RESEARCH ARTICLE

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Key Points:

- Geochemical anomalies observed in coral core records indicate the significance of "vital" effects in paleoclimate reconstructions
- Anomalous increases and decreases in coral Sr/Ca and Mg/Ca ratios provide a distinct signature of past thermal stress events
- Sr/Ca and Mg/Ca anomalies can be explained by a decrease in active Ca^{2+} transport and decreased Rayleigh Fractionation

Supporting Information:

- Dataset S1

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Differential response of corals to regional mass-warming events as evident from skeletal Sr/Ca and Mg/Ca ratios

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Abstract During the summer of 2010/2011, a regional marine heat wave resulted in coral bleaching of variable severity along much of the western coastline of Australia. At Ningaloo Reef, a 300 km long fringing reef system and World Heritage site, highly contrasting coral bleaching was observed between two morphologically distinct nearshore reef communities located on either side of the Ningaloo Peninsula: Tantabiddi (~20% bleaching) and Bundegi (~90% bleaching). For this study, we collected coral cores (*Porites* sp.) from Tantabiddi and Bundegi reef sites to assess the response of the Sr/Ca temperature proxy and Mg/Ca ratios to the variable levels of thermal stress imposed at these two sites during the 2010/2011 warming event. We found that there was an anomalous increase in Sr/Ca and decrease in Mg/Ca ratios in the Bundegi record that was coincident with the timing of severe coral bleaching at the site, while no significant changes were observed in the Tantabiddi record. We show that the change in the relationship of Sr/Ca and Mg/Ca ratios with temperature at Bundegi during the 2010/2011 event reflects changes in related coral "vital" processes during periods of environmental stress. These changes were found to be consistent with a reduction in active transport of Ca^{2+} to the site of calcification leading to a reduction in calcification rates and reduced Rayleigh fractionation of incorporated trace elements.

Plain Language Summary In this paper, we compare coral-core geochemical records (Sr/Ca and Mg/Ca) from two reef sites at Ningaloo Reef, Western Australia, which showed highly contrasting coral bleaching severities following a regional heat wave during the summer of 2010/11. We show that anomalous increases in Sr/Ca ratios and decreases in Mg/Ca ratios can provide a distinct signature of past thermal stress events making core records useful for understanding the variable impacts of regional ocean warming events within reef ecosystems. Furthermore, by using a novel approach we were able to explain the formation of these anomalies during periods of thermal stress through changes in coral physiological and kinetic processes, which, along with temperature, also effect the incorporation of trace elements in coral skeleton. This is of particular importance as coral core records are heavily relied upon for the understanding of climate change, yet the mechanisms responsible for acute changes in coral trace element ratios during periods of thermal stress have previously not been discussed. We thus hope our work will contribute to the understanding of coral physiology and the development of more robust records of climate change in the future.

1. Introduction

Coral reefs are undergoing rapid decline worldwide [Hoegh-Guldberg, 1999; Hughes et al., 2003; Pandolfi et al., 2003]. This decline has been attributed largely to an increase in the frequency and severity of widespread coral bleaching events as a result of the increased occurrence of acute, regional ocean-warming events [Veron et al., 2009; Hoegh-Guldberg, 1999; Feng et al., 2013]. These large-scale marine heat waves are often driven by regionally specific and transient climate phenomena superimposed on longer-term trends in global warming. For example, the El Niño Southern Oscillation (ENSO) has been shown to drive periodic (around 3–7 years) warm sea surface temperature (SST) anomalies of up to several degrees across the Indo-Pacific, Caribbean, and Red Sea [Rasmusson and Carpenter, 1982; Wilkinson, 1999], which, in turn, have caused mass coral bleaching events across the globe. In Australia, the most noteworthy coral bleaching events occurred during the summers of 1998 and 2002 [Hoegh-Guldberg, 1999; Bruno et al., 2001; Veron

et al., 2009; *Oliver et al.*, 2009] as well as 2011 [*Moore et al.*, 2012] and most recently during the summer of 2016 [e.g., *Hoegh-Guldberg and Ridgway*, 2016; *Normile*, 2016].

