawater [*Moore et al.*, 2000]. This results in sclerosponge δ^{18}O being used primarily as a recorder of seawater temperature in some locations [*Böhm et al.*, 1996; *Moore et al.*, 2000; *Wörheide*, 1998] but not in others [*Grottoli*, 2006; *Haase-Schramm et al.*, 2003; *Swart et al.*, 2002]. The ratio of strontium to calcium (Sr/Ca) in sclerosponge skeletons appears to reliably record temperature variations in the Caribbean species *Ceratoporella nicholsoni* [*Haase-Schramm et al.*, 2003; *Rosenheim et al.*, 2004, 2009; *Swart et al.*, 2002] but not in the Pacific species *Astrosclera willeyana* [*Fallon et al.*, 2005].

[3] Close examination of skeletal accretion rates indicate that sclerosponges have annual growth rates that range by more than an order of magnitude, from 0.05 to 1.9 mm/yr [*Benavides and Druffel*, 1986; *Böhm et al.*, 1996, 2002; *Fallon et al.*, 2003; *Fallon and Guilderson*, 2005; *Hughes and Thayer*, 2001; *Reitner and Gautret*, 1996; *Willenz and

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Hartman, 1985; *Wörheide et al.*, 1997]. Published growth rates for *A. wellsi, A. willeyana,* and *C. nicholsoni* range from 0.05 to 1.9, 0.35 to 1.9, and 0.1 to 0.4 mm/yr, respectively. *A. wellsi* deposits a high-Mg calcite skeleton [*Reitner and Gautret*, 1996] at a density of 1 g/cm^3 (Grottoli, unpublished) and does not incorporate its siliceous spicules into the skeleton [*Hartman*, 1983]. As the *A. wellsi* animal and skeleton increase in size, portions of the calices below the living tissue are separated by a series of horizontal skeletal partitions resembling layers, with little to no secondary infilling of the calices [*Hartman*, 1983]. However, the periodicity of the horizontal skeletal layers is unknown. In contrast, both *A. willeyana* and *C. nicholsoni*, the other two main species used for paleo-reconstructions, have aragonitic skeletons with densities that probably approach that of pure calcite (2.7 g/cm^3) [*Fallon and Guilderson*, 2005]; these species do incorporate their siliceous spicules into the skeleton, have significant secondary infilling of the skeleton, and have no horizontal skeletal partitions [*Hartman*, 1983; *Willenz and Hartman*, 1989; *Wörheide et al.*, 1997].

[4] Such variations in skeletal architecture, mineralogy, and growth rate could have significant effects on the isotopic and elemental proxy records generated from these organisms, possibly dramatically influencing our ability to compare proxy records generated from multiple specimens or species. Yet, few studies have systematically examined the natural variability in sclerosponge skeletal δ^{18}O, skeletal growth, and Sr/Ca content and how that variability may influence the interpretation of sclerosponge-based proxy records. Here, the variations in sclerosponge δ^{18}O, maximum linear skeletal extension (MLSE), and Sr/Ca were examined in multiple specimens of *A. wellsi* and *A. willeyana* sclerosponges grown in situ at The Grotto in Saipan and at the Short Drop Off Reef in Palau for 2 years. With these specimens, the following hypotheses were tested: (a) δ^{18}O, MLSE, and Sr/Ca significantly differ between species (*A. wellsi* versus *A. willeyana*) and locations (Saipan versus Palau), (b) sclerosponge skeletal δ^{18}O is deposited in isotopic equilibrium with seawater δ^{18}O ($\delta^{18}O_{sw}$), and (c) A 56-year-long high-resolution Palau sclerosponge δ^{18}O record is a proxy for the Southern Oscillation Index (SOI) in the northwestern quadrant of the western Pacific warm pool. In addition, species-specific and location-specific offsets were calculated, recommendations for δ^{18}O calibration and record interpretation were made, and the long δ^{18}O record generated from one large *A. wellsi* sclerosponge was evaluated.

2. Methods

2.1. Field Site

[5] Palau is located in the northwestern quadrant of the western Pacific warm pool (WPWP). Short Drop Off, Palau (7°16′N, 134°31′E) is a reef wall located 2 km offshore on the windward side of the Palauan island chain. Short Drop Off experiences good open ocean flushing by northward surface current flow driven by the North Equatorial Countercurrent in the winter and a southward flow driven by the Palau eddy in the summer [*Heron et al.*, 2006]. Short Drop Off also has a local current that travels the length of the wall, is unaffected by runoff from land, and is not influenced by temperature and salinity dynamics of caves or lagoons. *A. wellsi* sclerosponges are found in abundance within diving depth all along the reef wall. Sclerosponges used in this study were within 1 m of large crack/crevice openings at depths ranging from 5 to 20 m and were well within the minimum mixed-layer depth of 35 m (Patrick Collin, Coral Reef Research Foundation, unpublished data, 2006).

[6] Saipan is located 1,500 km northeast of Palau and is well outside of the WPWP. The Grotto, Saipan (15°2′N, 145°6′E), is a very large swim-through cavern with natural lighting located on the northeastern tip of the island of Saipan in the Central Northern Mariana Islands chain. The Grotto experiences vigorous flushing by the predominant North Equatorial Current waters that flow unimpeded past the site, is uninfluenced by temperature and salinity dynamics of closed caves or lagoons, and is only minimally affected by runoff from land. Both *A. wellsi* and *A. willeyana* sclerosponges (Figure 1) grow here in abundance between 6 and 33 m depths along the walls of the cavern.

2.2. Two Year Calibration Experiment

[7] Seven *A. wellsi* sclerosponges were identified between 11.5 and 18 m depths along the wall at Short Drop Off, Palau. The specimens were stained with Alizarin Red on 26 July 2001, cemented onto the reef at 11 m depth using Splash Zone® marine epoxy, and allowed to grow out past the stain line for 2 years. In Saipan, three *A. wellsi* were identified at 6 m depth and four *A. willeyana* sclerosponges were identified between 7 and 9 m depth, stained with Alizarin Red on 15 July 2001, cemented onto the reef at 8.3 m depth with marine epoxy, and also allowed to grow out past the stain line for 2 years (Figure 1). On 15 and 11 July 2003, all of the specimens were collected from Palau and Saipan, respectively, and returned to the lab for further analysis. In the absence of reliable annual skeletal banding, staining all of the specimens on a known date ensured that a clearly identifiable common time period was visible in each specimen. This ensured that each specimen could be sampled and compared over the exact same time period (Figures 1c and 1f). In addition, by allowing the specimens to grow in situ at the same depth ensured that the sclerosponges grew out under common natural conditions and removed any possible depth effects on the interpretation of the results.

[8] Seawater samples were collected two to four times per month at each site for seawater δ^{18}O ($\delta^{18}O_{sw}$) analysis. In brief, 25 mL of seawater was collected, filtered through a 0.2 μm filter, and preserved with anhydrous $MgCl_2$ under a nitrogen headspace. In situ submersible temperature loggers positioned beside the stained sclerosponges recorded seawater temperature every 2.5 h at each site.

[9] Once in the laboratory, each sclerosponge specimen was cut along its major axis of growth, cleaned with deionized water, and dried at 60°C for 3 days. The sclerosponges were sampled in two ways. First, bulk measurements spanning the common time period established with the stain lines were obtained from each specimen from each location. The MLSE was measured with calipers from the growing edge to the stain line under a dissecting microscope. A single bulk skeletal sample was milled from the stain line to the growing edge using a Dremmel tool fitted with a diamond-tipped dental bit. Each bulk sample was individually ground with an agate mortar and pestle to create a homogeneous

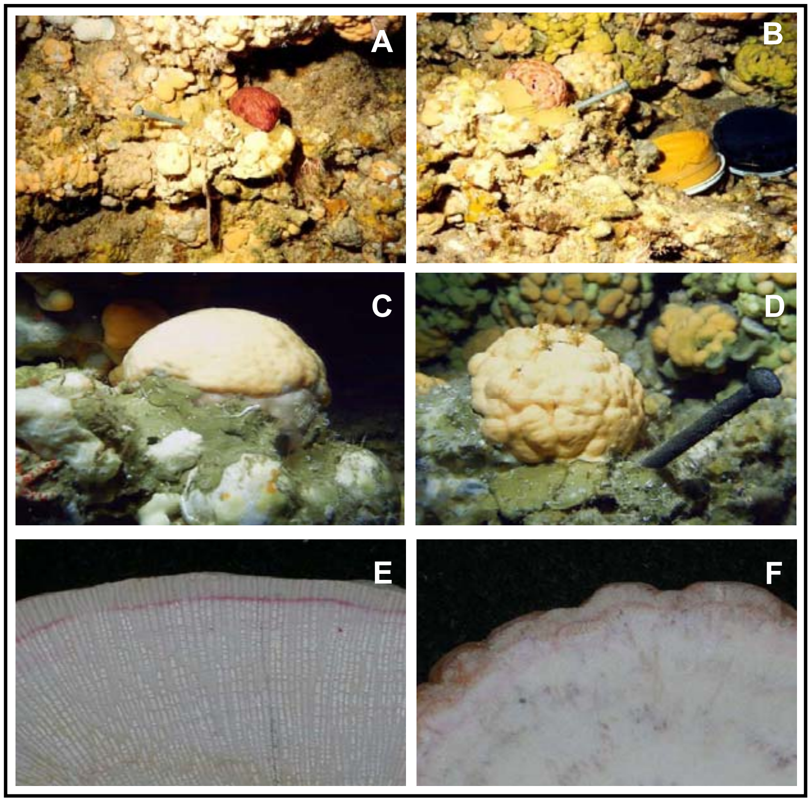

Figure 1. Sclerosponges (left, *Acanthocheatetes wellsi*, high Mg-calcite; right, *Astrosclera willeyana* aragonite) in situ and in cross section revealing the Alizarin Red stain lines. (a, b) Sclerosponges in situ immediately after staining, (c, d) 1 year after staining, and (e, f) in cross section. Note the clear vertical and horizontal skeletal features with little or no backfilling in Figure 1e and the absence of clear skeletal features and heavy backfilling of all spaces in Figure 1f. For both species, the pink stain line in Figures 1e and 1f corresponds to 15 July 2001 and the leading edge corresponds to 11 July 2003. Visible below the sclerosponges in Figures 1a–1d is the marine epoxy (seen in the yellow and black plastic containers in Figure 1b) used to cement the specimens back to the reef after staining, and the nails used to mark stained specimens (seen in Figures 1a, 1b, and 1d). Figures 1c and 1d were photographed by J.M.; Figures 1a, 1b, 1e, and 1f were photographed by A.G.G.

sample representing the entire 2 years of growth for δ^{18}O and Sr/Ca analyses. This sampling strategy ensured that comparisons among specimens, species, and locations were constrained to the same time period, irrespective of possible subannual variations in growth rates or skeletal morphology. Thus, each bulk-sample-derived data point was directly comparable with all others, and statistical analyses could be reliably performed. In addition, the bulk measurements were used to calibrate the sclerosponge δ^{18}O and Sr/Ca at biannual timescales (see section 2.7).

