



An apparent “vital effect” of calcification rate on the Sr/Ca temperature proxy in the reef coral *Montipora capitata*

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[1] Measuring the strontium to calcium ratio in coral skeletons reveals information on seawater temperatures during skeletal deposition, but studies have shown additional variables may affect the ratio. Here we measured Sr/Ca in the reef coral *Montipora capitata* grown in six mesocosms continuously supplied with seawater from the adjacent reef flat. Three mesocosms were ambient controls, and three had seawater chemistry simulating “ocean acidification” (OA). We found that Sr/Ca was not affected by the OA treatment and neither was coral calcification for these small colonies (larger colonies did show an OA effect). The lack of OA effects allowed us to test the hypothesis that coral growth rate can affect Sr/Ca using the natural range in calcification rates of the corals grown at the same temperature. We found that Sr/Ca was inversely related to calcification rate ($\text{Sr/Ca} = 9.385 - 0.0040 (\text{calcification rate})$). Using a previously published calibration curve for this species, a $22 \text{ mg d}^{-1} \text{ colony}^{-1}$ increase in calcification rate introduced a 1°C warmer temperature estimate, with the 27 corals reporting “temperatures” ranging from 24.9 to 28.9°C , with mean $26.6 \pm 0.9^\circ\text{C}$ standard deviation. Our results lend support to hypotheses invoking kinetic processes and growth rate to explain vital effects on Sr/Ca. However, uncertainty in the slope of the regression of Sr/Ca on calcification and a low R-squared value lead us to conclude that Sr/Ca could still be a useful proxy in this species given sufficient replication or by including growth rate in the calibration.

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1. Introduction

[2] Since most instrumental records of sea surface temperature (SST) only extend back a century or less, proxies are sought, such as the use of trace elemental ratios and isotopes in coral skeletons, for paleoreconstruction of SST [Druffel, 1997; Gagan et al., 2000; Corrège, 2006; Lough, 2010]. The elemental ratio between strontium and calcium in coral skeleton is now routinely used for this purpose [Weber, 1973; Smith et al., 1979; Beck et al., 1992; Alibert and McCulloch, 1997]. As with all proxies, there are assumptions that have to be made and tested regarding the influence of extraneous variables besides the desired environmental variable, but this process of questioning should not negate their usefulness in increasing knowledge of past climate change and variability [Schrag and Linsley, 2002]. Of particular concern are the constancy of Sr/Ca in seawater [de Villiers et al., 1994; Shen et al., 1996], and the possible influence of other environmental variables, e.g., salinity, pH, and nutrients. There are also those having to do with the biology of the organisms themselves, termed “vital” effects, such as growth rate [Houck et al., 1977; de Villiers et al., 1995], more specifically calcification rate [Cohen et al., 2001; Sinclair, 2005], and the activity of symbionts [Cohen et al., 2002].

[3] The premise behind the temperature-Sr/Ca relationship is that corals do not calcify in equilibrium with seawater, and the incorporation of Sr into the argonitic lattice has a temperature sensitive distribution coefficient [Smith et al., 1979]. This is mostly a physiochemical phenomenon since abiotically precipitated aragonite shows temperature dependence in Sr (and other alkaline earth cation) incorporation, but coral skeleton is thought to further deviate from equilibrium with seawater due to biological control of the calcification process [Cohen et al., 2006; Gaetani and Cohen, 2006]. This biological control seems to be species specific. While the slopes of the various calibrations conducted so far are very similar, the intercepts are not [Marshall and McCulloch, 2002]. There are several mechanisms that have been proposed to explain vital effects, most of which are linked to coral growth or some sort of kinetic process, but lack of