However, at smaller scales (hundreds of meters to several kilometers), spatial patterns of coral bleaching resulting from regional warming events can vary considerably within individual reef ecosystems [e.g., *Berkelmans et al.*, 2004; *Moore et al.*, 2012]. Corals have shown the ability to acclimatize to a wide range of local temperature regimes [*Brown*, 1997; *Guest et al.*, 2012; *Schoepf et al.*, 2015]. As such, coral bleaching thresholds can vary considerably for specific coral taxa between different reef environments [*Jokiel and Coles*, 1990; *Fitt et al.*, 2001; *Howells et al.*, 2012]. In addition, differences in reef environment can also affect the magnitude of reef-scale SST anomalies and hence, coral bleaching responses during regional ocean-warming events [e.g., *Depczynski et al.*, 2013; *Falter et al.*, 2014]. For instance, small-scale differences in the circulation and residence times of reef waters combined with variations in local atmospheric heating can drive strong spatial variations in SST anomalies across reef systems [e.g., *Davis et al.*, 2011; *Zhang et al.*, 2013; *Li and Reidenbach*, 2014], which can also cause similar variations in coral bleaching responses [*Berkelmans et al.*, 2004; *McClanahan et al.*, 2007; *Pineda et al.*, 2013].

Coral bleaching thresholds are typically calculated as 1° above the highest long-term (~7 year) average monthly SST (often referred to as the Maximum of the Monthly Mean (MMM) SST climatology) for any given reef environment [*Liu et al.*, 2003, 2006; *Skirving et al.*, 2006]. However, resolving small-scale variations in SST climatologies as well as variations in the magnitude of SST anomalies during regional warming episodes can sometimes be difficult using conventional SST products (i.e., satellite records and instrumental SST loggers) due to their spatial and temporal limitations. For example, although satellite temperature products have become invaluable for monitoring the development of ocean-basin and regional-scale SST anomalies [e.g., *Feng et al.*, 2013; *Liu et al.*, 2003], they often cannot resolve small-scale SST variability within reef systems due to their limited spatial resolution (typically >5 km). Similarly, instrumental temperature loggers require both the foresight and logistic support to provide the necessary spatial and temporal coverage in situ data, which can be particularly problematic when working in remote areas. Where such limitations are encountered, paleoclimate proxy records from coral cores offer an alternate method to assess fine-scale differences in SST climatologies between reef environments [e.g., *Alibert and McCulloch*, 1997; *Marshall and McCulloch*, 2002; *Fallon et al.*, 2003] as well as local variations in stress and bleaching responses of reef habitats following anomalous ocean-warming episodes [*Thompson and Woessik*, 2009; *D'Olivo et al.*, 2013; *Cantin and Lough*, 2014].

To date, the geochemical analysis of environmental proxies (e.g., Sr/Ca, Mg/Ca, U/Ca, and $\delta^{18}\text{O}$) from coral cores is a commonly used approach for generating long-term, high-resolution (bi-weekly to annual) records of tropical seawater temperatures and other environmental parameters for the period prior to when instrumental and remotely sensed data became available (i.e., before the 1980s) [*Gagan et al.*, 2000; *Eakin et al.*, 2009]. As such, coral geochemical proxy records have become an invaluable tool for assessing long-term ocean-warming trends, providing unequivocal evidence of global climate change related to the burning of fossil fuels since the onset of the industrial revolution (around mid-1700s) [*Gagan et al.*, 2000; *Grottoli and Eakin*, 2007]. Furthermore, the distinct annual density banding pattern observed in massive *Porites* sp. skeletons permits the measurement of skeletal growth parameters from coral cores (i.e., extension and calcification [*Lough and Barnes*, 1997; *Lough*, 2008; *D'Olivo et al.*, 2013]). This, in turn, provides a quantitative method by which to directly assess the impacts of acute warming events [*Cantin and Lough*, 2014; *Hetzinger et al.*, 2016] as well as the longer-term impacts of gradual changes in reef environmental conditions on coral growth [*Cantin et al.*, 2010; *Cooper et al.*, 2012; *D'Olivo et al.*, 2013].

While the incorporation of trace elements (Sr, Mg, U, etc.) in the aragonite crystals (CaCO_3) of coral skeletons have been shown to be related to a variety of environmental parameters such as ambient seawater temperatures [*Beck et al.*, 1992; *Fallon et al.*, 2003; *Felis and Pätzold*, 2003], they are also subject to varying levels of physiologic control. This is because corals precipitate their skeleton from a calcifying fluid which is partially isolated from the ambient seawater and then physiochemically modified [*Al-Horani et al.*, 2003; *Sinclair*, 2005; *Trotter et al.*, 2011; *McCulloch et al.*, 2012], thereby potentially influencing how trace elements are incorporated in the coral skeleton (i.e., via so-called “vital effects” [*Sinclair*, 2005; *Gaetani and Cohen*, 2006; *Allison and Finch*, 2007]). Although the exact mechanisms responsible for observed coral “vital effects” are not yet fully understood, their influence on skeletal trace element-calcium ratios (Te/Ca) is clear. For example, Sr/Ca ratios in coral skeletons are systematically lower (~10%) than that of inorganic aragonite

precipitated from an infinite reservoir of seawater [Kinsman and Holland, 1969; Cohen and Gaetani, 2010]. Similarly, the observed relationship between Mg/Ca and temperature for coral skeletons is the opposite of that expected for experimentally precipitated abiotic aragonite [Cohen and Gaetani, 2010].