[10] Second, high-resolution samples were collected for δ^{18}O by milling (with a Merchanteck Micromill) four *A. wellsi* specimens from Palau, three *A. wellsi* specimens from Saipan, and three *A. willeyana* specimens from Saipan at 100 μm increments from the growing edge to the stain line. Splits of each high-resolution sample from three *A. wellsi* sclerosponges from Palau were further analyzed for Sr/Ca ratios. The high-resolution measurements were used to calibrate the sclerosponge δ^{18}O in both species and Sr/Ca in *A. wellsi* (see section 2.7). No high-resolution Sr/Ca measurements or calibration were made for *A. willeyana*.

2.3. Multidecadal Sclerosponge δ^{18}O Record

[11] On 27 July 2001, a large *A. wellsi* sclerosponge was collected at 17 m at Short Drop Off, Palau, and transported back to the lab for further analysis. This specimen was not part of the collection of stained sclerosponges described in section 2.2. At 77 mm tall, this was the largest *A. wellsi* specimen collected at this site. Once in the laboratory, the sclerosponge specimen was cut along its major axis of growth, cleaned with deionized water, and dried at 60°C for 3 days. High-resolution samples were collected for δ^{18}O analysis by milling the sclerosponge at ~100 μm increments from the growing edge to the base of the specimen, using a Merchanteck Micromill, for a total of 758 samples (see section 2.4 for more details). Although others have successfully obtained sclerosponge samples at 0.03–0.5 mm resolution [*Hughes and Thayer*, 2001; *Swart et al.*, 2002], a sampling resolution of 0.1 mm increments seems to improve paleoceanographic pattern recognition [*Fallon et al.*, 2003]. Subsequent to the high-resolution sampling, additional 10 mg samples were drilled out at 10 mm increments along the entire 77 mm specimen and at 2 mm increments between

60 and 70 mm for use in radiocarbon analysis ($\Delta^{14}C$) to help establish the chronology.

2.4. Stable Isotopic and Sr/Ca Analyses

[12] Subsamples of 80–100 μg were analyzed for $\delta^{18}O$ ($\delta^{18}O$ = per mil deviation of $^{18}O/^{16}O$ relative to Vienna Pee Dee Belmnite Limestone standard (VPDB)) and $\delta^{13}C$ ($\delta^{13}C$ = per mil deviation of $^{13}C/^{12}C$ relative to VPDB) in A.G.G.'s lab using an automated Carbonate Kiel device coupled to a Finnigan MAT 252 stable isotope ratio mass spectrometer. Approximately 10% of all samples were run in duplicate. The standard deviation of repeated measurements of an internal standard was ±0.04‰ for $\delta^{13}C$ and ±0.07‰ for $\delta^{18}O$. Only the $\delta^{18}O$ data are reported here.

[13] For Sr/Ca measurements, an additional ~100 μg subsample was analyzed. Each subsample was dissolved in 5% HNO_3, supplemented with added ^{43}Ca and ^{87}Sr tracers; the ratio of Sr to Ca was determined at the California Institute of Technology (J.F.A's lab) using a Finnigan Element inductively coupled plasma—mass spectrometer (ICP-MS). A mixed spike technique was used to eliminate problems with long-term accuracy drift. The Sr/Ca precision (1σ) was ±0.02% for duplicate sclerosponge samples run on separate days, which was compatible with or better than the quoted precision for Sr/Ca analyses by ICP-optical emissions mass spectrometry methods [*Schrag*, 1999].

[14] For seawater isotopic analyses, a 2 mL subsample was transferred to a 5 dram vial under nitrogen and shipped to Columbia University for $\delta^{18}O_{sw}$ analysis in the Fairbanks laboratory; these analyses used a Fison Optima with a MultiPrep inlet system and an external precision of better than ±0.03‰ based on standard water replicates. Ten percent of all samples were run in duplicate and reported here relative to Vienna Standard Mean Ocean Water (VSMOW).

2.5. Radiocarbon Analyses

[15] Approximately 7 mg of each sclerosponge sample was acidified under vacuum at 90°C with orthophosphoric acid in individual containers [*Guilderson and Schrag*, 1998b]. The resulting CO_2 was cryogenically purified and reduced to graphite under hydrogen gas using an iron catalyst to produce a 0.8 mg graphite target [*Vogel et al.*, 1987]. The radiocarbon content of the graphite was measured using accelerator mass spectrometry (AMS) techniques and the results were reported as $\Delta^{14}C$ (the per mil deviation of $^{14}C/^{12}C$ of the sample relative to that of 95% oxalic acid-1 standard) [*Stuiver and Polach*, 1977] and include $\delta^{13}C$ and blank corrections. All of the AMS measurements were made at the Center for Accelerator Mass Spectrometry at Lawrence Livermore National Laboratories with a precision of ±4.0‰ or less (1 standard deviation). ^{14}C, produced naturally in the stratosphere, was also produced as a result of thermonuclear weapons explosions in the atmosphere in the 1950s and early 1960s. The base of the $\Delta^{14}C$ bomb curve is clearly identifiable in Pacific coral carbonate records by ~1955 [e.g., *Druffel*, 1987; *Grottoli and Eakin*, 2007] and can be used to anchor coral and sclerosponge chronologies.

2.6. Determination of Mg Concentration in *A. wellsi*

[16] The Mg concentration (i.e., Mg/(Mg + Ca)), in one *A. wellsi* sclerosponge from Palau (PAU1) and one *A. wellsi* sclerosponge from Saipan (SPNAc1) was determined by the frequency of the ν_4 vibrational mode with Fourier transform infrared (FTIR) spectroscopy at the National Synchrotron Light Source, Brookhaven National Laboratory by W.R.P. and D.M.R. according to methods by *Bottcher et al.* [1997]. Finely ground samples of each specimen were pressed into a 5-μm-thick plate with a diamond anvil cell. Spectra were collected with a custom long-working-distance IR microscope on a Bruker IFS66v spectrometer, using a KBr beamsplitter and a sychrotron source. FTIR spectroscopy analyses were performed at standard temperature and pressure between 2000 and 600 cm^{-1}. In addition, lattice constants measured via X-ray diffraction on all collected specimens further support the inferred Mg concentration of the carbonates and confirm the lack of intermixed high-Mg and low-Mg calcite.

2.7. Data Analysis: Two Year Calibration Experiment

[17] Significant differences in bulk $\delta^{18}O$, MLSE, and Sr/Ca between *A. wellsi* at Palau and Saipan (location effect), and between *A. wellsi* and *A. willeyana* species in Saipan (species effect), were each tested by one-way analysis of variance (ANOVA), where effects were statistically significant at $p < 0.05$. Direct comparison between locations could be done only with *A. wellsi* because *A. willeyana* did not occur at both sites. Direct comparison between species could only be done at Saipan, where both species occurred.

[18] To determine whether growth rate varied with specimen size, a correlation analysis was used to evaluate the relationship between MLSE and overall specimen size.

[19] For the high-resolution data, interpolation was used to evenly space the $\delta^{18}O$ data in each sclerosponge record. On the basis of the average number of days of growth represented by each 1 mm sample, the *A. wellsi* records from Palau were interpolated to 42-day intervals, the *A. wellsi* records from Saipan were interpolated to 24-day intervals, and the *A. willeyana* records from Saipan were interpolated to 29-day intervals. The individual interpolated records were averaged to produce a single average high-resolution sclerosponge $\delta^{18}O$ record for *A. wellsi* in Palau, for *A. wellsi* in Saipan, and for *A. willeyana* in Saipan. These are henceforth referred to as average sclerosponge $\delta^{18}O$ records.

[20] Predicted equilibrium skeletal $\delta^{18}O$ values were calculated for both the 2-year bulk samples and the 2-year high-resolution records, using equations by *Grossman and Ku* [1986] for the aragonitic *A. willeyana*, and equations by *Kim and O'Neil* [1997] for the high-Mg calcitic *A. wellsi* with the addition of 0.06‰ $\delta^{18}O$ for each mol% Mg according to *Tarutani et al.* [1969]. The mol% Mg used for the equilibrium calculations of *A. wellsi* at both Palau and Saipan was determined according to methods outlined in section 2.6. Average in situ seawater temperature and $\delta^{18}O_{sw}$ measurements made during the 2-year calibration period were used for the bulk equilibrium calculations. A correction factor of 0.27‰ was applied to $\delta^{18}O_{sw}$ values [*Hut*, 1987]. At high resolution, seawater temperature and in situ $\delta^{18}O$ records were interpolated in the same way as the sclerosponge data for each species and location, and the interpolated data were used to calculate the equilibrium skeletal $\delta^{18}O$ records. Regression analyses between the $\delta^{18}O_{sw}$-corrected average sclerosponge $\delta^{18}O$ records and the interpolated in situ seawater temperature values were also calculated for each

Table 1. Average Temperature and $\delta^{18}O$ Content of Seawater ($\delta^{18}O_{sw}$) for Palau and Saipan from July 2001 to July 2003 ± 1 Standard Deviation[a]

Variable	Palau	Saipan
Temperature (°C)	28.66 ± 0.62 (7680)	28.70 ± 0.79 (7718)
$\delta^{18}O_{sw}$ (‰, v-smow)	0.20 ± 0.06 (58)	0.33 ± 0.09 (69)

[a] The number of independent measurements is in parentheses.

species and location. All statistical analyses were generated using SAS software (SAS System for Windows, vers. 8.02; SAS Institute, Inc., Cary, NC].

