



## RESEARCH ARTICLE

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## Impact of warming events on reef-scale temperature variability as captured in two Little Cayman coral Sr/Ca records

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## Key Points:

- Susceptibility of corals to temperature stress varies on local and regional scales
- Coral data show that reef-scale SST variability can be much larger than suggested by satellite based SST
- Two corals respond differently to short-term thermal stress depending on their position in the reef

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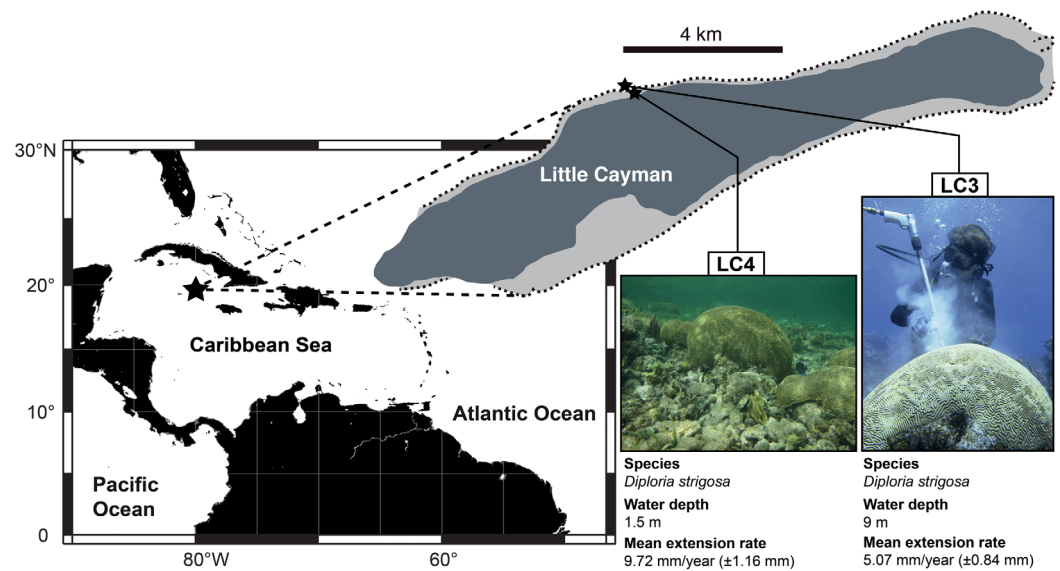
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**Abstract** The rising temperature of the world's oceans is affecting coral reef ecosystems by increasing the frequency and severity of bleaching and mortality events. The susceptibility of corals to temperature stress varies on local and regional scales. Insights into potential controlling parameters are hampered by a lack of long term in situ data in most coral reef environments and sea surface temperature (SST) products often do not resolve reef-scale variations. Here we use 42 years (1970–2012) of coral Sr/Ca data to reconstruct seasonal- to decadal-scale SST variations in two adjacent but distinct reef environments at Little Cayman, Cayman Islands. Our results indicate that two massive *Diploria strigosa* corals growing in the lagoon and in the fore reef responded differently to past warming events. Coral Sr/Ca data from the shallow lagoon successfully record high summer temperatures confirmed by in situ observations (>33°C). Surprisingly, coral Sr/Ca from the deeper fore reef is strongly affected by thermal stress events, although seasonal temperature extremes and mean SSTs at this site are reduced compared to the lagoon. The shallow lagoon coral showed decadal variations in Sr/Ca, supposedly related to the modulation of lagoonal temperature through varying tidal water exchange, influenced by the 18.6 year lunar nodal cycle. Our results show that reef-scale SST variability can be much larger than suggested by satellite SST measurements. Thus, using coral SST proxy records from different reef zones combined with in situ observations will improve conservation programs that are developed to monitor and predict potential thermal stress on coral reefs.

## 1. Introduction

Sea surface temperature (SST) in the tropical oceans is an important component in understanding tropical ocean-atmosphere dynamics and a key parameter for climate models in assessing future climate evolution linked to anthropogenic climate change [Deser et al., 2010; Enfield and Cid-Serrano, 2010; Latif and Keenlyside, 2011; IPCC, 2013]. Understanding past tropical climate variability beyond the period of instrumental observations or within regions lacking instrumental data requires the use of climate proxies. The geochemistry of coral skeletons provides such proxies. Corals record environmental fluctuations in ambient seawater and large-scale climate variability during growth. Geochemical records from corals offer reliable data on dominant large-scale climate modes and are used to detect impacts in the northern tropical Atlantic including the El Niño Southern-Oscillation (ENSO), the North Atlantic Oscillation (NAO) [Kuhnert et al., 2005; Hetzinger et al., 2006; Goodkin et al., 2008] or the Atlantic Multidecadal Oscillation (AMO) [Hetzinger et al., 2008]. One of the most commonly used geochemical parameters measured in coral aragonite are Sr/Ca ratios. Relative variations of coral Sr/Ca ratios follow thermodynamic principles and are influenced by temperature and the Sr/Ca of seawater. Over the past several hundred years seawater Sr/Ca changes are negligible [Gagan et al., 2000] and several studies have used the Sr/Ca ratios as paleothermometers for the reconstruction of SSTs on timescales ranging from seasonal and interannual to decadal in local to regional dimensions [Smith et al., 1979; Beck et al., 1992; de Villiers et al., 1994; Alibert and McCulloch, 1997; Gagan et al., 2000; Marshall and McCulloch, 2002; DeLong et al., 2012]. Coral Sr/Ca records are typically calibrated against SST records from local in situ measurements or reanalysis data and ideally resemble SST variability over the calibration period. In most cases local SST records are not available and reanalysis products calculated over a relatively large area are used. However, water temperatures can vary significantly at individual reef sites over small spatial and temporal scales because of the bottom topography and variable forcing parameters (e.g., tides, currents and insolation) [Monismith et al., 2006; McCabe et al., 2010]. Tidal forcing can play a role



**Figure 1.** Location of coral cores LC3 and LC4 (small stars) at Little Cayman, Cayman Islands (large star), Caribbean Sea. Coral cores are located 500 m apart. Images of the two colonies together with water depth and mean extension rates of the colonies over the common 42 year period.

in coral Sr/Ca variability on a daily and monthly scale [Cohen and Sohn, 2004]. Consequently, local effects on SST may hamper the use of coral colonies as recorders of regional/large-scale environmental variability. This study presents Sr/Ca time series from two *Diploria strigosa* coral cores drilled in different reef environments, the shallow lagoon and the fore reef of Little Cayman, Cayman Islands. These time series are used to examine how local environmental parameters may be imprinted in the coral record and which may be specific for each environment.

The questions addressed in this study include: (1) does satellite-based instrumental temperature data accurately capture the local- to regional-scale temperature variability? (2) which mechanisms influence seawater temperature and coral Sr/Ca in reef environments on a local scale (e.g., tides, insolation, water depth)? and (3) how does local-scale environmental variability affect the applicability of coral proxy data for regional and large-scale temperature reconstructions?

## 2. Materials and Methods

### 2.1. Setting of the Study Area

Little Cayman (Figure 1) is the smallest and least developed island of the three Cayman Islands with a human population of less than 200. It is a 17 km long and 1.6 km wide low-lying island with a maximum elevation of 13 m located in the pathway of the Caribbean Current. The island's climate is strongly moderated by the sea since no major land masses are present within a radius of 200 km. An almost continuously developed fringing reef encircles the island. The fore reef shelf is shallow and narrow and its edge is marked by the 20 m isobath from where it drops to great depths outside the euphotic zone. The width of the shelf averages 500 m, but extends to 1700 m off the east end of Little Cayman. Freshwater is scarce and the island lacks rivers and streams. Land based discharge of erosional products into lagoonal waters seems to be insignificant. Little Cayman has an average tidal amplitude of 26 cm while the range between highest and lowest tidal elevation is 1 m, representing a micro tidal environment typical for the Caribbean region [Kjerfve, 1981]. The tidal cycle generally shows a semidiurnal pattern although the diurnal component is often dominant. More than 50% of the nearshore waters are designated as marine park or no-take zone, ensuring minimal direct anthropogenic stress.