knowledge about and variability in calcification mechanisms among species greatly complicate our understanding of them. Experimental evidence suggests that the level of Sr incorporation is affected by a kinetic process linked to (and thus, perhaps, approximated by) calcification rate [Cohen et al., 2001]. Many of the studies explaining vital effects invoke a “reservoir” or Rayleigh fractionation effect, wherein calcium carbonate is precipitated from discrete batches of seawater within periodically enclosed calcifying spaces [Gaetani and Cohen, 2006]. When new seawater is brought into the calcicoblastic space for calcification, different rates of precipitation create different levels of kinetic disequilibrium. The faster the coral is growing, the more the calcifying fluid will diverge from equilibrium, and the more Sr depleted the resultant skeleton [Sinclair, 2005]. Differences in the mode of transport for specific ions have been proposed to explain vital effects. According to this idea, the transport of Ca^{2+} ions across coral membranes is active, versus passive uptake of Sr^{2+} , and thus the faster the coral is calcifying, the faster the Ca pumps are working, thereby diluting the Sr/Ca ratio inside the calcifying fluid [Sinclair, 2005]. However, new evidence suggests a minimal role for active transport of alkaline earth cations, and supports the hypotheses invoking the refreshment of new seawater in discrete batches within the calcicoblastic space [Gagnon et al., 2012], probably via paracellular pathways through the epithelial layers [Tambutté et al., 2012]. Various approaches have been proposed to deal with vital effects on the Sr/Ca proxy, including averaging the results of multiple coral cores taken within an area [Lough, 2004; Pfeiffer et al., 2009], by including linear extension rate in the Sr/Ca-temperature calibration [Goodkin et al., 2005; Saenger et al., 2008], and by using a statistical multiproxy approach [Gaetani et al., 2011].

[4] In most paleoreconstruction studies published thus far, coral “growth” rate is at least considered. Coral species show extreme variability in growth rates and forms, and there are numerous ways to express and measure growth, including increases in coral mass, length, volume, and area [Buddemeier and Kinzie, 1976]. Here we highlight and differentiate two measures of coral “growth”: linear extension (length of skeleton added per unit time) and calcification (mass of CaCO_3 gained per unit time). Patterns in calcification rate and linear extension

often do not correspond to one another [Barnes and Crossland, 1980], and neither are constant throughout the year [Shinn, 1966; Barnes and Crossland, 1980] particularly at high latitudes [Cohen *et al.*, 2004]. It is the subannual growth increments marked in the coral's skeleton by alternating bands of different densities that allows visualization of linear extension rates via X-ray imaging [Knutson *et al.*, 1972]. For example in Caribbean corals, there are thin, high-density bands produced in the late summer, and thick, lower-density bands produced throughout the rest of the year [Dodge and Brass, 1984; Leder *et al.*, 1996]. Calcification rates have not been directly measured in the wild very often, but mesocosm studies show that rates are positively related to temperature up until a thermal optimum, and then decline as the temperature approaches thermal tolerance thresholds [Jokiel and Coles, 1977]. In most coral paleoreconstruction studies evaluating coral growth, it is estimated by linear extension as visualized by X-ray or computerized tomography (CT) scan.

[5] It was suggested by *de Villiers et al.* [1994] that calcification rate, “the more difficult to quantify” growth parameter, would be the optimal one to measure when accounting for vital effects in the Sr/Ca proxy. Calcification rate, quantified by measuring the mass of skeleton gained per unit time [Jokiel *et al.*, 1978], would be a much more appropriate growth parameter than linear extension, which is influenced by variation in skeletal architecture not pertaining to the kinetic process. In one of the few studies where the importance of calcification rate on Sr/Ca was recognized and explicitly tested [Mitsuguchi *et al.*, 2003], the rate was calculated based upon measurements of skeletal density and linear extension. While common practice and useful for addressing many scientific questions [Lough, 2008], the calculation of calcification rate in this way necessitates assumptions about the time domain that are most likely not valid for most corals [e.g., Dodge and Brass, 1984], and linear extension can be highly variable even for corals of the same species living on the same reef [Hudson, 1981; Gagan *et al.*, 2012].

[6] Here we present data from a controlled mesocosm study that allowed for testing the effects of ocean acidification and whole-colony calcification rate on Sr/Ca in coral skeletons. Our replicated experiment allowed us to test the assumption that seawater carbonate chemistry and calcification rates (calcium carbonate mass gained per unit time for each whole colony) have a negligible effect on Sr/Ca. For the latter test, the corals were not

manipulated to obtain different growth rates (as in Reynaud *et al.* [2007]); rather, we used naturally varying rates of coral calcification in a series of mesocosm tanks with the same temperature regime as on the adjacent reef flat.