[21] To date, experimentally derived equilibrium equations are not available for Sr/Ca in high-Mg calcite. Thus, examination of the bulk and high-resolution Sr/Ca *A. wellsi* data was done qualitatively. High-resolution Sr/Ca measurements were not available for *A. willeyana.*

2.8. Data Analysis: Multidecadal Sclerosponge $\delta^{18}O$ Record

[22] The sclerosponge chronology was anchored by the base of the $\Delta^{14}C$ curve and the collection date. Assuming a constant growth rate between the collection date and the base of the bomb curve, dates were assigned to each $\delta^{18}O$ value for the entire record. No additional chronological adjustments were made to the $\delta^{18}O$ record. $\delta^{18}O$ values for the entire multidecadal sclerosponge record were fitted with a best fit second-order regression, and the residuals were calculated to produce a detrended $\delta^{18}O$ record. A monthly interpolated detrended $\delta^{18}O$ record was then produced using the Timer program from the free Arand software package (latest update, 2007; courtesy of Philip Howell, Brown University, http://www.ncdc.noaa.gov/paleo/softlib/arand/arand.html) and smoothed with a 5 point running mean. The monthly Southern Oscillation Index (SOI) data (www.bom.gov.aui/climate/current/soi2.shtml) was also smoothed with a 5-point running mean. Smoothing helped minimize noise in the data and facilitated comparison with SOI on interannual time scales. The statistical relationship between the smoothed sclerosponge $\delta^{18}O$ and SOI was evaluated by correlation analyses using the SAS System for Windows (Version 8.02). Analysis of cross-spectral coherence was performed on the monthly detrended $\delta^{18}O$ and SOI data using the Arand software.

3. Results

3.1. Mg Concentration in *A. wellsi*

[23] The Mg concentration was 21.6 (±0.6) mol% for one Palauan *A. wellsi* and 21.2 (±0.2) mol% for one *A. wellsi* from Saipan as determined by FTIR spectroscopy. Additional measurements by X-ray diffraction confirmed that all 10 *A. wellsi* specimens collected were a calcite structure with unit-cell volumes consistent with 21 mol% Mg. To be conservative, a value of 21 mol% Mg was used for all *A. wellsi* sclerosponges in this study. This is a higher Mg concentration than the previously reported 19 mol% for *A. wellsi* [*Reitner and Gautret*, 1996]. Thus, Mg concentration in sclerosponge skeletons can vary between studies and needs to be quantitatively determined for each specimen because method calibration is sensitive to Mg content.

3.2. Two-Year Calibration Experiment

[24] Sclerosponges were observed to be well stained in the field (Figures 1a and 1b), and readily grew beyond the stain

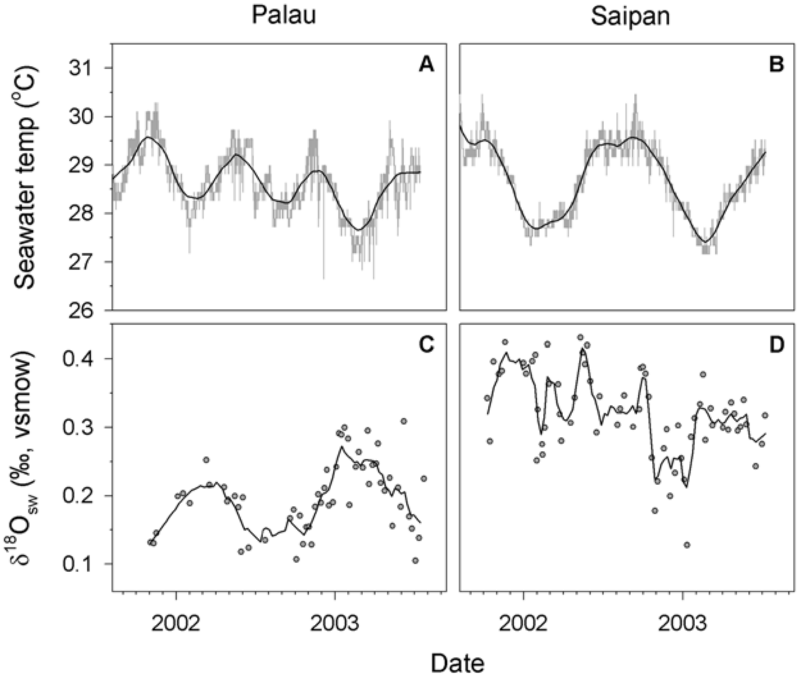

Figure 2. Hourly seawater temperature (a) in Palau and (b) in Saipan, and near weekly $\delta^{18}O_{sw}$ measurements (c) in Palau and (d) in Saipan. Measurements were recorded from July 2001 to July 2003. Individual measurement values are plotted in gray. Smoothed treadline is plotted as black solid line in each panel.

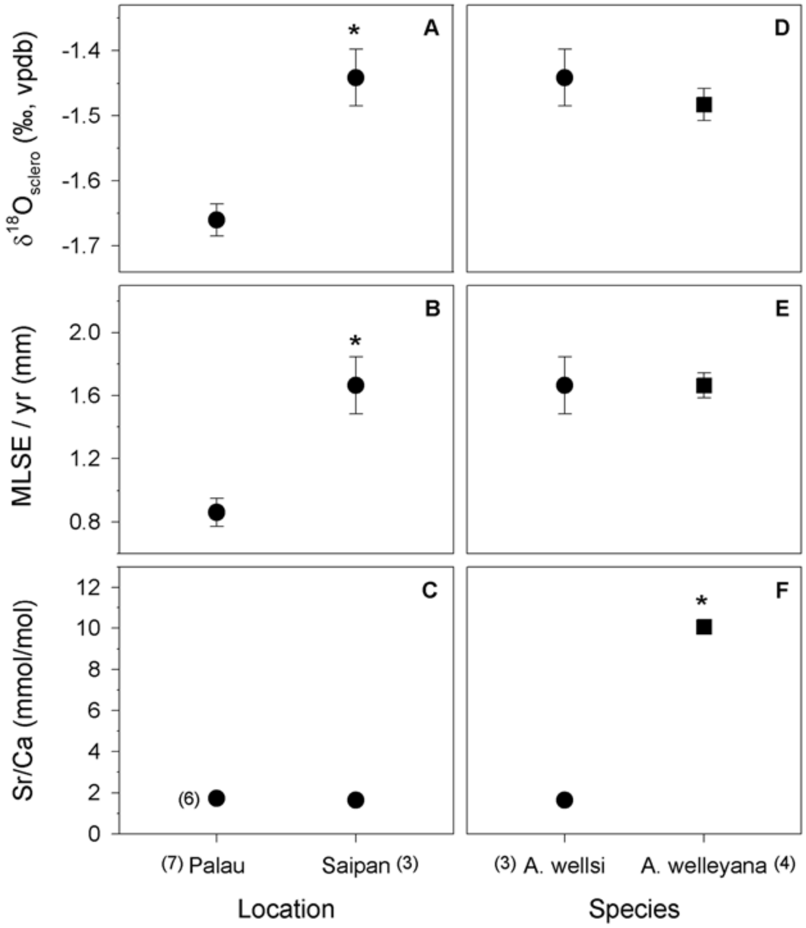

Figure 3. (a–c) Interlocation (Palau versus Saipan *A. wellsi* sclerosponges) and (d–f) interspecies (Saipan *A. wellsi* versus *A. willeyana*) variation in mean bulk sclerosponge skeletal $\delta^{18}O$, maximum linear skeletal extension per year (MLSE), and Sr/Ca. All averages are reported ±1 standard error. In some cases error bars are smaller than the symbol size. Sample sizes are indicated in parentheses on the *x* axis. Circles, *A. wellsi*; squares, *A. willeyana*; asterisks, significant differences between averages within a panel by one-way ANOVA.

line (Figures 1c–1f) at both sites. Thus, the staining process appeared to have had minimal impact on the specimens. Even if some stress was caused by the staining and field manipulations, its expression was consistent among all specimens studied. Thus, differences among species or locations were independent of field manipulations. Location and retrieval of the sclerosponges in 2003 was without incident.

[25] Average seawater temperatures over the 2-year period were similar at both sites (Table 1), though the subannual variability was quite different (Figures 2a and 2b). In Palau, seawater temperatures had two seasonal maxima and minima per year (Figure 2a), whereas Saipan had only a single yearly seasonal maximum and minimum period (Figure 2b), which is consistent with overhead insolation in the tropics and subtropics, at both sites. In comparison, average $\delta^{18}O_{sw}$ in Palau was slightly more depleted than in Saipan and experienced a single pronounced seasonal maximum and minimum period each year (Table 1 and Figures 2c and 2d). No specific seasonal variation was detected in the $\delta^{18}O_{sw}$ variability in Saipan (Figure 2d). Thus, the origin of the variability in $\delta^{18}O_{sw}$ in Palau must be nonlocal in origin, suggesting that water mass advection is a significant portion of the paleoceanographic record at this site.

[26] Average bulk sclerosponge $\delta^{18}O$ and MLSE values were significantly greater in *A. wellsi* from Saipan than in *A. wellsi* from Palau (Figures 3a and 3b), whereas bulk Sr/Ca did not differ significantly between locations (Figure 3c). Within the Saipan site, average bulk sclerosponge $\delta^{18}O$ and MLSE did not significantly differ between the two species (Figures 3d and 3e), while average bulk Sr/Ca levels were significantly higher in *A. willeyana* than in *A. wellsi* (Figure 3f). Correlation analyses revealed that MLSE was independent of specimen size for all data combined ($p = 0.39$), and for each species alone (*A. wellsi*, $p = 0.78$; *A. willeyana* $p = 0.30$).

[27] Averaged over the entire 2-year study, measured bulk sclerosponge $\delta^{18}O$ values were similar to predicted equilibrium values for *A. wellsi*, but were 0.26‰ enriched relative to predicted values for *A. willeyana* (Table 2). Closer examination of the high-resolution data revealed that the average 2-year pattern in the measured sclerosponge $\delta^{18}O$ record in Palau was similar to the 2-year predicted pattern, but the data did not capture the predicted subannual variability (Figure 4a). In Saipan, however, the average high-

Table 2. Comparison of Observed Average Bulk Sclerosponge *Acanthocheatetes wellsi* and *Astrosclera willeyana* δ^{18}O Relative to Predicted Equilibrium Values[a]

	A. wellsi - Palau		*A. wellsi* - Saipan		*A. willeyana* - Saipan	
	Observed	Predicted	Observed	Predicted	Observed	Predicted
δ^{18}O (‰, v-pdb)	−1.66 ± 0.06	−1.67[b]	−1.44 ± 0.07	−1.54[b]	−1.48 ± 0.05	−1.74[c]

[a] Observed values (21 mol% Mg, this study) are reported ±1 standard deviation. Predicted values are calculated using the average seawater temperature and $\delta^{18}O_{sw}$ values (from Table 1) plus the enrichment factors ($\varepsilon = 1000 \ln \alpha$) reported by various authors as indicated.