### 2.2. Coral Sampling

In July 2012, coral cores LC3 and LC4 were extracted from two separate hemispherical colonies of *Diploria strigosa* on the north central coast of Little Cayman. Colonies are located 500 m from each other. LC3 had a

diameter of 0.8 m and grows in a water depth of 9 m in the fore reef (Figure 1) 200 m off the fringing reef. LC4 had a diameter of 1 m and grows in a water depth of 1.5 m in the backreef inside the lagoon. At this site the lagoon is shallow and only 140 m wide. Here tidal currents are believed to be relatively strong despite the micro tidal environment owing to the lagoons shallow cross section and the proximity to a tidal inlet 300 m to the east of the corals location. Both cores were drilled approximately parallel to the central growth axis of the colony. The pneumatic drill was equipped with a 3.6 cm diameter core drill. Cores LC3 and LC4 have a length of 69 cm and 61.5 cm, respectively. The coral slabs were x-rayed in order to expose annual density band couplets which are slightly inclined. A chronology was generated by counting the well-developed annual density bands. Core LC3 extends continuously from 1871 to 2012, core LC4 from 1970 to 2012. For this study only the chronologically overlapping parts of both cores were considered. The skeletal extension rate measured from the annual density bands averages  $5.07 \text{ mm yr}^{-1}$  ( $\pm 0.84 \text{ mm}$ ) and  $9.72 \text{ mm yr}^{-1}$  ( $\pm 1.16 \text{ mm}$ ) for LC3 and LC4, respectively.

### 2.3. Coral Sr/Ca

Powdered samples were collected for trace element analysis using a low-speed micro drill with a diamond-coated 0.5 mm diameter drill bit. The samples were drilled every 0.5 mm along the corallite walls (parallel to the growth axis), yielding on average 10 samples per year for LC3 and 19 samples per year for LC4. Since the longitudinal axis of either core was slightly inclined to the growth axis of the coral, it was necessary to track jump downcore to stay in the growth axis. The molar Sr/Ca ratios were determined by inductively coupled plasma optical emission spectrometry (ICP-OES, Spectro Ciros SOP) at the University of Kiel. Element emission signals were simultaneously collected and subsequently drift corrected by sample-standard bracketing every five samples following a combination of techniques described by Schrag [1999] and de Villiers *et al.* [2002]. Analytical precision on Sr/Ca determinations was 0.15% RSD or  $0.01 \text{ mmol mol}^{-1}$  ( $1\sigma$ ). The average Sr/Ca value of the JcP-1 standard [Inoue *et al.*, 2004] from multiple measurements on the same day and on consecutive days was  $8.855 \text{ mmol mol}^{-1}$  with a RSD of 0.09%.

### 2.4. Coral Chronology

The coral chronologies were developed based on the pronounced seasonal cycle in the Sr/Ca record. The highest (lowest) measured Sr/Ca value was assigned to February (September) of any given year, which on average is the coldest (warmest) month according to HadISST. The Sr/Ca time series were linearly interpolated between these anchor points using the Analyseries software [Paillard *et al.*, 1996] to obtain monthly proxy time series. The uncertainty of the age model is approximately 1–2 months in any given year due to interannual differences in the exact timing of maximum (minimum) SST.

### 2.5. In Situ and Gridded Temperature Data

In situ water temperature data for Little Cayman Island are available from the Coral Reef Early Warning System (CREWS) station located within the fore reef zone of the Bloody Bay Marine Park <300 m off the reef crest and <400 m apart from coral colony LC3. The station is part of the Integrated Coral Observing Network (ICON) of the National Oceanic and Atmospheric Administration (NOAA) and is equipped with a variety of meteorological and oceanographic instruments. Hourly water temperatures were recorded by an NXIC-CTD (Conductivity, Temperature, Depth) from Falmouth Scientific at a depth of approximately 5 m. The employed data set comprises 3 years of measurements. The record starts in August 2009 when the station was newly brought into service and ends in October 2012 due to storm damage 3 months after retrieval of the coral cores. For this study the water temperature data were averaged to produce a monthly time series. Mean annual SST for the time interval is  $28.21^\circ\text{C}$  with an average seasonal variation of  $3.91^\circ\text{C}$ . Monthly SST data for the calibration of the Sr/Ca record were extracted from the HadISST data set for the  $1^\circ \times 1^\circ$  grid box at  $19\text{--}20^\circ\text{N}$  and  $79\text{--}80^\circ\text{E}$  including the coral sites [Rayner *et al.*, 2003]. A comparison of the CREWS and HadISST data for the 2009–2012 period reveals similar mean annual SSTs but different average seasonal variations with the gridded SST product underestimating the in situ data by almost  $0.8^\circ\text{C}$  (Table 1). Accordingly these data were adjusted using an ordinary least squares (OLS) regression relationship between the HadISST and the CREWS data to create an augmented SST data set (referred to as such hereafter) following previous examples [e.g., Smith *et al.*, 2006; Maupin *et al.*, 2008]. The discrepancy in the average seasonal variation between the (augmented) gridded and the in situ data could thus be reduced to  $0.2^\circ\text{C}$ . A regression of monthly augmented and in situ SST yields a high correlation coefficient of 0.98.

**Table 1.** Basic Statistics of the (Calibrated) Sr/Ca and Temperature Data Sets for the Seasonal Cycle and Full Records for the 1969–2011 and the 2009–2012 Time Period<sup>a</sup>

Data Set	Period	Seasonal Cycle							Max	Min	Range	$\Delta_{\text{Range}}$	$\sigma_{\text{AMV}}$
		Summer	Winter	$\Delta_S$	$\Delta_W$	Average	Range	$\Delta_{\text{Range}}$					
<i>Sr/Ca</i>													
LC4	1969–2011	9.182	9.024			9.111	0.158		9.330	8.899	0.431		0.05
LC3	1969–2011	8.941	8.867			8.901	0.074		9.029	8.814	0.215		0.02
<i>SST</i>													
CREWS	2009–2012	30.26	26.35			28.21	3.91	–	30.50	25.79	4.71	–	0.01
HadISST	2009–2012	29.74	26.61	–0.52	0.26	28.26	3.13	0.78	30.16	26.37	3.79	–0.92	0.03
HadISST <sub>aug</sub>	2009–2012	29.97	26.25	–0.29	–0.10	28.22	3.71	0.20	30.46	25.97	4.50	–0.21	0.04
HadISST <sub>aug</sub>	1969–2011	29.74	26.25			28.08	3.49	–	30.52	25.73	4.79	–	0.19
LC4	1969–2011	30.35	26.40	0.61	0.15	28.17	3.95	0.46	33.48	22.71	10.78	5.98	1.13
LC3	1969–2011	29.28	25.36	–0.46	–0.89	27.49	3.92	0.43	32.05	20.74	11.32	6.52	1.12

<sup>a</sup>Sr/Ca in mmol/mol; SST in °C;  $\Delta$  is difference to CREWS (HadISSTaug);  $\sigma_{\text{AMV}}$  is standard deviation of annual mean values.

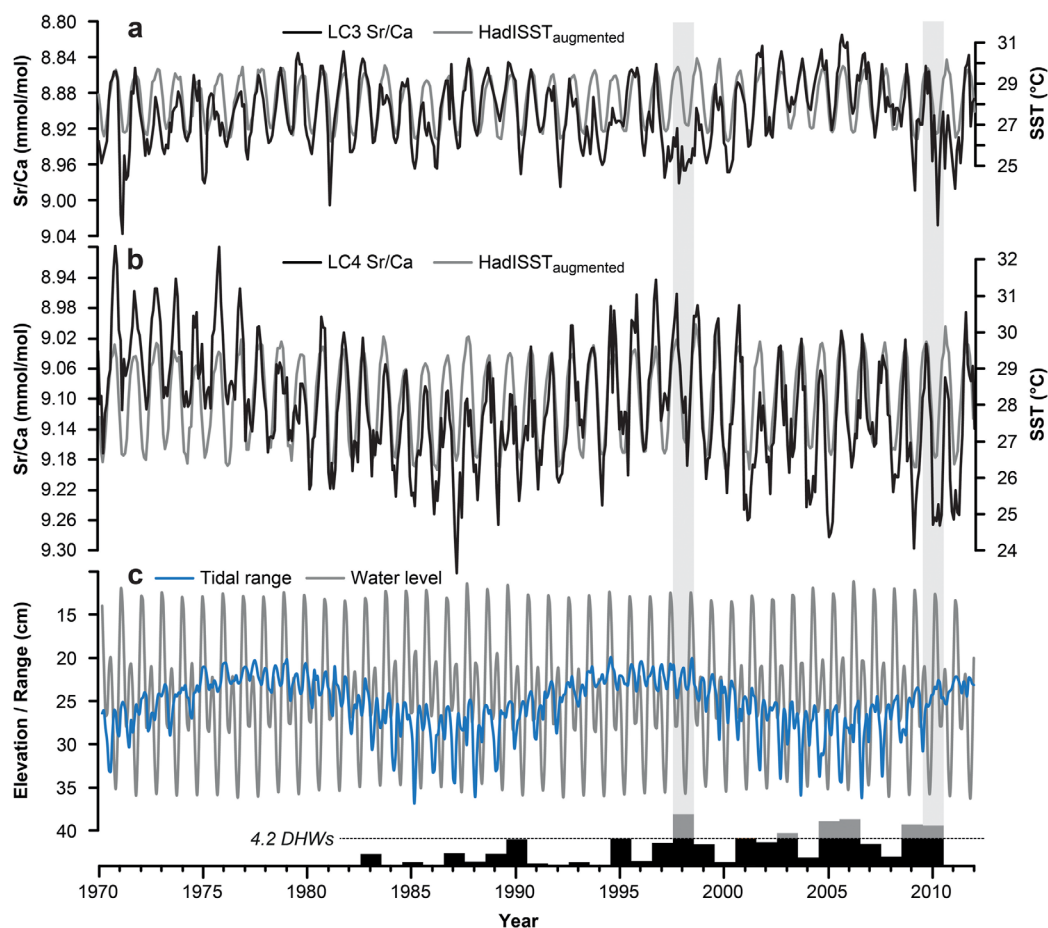
Since no systematic tidal measurements from tide gauges were available for Little Cayman, tidal data were generated using the Mr. Tides software (Hahn Software, Seattle, WA, USA). The program predicts tides based only on harmonics data for a particular location and the used algorithm does not take into account anything other than the Sun and the Moon.