2. Materials and Methods

[7] The experiment took place at the Hawaii Institute of Marine Biology from November 2005 to August 2006 [Jokiel *et al.*, 2008; Kuffner *et al.*, 2008; Andersson *et al.*, 2009]. One small (approximately 5 cm tall × 1 cm wide) branch (nubbin) was taken from each of 30 morphologically distinct colonies of the reef coral *Montipora capitata* growing on the reef flat (<1 to 2 m depth) of Moku O Lo'e (Coconut Island), Kāne'ohe Bay, Hawai'i (21.4°N, 157.8°W). *Montipora capitata* is a fast growing, branching species of coral with a very perforate skeleton. The coral nubbins were fixed to ceramic tiles with Splash Zone® underwater epoxy and randomly assigned to one of six mesocosm tanks. By the end of the 9 month experiment, the nubbins had more than doubled in size. Five corals were maintained in each tank, which were flushed with seawater from the adjacent coral reef at a rate of eight liters min⁻¹ per mesocosm (complete turnover rate ≈ 1 h). The open system, replicated (n = 3 tanks per treatment), mesocosm approach was chosen for the study to achieve realistic diurnal and seasonal fluctuations in seawater temperature and chemistry similar to those occurring on reef flats [Ohde and van Woessik, 1999; Andersson and Mackenzie, 2012], making the study as close to a field experiment as possible while allowing estimates of variability between multiple tanks.

[8] Three mesocosms were randomly chosen to be maintained at an ambient (control, mean midday pCO₂ ± SD = 374 ± 31 μatm) chemical state, and the remaining three were maintained at a daytime pCO₂ exceeding control conditions by 240 ± 49 μatm (Table 1). The mean pCO₂ level in the treatment tanks at midday was near that expected sometime in the second half of the 21st century [Intergovernmental Panel on Climate Change, 1992] assuming equilibrium between the atmosphere and surface seawater, and was 614 ± 74 μatm during this time period. Note that the pCO₂ of Kāne'ohe Bay and many other coral reef environments, on average, is greater than the overlying atmosphere [Fagan and Mackenzie, 2007]. Furthermore, the surface seawater pCO₂ (and thus pH) fluctuates diurnally on coral reefs owing to shifts in organismal metabolism (photosynthesis and respiration) between day and

Table 1. Carbonate Chemistry in the Mesocosm Tanks During the Estimated Growth Period for the Coral Samples Analyzed for Sr/Ca^a

	Control		Treatment	
	Mean	SD	Mean	SD
$p\text{CO}_2$ (μatm)	374.2	30.8	613.9	74.4
$\Omega_{\text{aragonite}}$	3.16	0.15	2.11	0.22
TA ($\mu\text{mol kg}^{-1}$)	2104.8	34.5	1986.2	39.3
pH	8.19	0.03	8.00	0.05
$[\text{CO}_3^{2-}]$ ($\mu\text{mol kg}^{-1}$)	206.8	10.3	138.2	14.7

^aThe six mesocosms were sampled once per week at midday, and conditions in the tanks varied diurnally [see *Andersson et al.*, 2009, Figure 4]. $\Omega_{\text{aragonite}}$ = aragonite saturation state and TA = total alkalinity.

night [Ohde and van Woessik, 1999; Hofmann et al., 2011]. Carbonate chemistry was altered with hydrochloric acid (HCl) diluted with tap water to a 10% solution added at 1.3 ml min^{-1} via peristaltic pump to the inflow pipes of each treatment mesocosm (control mesocosms received tap water at the same rate). The carbonate chemistry in the mesocosms was well characterized (by measuring pH, total alkalinity, and DIC) at least once per week, and occasionally on a 24 h basis that revealed pronounced diurnal fluctuations driven by photosynthesis, respiration, and calcification inside the mesocosms [Andersson et al., 2009]. In an example 24 h sampling, $p\text{CO}_2$ approximately doubled and aragonite saturation state decreased by 1 during the night in control and treatment mesocosms [see *Andersson et al.*, 2009, Figure 4]. Water

temperature was measured with HOBO[®] Water Temp temperature loggers (Onset Computer Corporation), set to record temperature every 5 min in two randomly chosen mesocosm tanks, as well as on the adjacent reef flat near the intake pipe for the seawater system. The diurnal variation in temperature was pronounced, both in the tanks and on the reef flat (Figure 1). Temperature differences between the two tanks during the last month growth period were negligible (mean \pm SD difference tank T2 minus tank T3 = $0.22 \pm 0.34^\circ\text{C}$) and close to the uncertainty of the Sr/Ca proxy (0.18°C precision).