[b] *Kim and O'Neil* [1997], $\varepsilon_{calcite\text{-}water}$ = 27.312‰ at 28.7°C, $\varepsilon_{calcite\text{-}water}$ = 27.349‰ at 28.66°C; *Tarutani et al.* [1969], $\varepsilon_{Mg\text{-}calcite\text{-}water}$ = 0.06‰ per mol% Mg.

[c] *Grossman and Ku* [1986], Temperature (°C) = 20.6–4.34 [$\delta^{18}O_{arag}$ − ($\delta^{18}O_{sw}$ − 0.2‰)].

resolution sclerosponge δ^{18}O records closely matched both the predicted equilibrium 2-year and seasonal variability patterns in both species (Figures 4b and 4c), though with an average 0.27‰ offset in the case of *A. willeyana* (Figure 4c). Despite some slight differences in the δ^{18}O records among specimens of the same species within each site, their overall patterns were very similar and well represented by their respective average δ^{18}O record (Figure 4).

[28] Regression analyses revealed that seawater temperature was not well correlated with $\delta^{18}O_{sw}$-corrected average high-resolution *A. wellsi* δ^{18}O in Palau (Figure 5a), but was significantly correlated with that for *A. wellsi* δ^{18}O (Figure 5b) and *A. willeyana* δ^{18}O (Figure 5c) in Saipan. Propagating all of the error terms results in δ^{18}O-based temperatures estimates of ±0.79°C and ±0.88°C for *A. willeyana* and *A. wellsi* in Saipan, respectively.

[29] The 2-year high-resolution Sr/Ca records were fairly consistent among the three Palauan *A. wellsi* specimens (Figure 6). However, the large error bars associated with many of the individual measurements made interpretation of the overall record more difficult. In broad terms, the average Sr/Ca record (Figure 6) did not appear to match either the seawater temperature or the $\delta^{18}O_{sw}$ record measured over the same time period (Figure 2).

3.3. Multidecadal Sclerosponge δ^{18}O Record

[30] Radiocarbon (Δ^{14}C) measurements showed that the onset of the Δ^{14}C bomb curve, which occurred in 1955, started at 63 mm distance from the surface (Figure 7a). Assuming a linear growth rate between 1955 and the collection date, the mean annual growth rate was calculated to be 1.355 mm/year. Given that MLSE did not vary with specimen size (see section 3.2), this assumption of linear growth rate over the course of the lifetime of the specimen is reasonable. Thus, at a 100 μm sampling resolution, an average of 13.6 samples are sampled per year (i.e., submonthly resolution); the total record is 56.5 years long and spans the years 1945–2001.58. Consistency between the

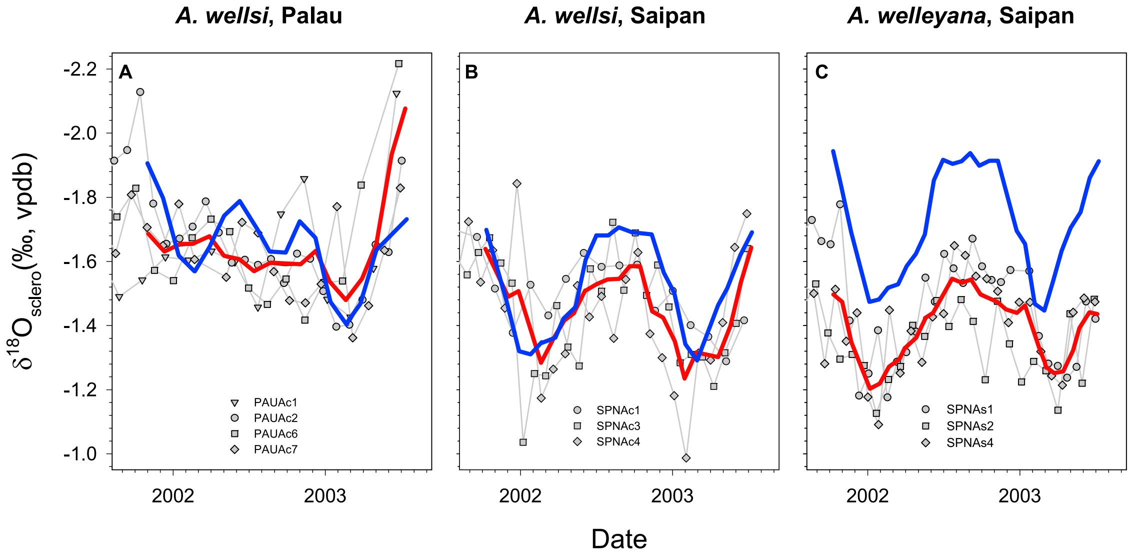

Figure 4. High-resolution sclerosponge δ^{18}O for (a) *A. wellsi* in Palau, (b) *A. wellsi* in Saipan, and (c) *A. willeyana* in Saipan. Measurements made at 0.1 mm increments in all specimens are shown with gray symbols. Each record was interpolated before calculating the average sclerosponge δ^{18}O record (solid red line) in each panel according to methods outlined in section 2.7. Predicted equilibrium skeletal δ^{18}O values (blue lines) were calculated by using equations by *Grossman and Ku* [1986] for the aragonitic *A. willeyana* and equations by *Kim and O'Neil* [1997] for the high-Mg calcitic *A. wellsi*, with the addition of 0.06‰ for each mol% Mg according to *Tarutani et al.* [1969]. *A. wellsi* were 21 mol% Mg in this study. Seawater temperature and in situ $\delta^{18}O_{sw}$ records (data shown in Figure 2) were interpolated in the same way as the sclerosponge data for each species and location, and the interpolated data were used to calculate the equilibrium skeletal δ^{18}O records.

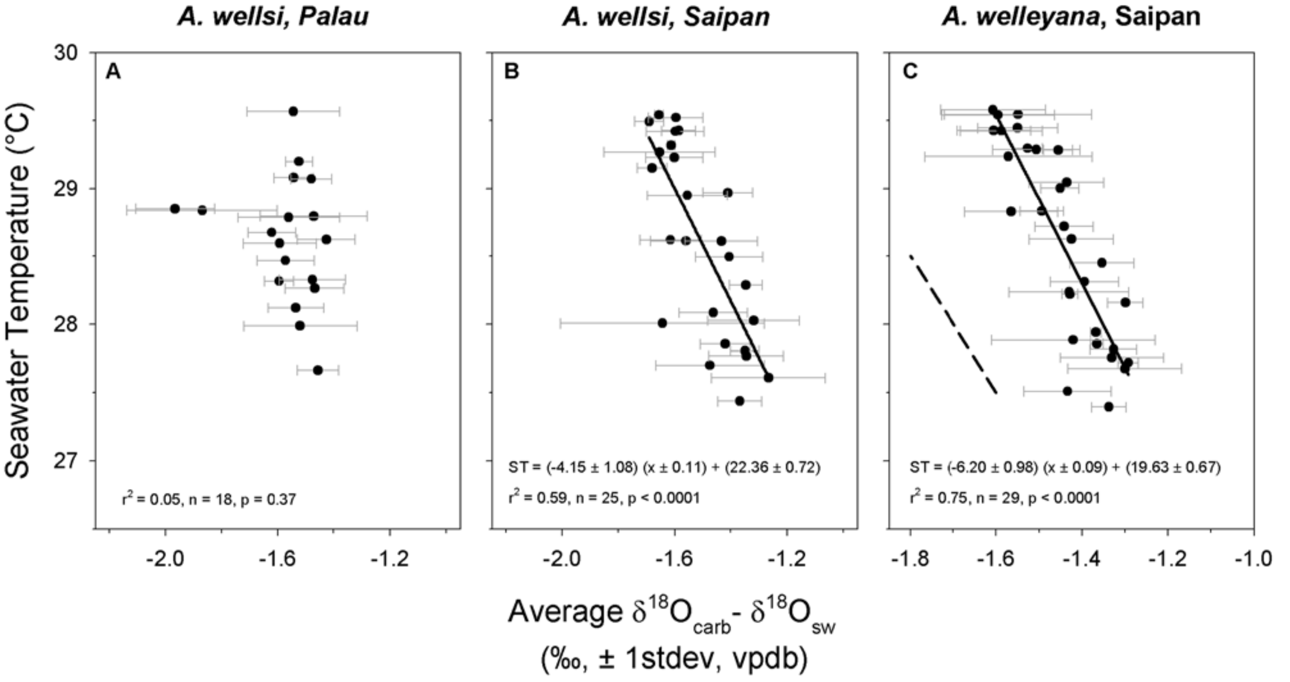

Figure 5. Regression of seawater temperature versus average sclerosponge $\delta^{18}O_{carb}$ corrected for $\delta^{18}O_{sw}$ (i.e., $\delta^{18}O_{carb} - \delta^{18}O_{sw}$) for *A. wellsi* in (a) Palau and (b) Saipan and (c) for *A. willeyana* in Saipan. In all cases, the data were interpolated to be evenly spaced according to methods described in section 2.7. Regression lines (solid black) and equations shown were statistically significant at $p < 0.05$. Published relationship between temperature and aragonite-water fractionation for the sclerosponge species *C. nicholsoni* of *Böhm et al.* [2000] is indicated (dashed line) in Figure 1c. ST, seawater temperature.

peak of the bomb curve in western Pacific tropical seawater (late 1970s) [*Grottoli and Eakin*, 2007] and the peak in the sclerosponge $\Delta^{14}C$ values corroborates the chronology.

[31] Overall, sclerosponge $\delta^{18}O$ gradually increased by ~0.2‰ from 1945 to 1977 and then decreased by ~0.13‰ from 1977 to 2001.5 (Figure 7b). In addition, interannual variability relative to the best fit curve was much lower in the pre-1977 portion of the record than in the post-1977 portion. Detrended sclerosponge $\delta^{18}O$ was inversely correlated with SOI (Table 3 and Figure 7c). Examined more closely, the relationship between sclerosponge $\delta^{18}O$ and SOI differed in the pre- and post-1977 portions of the record. No significant correlation was detected pre-1977, but a strong inverse correlation was present post-1977 (Table 3), such that when the SOI was strongly negative (positive), sclerosponge $\delta^{18}O$ was strongly positive (negative) during strong warm (cool) phases of the El Niño–Southern Oscillation (ENSO) (Figure 7c). These data were further supported by cross-spectral analysis that revealed significant coherence between monthly sclerosponge $\delta^{18}O$ and SOI post-1977 at a frequency of 4–6 years (95% confidence interval) and no significant coherence, in either the pre-1977 portion of the data or for the entire time series as a whole.