### 3. Results and Discussion

#### 3.1. Calibration of Coral Sr/Ca Records With Temperature

Both LC3 and LC4 show clear seasonal cycles in the monthly time series (Figure 2). The two records strongly correlate over the entire length on the monthly scale ( $r = 0.75$ ,  $p < 0.0001$ ). However, the correlation is much reduced ( $r = 0.24$ ,  $p < 0.05$ ) on the mean annual scale. To evaluate the applicability of Sr/Ca ratios as a proxy for regional temperature variability, both records were calibrated against the augmented SST data set. A comparison of the resulting transfer functions for monthly, annual mean, and extreme values is given in Table 2.

Regressions of monthly Sr/Ca with gridded SST yield significant relationships for both records ( $r = -0.67$  and  $-0.70$ , LC3 and LC4 respectively;  $p < 0.0001$ ). The resulting regression slopes show significant differences between coral records with  $-0.04 \text{ mmol mol}^{-1} \text{ } ^\circ\text{C}^{-1}$  for LC4 and  $-0.019$  for LC3. A regression using only the warmest and coldest months in SST (September and February) and the corresponding minimum and maximum Sr/Ca values further enhances the relationship and also confirms the regression slopes obtained using monthly data (Table 2). The correlation of annual mean Sr/Ca values to SST, however, is weaker (Table 2) and insignificant for both records. Published relationships between Sr/Ca from different tropical Atlantic coral genera and water temperatures show slopes ranging from  $-0.023$  to  $-0.084 \text{ mmol mol}^{-1} \text{ } ^\circ\text{C}^{-1}$  [Cardinal *et al.*, 2001; Swart *et al.*, 2002; Cohen *et al.*, 2004; Goodkin *et al.*, 2005; Smith *et al.*, 2006; Maupin *et al.*, 2008; DeLong *et al.*, 2011]. Previously published slopes for modern Caribbean *Diploria strigosa* from Guadeloupe [Hetzinger *et al.*, 2006] and Bonaire [Giry *et al.*, 2012] range from  $-0.034$  to  $-0.042 \text{ mmol mol}^{-1} \text{ } ^\circ\text{C}^{-1}$ . The Sr/Ca-SST slope from the lagoon coral LC4 obtained in this study falls within this range while that from the fore reef coral LC3 is notably lower. The applicability of these calibrations, however, needs to be scrutinized, e.g., Smith *et al.* [2006] explained similar differences in calibrations (for *Montastraea*) with variations in water chemistry not accounted for in the regression analysis. Their explanation is supported by the work of several investigators indicating that Sr/Ca of seawater, especially in the realm where corals grow, cannot be considered constant through time and space [de Villiers *et al.*, 1994; Shen *et al.*, 1996; de Villiers, 1999; De Deckker, 2004]. Furthermore, the strength and pattern of surface water circulation and therefore heat fluxes and associated heat accumulation within a reef system are strongly dependent on the systems morphology and its exposure to the open ocean [Roberts *et al.*, 1975; Farrow and Patterson, 1993; Monismith *et al.*, 2006; McCabe *et al.*, 2010]. As a result, the maximum temperatures in shallow lagoon waters, which are separated from the open ocean, can be several degrees higher than in the fore reef environment. In situ temperature logger data from a survey in summer 2014 at Grape Tree Bay, Little Cayman, confirm this assumption, indicating that daily maximum



**Figure 2.** Monthly mean Sr/Ca time series of coral cores (a) LC3 and (b) LC4 together with monthly mean SST time series from the HadISST reanalysis data set. SST has been scaled according to each core regression equation. (c) Tidal range and water level for Little Cayman. Note that for better comparison with Sr/Ca and SST variability tidal ranges are shown with inverse scale. Black bars represent Maximum Degree Heating Weeks (DHW) per year for the period 1982–2010 calculated from OISST v2 data at Little Cayman [van Hooidonk et al., 2012]. The horizontal line is the optimal bleaching threshold of 4.2 DHWs. DHWs above this threshold are grey, indicating that bleaching is predicted. Light grey bars mark the El Niño years 1998 and 2010.

temperatures are much higher in the lagoon than in the fore reef environment at the same water depth exceeding 33°C during the summer (unpublished data). Water exchange of lagoonal waters with the open ocean is limited at this location through the shallow water depth on the reef crest (0.5–1 m). Particularly a calibration of the lagoon Sr/Ca record with gridded SST, although augmented with in situ fore reef data, will therefore lead to an underestimation of the true temperature range in the surrounding waters.

**Table 2.** Linear Regression Equations Between Coral Sr/Ca Ratios and Augmented HadISST Data Set<sup>a</sup>

Coral Core	Data Set	Period	Resolution	Regression Equation	r	r <sup>2</sup>	p	σ <sup>b</sup>
LC3	HadISST <sub>aug</sub>	1969–2011	monthly	Sr/Ca = -0.019(0.001) × SST + 9.423(0.028)	-0.67	0.45	<0.0001	0.028
			extreme values	Sr/Ca = -0.021(0.002) × SST + 9.497(0.048)	-0.83	0.69	<0.0001	0.026
			annual	Sr/Ca = 0.003(0.019) × SST + 8.823(0.539)	0.03	0.00	0.86	0.022
LC4	HadISST <sub>aug</sub>	1969–2011	monthly	Sr/Ca = -0.04(0.002) × SST + 10.238(0.051)	-0.70	0.49	<0.0001	0.055
			extreme values	Sr/Ca = -0.045(0.004) × SST + 10.369(0.099)	-0.81	0.66	<0.0001	0.057
			annual	Sr/Ca = -0.037(0.037) × SST + 10.163(1.03)	0.16	0.03	0.30	0.046

<sup>a</sup>Equations are computed using ordinary least squares (OLS) regression with zero-lag, 95% confidence limits for slope and intercept are given.  
<sup>b</sup>The residual standard errors are given as σ.



### 3.2. Comparison of Coral Sr/Ca Between the Fore Reef and the Lagoon Record

Due to their location within different sectors of the reef (Figure 1) the two *D. strigosa* colonies are exposed to different environmental conditions (e.g., tides, seawater temperature, water depth, insolation) causing apparent differences between both records. Different seasonal amplitudes in coral Sr/Ca, for instance, point to local temperature variability in distinct reef sectors, which is not captured by reanalysis SST data. Other differences include disparities in linear extension, mean Sr/Ca values (LC3 = 8.901 and LC4 = 9.111 mmol mol<sup>-1</sup>) and deviating variability of Sr/Ca on decadal scales (Table 1 and Figure 2).