[9] Whole-colony calcification rate was measured using the buoyant weight technique [Jokiel et al., 1978]. Using this method, the coral being weighed is suspended in a container of seawater from a line that hangs from an under-loading balance. We realize that whole-colony calcification rate is not the same as directly measuring precipitation rates in the calcifying space (see section 1), but it should be a good indicator of the average microcalcification rates across the colony and during the time between weighings.

[10] At the end of the experiment, the coral nubbins were cleaned of tissue with a jet of tap water, air dried in the sun, and placed in plastic bags for storage in the dark. In January 2011, approximately 3 mm of a distal growing verruca (skeletal projection characteristic of this species) of each coral was removed using a dremel tool, reflecting growth during the last month of the experiment (using an

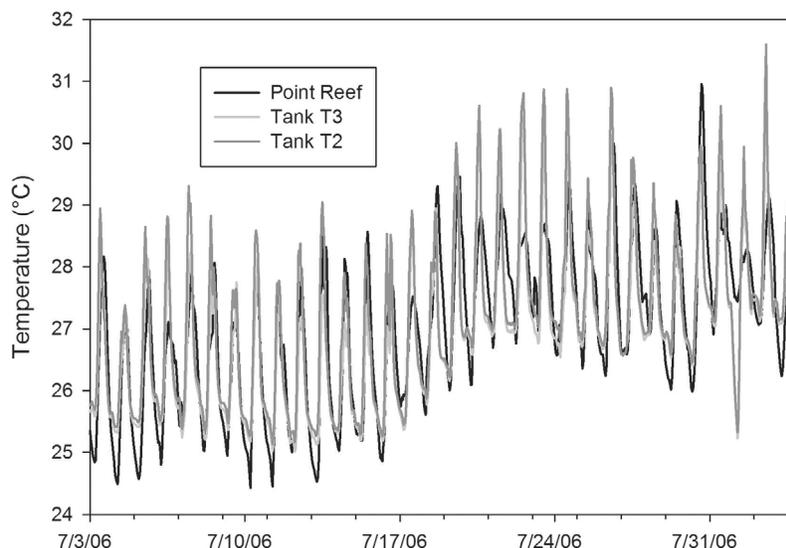


Figure 1. Water temperature (degrees Celsius) in two of the mesocosm tanks and the adjacent reef flat (source water for seawater system). The two spikes in early August are due to temporary stoppage of flow in the system, reflecting cooling at night and heating during the day.

Table 2. Thirty *Montipora capitata* Colonies Subjected to Control (Tanks C1, C2, and C3) or Ocean Acidification Treatment (Tanks T1, T2, and T3) Conditions^a

Coral Number	Mesocosm Tank	Calcification Rate (mg d ⁻¹)	Sr/Ca (mmol/mol ± SE)
1	T2	17.1	9.286 ± 0.0006
2	C3	37.9	9.364 ± 0.0028
3	C3	46.8	9.225 ± 0.0059
4	T1	dead	NA
5	C2	21.7	9.207 ± 0.0001
6	C3	17.5	9.424 ± 0.0207
7	C2	35.4	9.255 ± 0.0062
8	C3	38.0	9.299 ± 0.0079
9	C2	27.4	9.251 ± 0.0062
10	C2	35.2	9.265 ± 0.0073
11	T2	33.4	9.205 ± 0.0255
12	T2	37.9	9.254 ± 0.0202
13	T2	14.8	9.359 ± 0.0226
14	C1	19.8	9.330 ± 0.0236
15	T3	24.4	9.350 ± 0.0207
16	T2	15.2	9.315 ± 0.0149
17	C1	41.6	9.288 ± 0.0187
18	T1	dead	NA
19	C1	24.9	9.233 ± 0.0281
20	C3	23.5	9.315 ± 0.0012
21	T3	41.1	9.159 ± 0.0043
22	T1	21.0	9.150 ± 0.0065
23	C1	15.1	9.350 ± 0.0214
24	C1	33.2	9.204 ± 0.0020
25	T2	17.8	9.321 ± 0.0249
26	C2	12.6	9.330 ± 0.0080
27	T3	dead	NA
28	T1	14.9	9.382 ± 0.0028
29	T3	16.9	9.233 ± 0.0257
30	T1	52.0	9.065 ± 0.0085