4. Discussion

4.1. Two-Year Calibration Experiment: *A. wellsi*

[32] *A. wellsi* deposited its skeleton $\delta^{18}O$ in isotopic equilibrium with seawater at both the bulk 2-year and the high-resolution monthly timescales based on predicted equilibrium values derived from the $\varepsilon_{\text{calcite-water}}$ values of *Kim and O'Neil* [1997] coupled with the $\varepsilon_{\text{Mg-calcite-water}}$ value of *Tarutani et al.* [1969] (Table 2 and Figures 4a and 4b). This

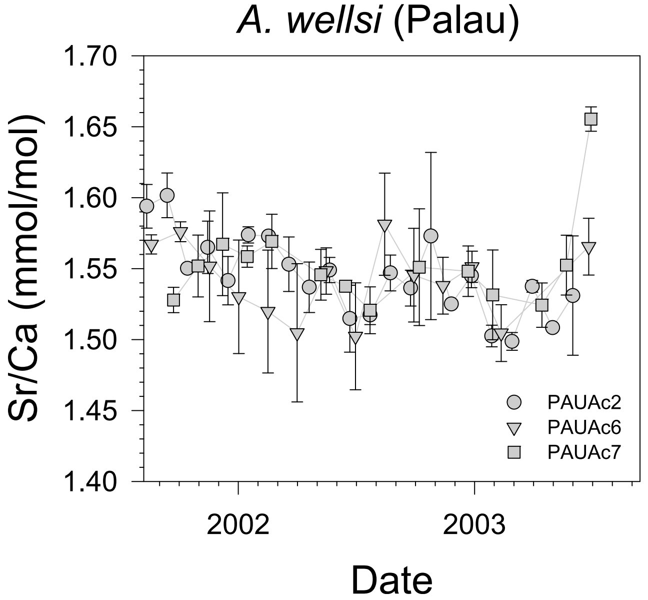

Figure 6. Palau *A. wellsi* sclerosponge Sr/Ca (±1 standard deviation). Measurements made at 0.1 mm increments in all specimens are shown with gray symbols.

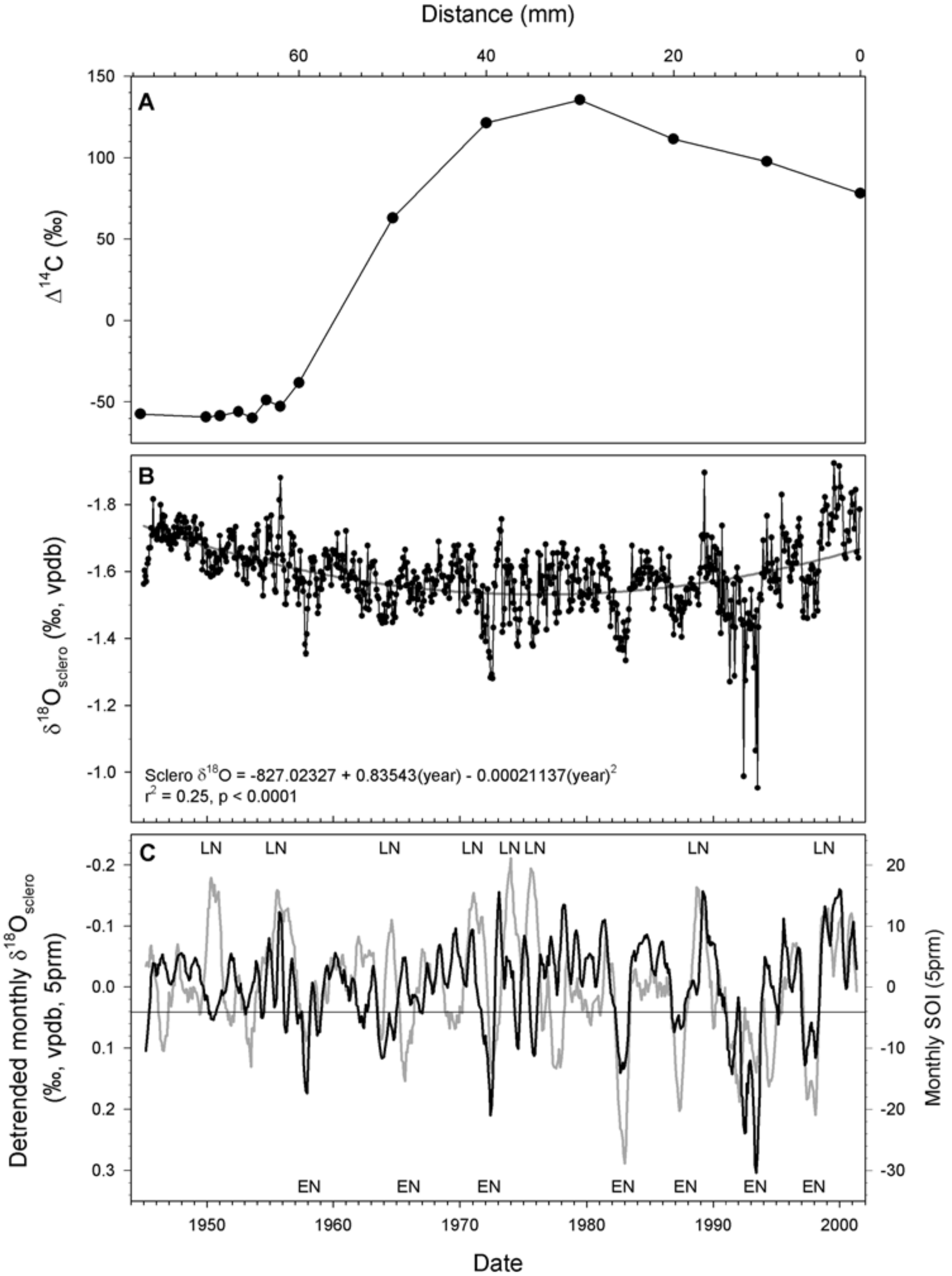

Figure 7. (a) Palauan *A. wellsi* sclerosponge radiocarbon values (Δ^{14}C) measured along the major axis of growth. Analytical precision of each Δ^{14}C measurement is ±4‰ (1 standard deviation) or less. (b) High-resolution *A. wellsi* δ^{18}O values (black line) for the entire record fitted with a best fit second-order regression (gray line, equations listed). (c) Detrended monthly *A. wellsi* sclerosponge δ^{18}O (black line) and SOI (gray line) both smoothed with a 5 point running mean. Note that δ^{18}O *y*-axes are inverted in Figures 7b and 7c, as is the convention in the coral and sclerosponge literature. LN, La Niña; EN, El Niño.

supports our initial hypothesis. *Moore et al.* [2000] also found good agreement between the observed and predicted equilibrium δ^{18}O values for *A. wellsi* sclerosponges from various locations using the $\varepsilon_{\text{calcite-water}}$ values of *Friedman and O'Neil* [1977] also coupled with the $\varepsilon_{\text{Mg-calcite-water}}$ value of *Tarutani et al.* [1969]. Large disagreement between observed values and predicted equilibrium values generated by enrichment factors of *Zhou and Zheng* [2002, 2003, 2005] and *Jiménez-López et al.* [2004] are most likely due to the result of the approach used in the inorganic laboratory experiments [*Horita and Clayton*, 2007], and not the result of biological effects.

[33] Differences in bulk skeletal δ^{18}O between *A. wellsi* in Palau and Saipan were a result of differences in the temperature and/or $\delta^{18}O_{sw}$ between the sites, differences in skeletal growth rates, or some combination of both (Figures 3a, 4a, and 4b). Since sclerosponge δ^{18}O was independent of specimen size (see section 3.2), it is unlikely

Table 3. Spearman Correlation Coefficients Between Smoothed Monthly *A. wellsi* Sclerosponge δ^{18}O and Smoothed Monthly Southern Oscillation Index

Data Period	Spearman Correlation Coefficient	*p*-Value
1945–2001.5	−0.263	<0.0001
1945–1976.9	0.05	0.28
1977–2001.5	−0.647	<0.0001

that differences in growth rate contributed to the δ^{18}O values. In situ measurements confirm that the 2-year average seawater temperature did not differ between the sites but that $\delta^{18}O_{sw}$ did (Table 1). Thus, biannual average $\delta^{18}O_{sw}$ was most likely the primary driving factor contributing to the difference in the bulk sclerosponge δ^{18}O values (Figure 3a). However, at high-resolution, the temperature dependence of the *A. wellsi* δ^{18}O signature was apparent in Saipan (Figures 4b and 5b). This is because seasonal variability in seawater temperature is very pronounced at this site with no corresponding seasonal variability in $\delta^{18}O_{sw}$ (Figures 2b and 2d). In Palau where the seasonal seawater temperature range is much smaller and the $\delta^{18}O_{sw}$ variability is pronounced (Figures 2a and 2c), the sclerosponge δ^{18}O signature was driven predominantly by $\delta^{18}O_{sw}$ (i.e., salinity) on annual and longer time scales (Figure 4a) and no statistical relationship to seawater temperature was detectable (Figure 5a). In Palau, the strong influence of $\delta^{18}O_{sw}$ muted any subannually driven sea surface temperature (SST) patterns in the *A. wellsi* δ^{18}O record. In both Palau and Saipan, reproducibility among high-resolution *A. wellsi* sclerosponge specimen skeletal δ^{18}O records was generally quite good (Figures 4a and 4b). Even though the average sclerosponge δ^{18}O record of multiple specimens gave the most representative record for each site relative to the predicted equilibrium record (Figures 4a and 4b) and gave a more robust temperature calibration curve in Saipan (Figure 5b), the data suggest that a single *A. wellsi* sclerosponge record could be sufficient for reconstructing annually resolved sclerosponge δ^{18}O records from Palau or Saipan and for reconstructing subannually resolved temperature records from Saipan. However, any temperature reconstruction would have an error term of ±0.88°C that would need to be incorporated into any *A. wellsi*-based temperature reconstruction from locations with environmental characteristics similar to Saipan.