#### 3.2.1. Differences in Mean Values

The incorporation of Sr into the coral skeleton is partially related to the annual extension rate [Emiliani *et al.*, 1978; de Villiers *et al.*, 1995; Felis *et al.*, 2003; Goodkin *et al.*, 2007]. Considering the mean value of each entire coral record (overall mean) considerable differences exist between both coral cores regarding Sr/Ca and extension, with higher values for LC4 for both parameters (Table 1 and Figure 1). This points to a direct relation between extension rates and Sr/Ca, in which the nearly two times faster growing coral LC4 is more enriched in Sr than the slower growing coral LC3. This observation is in good agreement with results of other studies [Oomori *et al.*, 1982; Cross and Cross, 1983; de Villiers *et al.*, 1995, DeLong *et al.*, 2011]. In the present context, water depth seems an important factor of influence since light intensity is reduced with increasing water depth causing corals to grow more slowly [Huston, 1985]. Weber [1973] named this relationship the “depth effect,” although he observed a direct relation between Sr/Ca and depth contrary to the result of the present study. His observation may be explained by pronounced influence of temperature on the overall mean coral Sr/Ca, assuming colder temperatures in the fore reef and warmer mean temperatures in the lagoon. However, in the present case growth may be the more important parameter causing the differences between overall mean Sr/Ca values of LC3 and LC4. Differences in growth may also have been affected by the coral microbiology. For example, studies on coral response to increased temperature extremes could show that some corals can shuffle or substitute symbiont types and that this may be a mechanism of thermal acclimatization/adaptation to a changing environment [Berkelmans and van Oppen, 2006; Edmunds and Gates, 2008; Weis, 2010] (see further discussion on this topic in section 3.1.4). Distinct lineages of *Symbiodinium* differ in the contribution of photosynthetic products to the coral host [Loram *et al.*, 2007] and calcification is considered to be a “photosynthesis-driven” process [Colombo-Pallotta *et al.*, 2010]. These considerations also lead to the question of how growth-rate-related kinetic effects [Cohen and McConnaughey, 2003] as well as vital effects [Urey *et al.*, 1951] affect the quality of the Sr/Ca records as monitors of local- to regional-scale, temperature variability. Several authors recommend some level of replication of geochemical proxies at each site to enhance the reliability of the coral paleoclimate record [Lough, 2004; DeLong *et al.*, 2007; Pfeiffer *et al.*, 2009]. For example, Cahyarini *et al.* [2009] averaged Sr/Ca records from three different coral cores taken from the lagoon of Tahiti (French Polynesia) resulting in a better correlation with grid-SST and a lower residual SST compared to any of the single-core Sr/Ca records. In the present study only one coral record from each part of the reef was available due to limited sampling permits, making replication with several cores impossible. However, DeLong *et al.* [2007] and Pfeiffer *et al.* [2009] also found that multiple single-core Sr/Ca records from the same reef location are highly reproducible. Their results indicate that coral Sr/Ca variations from multiple cores from the same location are recording the same Sr/Ca signal.

Another factor that could potentially influence the overall mean Sr/Ca values is the width of the thecal wall and the exact position of the sampling line. In order to identify complications associated with the complex skeletal architecture of *Diploria strigosa*, Giry *et al.* [2010] performed micro-sampling experiments along and across individual skeletal elements. The study showed that the thecal wall is systematically depleted in Sr while samples derived from the center of the theca exhibited enriched Sr/Ca values. This observation may be relevant for interpreting the present results even though the corals were sampled along the center of the thecal wall. The slower growing coral LC3 displayed a generally thicker structure of its skeletal elements, with specifically the thecal wall being much wider than in the faster growing coral. Consequently the sampled portion of depleted material from the center of the theca was relatively larger, possibly leading to the reduced mean Sr/Ca values when compared to the faster growing coral LC4.

A comparison of annual Sr/Ca and annual extension variability reveals a moderate, but still apparent, direct relationship between both parameters for LC3 ( $r = 0.4$ ,  $p = 0.02$ ), whereas it is weak and insignificant for LC4 ( $r = 0.23$ ,  $p = 0.14$ ). Similar results are provided by studies from *Diploria strigosa* from Guadeloupe and

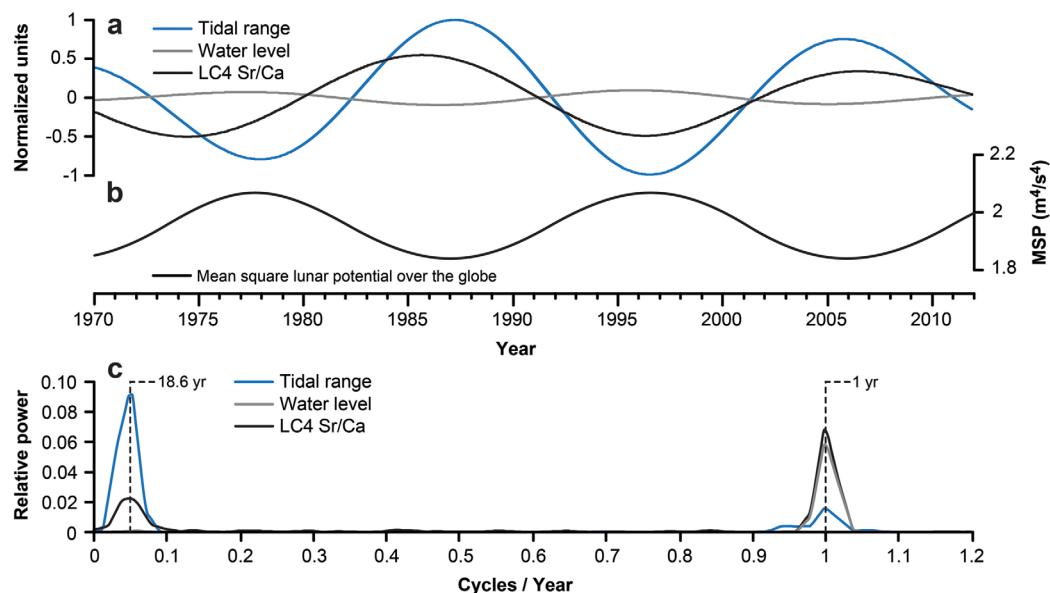
Bonaire which found positive but weak relationships between annual mean Sr/Ca and annual mean extension rate [Hetzinger *et al.*, 2006; Giry *et al.*, 2010; Hetzinger *et al.*, 2010; Giry *et al.*, 2012]. This is also in good agreement with results from Cohen and Gaetani [2010] who, under controlled experimental conditions, could show that coral Sr/Ca ratios increased with increasing crystal growth rate and decreased with increasing seawater temperature. Furthermore, Hayashi *et al.* [2013] and Hirabayashi *et al.* [2013] found that the skeletal Sr/Ca ratio from cultivated and noncultivated *Porites* is stable in relation to temporal intracolony variation in the skeletal extension rate. Accordingly, a reasonable explanation for the direct relation between annual mean Sr/Ca and annual mean extension rate observed in the present study is that in a given year the coral grew faster when the years mean SST was lower (and *vice versa*) as it is the case with other genera from different locations in the western Atlantic [Dodge and Vaisnys, 1975; Carricart-Ganivet, 2004; Crueger *et al.*, 2006; Saenger *et al.*, 2009]. For LC3 this assumption is supported to some extent by a weak inverse correlation ( $r = -0.3$ ) between linear extension and HadISST, significant at the 90% level. The correlation for LC4 is also negative but very weak and insignificant ( $r = -0.16$ ,  $p = 0.28$ ).

### 3.2.2. Seasonal Scale Differences

The slower growing coral LC3 has a seasonal Sr/Ca cycle with only half the amplitude of the faster growing coral LC4 (Figure 2 and Table 1). Due to the shallower water depth in lagoon environments, short-scale temperature variability from diurnal solar forcing and cooling is amplified [McCabe *et al.*, 2010; Zhang *et al.*, 2013] while in the deeper fore reef temperature amplitudes are dampened and mean values are lower. Hence, the observed differences between the coral Sr/Ca records are reasonable. However, there are most likely additional reasons, which would also explain the unusually reduced slope of the Sr/Ca-SST relationship of colony LC3. Referring to a similar case [Cardinal *et al.*, 2001], DeLong *et al.* [2011] suggested a significant influence of the sampling strategy on measured amplitude differences between records derived from corals with different extension rates. Cohen *et al.* [2004] could show that micro-sampling two colonies of *Diploria labyrinthiformis* with the same sampling interval would lead to a dampened amplitude of the seasonal Sr/Ca cycle in the slower growing colony as a result of more time averaging. Consequently each Sr/Ca record would also be biased to the season of higher growth with a possibly larger effect for the slower growing coral.