^aNet calcification rate (mg d⁻¹) was measured using buoyant weight at the beginning and end of the 9 month experiment. Sr/Ca value is the mean ± SE of n = 2 subsamples (except for n = 3 for coral numbers 19 and 23, see section 2) from the homogenized powder of a 3 mm distal tip of the coral's growing edge. NA = not available.

average 90 μm d⁻¹ summer growth rate as reported in Jokiel *et al.* [2008]). Each coral piece was placed in a 1 mL vial, and 0.5 mL of deionized water was added to ensure that the sample was completely covered. The vials were placed in a sonicator for 15 min to remove any remaining organic material present in the coral matrix; further cleaning with organic solvents is not necessary for Sr/Ca analyses of coral samples [Watanabe *et al.*, 2001]. Any detritus was allowed to settle out and the remaining water was removed with a pipette. The vials were placed into a 50°C oven for 4 h to dry the skeletal material. Each sample was then transferred to a 0.25 mL vial, crushed, and homogenized using a metal spatula. Two aliquots of each coral powder sample were weighed out (between 88 and 237 μg) and diluted in a volume of 2% trace metal grade HNO₃ to obtain a target sample solution of ~20 ppm calcium.

[11] Elemental ratio Sr/Ca determinations were made using a PerkinElmer 7300 Dual View Inductively Coupled Plasma Optical Emission Spectrometer (ICP-OES) at the U.S. Geological Survey in St. Petersburg, FL. A reference solution prepared gravimetrically was measured for Sr/Ca before and after each dissolved coral sample to correct for instrumental drift and noise [Schrag, 1999]. The long-term average corrected precision for this gravimetric reference solution was 0.007 mmol mol⁻¹ (1σ, n = 105) Sr/Ca. We used homogenized powder from a *Porites lutea* specimen as a secondary measure of precision by analyzing a subsample after every five experimental samples to test for any potential coral matrix effects. The Schrag correction method [Schrag, 1999] was applied to this precision estimate as well, and produced a long-term average corrected precision of 0.016 mmol mol⁻¹ (1σ, n = 140). The temperature equivalent of this precision is 0.18°C using the calibration for this species in Smith *et al.* [1979]. The Sr/Ca value reported in Table 2 is an average of the two experimental subsamples from each coral. Samples with a standard deviation greater than 0.05 mmol mol⁻¹ had a third aliquot weighed out and analyzed for Sr/Ca, and all three subsamples were then averaged.

3. Results and Discussion

[12] For the coral nubbins in this study, there was not a statistically significant effect of ocean acidification treatment on coral calcification rate (Figure 2a; one-way ANOVA, p = 0.88). Small sample size, and the small size of the coral nubbins themselves, contributed to high variance in calcification, probably swamping out any OA effect. While this result did not agree with the results for the bigger corals growing in the same mesocosms [Jokiel *et al.*, 2008], it gave us the opportunity to test the effects of ocean acidification treatment on Sr/Ca, and the effects of coral calcification rate on Sr/Ca.