Current knowledge about the role of coral “vital effects” have been largely limited to inferences based on comparisons between the geochemical composition of aragonite in coral skeletons collected in situ and laboratory inorganic experiments abiotically precipitating aragonite under known physicochemical conditions [e.g., Sinclair, 2005; Cohen and Gaetani, 2010]. Consequently, the significance of “vital effects” on long-term geochemical proxy records is poorly understood. For example, the slope and intercept of regressions of Sr/Ca and Mg/Ca versus temperature can vary significantly between different corals of the same species [Corrège, 2006], which may either reflect physiological differences between coral colonies or differences in their local habitat. Geochemical anomalies observed in monthly-to-seasonal resolution coral core records that correspond with the timing of past coral bleaching events [e.g., Marshall and McCulloch, 2002; Hetzinger et al., 2016] allude to the importance of vital effects to modulate the climate signal preserved in proxy records; however, they have yet to be studied in detail. Thus, the transient effects of environmental perturbations such as ocean-warming events on coral core geochemical records are potentially useful for understanding the mechanisms responsible for coral “vital effects” and the impact of elevated thermal stress on coral physiological and calcification processes.

In this study, we report records of Sr/Ca and Mg/Ca at monthly resolution from coral cores collected from Tantabiddi and Bundegi reef sites at Ningaloo Reef, each located ~20 km apart in the northwest region of Western Australia. Despite their relatively close proximity, these reef sites experienced highly contrasting severities of coral bleaching (around 20% of colonies at Tantabiddi versus 90% at Bundegi [Moore et al., 2012; Depczynski et al., 2013]) during an unprecedented regional ocean-warming event, associated with strong La Nina conditions during the austral summer of 2010/2011 [Feng et al., 2013]. We compare the response of the Sr/Ca and Mg/Ca proxies and coral growth rates during the summer of 2010/2011 at the two sites. We assess the veracity with which geochemical records can act as short-term recorders of extreme temperatures and the response of coral Te/Ca temperature calibrations to assess thermal stress of coral colonies. We then discuss the potential role of the coral Ca^{2+} ATPase enzyme and kinetic processes to explain the anomalous Sr/Ca and Mg/Ca ratios observed during the thermal stress event of 2010/2011.

2. Materials and Methods

2.1. Study Sites

Tantabiddi reef is located on the offshore side of the Ningaloo Peninsula (Figure 1) and forms part of the nearshore lagoon complex of the larger Ningaloo fringing reef system [Wyrwoll et al., 1993]. Significant swells (heights >1 m) impact the outer reef edge at Ningaloo for much of the year [Collins et al., 2003], which drives wave-driven circulation patterns that lead to rapid water exchange and ventilation of the inner lagoon at Tantabiddi with waters from offshore [Taebi et al., 2011].

Conversely, Bundegi Reef is situated on the protected northeastern coastline of the Ningaloo Peninsula within the Exmouth Gulf (Figure 1); a shallow (mean depth 12 m), inverse estuarine embayment [Brunskill et al., 2001]. Bundegi Reef is protected from offshore wave energy and as such circulation at the reef is predominantly driven by tides [Masse et al., 1997]. However, locally generated wind waves within the Exmouth Gulf probably also influence nearshore circulation at Bundegi to a lesser degree, although this has yet to be quantified at the site.

2.2. Coral Sample Collection and Preparation

During August of 2008, the Australian Institute of Marine Science (AIMS) recovered coral cores from massive *Porites* sp. corals located in shallow waters (within 200–300 m of their respective shorelines) at Tantabiddi (5 m, 21°54′ 35″S, 113°58′ 12″E) and Bundegi (3.5 m, 21°52′ 11″S, 114°09′ 23″E) reef sites at Ningaloo (Figure 1). The University of Western Australia recovered additional coral cores from the same coral colonies in August 2013 several years after the 2010/2011 bleaching event. All coral cores were sliced along to their main growth axes into rectangular slabs approximately 6 mm thick and soaked in a sodium hypochlorite solution to remove residual organic matter. The slabs were then rinsed repeatedly with deionised water in an ultrasonic bath and dried at 45°C in an oven for 24 h.