### 3.2.3. Decadal Variability

On longer time scales, however, a pronounced decadal variation of Sr/Ca values is apparent in core LC4 that is not seen in LC3 or the augmented SST data set (Figure 2). The disparity between the records indicates that LC4, the lagoon record, is responding to a forcing not present or negligible in the fore reef of LC3 at greater depth. Inside the lagoon the corals physical environment is subject to the tides, which change the water level and flush water into and out of the lagoon. Cohen and Sohn [2004] proposed that variations in tidal water level within shallow lagoonal settings might indirectly influence Sr/Ca by modulation of photosynthetically active radiation (PAR), which in turn drives large changes in zooxanthellate photosynthesis. This means that skeletons accreted during phases of low water level and high photosynthesis have lower Sr/Ca ratios [Cohen and McConnaughey, 2003]. However, the tidally varying depth of the lagoon and the volume of relatively cooler ambient water masses from the ocean entering the lagoon can significantly influence the mean lagoon temperature through tidal mixing [Smith and Kierspe, 1981; McCabe *et al.*, 2010; Zhang *et al.*, 2013], which has an additional effect on coral Sr/Ca values. To evaluate a potential tidal effect on Sr/Ca two aspects of tidal variability were considered: water level and tidal range (Figure 2). The mean water level provides information about water depth while the mean tidal range is an indicator for the water volume exchange between the lagoon and open waters, although it is not a direct relation since water volume is also dependent on the cross section/topography of the lagoons basin. Mean water level and mean tidal range have an inverse relationship, i.e., high (low) water levels correspond to low (high) tidal ranges. Coral Sr/Ca and tidal data were filtered and normalized (Figure 3a) to allow a direct comparison of signal variability in the low frequency band. The time series show a clear covariance over the largest part of the record, with the LC4 record directly (inversely) mimicking the oscillating tidal signals. However, before 1977 Sr/Ca show persistently low mean values with the result that tidal and Sr/Ca signals are not covarying like in the subsequent part of the record (Figure 2). This oldest portion of the core is from near the basement of the coral, which corresponds to the corals postsettlement juvenile period. Ourbak *et al.* [2008] found significant differences in the magnitude of the Sr/Ca signature between the modern part and the basement of a New Caledonian *Porites* sp. coral that could unlikely be caused by environmental factors alone. Similar differences were observed between small juvenile *Porites* sp. and their larger, more mature counterparts in



**Figure 3.** (a) Filtered and normalized (zero mean, unit variance) data records of tidal range, water level and LC4 Sr/Ca. A Low-pass filter (band-pass Gaussian filter with a center frequency of 0.05 and a bandwidth of 0.02) was applied. (b) Mean square potential (virtually the tidal force exerted by the moon) over the globe averaged over each year for semidiurnal tides (after Ray [2007]) with the 18.6 year modulation being the main feature. (c) Power-Spectral-Density of normalized monthly data. Spectral estimates formed using the simple periodogram method. Dashed lines indicating 1 yr seasonal cycle and 18.6 yr lunar nodal cycle.

New Caledonia [Ourbak *et al.*, 2006] and the Great Barrier Reef [Marshall and McCulloch, 2002]. Both studies conclude that the differences seem to be caused by ontogenic effects and that temperature does not have the same effect on Sr incorporation at the early stage of the corals life compared to today. Therefore, in the case of LC4 the divergence between Sr/Ca and the tidal signal, restricted only to the oldest portion of the core, possibly is a result of ontogenic effects altering the geochemistry. In the low pass filtered data this leads to Sr/Ca being slightly out of phase with water level and out of a half phase shift with tidal range, respectively (Figure 3).

The observed direct relation between coral Sr/Ca and tidal range potentially shows the modulation of temperature inside the lagoon through a varying volume of entering ambient water masses. Modulation by PAR on the other hand does not seem to play a significant role because the relation of Sr/Ca and water level is negative. Cohen and Sohn [2004] found Sr/Ca to correlate with both water temperature and water level at subannual periods >50 days. This was not observed in the present study over the much longer periods.

To express the combined lunar plus solar potentials/tidal forces integrated over the earth's surface, Ray [2007] calculated the mean square potential (MSP) which is shown in Figure 3b, it has a period of 18.6 years. From the figure it can clearly be seen that the tidal force is virtually in phase with the water level and out of phase with the tidal range. Thus, the 18.6 year period nodal tidal cycle is a potential cause of the decadal Sr/Ca variability since it considerably modulates the amplitude of the tide on this time scale [Doodson, 1928; Loder and Garrett, 1978]. This assumption is corroborated by the analysis of the Power-Spectral-Density (PSD) of the water level, tidal range and LC4 Sr/Ca data (Figure 3c), which reveals two major frequency domains: around 1 and around 0.05 cycle(s) per year representing the seasonal cycle and a variation with a period of about 20 years, respectively.

### 3.2.4. Coral Susceptibility to Positive Thermal Anomalies

Coral reefs in Little Cayman have shown different levels of coral bleaching during phases of sustained high temperatures. Bleaching has been reported since 1987 with subsequent observations in 1995, 1998, 2003, 2005, and 2009 [Ghiold and Smith, 1990; Coelho and Manfrino, 2007; Eakin *et al.*, 2010; van Hooidonk *et al.*, 2012]. In 2002, 2004, and 2007 low levels of bleaching were reported when less than 5% of colonies under observation were affected. In order to improve the forecast of imminent bleaching van Hooidonk and Huber [2009] and van Hooidonk *et al.* [2012] refined the Degree Heating Weeks (DHW) method [Gleeson and Strong, 1995; Goreau and Hayes, 1994], an accumulative stress index based on the sum of the positive



anomalies above the maximum summertime temperature of the previous 12 weeks, by establishing a local threshold above which bleaching was expected to occur at Little Cayman. By combining the reanalysis of the existing reports with own observations from the bleaching year 2009 and OISST V2 temperature data for the period 1982–2010, *van Hooidonk et al.* [2012] has established a site specific optimal bleaching threshold of 4.2 DHW's with SST's above 29.5°C. From observations of site-specific recovery in March 2010 they also found the corals with a prevalence (number of affected colonies divided by total number of colonies) of bleaching or paling of more than 25% to be *Siderastrea siderea*, *Montastraea annularis*, *Montastraea faveolata*, *Diploria strigosa* and *Agaricia* spp. The bleaching extent was quantified at different spur and groove reef sites at a depth between approximately 10 and 18 m in the fore reef zone. While *van Hooidonk et al.* [2012] distinguished between coral species, the present study assesses different responses and their geochemical imprints within one coral species as a function of the colonies environment. On the assumption of a local optimal bleaching threshold of 4.2 DHW the considered colonies/corals may show signs of stress either in Sr/Ca or calcification or both in years when the threshold was passed.