[13] In our study there was no significant effect of ocean acidification treatment on Sr/Ca values (Figure 2b; one-way ANOVA, p = 0.41). In a similar study to ours, Cohen *et al.* [2009] subjected coral recruits to varying ocean chemistry (aragonite saturation state). They found that Sr/Ca ratios in skeleton deposited during the treatment interval varied inversely with aragonite saturation state. They accounted for this variability in skeletal composition with predictions using Rayleigh mass fractionation calculations, thereby attributing the patterns in Sr/Ca to the rate at which the corals were

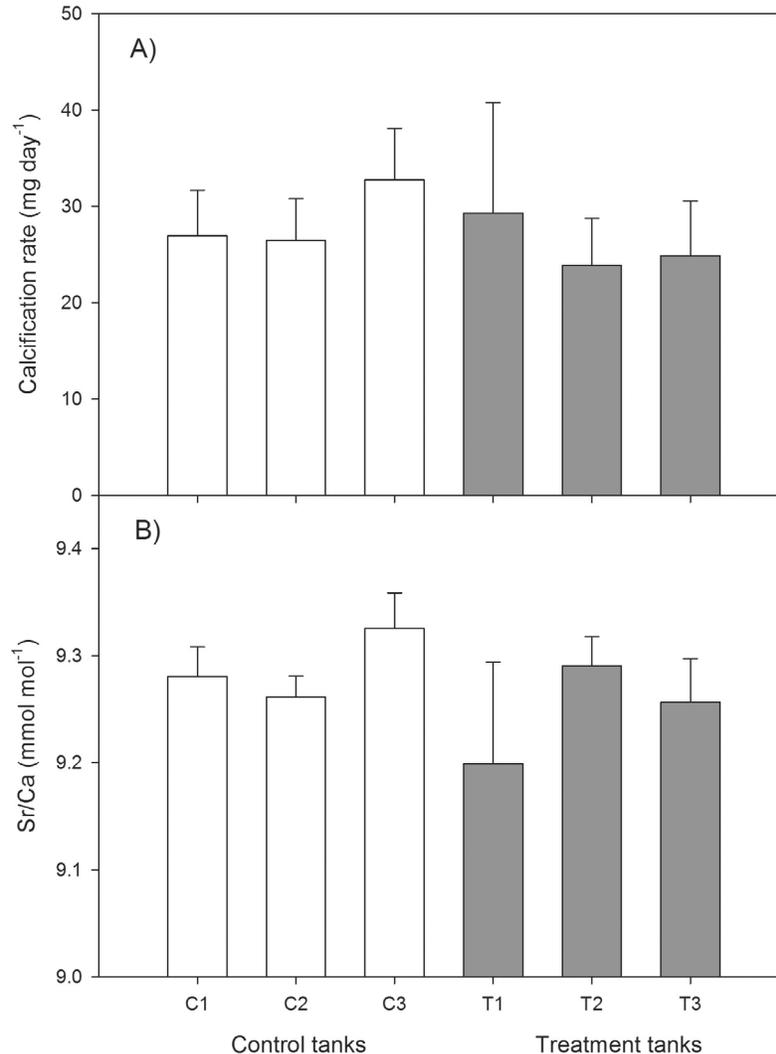


Figure 2. (a) Mean calcification rate ($\text{mg d}^{-1} \pm \text{SE}$) and (b) Sr/Ca ($\text{mmol mol}^{-1} \pm \text{SE}$) of *Montipora capitata* coral colonies grown in six mesocosm tanks: three at ambient control conditions (C1, C2, and C3) and three under ocean acidification treatment (T1, T2, and T3). Mean midday $p\text{CO}_2 \pm \text{SD}$ for control mesocosms = $374 \pm 31 \mu\text{atm}$ and $614 \pm 74 \mu\text{atm}$ for treatment mesocosms (see Table 1 for other carbonate chemistry variables). $N = 5$ coral colonies in each tank except $n = 3$ in T1 and $n = 4$ in T3 due to natural mortality.

growing (i.e., the fraction of calcifying fluid that was precipitated per batch). These results are consistent with ours in that they do not suggest a direct influence of ocean chemistry on the Sr/Ca proxy, but do predict indirect influence of ocean chemistry via controls on calcification rates. While our study and the Cohen *et al.* [2009] study suggest no direct effect of ocean acidification treatment on the Sr/Ca temperature proxy, there is evidence that other paleoproxies are affected by pH. Krief *et al.* [2010] found that $\delta^{18}\text{O}$ was sensitive to seawater pH (adjusted by bubbling with CO_2) in two species of corals from the Red Sea when grown at a constant temperature. Inoue *et al.* [2011] measured U/Ca in

Acropora spp. recruits, and proposed that in combination with measurement of Sr/Ca, it has potential as a pH paleoproxy.