Figure 1. Location of Tantabiddi and Bundegi coral sites in the northern region of Ningaloo Reef (left) and core slab X-rays (right). Coral cores were collected from massive *Porites* sp. colonies from the two sites in 2008 (08BND and 08TNT) and again in 2013 (13BND and 13TNT). The red lines indicate sampling transects for Sr/Ca and Mg/Ca analysis and approximate start and end dates for the core records (years) are provided alongside.

Annual density band couplets (evident as alternating light and dark colored bands from X-ray images of coral slices) (Figure 1) were used to make preliminary determinations of core chronology and growth axis orientation [see Lough and Cooper, 2011]. Coral slices were sampled continuously along major growth axes using a Zenbot[®] Precision Mill equipped with a ~3 mm diameter drill bit. Sample powders were collected at millimeter increments (~monthly resolution) along major growth axis (sampling tracts shown in Figure 1). A temporal overlap (2–4 years) between the new (2013) and old (2008) samples was ensured to check the agreement between trace element ratios measured between the pairs of cores from the two sites. One hundred and fifty samples were collected from each of the Tantabiddi and Bundegi cores collected in 2008 (hereafter referred to as 08TNT and 08BND cores) covering growth periods of 1996–2008 and 1998–2008, respectively. For the coral cores collected in 2013 (hereafter referred to as 13TNT and 13BND), 112 samples were collected from the 13TNT core, covering the 2004–2013 period and 75 were collected from the 13BND core, which covered the 2006–2013 period.

Sample powders were weighed to 5 ± 0.25 mg for cores obtained in 2008 and to 10 ± 0.25 mg for cores obtained in 2013. Samples were then dissolved in nitric acid and diluted through two stages to produce 100 and 10 ppm Ca^{2+} solutions for trace element analysis [Holcomb et al., 2015]. Sr/Ca and Mg/Ca was analyzed from the 10 ppm Ca^{2+} solutions using a Thermo Fisher Scientific (Bremen, Germany) X Series II quadrupole inductively coupled plasma mass spectrometer using the standard Xt interface and plasma screen fitted at the University of Western Australia AGFIOR laboratory. Long-term reproducibility (RSD, 2 sigma) was derived from the repeated analyses of a gravimetrically prepared standard and yielded up to 0.3% for Sr/Ca and Mg/Ca for the analysis of the cores collected in 2008 ($n = 300$) and up to 0.2 and 0.3% for the Sr/Ca and Mg/Ca analysis of the cores collected in 2013 ($n = 187$).

2.3. Tantabiddi and Bundegi In Situ and Remote SST Data

Approximately 18 months of in-continuous in situ temperature data were collected from the Tantabiddi coral site between January 2012 and April 2014. The in situ temperature data were used to validate a separate, remotely sensed (OISST) sea surface temperature (SST) record for the calibration of the Tantabiddi Sr/Ca and Mg/Ca core records. The average of two, long-term (1996–2013), monthly resolution OISST (50 km²) records (within coordinates: 113.5°E, 21.5°S, and 113.5°E, and 22.5°S) was taken to give the closest SST record to the Tantabiddi site (OISST v2, <http://apdrc.soest.hawaii.edu/las/v6/dataset>) which showed good agreement with the in situ data within the range of “normal” temperatures (~22–30°C) for the reef site ($\text{SST} = 1.078 \times T_{\text{in situ}} - 2.0$, $R^2 = 0.93$).

For the Bundegi site, we collected approximately 2 years (January 2012 to March 2014) of near continuous in situ temperature data. This in situ data were combined with a prior 12 month record of in situ temperature previously reported in *Depczynski et al.* [2013] to generate a 3 year, continuous, record of monthly average in situ (nearshore) SST for the period February 2011 to March 2014. To extend the temperature record for Bundegi further back in time, the in situ data were used to adjust a longer-term OISST record (1998–2013), which provided complete temporal overlap with the two core records. We took the average of two OISST data sets generated for the coordinates: 114.5°E and 21.5°S and 114.5°E and 22.5°S, which gave the closest possible, long-term SST record for the Bundegi coral site (i.e., at 114.5°E, 22°S). For the period of overlap between the Bundegi in situ and OISST records, maximum annual SSTs were in good agreement (average of 29.3°C during February for OISST versus 29.4°C during February for in situ record); however, strong differences were observed between the records during winter months where the in situ temperature record showed an average annual SST minimum of 21°C occurring during July compared to 23.2°C during August for the OISST record. We thus adjusted the OISST record by subtracting the average monthly difference in SST between the OISST and in situ records from the long-term OISST record to generate a pseudo nearshore temperature record for Bundegi reef for the period from 1998–2013 (hereafter referred to as the nearshore SST record).