Within the reconstructed DHW period 1982–2010 the years in which bleaching is predicted are confined to a period limited by the years 1998 and 2010, both coincident with recorded El Niño events in the tropical Pacific. There is no direct evidence that either of the two sampled corals bleached during these years. However, these two thermal events (high SST) are characterized in LC3 by considerably reduced seasonal amplitudes and increased Sr/Ca ratios during the warm summer season when lower Sr/Ca values are expected. At very high temperatures the corals Ca-transport enzymes may become less efficient, thereby lowering the active  $\text{Ca}^{2+}$  transport and decreasing calcification [*Sinclair*, 1999]. The observed elevated Sr/Ca ratios could be a result of passively transported  $\text{Sr}^{2+}$ , which would not be affected in the same way as  $\text{Ca}^{2+}$  [*Ip and Lim*, 1991; *Sinclair*, 1999; *Fallon et al.*, 2003]. Interestingly, above threshold DHW's in 2001, 2003, 2005, and 2006 do not seem to inhibit the Sr/Ca "recorder." The coral presumably could tolerate the persisting high temperatures in the respective 4 years between the two El Niño events. This does not contradict the corals behavior during the El Niño years. Although *Diploria strigosa* was found to be one of the more susceptible corals, its observed prevalence of bleaching was about 37% [*van Hooidonk et al.*, 2012], implying that not all colonies of this species are affected equally. Additionally, in the years 2001 and 2006 none of the coral colonies observed where reported bleached, only some were reported pale or patchy [*van Hooidonk et al.*, 2012]. Different from the fore reef record, the lagoon Sr/Ca record (LC4) does not show the pronounced response to the thermal events in 1998 and 2010. These discrepancies between the records together with generally higher thermal maxima inside the lagoon suggest that LC4 may be equipped with an improved tolerance for thermal extremes relative to LC3. *Oliver and Palumbi* [2011] summarized three mechanisms corals and their endosymbionts may deploy to raise thermal tolerance: *coral adaption* and *Symbiodinium adaption* through the natural selection for heat-tolerant lineages of either partner and physiological *acclimatization* to differences in the thermal climate by living individuals of either or both partners [*Gates and Edmunds*, 1999; *Edmunds and Gates*, 2008; *Weis*, 2010]. As LC3 and LC4 were both drilled from colonies of the same species, differences between cores may partly be explained by the presence of distinct lineages of *Symbiodinium* incorporated within the coral host. However, there are likely additional factors. The apparent differences in seasonal Sr/Ca amplitudes and overall mean Sr/Ca ratios between both cores point to processes leading to physiological acclimatization of the coral as suggested by results from experimentally applied long-term treatments [*Coles and Jokiel*, 1978; *Middlebrook et al.*, 2008]. These results imply that corals which are exposed to elevations in mean temperatures for long (56 days) or short (2 days) periods develop elevated thermal stress tolerances. Furthermore, comparisons of corals from habitats with more rapid thermal fluctuations and higher daily thermal maxima with those from thermally moderate fore reefs indicate that temperature fluctuations resulting from daily or tidal changes expose corals to extreme temperatures below a critical amount of time avoiding coral mortality but for a beneficial amount of time stimulating acclimatization or adaption processes [*Coles*, 1975; *Warner et al.*, 1996; *Castillo and Helmuth*, 2005] Thus, exposure to an environmentally variable microhabitat adds substantially to coral-algal thermal tolerance [*Oliver and Palumbi*, 2011]. Arguing from these findings and from the observations of the present study it seems plausible to suggest that at Little Cayman *D. strigosa* from an environment with more rapid thermal fluctuations and higher maximum temperatures may be less susceptible to exceptionally high temperatures during a thermal event also

because it is accustomed to extreme temperatures, while *D. strigosa* from the thermally moderate fore reef is not and hence reacts with stress symptoms.

#### 4. Conclusions

A comparison between Sr/Ca variability from massive *Diploria strigosa* corals growing in different reef environments and augmented SST data from 1970 to 2012 point to local temperature variability in the respective reef sectors which cannot be resolved by augmented instrumental SST data. More specifically, our data show that a calibration of the lagoon Sr/Ca record with gridded SST, although augmented with in situ observations from the fore reef, would lead to an underestimation of the true temperature range in the lagoon.

The two corals respond differently to El Niño related thermal events influencing the magnitude of Sr/Ca ratios and seasonal amplitudes: *D. strigosa* from the fore reef seems to be more susceptible to such short-term events displaying significantly reduced seasonal amplitudes and increased Sr/Ca ratios in the same year suggesting cooler SSTs than expected. In contrast the lagoon Sr/Ca record does successfully capture the expected seasonal temperature variability during the thermal events in 1998 and 2010 related to El Niño.

The results suggest that *D. strigosa* from the deeper fore reef, where seasonal temperature amplitudes are dampened compared to the lagoon, is more susceptible to short-term high temperature events and consequently reacts with stress symptoms (high mean Sr/Ca and reduced seasonal amplitude). *D. strigosa* from the shallow lagoon environment shows a higher level of resilience because it may already be adapted to an environment with rapid thermal fluctuations and higher maximum temperatures.

On longer time scales the lagoon coral shows decadal variations in Sr/Ca which are absent in the fore reef coral. A comparison of the coral Sr/Ca record and tidal data indicates that modulation of temperature inside the lagoon through a varying volume of entering ambient water masses is presumably the underlying mechanism. The 18.6 year period lunar nodal cycle may be the forcing factor.

Further studies concerning coral physiology and bleaching thresholds could benefit from a systematic investigation of potential controls of these shallow lagoon sites where environmental conditions appear to promote coral resilience during thermal events. This could also help to improve monitoring systems such as NOAA's Coral Reef Watch, which provides coral reef managers and other stakeholders with tools to understand, monitor and better manage the complex interactions leading to coral bleaching.

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#### References

- Alibert, C., and M. T. McCulloch (1997), Strontium/calcium ratios in modern Porites corals from the Great Barrier Reef as a proxy for sea surface temperature: Calibration of the thermometer and monitoring of ENSO, *Paleoceanography*, *12*(3), 345–363.
- Beck, J. W., L. R. Edwards, E. Ito, F. W. Taylor, J. Recy, F. Rougerie, P. Joannot, and C. Henin (1992), Sea-surface temperature from coral skeletal strontium/calcium ratios, *Science*, *257*, 644–647.
- Berkelmans, R., and M. J. H. van Oppen (2006), The role of zooxanthellae in the thermal tolerance of corals: A 'nugget of hope' for coral reefs in an era of climate change, *Proc. R. Soc. B*, *273*(1599), 2305–2312.
- Cahyarini, S. Y., M. Pfeiffer, and W.-C. Dullo (2009), Improving SST reconstructions from coral Sr/Ca records: Multiple corals from Tahiti (French Polynesia), *Int. J. Earth Sci.*, *98*, 31–40, doi:10.1007/s00531-00008-00323-00532.
- Cardinal, D., B. Hamelin, E. Bard, and J. Pätzold (2001), Sr/Ca, U/Ca and  $\delta^{18}\text{O}$  records in recent massive corals from Bermuda: Relationships with sea surface temperature, *Chem. Geol.*, *176*(213–233), 213–233.
- Carricart-Ganivet, J. P. (2004), Sea surface temperature and the growth of the West Atlantic reef-building coral *Montastraea annularis*, *J. Exp. Mar. Biol. Ecol.*, *302*(2), 249–260.
- Castillo, K. D., and B. S. T. Helmuth (2005), Influence of thermal history on the response of *Montastraea annularis* to short-term temperature exposure, *Mar. Biol.*, *148*(2), 261–270.
- Coelho, V. R., and C. Manfrino (2007), Coral community decline at a remote Caribbean island: Marine no-take reserves are not enough, *Aquat. Conserv. Mar. Freshwater Ecosyst.*, *17*(7), 666–685.
- Cohen, A. L., and G. A. Gaetani (2010), Ion partitioning and the geochemistry of coral skeletons: Solving the mystery of the vital effect, *EMU Notes Mineral.*, *11*, 377–397.
- Cohen, A. L., and T. A. McConnaughey (2003), Geochemical perspectives on coral mineralization, *Rev. Mineral. Geochem.*, *54*, 151–187.
- Cohen, A. L., and R. A. Sohn (2004), Tidal modulation of Sr/Ca ratios in a Pacific reef coral, *Geophys. Res. Lett.*, *31*, L16310, doi:10.1029/2004GL020600.
- Cohen, A. L., S. R. Smith, M. S. McCartney, and J. van Etten (2004), How brain corals record climate: An integration of skeletal structure, growth and chemistry of *Diploria labyrinthiformis* from Bermuda, *Mar. Ecol. Prog. Ser.*, *271*, 147–158.
- Coles, S. (1975), A comparison of effects of elevated temperature versus temperature fluctuations on reef corals at Kahe Point, Oahu, *Pac. Sci.*, *29*, 15–18.