[14] In our study there was a statistically significant relationship between calcification rate and Sr/Ca (simple linear regression, R-squared = 0.32, $p = 0.002$, $\text{Sr/Ca} = 9.385 - 0.0040$ (calcification rate); Table 2 and Figure 3). If the point with the extreme value in calcification rate (coral #30) that is influential on the slope of the line is eliminated, the slope is more shallow and less variance in Sr/Ca is explained but the regression is still significant (simple linear regression, R-squared = 0.20, $p =$

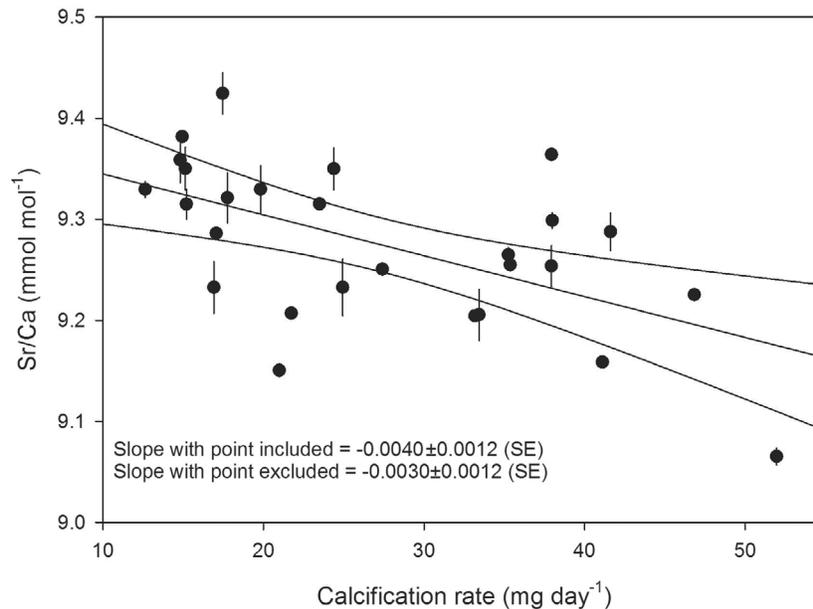


Figure 3. Sr/Ca (mean $\text{mmol mol}^{-1} \pm \text{SE}$ of two subsamples) of 27 different *Montipora capitata* coral colonies grown in six mesocosm tanks as a function of coral calcification rate (mg d^{-1}) measured during the 9 month experiment. The simple linear regression line is shown ($\text{Sr/Ca} = 9.385 - 0.0040$ (calcification rate)) with 95% confidence intervals. If the fastest growing coral (#30) is eliminated from the analysis (influential point), the regression equation is $\text{Sr/Ca} = 9.362 - 0.0030$ (calcification rate).

0.0235, $\text{Sr/Ca} = 9.362 - 0.0030$ (calcification rate)). The corals in our study that calcified more rapidly over the long-term experiment had lower Sr/Ca values, falsely indicating warmer temperatures. Using the *Smith et al.* [1979] calibration for this species (former name *Montipora verrucosa*, now named *Montipora capitata*), the range we observed in our Sr/Ca data from 9.42 to 9.06 mmol mol^{-1} corresponds to a predicted “temperature” range of 24.9 to 28.9°C. The actual temperatures experienced by the corals ranged from 24.3 to 29.0°C (see diurnal fluctuation in Figure 1). The significance of this correspondence is hard to deduce, since it is hard to imagine that the slower growing corals were calcifying more when experiencing cooler temperatures and vice versa.