2.4. Sr/Ca and Mg/Ca Age Model Determination

Age models for the Tantabiddi and Bundegi Sr/Ca and Mg/Ca data sets were determined by aligning the seasonal minima and maxima in the Sr/Ca records with maxima and minima in the respective SST records for the two sites using *Analyseries* software [Paillard *et al.*, 1996]. To further refine the seasonality of the coral core age models, additional “anchor points” were added between matching sections of the Sr/Ca and temperature records [Alibert and McCulloch, 1997] until the strongest correlation coefficients were obtained. Trace element data from the top ~1 cm of both the 13TNT and 13BND core records (June 2012 to April 2013) were omitted from the final data sets to exclude the possibility of contamination from the presence of organic material [e.g., Alibert and McCulloch, 1997; Marshall and McCulloch, 2002]. Lastly, the Sr/Ca and Mg/Ca data sets were interpolated to monthly resolution, using *Analyseries*, to produce two continuous monthly Sr/Ca records for each of the 08TNT and 08BND core records that covered the periods April 1996 to July 2008 (08TNT) and April 1998 to October 2008 (08BND) and two Sr/Ca and Mg/Ca records for the 13TNT and 13BND records that covered the periods March 2004 to May 2012 (13TNT) and October 2005 to May 2012 (13BND).

2.5. Calibration of the Sr/Ca Temperature Proxy and Mg/Ca Relationships

Bulk Sr/Ca and Mg/Ca-SST correlations were calculated for each of the Sr/Ca and Mg/Ca data sets from Tantabiddi and Bundegi. For the 13BND record, anomalous Sr/Ca and Mg/Ca data observed from November 2010 to April 2011 were excluded from the calculation of the bulk 13BND Sr/Ca-SST and Mg/Ca-SST correlations. The linear regression equations of the bulk correlations were used to separately calibrate each of the Sr/Ca and Mg/Ca records with temperature from Tantabiddi and Bundegi to produce two long-term Sr/Ca-SST reconstructions and one long-term Mg/Ca-SST reconstruction for each site. Monthly temperature residuals (Sr/Ca-SST minus instrumental SST and Mg/Ca-SST minus instrumental SST) were calculated for each of these long-term temperature reconstructions to highlight periods where changes in the Sr/Ca-SST and Mg/Ca-SST relationships occurred.

To analyze the effects of thermal stress on the Sr/Ca and Mg/Ca temperature proxies, for the 2013 core records from Tantabiddi and Bundegi, we calculated short-term (6 months) Sr/Ca and Mg/Ca-SST correlations that corresponded with the timing of the 2010/2011 Ningaloo Niño event and severe coral bleaching at Bundegi (i.e., from November 2010 to April 2011). For the 13BND record, we also calculated additional short-term Sr/Ca and Mg/Ca-SST correlation for the 12 months following the suspected bleaching of the coral (i.e., from May 2011 to May 2012), to see if and how the function of the two proxies changed once temperatures at the coral site returned below bleaching thresholds.

2.6. Linear Extension Rates

Annual rates of linear extension were calculated from the monthly interpolated Sr/Ca records by measuring the distance between Sr/Ca maxima (i.e., temperature minima) in each record. For the period of overlap for the 08BND and 13BND core records (July 2006 to June 2007 and July 2007 to June 2008), the 13BND record showed reduced (slower) linear extension rates compared to the 08BND record (i.e., –2.27 and –3.42 mm

yr⁻¹, respectively), presumably reflecting the effects of sampling different growth axes. We therefore proportionally adjusted all linear extension rates measured in the 13BND record by a factor of 1.29 to account for the observed differences in average linear extension rates during the overlap period. It was not necessary to make any such adjustment for the two Tantabiddi core records.