- Coles, S. L., and P. L. Jokiel (1978), Synergistic effects of temperature, salinity and light on the hermatypic coral *Montipora verrucosa*, *Mar. Biol.*, *49*(3), 187–195.
- Colombo-Pallotta, M. F., A. Rodríguez-Román, and R. Iglesias-Prieto (2010), Calcification in bleached and unbleached *Montastraea faveolata*: Evaluating the role of oxygen and glycerol, *Coral Reefs*, *29*(4), 899–907.
- Cross, T. S., and B. W. Cross (1983), U, Sr, and Mg in Holocene and Pleistocene corals *A. palmata* and *M. annularis*, *J. Sediment. Petrol.*, *53*, 587–594.
- Crueger, T., H. Kuhnert, J. Pätzold, and E. Zorita (2006), Calibrations of Bermuda corals against large-scale sea surface temperature and sea level pressure pattern time series and implications for climate reconstructions, *J. Geophys. Res.*, *111*, D23103, doi:10.1029/2005JD006903.
- De Deckker, P. (2004), On the celestite-secreting *Acantharia* and their effect on seawater strontium to calcium ratios, *Hydrobiologia*, *517*(1), 1–13.
- DeLong, K. L., T. M. Quinn, and F. W. Taylor (2007), Reconstructing twentieth-century sea surface temperature variability in the southwest Pacific: A replication study using multiple coral Sr/Ca records from New Caledonia, *Paleoceanography*, *22*, PA4212, doi:10.1029/2007PA001444.
- DeLong, K. L., J. A. Flannery, C. R. Maupin, R. Z. Poore, and T. M. Quinn (2011), A coral Sr/Ca calibration and replication study of two massive corals from the Gulf of Mexico, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, *307*(1–4), 117–128.
- DeLong, K. L., T. M. Quinn, F. W. Taylor, K. Lin, and C.-C. Shen (2012), Sea surface temperature variability in the southwest tropical Pacific since AD 1649, *Nat. Clim. Change*, *2*(11), 799–804.
- Deser, C., M. A. Alexander, S.-P. Xie, and A. S. Phillips (2010), Sea surface temperature variability: Patterns and mechanisms, *Annu. Rev. Mar. Sci.*, *2*(1), 115–143.
- de Villiers, S. (1999), Sewater strontium and Sr/Ca variability in the Atlantic and Pacific oceans, *Earth Planet. Sci. Lett.*, *171*, 623–634.
- de Villiers, S., G. T. Shen, and B. K. Nelson (1994), The Sr/Ca-temperature relationship in coralline aragonite: Influence of variability in (Sr/Ca)<sub>seawater</sub> and skeletal growth parameters, *Geochim. Cosmochim. Acta*, *58*, 197–208.
- de Villiers, S., B. K. Nelson, and A. R. Chivas (1995), Biological Controls on Coral Sr/Ca and  $\delta^{18}\text{O}$  Reconstructions of Sea Surface Temperature, *Science*, *269*, 1247–1249.
- de Villiers, S., M. Greaves, and H. Elderfield (2002), An intensity ratio calibration method for the accurate determination of Mg/Ca and Sr/Ca of marine carbonates by ICP-AES, *Geochem. Geophys. Geosyst.*, *3*(1), 1001, doi:10.1029/2001GC000169.
- Dodge, R. E., and J. R. Vaisnys (1975), Hermatypic coral growth banding as environmental recorder, *Nature*, *258*(5537), 706–708.
- Doodson, A. T. (1928), The analysis of tidal observations, *Philos. Trans. R. Soc. London A*, *227*, 223–279.
- Eakin, C. M., et al. (2010), Caribbean corals in crisis: Record thermal stress, bleaching, and mortality in 2005, *PLoS ONE*, *5*(11), e13969.
- Edmunds, P. J., and R. D. Gates (2008), Acclimatization in tropical reef corals, *Mar. Ecol. Prog. Ser.*, *361*, 307–310.
- Emiliani, C., J. H. Hudson, E. A. Shinn, and R. Y. George (1978), Oxygen and carbon isotopic growth record in a reef coral from the Florida Keys and a deep-sea coral from Blake Plateau, *Science*, *202*, 627–629.
- Enfield, D. B., and L. Cid-Serrano (2010), Secular and multidecadal warmings in the North Atlantic and their relationships with major hurricane activity, *Int. J. Climatol.*, *30*(2), 174–184.
- Fallon, S., M. T. McCulloch, and C. Alibert (2003), Examining water temperature proxies in *Porites* corals from the Great Barrier Reef: A cross-shelf comparison, *Coral Reefs*, *22*, 389–404.
- Farrow, D. E., and J. C. Patterson (1993), On the response of a reservoir sidearm to diurnal heating and cooling, *J. Fluid Mech.*, *246*, 143–161.
- Felis, T., J. Pätzold, and Y. Loya (2003), Mean oxygen-isotope signatures in *Porites* spp. corals: Inter-colony variability and correction for extension-rate effects, *Coral Reefs*, *22*(4), 328–336.
- Gagan, M. K., L. K. Ayliffe, J. W. Beck, J. E. Cole, E. R. M. Druffel, R. B. Dunbar, and D. P. Schrag (2000), New views of tropical paleoclimates from corals, *Quat. Sci. Rev.*, *19*, 45–64.
- Gates, R. D., and P. J. Edmunds (1999), The physiological mechanisms of acclimatization in tropical reef corals, *Am. Zool.*, *39*(1), 30–43.
- Ghiold, J., and S. Smith (1990), Bleaching and recovery of deep-water, reef dwelling invertebrates in the Cayman Islands, *British West Indies Caribbean J. Sci.*, *26*, 52–61.
- Giry, C., T. Felis, M. Kölling, and S. Scheffers (2010), Geochemistry and skeletal structure of *Diploria strigosa*, implications for coral-based climate reconstruction, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, *298*(3–4), 378–387.
- Gleeson, M. W., and A. Strong (1995), Applying MCSST to coral-reef bleaching, *Adv. Space Res.*, *16*, 151–154.
- Giry, C., T. Felis, M. Kölling, D. Scholz, W. Wei, G. Lohmann, and S. Scheffers (2012), Mid- to late Holocene changes in tropical Atlantic temperature seasonality and interannual to multidecadal variability documented in southern Caribbean corals, *Earth Planet. Sci. Lett.*, *331*–*332*, 187–200.
- Goodkin, N. F., K. A. Hughen, A. L. Cohen, and S. R. Smith (2005), Record of Little Ice Age sea surface temperatures at Bermuda using a growth-dependent calibration of coral Sr/Ca, *Paleoceanography*, *20*, PA4016, doi:10.1029/2005PA001140.
- Goodkin, N. F., K. A. Hughen, and A. L. Cohen (2007), A multicoral calibration method to approximate a universal equation relating Sr/Ca and growth rate to sea surface temperature, *Paleoceanography*, *22*, PA1214, doi:10.1029/2006PA001312.
- Goodkin, N. F., K. A. Hughen, S. C. Doney, and W. B. Curry (2008), Increased multidecadal variability of the North Atlantic Oscillation since 1781, *Nat. Geosci.*, *1*(12), 844–848.
- Goreau, T., and R. Hayes (1994), Coral bleaching and ocean hot-spots, *Ambio*, *23*, 176–180.
- Hayashi, E., et al. (2013), Growth-rate influences on coral climate proxies tested by a multiple colony culture experiment, *Earth Planet. Sci. Lett.*, *362*, 198–206.
- Hetzinger, S., M. Pfeiffer, W.-C. Dullo, E. Ruprecht, and D. Garbe-Schönberg (2006), Sr/Ca and  $\delta^{18}\text{O}$  in a fast-growing *Diploria strigosa* coral: Evaluation of a new climate archive for the tropical Atlantic, *Geochem. Geophys. Geosyst.*, *7*, Q10002, doi:10.1029/2006GC001347.
- Hetzinger, S., M. Pfeiffer, W.-C. Dullo, N. S. Keenlyside, M. Latif, and J. Zinke (2008), Caribbean coral tracks Atlantic Multidecadal Oscillation and past hurricane activity, *Geology*, *36*(1), 11–14, doi:10.1130/G24321A.24321.
- Hetzinger, S., M. Pfeiffer, W.-C. Dullo, D. Garbe-Schönberg, and J. Halfar (2010), Rapid 20th century warming in the Caribbean and impact of remote forcing on climate in the northern tropical Atlantic as recorded in a Guadeloupe coral, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, *296*(1–2), 111–124.
- Hirabayashi, S., Y. Yokoyama, A. Suzuki, Y. Kawakubo, Y. Miyairi, T. Okai, and S. Nojima (2013), Coral growth-rate insensitive Sr/Ca as a robust temperature recorder at the extreme latitudinal limits of *Porites*, *Geochem. J.*, *47*(3), e1–e5.
- Huston, M. (1985), Variation in coral growth rates with depth at Discovery Bay, Jamaica, *Coral Reefs*, *4*(1), 19–25.
- Inoue, M., M. Nohara, T. Okai, A. Suzuki, and H. Kawahata (2004), Concentrations of trace elements in carbonate reference materials coral JCP-1 and giant clam JCT-1 by inductively coupled plasma-mass spectrometry, *Geostand. Geoanal. Res.*, *28*(3), 411–416.