[15] There is much conflicting information regarding the importance of vital effects and whether their influence is significant enough to invalidate the use of Sr/Ca in corals as a temperature proxy. The most substantial demonstration of vital effects came from the work of *de Villiers et al.* [1994, 1995]. The later paper showed that transects along different growth axes of the same colony of *Pavona clavus* could vary greatly in Sr/Ca, and the slower growing axis on the side of the coral estimated temperatures much cooler than the fast growing main coral axis. The *de Villiers et al.* [1995] study

also demonstrated intrareef variability in Sr/Ca by documenting differences between two individual corals living on the same reef. However, there are critics of the *de Villiers et al.* [1995] sampling technique in that they did not follow the same skeletal components in their drilling transects [*Marshall and McCulloch, 2002*]. Later studies have concluded that vital effects are negligible or not important enough to invalidate the proxy. Temperature dependence of Sr/Ca was found to be robust to growth (linear extension) rate and species (within the genus *Porites*) when corals were cultured at a range of temperatures [*Inoue et al., 2007*]. However, there was a large amount of variation in Sr/Ca among corals grown at the same temperature that could not be accounted for by any variable measured. The same corals were previously analyzed for $\delta^{18}\text{O}$, revealing that intercolony variance in coral oxygen isotope ratio could be largely explained by kinetic effects as determined by linear extension rate [*Suzuki et al., 2005*].

[16] Studies have recommended the inclusion of growth rate into the calibration of the Sr/Ca proxy [*Goodkin et al., 2005; Saenger et al., 2008*]. It has also been suggested that sampling during the periods of reduced growth (e.g., wintertime) would yield more accurate reconstructions of SST due to decreased vital effects on Sr/Ca [*Meibom et al.,*

2003]. Despite the difficulty in measuring calcification rate directly, there seems to be a consensus that it would be the best choice for estimating kinetic effects rather than linear extension [Suzuki *et al.*, 2005]. There was one study that measured both calcification rate (buoyant weight over time) and Sr/Ca. However, they achieved different calcification rates through the application of different temperature and light regimes, and only had one genotype (a single colony) represented in the study [Reynaud *et al.*, 2007]. Species-specific studies (field or culture) where all three growth parameters (density via X-ray, linear extension via alizarin Red S staining, and calcification rate via buoyant weighing) were independently measured, plus in situ temperature, would yield the best chance for a growth-corrected temperature calibration for Sr/Ca in coral skeletons.

[17] The results of our investigation suggest that in this species of coral, whole-colony calcification rate (as an indicator of microcalcification rate, which can be highly heterogeneous [Gagnon *et al.*, 2012]) could explain some of the variance in Sr/Ca values that is independent of temperature. However, the slope of the regression between Sr/Ca and calcification was highly uncertain, and in fact could be quite shallow. Calcification rates and skeletal architecture vary greatly among coral species, so it is not surprising that some coral species will act as better paleorecorders than others. *Montipora capitata*, which has not been further used as a temperature recorder since the original work by Smith *et al.* [1979], is in the family *Acroporidae* along with *Acropora palmata*, which has likewise proven not particularly valuable for Sr/Ca temperature proxy work [Gallup *et al.*, 2006]. Obtaining reliable chronologies for branching species such as these also presents a problem for paleoclimate work, making the issue fairly moot. Our data do support, however, the proposed mechanisms for vital effects involving the mass fraction of calcium carbonate precipitated from discrete batches of seawater within periodically enclosed calcifying spaces [Gaetani and Cohen, 2006]. Our study also demonstrates that whole-colony calcification rate could be a good way to estimate and correct for vital effects, particularly in culture experiments using small corals.

[18] Continued work using *Porites* spp. in the Pacific [Inoue *et al.*, 2007; Pfeiffer *et al.*, 2009], and *Siderastrea siderea* and *Montastraea faveolata* in the Atlantic [Saenger *et al.*, 2009; DeLong *et al.*, 2011] supports the utility of Sr/Ca as a paleoproxy. As long as studies are replicated (i.e., cores taken from multiple corals across a reef area experiencing

similar oceanographic and hydrographic settings) to account for the natural variability in growth rates of individual corals [Lough, 2004], or growth rates are somehow incorporated into the calibration exercise [Goodkin *et al.*, 2005; Saenger *et al.*, 2008; Gaetani *et al.*, 2011], and coral species (ideally more than one) are chosen carefully, Sr/Ca measured in large, density banding corals will continue to yield useful information on sea surface temperatures over the past several centuries.

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