3. Results

3.1. Skeletal Trace Element Abundances at Tantabiddi

The 08TNT and 13TNT Sr/Ca records were generally in good agreement with the offshore SST record ($r^2 = 0.94$ and 0.87 , respectively; Figure 2a and Table 1). Both the slope and y intercept terms of the linear regressions for the 08TNT and 13TNT bulk Sr/Ca-SST data indicated the two bulk calibrations were not statistically different from one another ($p > 0.05$, Figure 2a and Table 1). Root mean squared errors (RMSE) for the individual monthly Sr/Ca-SST estimates for the two records were 0.5 and 0.8°C for the 08TNT and 13TNT records, respectively. Both Sr/Ca records showed strong interannual and interdecadal variability in the magnitude of their respective seasonal maxima and minima (equivalent to $\sim 3^\circ\text{C}$) over the 1996–2013 period; results consistent with the seasonal warming and cooling trends displayed in the instrumental SST record (Figure 3a). For the 13TNT Sr/Ca record, Sr/Ca-SST estimates from the bulk calibration showed a cool bias of -0.5°C on average compared to the offshore SST record for the period from April 2004 to June 2008 ($-0.53 \pm 0.49^\circ\text{C}$, average ± 1 S.E., $p < 0.01$, $n = 51$, Figure 3b). This was followed by a warm bias in Sr/Ca-SST estimates from the bulk calibration of $+0.6^\circ\text{C}$ on average from July 2008 to May 2012 (0.58 ± 0.51 , average ± 1 S.E. $p < 0.01$, $n = 47$). For the bulk 13TNT Mg/Ca-SST calibration, temperature estimates were largely consistent across the entire record and showed good general agreement with OISST record (RMSE = 0.7°C , $R^2 = 0.87$; Figures 2b and 3a). During the summer of 2010/2011 (when mass coral bleaching occurred at Bundegi), no anomalous Sr/Ca or Mg/Ca values were observed in the 13TNT record (see red markers, Figures 2a and 2b). From November 2010 to April 2011, Sr/Ca and Mg/Ca temperatures derived from the bulk calibrations were within 1°C of the remote SST record (see red markers, Figure 3a), suggesting no short-term changes to the temperature relationship of either proxy occurred.

For the subdivided 13TNT record, a significant decline in the slope of the Sr/Ca-SST regression was observed for the period from July 2008 to May 2012 compared to the period from April 2004 to June 2008 (i.e., -0.12 , $p < 0.05$, Figure 2a and Table 1). The change in the coral Sr/Ca-SST sensitivity recorded between these two periods corresponded with a change in the direction of the coral growth axis evident around the year 2008 in the core X-ray (Figure 1). Conversely, no significant changes in Mg/Ca-SST relationships were observed between these same periods in the 13TNT Mg/Ca record ($p > 0.05$) (Figure 2b and Table 1). For the short-term Sr/Ca-SST and Mg/Ca-SST linear regressions calculated for the period in the 13TNT record from November 2010 to April 2011, no

Figure 2. (A) Sr/Ca-SST correlations for the two Tantabiddi (08TNT and 13TNT) coral core records; and (B) Mg/Ca-SST correlations calculated for the 13TNT coral core record (linear regression equation coefficients are shown in Table 1). For the subdivided 13TNT Sr/Ca and Mg/Ca records, no significant change in the linear regressions of the Sr/Ca-SST and Mg/Ca-SST correlations was observed from November 2010 to April 2011 as indicated by the (A) red circles and the (B) red squares; thus, suggesting thermal stress did not have a significant impact on coral “vital effects” during the 2010/2011 warming event.

Table 1. Slope (m) and y Intercept (b) Terms for the Sr/Ca-SST and Mg/Ca-SST Linear Regressions Equations Calculated for the Two Tantabiddi Core Records (08TNT and 13TNT)^a

Period	Bulk TNT Calibrations							
	Sr/Ca					Mg/Ca		
	n	m	b	r ²	p	m	b	r ²
08TNT, Apr 1996 to Jul 2008	148	−0.057 (±0.002)	10.552 (±0.061)	0.94	<0.001			
13TNT, Apr 2004 to May 2012	98	−0.056 (±0.004)	10.549 (±0.104)	0.87	<0.001	0.152 (±0.011)	0.587 (±0.288)	0.88
Subdivided 13TNT Core Record Calibrations								
Apr 2004 to Jun 2008	51	−0.061 (±0.004)	10.692 (±0.099)	0.95	<0.001	*0.150 (±0.016)	*0.591 (±0.399)	0.88
Jul 2008 to May 2012	47	−0.049 (±0.004)	10.332 (±0.098)	0.94	<0.001	*0.150 (±0.016)	*0.670 (±0.401)	0.90
Nov 2010 to Apr 2011	6	−0.061 (±0.019)	10.642 (±0.520)	0.95	<0.001	0.178 (±0.071)	−0.116 (±1.988)	0.92

^aThe bulk Sr/Ca-SST and Mg/Ca-SST linear regression equations were used to calibrate the coral temperature records shown in Figure 3a and included all Sr/Ca and Mg/Ca data up to May 2012. For the subdivided 13TNT record, the periods listed above correspond to the linear regressions shown in Figure 2 (except coefficients for Mg/Ca-SST equations indicated by asterisks which are not shown in Figure 2b).

significant changes were observed compared to the bulk calibrations ($p > 0.05$) (Figures 2a and 2b and Table 1). Similarly, no change in the linear regression of the Sr/Ca versus Mg/Ca correlation was observed across this period compared to the bulk 13TNT Sr/Ca versus Mg/Ca correlation ($p > 0.05$) (Figure 4).