- Ip, Y. K., and A. L. L. Lim (1991), Short Communication: Are calcium and strontium transported by the same mechanism in the hermatypic coral *Galaxea Fascicularis*?, *J. Exp. Biol.*, *159*(1), 507–513.
- IPCC (2013), *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, 1535 pp., Cambridge Univ. Press, Cambridge, U. K.
- Kjerfve, B. (1981), Tides of the Caribbean Sea, *J. Geophys. Res.*, *86*(C5), 4243–4247.
- Kuhnert, H., T. Crüger, and J. Pätzold (2005), NAO signature in a Bermuda coral Sr/Ca record, *Geochem. Geophys. Geosyst.*, *6*, Q04004, doi:10.1029/2004GC000786.
- Latif, M., and N. S. Keenlyside (2011), A perspective on decadal climate variability and predictability, *Deep Sea Res., Part II*, *58*(17–18), 1880–1894.
- Loder, J. W., and C. Garrett (1978), The 18.6-year cycle of sea surface temperature in shallow seas due to variations in tidal mixing, *J. Geophys. Res.*, *83*(C4), 1967–1970.
- Loram, J. E., H. G. Trapido-Rosenthal, and A. E. Douglas (2007), Functional significance of genetically different symbiotic algae Symbiodinium in a coral reef symbiosis, *Mol. Ecol.*, *16*(22), 4849–4857.
- Lough, J. M. (2004), A strategy to improve the contribution of coral data to high-resolution paleoclimatology, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, *204*(1–2), 115–143.
- Marshall, J. F., and M. T. McCulloch (2002), An assessment of the Sr/Ca ratio in shallow water hermatypic corals as a proxy for sea surface temperature, *Geochim. Cosmochim. Acta*, *66*(18), 3263–3280.
- Maupin, C. R., T. M. Quinn, and R. B. Halley (2008), Extracting a climate signal from the skeletal geochemistry of the Caribbean coral *Siderastrea siderea*, *Geochem. Geophys. Geosyst.*, *9*, Q12012, doi:10.1029/2008GC002106.
- McCabe, R. M., P. Estrade, J. H. Middleton, W. K. Melville, M. Roughan, and L. Lenain (2010), Temperature variability in a shallow, tidally isolated coral reef lagoon, *J. Geophys. Res.*, *115*, C12011, doi:10.1029/2009JC006023.
- Middlebrook, R., O. Hoegh-Guldberg, and W. Leggat (2008), The effect of thermal history on the susceptibility of reef-building corals to thermal stress, *J. Exp. Biol.*, *211*(7), 1050–1056.
- Monismith, S. G., A. Genin, M. A. Reidenbach, G. Yahel, and J. R. Koseff (2006), Thermally Driven Exchanges between a Coral Reef and the Adjoining Ocean, *J. Phys. Oceanogr.*, *36*(7), 1332–1347.
- Oliver, T. A., and S. R. Palumbi (2011), Do fluctuating temperature environments elevate coral thermal tolerance?, *Coral Reefs*, *30*(2), 429–440.
- Oomori, T., K. Kaneshima, Y. Nakamura, and Y. Kitano (1982), Seasonal variation of minor elements in coral skeletons, *Galaxea*, *1*, 77–86.
- Ourbak, T., T. Corregge, B. Malaize, F. Le Cornec, K. Charlier, and J. P. Peypouquet (2006), ENSO and interdecadal climate variability over the last century documented by geochemical records of two coral cores from the South West Pacific, *Adv. Geosci.*, *6*, 23–27.
- Ourbak, T., K. Delong, T. Corregge, B. Malaize, K. Kilbourne, S. Caquineau, and D. Hollander (2008), The significance of geochemical proxies in corals, does size (age) matter, in *Proceedings of 11th International Coral Reef Symposium*, edited by B. Riegl, and R. E. Dodge, Nova South-eastern University National Coral Reef Institute, vol. 1, pp. 85–89, Lauderdale, Fla.
- Paillard, D., L. Labeyrie, and P. Yiou (1996), Macintosh program performs time-series analysis, *Eos Trans. AGU*, *77*, 379.
- Pfeiffer, M., W.-C. Dullo, J. Zinke, and D. Garbe-Schönberg (2009), Three monthly coral Sr/Ca records from the Chagos Archipelago covering the period of 1950–1995 A.D.: Reproducibility and implications for quantitative reconstructions of sea surface temperature variations, *Int. J. Earth Sci.*, *98*, 53–66, doi:10.1007/s00531-00008-00326-z.
- Ray, R. D. (2007), Decadal climate variability: Is there a tidal connection?, *J. Clim.*, *20*(14), 3542–3560.
- Rayner, N. A., D. E. Parker, E. B. Horton, C. K. Folland, L. V. Alexander, D. P. Rowell, E. C. Kent, and A. Kaplan (2003), Global analyses of sea surface temperature, sea ice, and night marine air temperature since the late nineteenth century, *J. Geophys. Res.*, *108*(D14), 4407, doi:10.1029/2002JD002670.
- Roberts, H. H., S. P. Murray, and J. N. Suhayda (1975), Physical processes in fringing reef systems, *J. Mar. Res.*, *33*(2), 233–260.
- Saenger, C., A. L. Cohen, D. W. Oppo, R. B. Halley, and J. E. Carilli (2009), Surface-temperature trends and variability in the low-latitude North Atlantic since 1552, *Nat. Geosci.*, *2*(7), 492–495.
- Schrag, D. P. (1999), Rapid analysis of high-precision Sr/Ca ratios in corals and other marine carbonates, *Paleoceanography*, *14*(2), 97–102.
- Shen, C.-C., T. Lee, C.-Y. Chen, C.-H. Wang, C.-F. Dai, and L.-A. Li (1996), The calibration of D[Sr/Ca] versus sea surface temperature relationship for *Porites* corals, *Geochim. Cosmochim. Acta*, *60*(20), 3849–3858.
- Sinclair, D. J. (1999), High Spatial-Resolution Analysis of Trace Elements in Corals Using Laser Ablation ICP-MS, Aust. Natl. Univ., Canberra, 1–414.
- Smith, J. M., T. M. Quinn, K. P. Helmle, and R. B. Halley (2006), Reproducibility of geochemical and climatic signals in the Atlantic coral *Montastrea faveolata*, *Paleoceanography*, *21*, PA1010, doi:10.1029/2005PA001187.
- Smith, N. P., and G. H. Kierspe (1981), Local energy exchanges in a shallow, coastal lagoon: Winter conditions, *Estuarine Coastal Shelf Sci.*, *13*(2), 159–167.
- Smith, S. V., R. W. Buddemeier, R. C. Redalje, and J. E. Houck (1979), Strontium-calcium thermometry in coral skeletons, *Science*, *204*, 404–407.
- Swart, P. K., H. Elderfield, and M. J. Greaves (2002), A high-resolution calibration of Sr/Ca thermometry using the Caribbean coral *Montastrea annularis*, *Geochem. Geophys. Geosyst.*, *3*(11), 8402, doi:10.1029/2002GC000306.
- Urey, H. C., H. A. Lowenstam, S. Epstein, and C. R. McKinney (1951), Measurement of paleotemperatures and temperatures of the Upper Cretaceous of England, Denmark and the southeastern United States, *Geol. Soc. Am. Bull.*, *62*(4), 399–416.
- van Hooidonk, R., and M. Huber (2009), Quantifying the quality of coral bleaching predictions, *Coral Reefs*, *28*(3), 579–587.
- van Hooidonk, R. J., D. P. Manzello, J. Moye, M. E. Brandt, J. C. Hendee, C. McCoy, and C. Manfrino (2012), Coral bleaching at Little Cayman, Cayman Islands 2009, *Estuarine Coastal Shelf Sci.*, *106*, 80–84.
- Warner, M. E., W. K. Fitt, and G. W. Schmidt (1996), The effects of elevated temperature on the photosynthetic efficiency of zooxanthellae in hospite from four different species of reef coral: A novel approach, *Plant Cell Environ.*, *19*(3), 291–299.
- Weber, J. N. (1973), Incorporation of strontium into reef coral skeletal carbonate, *Geochim. Cosmochim. Acta*, *37*, 2173–2190.
- Weis, V. M. (2010), The susceptibility and resilience of corals to thermal stress: Adaptation, acclimatization or both?, *Mol. Ecol.*, *19*(8), 1515–1517.
- Zhang, Z., J. Falter, R. Lowe, G. Ivey, and M. McCulloch (2013), Atmospheric forcing intensifies the effects of regional ocean warming on reef-scale temperature anomalies during a coral bleaching event, *J. Geophys. Res. Oceans*, *118*, 4600–4616, doi:10.1002/jgrc.20338.