[34] Caribbean aragonitic sclerosponge Sr/Ca is typically a strong recorder of seawater temperature, independent of changes in $\delta^{18}O_{sw}$ [*Rosenheim et al.*, 2004]. Even though the lack of any significant difference in the bulk *A. wellsi* Sr/Ca values from Saipan and Palau (Figure 3c) is consistent with the lack of any significant difference in the 2 year mean temperatures at both sites (Table 2), the high-resolution Sr/Ca records from Palau did not track seawater temperatures over the 2-year period (Figure 6). Two factors could be contributing to the poor performance of Sr/Ca as temperature proxy in *A. wellsi*. First, the high Mg content of *A. wellsi* sclerosponges interfered with the accurate measurement of Sr/Ca by ICP-MS. The second and most likely factor is that the high Mg content of the skeleton interferes with the uptake of Sr into the skeletal matrix independent of temperature [*Morse and Bender*, 1990].

4.2. Two Year Calibration Experiment: *A. willeyana*

[35] *A. willeyana* deposited its skeleton δ^{18}O with a 0.27‰ offset from isotopic equilibrium with seawater at both the bulk 2-year and the high-resolution monthly time scales (Table 2 and Figure 4c), based on predicted equilibrium values derived from the equation of *Grossman and Ku* [1986]. When the offset is taken into account, the findings are consistent with the initial hypothesis. The aragonitic *C. nicholsoni* from the Caribbean and *A. willeyana* from other Pacific locations have also been shown to deposit their skeleton in isotopic equilibrium, but without a consistent offset [*Böhm et al.*, 2000; *Moore et al.*, 2000]. *Moore et al.* [2000] found *A. willeyana* δ^{18}O to be deposited in isotopic equilibrium (±0.1‰ to 0.3‰), using $\varepsilon_{calcite\text{-}water}$ values of *Friedman and O'Neil* [1977] coupled with a calcite-to-aragonite fractionation factor correction by *Tarutani* [1969]. Slight differences between this study and that by *Moore et al.* [2000] may be due to the different sources used to generate the equilibration equations (i.e., *Moore et al.* [2000] used equations derived from inorganic precipitation experiments under laboratory conditions, whereas *Grossman and Ku*'s [1986] equation was derived from biogenically precipitated aragonite under natural conditions) or because Moore's $\delta^{18}O_{sw}$ values in some cases had to be derived from atlas salinity data [*Levitus et al.*, 1994] and not from direct in situ measurements.

[36] Assuming that the equilibration equations of *Grossman and Ku* [1986] are more appropriate, and that our equilibrium δ^{18}O values are more accurate because they were all calculated using in situ $\delta^{18}O_{sw}$ values, then the 0.27‰ offset for *A. willeyana* sclerosponge δ^{18}O from equilibrium is real. The offset between the average *A. willeyana* δ^{18}O record (Figure 5c), the equilibrium equation for *C. nicholsoni* (0.25‰; data not shown), and the equilibrium equation for all aragonitic organisms (0.37‰; data not shown) of *Böhm et al.* [2000] are similar to the offset from the *Grossman and Ku* [1986] equilibrium (0.27‰; Figure 4c). The offset could be due to the following: (1) a species-specific effect since none of the previous equilibrium equations were constructed using δ^{18}O of *A. willeyana* sclerosponges, (2) the type of $\delta^{18}O_{sw}$ values used (i.e., collected in situ over the duration of the entire calibration period in this study compared to using derived $\delta^{18}O_{sw}$ values or $\delta^{18}O_{sw}$ values that did not represent the entire growth period), or (3) some combination of both. In addition, offsets from equilibrium are higher in summer for *A. willeyana*, which might indicate the presence of a "vital effect" in this species that is related to the 0.27‰ mean offset. As such, paleotemperature reconstruction and interpretation of *A. willeyana*-based δ^{18}O records should use the new calibration equation presented in this study. By taking the offset into account, high-resolution *A. willeyana* δ^{18}O records can be reliably used to reconstruct seawater temperature proxy records (Figures 4c and 5c). As with *A. wellsi*, reproducibility among high-resolution *A. willeyana* sclerosponge specimen skeletal δ^{18}O records was generally quite good (Figure 4c) and suggests that a single *A. willeyana* sclerosponge record would probably be sufficient for reconstructing subannually resolved seawater temperature records from Saipan. However, any temperature reconstruction would have an error term of ±0.79°C that would need to be considered for any

A. willeyana–based temperature reconstruction from locations with environmental characteristics similar to Saipan. This temperature error term is four times smaller than previous calibrations estimates based on the aragonitic *C. nicholsoni* [*Böhm et al.*, 2000] (Figure 5c) and is consistent with the temperature error term generated using a wide range of aragonitic organisms [*Böhm et al.*, 2000].

[37] Interestingly, δ^{18}O and MLSE did not significantly differ between the two species (Figures 3d and 3e). Thus, neither the mineralogy of the skeleton nor growth-rate-dependent fractionation influenced the interpretation of sclerosponge δ^{18}O values. However, the large difference in Sr/Ca between the two species at the same site suggests that mineralogy does influence Sr incorporation into the skeleton, possibly by interference of Mg with Sr incorporation in the high-Mg calcite of *A. wellsi* [*Morse and Bender*, 1990]. Inorganic precipitation studies are needed to further investigate the mineralogical influences on skeleton Sr/Ca values. Sr/Ca values of *A. willeyana* in Saipan overlap with the Sr/Ca values of *A. willeyana* from Australia and Truk [*Fallon et al.*, 2005] and are 0.1–0.6 mmol/mol higher than the highest Sr/Ca values in *C. nicholsoni* from Jamaica [*Haase-Schramm et al.*, 2003; *Rosenheim et al.*, 2004]. Even though high-resolution elemental measurements were not performed on *A. willeyana* in this study, previous work on this species from Australia and Truk indicated that Sr/Ca does record seawater temperature, but because of the 2–3 year skeletal infilling, which smoothes the elemental signal, reliable Sr/Ca-based temperature reconstructions are not possible using this species [*Fallon et al.*, 2005].

4.3. Multidecadal Sclerosponge δ^{18}O Record

[38] The Palauan *A. wellsi* skeletal δ^{18}O record exhibited multidecadal variability (Figures 7b and 7c). Given the calibration findings in this study, we would expect the bulk of this variability to have been driven by local changes in $\delta^{18}O_{sw}$ caused by variation in the water masses advected to Palau on those time scales. This is supported by the following argument. If changes in sclerosponge δ^{18}O in multidecadal time scales were due to temperature alone, then on the basis of a relationship of −0.22‰ per °C [*Kim and O'Neil*, 1997], Palau seawater cooled by ~1°C from 1945 to 1977 and warmed by ~0.6°C from 1977 to 2001 (Figure 7b). Unfortunately, instrumental seawater temperatures do not exist for Palau before 1981. Nevertheless, no cooling was observed in the global oceans from 1945 to 1977 [*Folland and Karl*, 2001]. Post-1977, mean global sea surface temperature increased by 0.3°C [*Folland and Karl*, 2001] and sea surface temperatures in the greater Palau regions increased by ~0.4°C from 1981 to 2001 (Integrated Global Ocean Services System Products Bulletin's Global SST data by *Reynolds et al.* [2002] available at http://iridl.ldeo.columbia.edu/SOURCES/.IGOSS/.nmc/.Reyn_SmithOIv2/.monthly/.sst). Under this scenario, the sclerosponge record indicates a cooling from 1945 to 1977 where none seem to have existed, and overestimates the average warming over the last 24 years of its record by ~33%. Clearly seawater temperature is not the main driver of the skeletal δ^{18}O in Palau on multidecadal time scales, which suggests that $\delta^{18}O_{sw}$ is the driver. This is consistent with findings in section 4.1. In the WPWP, the mean monsoon convection state tends to vary on decadal time scales [*Chu and Wang*, 1997], which can modulate rainfall (and thus $\delta^{18}O_{sw}$) on decadal time scales in the waters being entrained to Palau. The influence of both temperature and $\delta^{18}O_{sw}$ on sclerosponge δ^{18}O records in the WPWP was also detected in *A. willeyana* specimens in the Indonesian Throughflow [*Moore et al.*, 2000]. Thus, Palau appears to have experienced a 32-year period of little or no cooling with higher salinity water entrained into the region before 1977, followed by a 24-year period of warming conditions with lower salinity water. The timing of the change in these multidecadal climate regimes coincides with a switch from a negative to a positive phase in the Pacific Decadal Oscillation (PDO) in ~1976 [*Hare et al.*, 1999; *Mantua et al.*, 1997; *Wooster and Zhang*, 2004], highlighting the influence of basin-scale multidecadal climate phenomenon on local oceanographic conditions. As a whole, this is the first evidence that the 1976 PDO phase shift influenced water mass advection in the WPWP and that sclerosponges, like eastern Pacific corals [*Guilderson and Schrag*, 1998a], are sensitive to PDO-driven water mass changes. Additional records from additional sclerosponges in the region are needed to confirm these findings.

[39] On interannual time scales, large deviations from the long-term mean (Figure 7c) were caused primarily by interannual time scale changes in $\delta^{18}O_{sw}$. Given that SST is known to be relatively constant in the WPWP on interannual time scales [*McGregor and Nieuwolt*, 1998], interannual variability in sclerosponge δ^{18}O in Palau should be driven primarily by changes in salinity. This is supported by four pieces of evidence. First, recent work by *Morimoto et al.* [2002] showed that 93% of the variability in $\delta^{18}O_{sw}$ in Palau is due to changes in salinity. Second, modeling studies show that changes in salinity in the broader region are largely the result of large-scale shifts in the amount of monsoon rains associated with ENSO variability on interannual time scales [*Feely et al.*, 2002; *McGregor and Nieuwolt*, 1998]. Third, the maximum change in the sclerosponge δ^{18}O anomalies is 0.53‰, the maximum value having been observed in early 1989 and the minimum in mid-1994 (Figure 7b), which would be equivalent to 2.4°C if the δ^{18}O variability were all the result of changes in SST. However, comparison with the Integrated Global Ocean Station System (IGOSS) seawater temperature record shows that the same time periods correspond to a change in temperature of only 1°C. Hence, the change in sclerosponge δ^{18}O is much greater than would be expected from temperature alone and indicates that on interannual time scales, the majority of the δ^{18}O variability appears to be driven by changes in $\delta^{18}O_{sw}$ (i.e., salinity). Fourth, results of the 2 year calibration (sections 3.2 and 4.1) strongly show that $\delta^{18}O_{sw}$ is the primary driver of sclerosponge δ^{18}O variability.