Figure 3. (A, C) Sr/Ca-SST records (black circles—08TNT and 08BND records, blue circles—13TNT and 13BND records) and Mg/Ca-SST records (light blue squares—13TNT and 13BND records) for the (A) Tantabiddi and (C) Bundegi coral core records. (B, D) Monthly temperature residuals (i.e., Sr/Ca-SST and Mg/Ca-SST minus instrumental SST) for (B) Tantabiddi and (D) Bundegi Sr/Ca-SST and Mg/Ca-SST records. The Sr/Ca-SST and Mg/Ca-SST records were calibrated using the respective linear regression equations of the bulk correlations obtained for each of the core records from the two sites (see Figures 2 and 5 and Tables 1 and 2). For the 13TNT and 13BND records, Sr/Ca-SST's and Mg/Ca-SST's recorded during the 2010/2011 marine heat wave are indicated by marker points with red fill. For the 13BND record, the anomalous increase and decrease in Sr/Ca and Mg/Ca ratios recorded during the summer of 2010/2011 (see red markers, Figures 5a and 5b) lead to Sr/Ca-SSTs and Mg/Ca-SSTs underestimating the instrumental temperature record by up to ~5°C (D) during this period. Where no such changes in Sr/Ca and Mg/Ca ratios were observed in the Tantabiddi record, this was consistent with reports of increased coral bleaching (and hence thermal stress) at Bundegi (~90% bleaching) compared to Tantabiddi (~20% bleaching) [Moore et al., 2012].

Figure 4. Sr/Ca versus Mg/Ca for the 13TNT (blue) and 13BND (black) core records. The red markers indicate values recorded during the 2010/2011 marine heatwave at Ningaloo.

3.2. Skeletal Trace Element Abundances at Bundegi

Unlike the Tantabiddi records, the 13BND bulk Sr/Ca-SST calibration showed a significant reduction in Sr/Ca-SST sensitivity compared to the 08BND bulk calibration (-0.052 ± 0.003 versus -0.058 ± 0.003 mmol/ $^{\circ}\text{C}$, $p \leq 0.05$, Figure 5a and Table 2). Errors (RMSE) were 0.7°C for all Sr/Ca-SST predictions made from the 08BND time series ($n = 125$) and 1.0°C for the 13BND time series ($n = 84$); or just ~ 6 and $\sim 13\%$ of the total variance in the nearshore SST record. Compared to the Tantabiddi records, the 08BND and 13BND records on average showed increased seasonal variability

of Sr/Ca maxima and minima (Figures 2a and 5a). This contributed to Sr/Ca-SST minima that were $\sim 1.5^{\circ}\text{C}$ cooler and maxima that were $\sim 0.5^{\circ}\text{C}$ warmer than the Tantabiddi records on average (Figures 3a and 3c). However, the Bundegi records also showed reduced interannual variability of Sr/Ca-SST maxima and minima ($\sim 2^{\circ}\text{C}$ versus $\sim 3^{\circ}\text{C}$ for Tantabiddi records) over the 1998–2013 period (Figures 3a and 3c).

During the 2010/2011 warming event from November 2010 to April 2011, an anomalous increase in Sr/Ca ratios (up to $+2.5\%$) and decrease in Mg/Ca ratios (up to -10.8%) was observed in the 13BND record (see red markers, Figures 5a and 5b). This, in turn, resulted in predicted Sr/Ca-SSTs and Mg/Ca-SSTs from the bulk calibrations underestimating observed SSTs by up to 3.5 and 4.5°C , respectively, during this period (see red markers, Figures 3c and 3d). These Sr/Ca and Mg/Ca anomalies were observed to correspond with significant short-term declines ($\sim 70\%$, $p < 0.05$) in the slopes of both the Sr/Ca-SST and Mg/Ca-SST regressions