[40] As another point of interest, the interannual component of the sclerosponge δ^{18}O record was coherent and inversely correlated with SOI post-1977, but not pre-1977 (Figure 7c). The post-1977 correlation with SOI is consistent with the initial hypothesis, but the decoupling of the relationship pre-1977 is intriguing. Post-1977, Palau experienced lower (higher) $\delta^{18}O_{sw}$ (i.e., salinity) conditions during El Niño (La Niña). Pre-1977, however, local oceanographic conditions in Palau appear to be decoupled from ENSO variability. Once again, the transition period coincides with the switch in PDO in 1976, highlighting the connection

between interdecadal and interannual basin-scale oceanographic and climatic processes. The sensitivity of sclerosponge δ^{18}O records to ENSO variability has also been reported for *A. willeyana* from the Great Barrier Reef [*Wörheide*, 1998]. However, the resolution of this latter record was not sufficient to statistically evaluate the relationship between SOI and skeletal δ^{18}O.

4.4. Sclerosponge Growth and Implications for Chronology Development

[41] Compared to the Caribbean sclerosponge *C. nicholsoni* [*Benavides and Druffel*, 1986; *Böhm et al.*, 2002; *Haase-Schramm et al.*, 2003; *Joachimski et al.*, 1995; *Lazareth et al.*, 2000; *Swart et al.*, 2002; *Willenz and Hartman*, 1985], *A. wellsi* and *A. willeyana* growth rates in Palau and Saipan are typically 4 to 8 times greater. In addition, *A. wellsi* growth rates from both Saipan and Palau were 90–380% higher than in New Caledonia [*Böhm et al.*, 1996] and Australia [*Reitner and Gautret*, 1996]. Observed average growth rates in *A. willeyana* were 4.8 to 7.3 times greater than that previously reported for Australian specimens [*Wörheide et al.*, 1997; *Wörheide*, 1998] but consistent with results for other *A. willeyana* specimens from Australia and Truk [*Fallon and Guilderson*, 2005]. Observed average growth rates in Palauan *A. wellsi* were 36% lower than previously reported for *A. wellsi* from that region [*Hughes and Thayer*, 2001] and 43% lower than growth rates in a Vanuatu specimen [*Fallon et al.*, 2003]. However, Saipan *A. wellsi* growth rates were very similar to those previously reported for that species in Palau [*Hughes and Thayer*, 2001] and Vanuatu [*Fallon et al.*, 2003]. Closer examination of our data and of the reported literature as a whole reveals two features: not only can growth rates vary by 50% among specimens of the same species at the exact same location, but also they appear to increase as flow rates increase. Sclerosponges collected at the mouths of caves or from shallow cracks along walls appear to have higher growth rates than do specimens collected from the back of quiescent caves. At the same time, however, the growth rate within a specimen appears to be constant over the lifetime of the organism (see section 3.2).

[42] In the multidecadal sclerosponge specimen, visible horizontal skeletal structures were separated by an average of 1.40 mm ± 0.36 mm (1 standard deviation), calculated from measurements of the distance between horizontal structures at 20 randomly selected locations along the growth axis, which is within the range of error identical to the calculated 1.355 mm/yr growth rate based on the Δ^{14}C curve. These "annual" layers have also been observed in a New Caledonian *A. wellsi* sclerosponge [*Fallon et al.*, 2003]. The relatively high and constant growth rate in *A. wellsi* from open flushing environments coupled with what might be annual layers, allows for monthly or more frequent sampling resolution through use of microdrilling techniques for stable isotope analysis in *A. wellsi*. Further research is needed to confirm that the skeletal layers are annual.

[43] Overall, these findings have three implications for establishing sclerosponge chronologies: (1) The high degree of natural variability in growth rates among sclerosponge specimens must be taken into consideration when establishing growth chronologies to sclerosponge proxy records. The standard error about the MLSE means varied such that age estimates for a hypothetical 5 cm tall *A. wellsi* or *A. willeyana* specimen could differ by up to 34 and 6 years, respectively, if estimated from growth rates alone. Therefore, modern bomb-signal Δ^{14}C dating techniques [e.g., *Druffel and Benavides*, 1986; *Fallon et al.*, 2003; *Fallon and Guilderson*, 2005; *Grottoli*, 2006] are necessary to anchor the sclerosponge record to known time points in the record. (2) Since growth rates within a specimen were shown to be constant over the life of a specimen, the average annual growth rate can be calculated from the bomb-curve dates and used to establish a chronology for the entire sclerosponge record, even for the prebomb portion of the record. (3) *A. wellsi* sclerosponges may in fact have annual banding patterns that could be used in conjunction with Δ^{14}C analyses to further refine the chronology.

4.5. Summary

[44] The higher growth rates among *A. wellsi* and *A. willeyana* sclerosponges collected from well-flushed open sites allows for higher resolution isotopic or elemental analyses over shorter time periods compared to the Caribbean *C. nicholsoni* and compared to *A. wellsi* or *A. willeyana* collected from quiescent caves. Thus, the fast-growing Pacific species are best suited for studying interannual to interdecadal paleoceanographic variability. Since growth rates can vary among specimens of the same species and from the same location, a combination of geochemical measurements (e.g., Δ^{14}C dating, skeletal staining) must be used to calibrate the chronology of each specimen.

[45] Both *A. wellsi* and *A. willeyana* deposit their skeletal δ^{18}O according to the trends of isotopic equilibrium with seawater, independent of specimen size or growth rate. In the WPWP (i.e., Palau), sclerosponge δ^{18}O is primarily a recorder of $\delta^{18}O_{sw}$ on interannual to interdecadal time scales. In Saipan, sclerosponge δ^{18}O is primarily a recorder of seawater temperatures on subannual and longer time scales, though a −0.27‰ correction needs to be applied to *A. willeyana* δ^{18}O records to generate accurate temperature proxy records. Given the strong reproducibility of δ^{18}O records among specimens of a given species at a given site, a single *A. wellsi* or *A. willeyana* is sufficient to produce a reliable sclerosponge δ^{18}O record. Sr/Ca in *A. wellsi* does not appear to be a reliable recorder of paleoceanographic conditions, presumably because of the interference of Mg with Sr incorporation into the calcite.

[46] Overall, sclerosponge-derived proxy records may lend insight into the spatial and temporal variability in seawater temperature outside of the WPWP and in $\delta^{18}O_{sw}$ within the WPWP, thus extending existing instrumental sets by several decades. For example, the 56-year-long *A. wellsi* sclerosponge δ^{18}O record from Palau revealed for the first time that the 1976 PDO phase shift influenced water mass advection in the WPWP, mirroring circulation changes observed during the same period in the eastern tropical Pacific.

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References

Benavides, L. M., and E. R. M. Druffel (1986), Sclerosponge growth rate as determined by ^{210}Pd and Δ^{14}C chronologies, *Coral Reefs*, *4*, 221–224, doi:10.1007/BF00298080.

Böhm, F., M. Joachimski, H. Lehnert, G. Morgenroth, W. Kretschmer, J. Vacelet, and W.-C. Dullo (1996), Carbon isotope records from extant Caribbean and South Pacific sponges: Evolution of δ^{13}C in surface water DIC, *Earth Planet. Sci. Lett.*, *139*, 291–303, doi:10.1016/0012-821X(96)00006-4.

Böhm, F., M. M. Joachimski, W.-C. Dullo, A. Eisenhauer, H. Lehnert, J. Reitner, and G. Wörheide (2000), Oxygen isotope fractionation in marine aragonite of coralline sponges, *Geochim. Cosmochim. Acta*, *64*, 1695–1703, doi:10.1016/S0016-7037(99)00408-1.

Böhm, F., A. Haase-Schramm, A. Eisenhauer, W.-C. Dullo, M. M. Joachimski, H. Lehnert, and J. Reitner (2002), Evidence for preindustrial variations in the marine surface water carbonate system from coralline sponges, *Geochem. Geophys. Geosyst.*, *3*(3), 1019, doi:10.1029/2001GC000264.

Bottcher, M. E., P. L. Gehlken, and D. F. Steele (1997), Characterization of inorganic and biogenic magnesian calcites by Fourier Transform infrared spectroscopy, *Solid State Ion.*, *101–104*, 1379–1385, doi:10.1016/S0167-2738(97)00235-X.

Chu, P.-S., and J.-B. Wang (1997), Recent climate change in the tropical western Pacific and Indian ocean regions as detected by outgoing long-wave radiation records, *J. Clim.*, *10*, 636–646, doi:10.1175/1520-0442(1997)010<0636:RCCITT>2.0.CO;2.

Druffel, E. R. M. (1987), Bomb radiocarbon in the Pacific: Annual and seasonal timescale variations, *J. Mar. Res.*, *45*, 667–698, doi:10.1357/002224087788326876.

Druffel, E. R. M., and L. M. Benavides (1986), Input of excess CO_2 to the surface ocean based on $^{13}C/^{12}C$ ratios in a banded Jamaican sclerosponge, *Nature*, *321*(6065), 58–61, doi:10.1038/321058a0.

Fallon, S. J., and T. P. Guilderson (2005), Extracting growth rates from the non-laminated coralline sponge *Astrosclera willeyana* using bomb radiocarbon, *Limnol. Oceanogr. Methods*, *3*, 455–461.

Fallon, S. J., T. P. Guilderson, and K. Caldeira (2003), Carbon isotope constraints on vertical mixing and air-sea CO_2 exchange, *Geophys. Res. Lett.*, *30*(24), 2289, doi:10.1029/2003GL018049.

Fallon, S. J., M. T. McCulloch, and T. P. Guilderson (2005), Interpreting environmental signals from the coralline sponge *Astrosclera willeyana*, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, *228*(1–2), 58–69, doi:10.1016/j.palaeo.2005.03.053.

Feely, R. A., et al. (2002), Seasonal and interannual variability of CO_2 in the equatorial Pacific, *Deep Sea Res., Part II*, *49*, 2443–2469, doi:10.1016/S0967-0645(02)00044-9.

Folland, C. K., and T. R. Karl (2001), Recent rates of warming in marine environment meet controversy, *Eos Trans. AGU*, *82*(40), 453–459, doi:10.1029/01EO00270.

Friedman, I., and J. R. O'Neil (1977), Compilation of stable isotope fractionation factors of geochemical interest, in *Data of Geochemistry*, 6th ed., edited by M. Fleischer, U.S. Government Printing Office, Washington, DC.

Grossman, E. L., and T. L. Ku (1986), Oxygen and carbon isotope fractionation in biogenic aragonite: Temperature effects, *Chem. Geol.*, *59*(1), 59–74, doi:10.1016/0009-2541(86)90044-6.

Grottoli, A. G. (2006), Monthly resolved stable oxygen isotope record in a Palauan sclerosponge *Acanthocheatetes wellsi* for the period of 1977–2001, In *Proc. 10th Int. Coral Reef Symp., 2004*, pp. 572–579.

Grottoli, A. G., and C. M. Eakin (2007), A review of modern coral δ^{18}O and Δ^{14}C proxy records, *Earth Sci. Rev.*, *81*, 67–91, doi:10.1016/j.earscirev.2006.10.001.

Guilderson, T. P., and D. P. Schrag (1998a), Abrupt shift in subsurface temperatures in the tropical Pacific associated with changes in El Niño, *Science*, *281*, 240–243, doi:10.1126/science.281.5374.240.

Guilderson, T. P., and D. P. Schrag (1998b), Radiocarbon variability in the western equatorial Pacific inferred from a high-resolution coral record from Nauru Island, *J. Geophys. Res.*, *103*(C11), 24,641–624,650, doi:10.1029/98JC02271.

Haase-Schramm, A., F. Böhm, A. Eisenhauer, W.-C. Dullo, M. M. Joachimski, B. Hansen, and J. Reitner (2003), Sr/Ca ratios and oxygen isotopes from sclerosponges: Temperature history of the Caribbean mixed layer and thermocline during the Little Ice Age, *Paleoceanography*, *18*(3), 1073, doi:10.1029/2002PA000830.

Hare, S. R., N. J. Mantua, and R. C. Francis (1999), Inverse production regimes: Alaskan and west coast Pacific salmon, *Fisheries*, *21*, 6–14, doi:10.1577/1548-8446(1999)024<0006:IPR>2.0.CO;2.

Hartman, W. D. (1983), Modern and ancient sclerospongiae, in *Sponges and Spongiomorphs*, edited by T. W. Broadhead, pp., Dept. of Geological Sciences, Univ. of Tennessee, Knoxville, *Stud. Geol.*, *7*, 116–129.

Heron, S. F., E. J. Metzger, and W. J. Skirving (2006), Seasonal variations of the ocean surface circulation in the vicinity of Palau, *J. Oceanogr.*, *62*, 413–426, doi:10.1007/s10872-006-0065-3.

Horita, J., and R. N. Clayton (2007), Comment on the studies of oxygen isotope fractionation between calcium carbonates and water at low temperatures by Zhou and Zheng (2003; 2005), *Geochim. Cosmochim. Acta*, *71*, 3131–3135, doi:10.1016/j.gca.2005.11.033.

Hughes, G. B., and C. W. Thayer (2001), Sclerosponges: Potential high-resolution recorders of marine paleotemperatures, in *Geological Perspectives of Global Climate Change*, edited by L. C. Gerhard, W. E. Harrison, and B. M. Hanson, pp. 137–151, AAPG Studies in Geology, Tulsa, OK.

Hut, G. (1987), *Consultants' group meeting on stable isotope reference samples for geochemical and hydrological investigations*, *Internal Report*, IAEA, Vienna.

Jiménez-López, C., C. S. Romanek, F. J. Huertas, H. Ohmoto, and E. Caballero (2004), Oxygen isotope fractionation in synthetic magnesian calcite, *Geochim. Cosmochim. Acta*, *68*, 3367–3377, doi:10.1016/j.gca.2003.11.033.

Joachimski, M. M., F. Bohm, and H. Lehnert (1995), Longterm isotopic trends from Caribbean desmosponges: Evidence for isotopic disequilibrium between surface waters and atmosphere, *Proc. 2nd Eur. Reg. Meet. ISRS, 29*, 141–147.

Kim, S.-T., and J. R. O'Neil (1997), Equilibrium and nonequilibrium oxygen isotope effects in synthetic carbonates, *Geochim. Cosmochim. Acta*, *61*(16), 3461–3475, doi:10.1016/S0016-7037(97)00169-5.

Lazareth, C., P. Willenz, J. Navez, E. Keppens, F. Dehairs, and L. Andre (2000), Sclerosponges as a new potential recorder of environmental changes: Lead in *Ceratoporella nicholsoni*, *Geology*, *28*, 515–518, doi:10.1130/0091-7613(2000)28<515:SAANPR>2.0.CO;2.

Levitus, S., R. Burgett, and T. Boyer (1994), *World Ocean Atlas*, vol. 3, *Salinity*, NOAA Atlas NESDIS 3 (CD-ROM), National Oceanic and Atmospheric Administration, Silver Spring, MD.

Mantua, N. J., S. R. Hare, Y. Zhang, J. M. Wallace, and R. C. Francis (1997), A Pacific interdecadal climate oscillation with impacts on salmon production, *Bull. Am. Meteorol. Soc.*, *78*, 1069–1079, doi:10.1175/1520-0477(1997)078<1069:APICOW>2.0.CO;2.

McGregor, G. R., and S. Nieuwolt (1998), *Tropical Climatology*, 339 pp., John Wiley, New York.

Moore, M. D., C. D. Charles, J. L. Rubenstone, and R. G. Fairbanks (2000), U/Th-dated sclerosponges from the Indonesian Seaway record subsurface adjustments to west Pacific winds, *Paleoceanography*, *15*, 404–416, doi:10.1029/1999PA000396.

Morimoto, M., O. Abe, H. Kayanne, N. Kurita, E. Matsumoto, and N. Yoshida (2002), Salinity records for the 1997–98 El Niño from western Pacific corals, *Geophys. Res. Lett.*, *29*(11), 1540, doi:10.1029/2001GL013521.

Morse, J. W., and M. L. Bender (1990), Partition-coefficients in calcite: Examination of factors influencing the validity of experimental results and their application to natural systems, *Chem. Geol.*, *82*(3–4), 265–277, doi:10.1016/0009-2541(90)90085-L.

Reitner, J., and P. Gautret (1996), Skeletal formation in the modern but ultraconservative chaetetid sponge *Spirastrella (Acanthochaetetes) wellsi* (Demospongiae, Porifera), *Facies*, *34*, 193–208, doi:10.1007/BF02546164.

Reynolds, R. W., N. A. Rayner, T. M. Smith, D. C. Stokes, and W. Wang (2002), An improved in situ and satellite SST analysis for climate, *J. Clim.*, *15*, 1609–1625, doi:10.1175/1520-0442(2002)015<1609:AIISAS>2.0.CO;2.

Rosenheim, B. E., P. K. Swart, S. R. Thorrold, P. Willenz, L. Berry, and C. Latkoczy (2004), High-resolution Sr/Ca records in sclerosponges calibrated to temperature in situ, *Geology*, *32*(2), 145–148, doi:10.1130/G20117.1.

Rosenheim, B. E., P. K. Swart, and P. Willenz (2009), Calibration of sclerosponge oxygen isotope records to temperature using high-resolution δ^{18}O data, *Geochim. Cosmochim. Acta*, *73*, 5308–5319, doi:10.1016/j.gca.2009.05.047.

Schrag, D. P. (1999), Rapid analysis of high-precision Sr/Ca ratios in coral and other marine carbonates, *Paleoceanography*, *14*, 97–102, doi:10.1029/1998PA900025.

Stuiver, M., and H. A. Polach (1977), Discussion reporting of ^{14}C data, *Radiocarbon*, *19*(3), 355–363.

Swart, P. K., J. L. Rubenstone, C. Charles, and J. Reitner (1998), Sclerosponges: A new proxy indicator of climate, *NOAA Climate and Global Change Program*, 20 pp, Univ. Miami, Miami, FL.

Swart, P. K., S. Thorrold, B. Rosenheim, A. Eisenhauer, C. G. A. Harrison, M. Grammer, and C. Latkoczy (2002), Intra-annual variation in the stable oxygen and carbon and trace element composition of sclerosponges, *Paleoceanography*, *17*(3), 1045, doi:10.1029/2000PA000622.

Tarutani, T., R. N. Clayton, and T. K. Mayeda (1969), The effect of polymorphism and magnesium substitution on oxygen isotope fractionation between calcium and carbonate and water, *Geochim. Cosmochim. Acta*, *33*, 987–996, doi:10.1016/0016-7037(69)90108-2.

Vogel, J. S., D. E. Nelson, and J. R. Southon (1987), ^{14}C background levels in an accelerator mass spectrometry system, *Radiocarbon*, *29*(3), 323–333.

Willenz, P., and W. D. Hartman (1985), Calcification rate of *Ceratoporella nicholsoni* (Porifera: Sclerospongiae): An *in situ* study with calcein, paper presented at Proceedings of the 5th International Coral Reef Congress, Tahiti.

Willenz, P., and W. D. Hartman (1989), Micromorphology and ultrastructure of Caribbean sclerosponges. I. *Ceratoporella nicholsoni* and *Stromatospongia norae* (Ceratoporellida: Porifera), *Mar. Biol. Berlin*, *103*, 387–401, doi:10.1007/BF00397274.

Wooster, W. S., and C. I. Zhang (2004), Regime shifts in the North Pacific: Early indications of the 1976–1977 event, *Prog. Oceanogr.*, *60*, 183–200, doi:10.1016/j.pocean.2004.02.005.

Wörheide, G. (1998), The reef cave dwelling ultraconservative coralline demosponge *Astrosclera willeyana* Lister 1900 from the Indo-Pacific. Micromorphology, ultrastructure, biocalcification, isotope record, taxonomy, biogeography, phylogeny, *Facies*, *38*, 1–88, doi:10.1007/BF02537358.

Wörheide, G., P. Gautret, J. Reitner, F. Böhm, M. Joachimski, V. Thiel, W. Michaelis, and M. Massault (1997), Basal skeletal formation, role and preservation of intracrystalline organic matrices, and isotopic record in the coralline sponge *Astrosclera willeyana* Lister, 1900, *Bol. R. Soc. Esp. Hist. Nat. (Sec. Geol.)*, *91*, 355–374.

Zhou, G.-T., and Y.-F. Zheng (2002), Kinetic mechanism of oxygen isotope disequilibirum in precipitated witherite and aragonite at low temperatures: An experimental study, *Geochim. Cosmochim. Acta*, *66*(1), 63–71, doi:10.1016/S0016-7037(01)00746-3.

Zhou, G.-T., and Y.-F. Zheng (2003), An experimental study of oxygen isotope fractionation between inorganically precipitated aragonite and water at low temperatures, *Geochim. Cosmochim. Acta*, *67*, 387–399, doi:10.1016/S0016-7037(02)01140-7.

Zhou, G.-T., and Y.-F. Zheng (2005), Effect of polymorphic transition on oxygen isotope fractionation between aragonite, calcite, and water: A low-temperature experimental study, *Am. Mineral.*, *90*, 1121–1130, doi:10.2138/am.2005.1410.

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