Figure 5. (A) Sr/Ca-SST correlations for the two Bundegi coral core records (08BND and 13BND); and (B) Mg/Ca-SST correlations calculated for the 13BND coral core record. For the subdivided 13BND Sr/Ca and Mg/Ca records, corresponding with the timing of the 2010/2011 marine heat wave at Ningaloo, a strong ($\sim 70\%$) decline in the slope of the Sr/Ca-SST and Mg/Ca-SST regressions was observed (see red markers, Table 2) suggesting thermal stress strongly affected coral “vital” processes, leading to changes in the incorporation of Sr and Mg in coral skeleton deposited during this period. For Sr/Ca-SST and Mg/Ca-SST regressions calculated for the 12 months following this warming event (see orange markers), both linear regressions returned to their pre-thermal stress configurations, suggesting that conditions within the calcifying fluid returned to “normal” shortly after SSTs at the site returned below bleaching thresholds.

Table 2. Slope (m) and y Intercept (b) Terms for the Sr/Ca-SST and Mg/Ca-SST Linear Regressions Equations Calculated for the Two Bundegi Core Records (08BND and 13BND)^a

Period	Bulk BND Calibrations								
	Sr/Ca					Mg/Ca			
	n	m	b	r ²	p	m	b	r ²	p
08BND, Apr 1998 to Aug 2008	125	−0.058 (±0.003)	10.572 (±0.07)	0.93	<0.001				
13BND, Jun 2005 to May 2012	78	−0.052 (±0.003)	10.4 (±0.063)	0.96	<0.001	0.102 (±0.013)	1.473 (±0.32)	0.77	<0.001
Subdivided 13BND Core Record Calibrations									
Jun 2005 to Oct 2010	65	−0.054 (±0.003)	10.425 (±0.07)	0.96	<0.001	0.102 (±0.015)	1.485 (±0.373)	0.74	<0.001
Nov 2010 to Apr 2011	6	−0.017 (±0.011)	9.544 (±0.313)	0.82	<0.05	0.039 (±0.026)	2.908 (±0.738)	0.81	<0.05
May 2011 to May 2012	13	−0.048 (±0.006)	10.291 (±0.153)	0.97	<0.001	0.104 (±0.024)	1.452 (±0.608)	0.89	<0.001

^aThe bulk Sr/Ca-SST and Mg/Ca-SST linear regression equations were used to calibrate the coral SST records shown in Figure 3c and included all Sr/Ca and Mg/Ca data up to May 2012 except anomalous values recorded during the 2010/2011 marine heat wave at Ningaloo from November 2010 to April 2011. For the subdivided 13BND record, the periods listed above correspond to the linear regressions shown in Figures 5a and 5b.

calculated from November 2010 to April 2011, compared to their prethermal stress values (i.e., from June 2005 to October 2010, Figures 5a and 5b and Table 2). Interestingly, no significant change in the relationship of Sr/Ca versus Mg/Ca was observed during or just after the severe warming event ($p > 0.05$, $n = 6$, Figure 4). Following the 2010/2011 event, no significant differences in the slopes of either Sr/Ca-SST or Mg/Ca-SST linear regressions were observed between the postthermal stress period (May 2011 to May 2012) and the prethermal stress period (June 2005 to October 2010, $p > 0.05$, Figures 5a and 5b and Table 2).

3.3. Linear Extension Rates

The Tantabiddi records (08TNT and 13TNT) showed a mean linear extension rate of $11.1 \pm 1.6 \text{ mm yr}^{-1}$ ($\pm 1 \text{ SD}$) for the 1996–2013 period (Figure 6) with no abrupt changes in extension rate observed in either record. The Bundegi records (08BND and 13BND) showed a mean linear extension rate of $12.3 \pm 2.4 \text{ mm yr}^{-1}$ for the 1998–2013 period (after adjusting for differences in the growth rate of separate primary growth axes, see section 2 and Figure 1) and $13.2 \pm 1.4 \text{ mm yr}^{-1}$ for the 12 years prior to the summer of 2010/2011 (i.e., from 1998 to mid-2010). However, there was a significant decrease in the rate of linear extension (7.5 mm yr^{-1}) observed in the 13BND record over the 12 month period following the warming event of 2010/2011. This abrupt decline in the linear extension rate was accompanied by a thin, high-density band, typically indicative of environmental stress [Lough and Cooper, 2011] that was evident in the X-ray image of the core (Figure 1). For the 2 years following the 2010/2011 thermal stress event, annual rates of linear extension in the Bundegi coral averaged just $9.0 \pm$

0.9 mm yr^{-1} between July 2011 and June 2013; i.e., the coral was growing at a significantly slower rate ($\sim 30\%$) than before the warming event (Welch's t-test, $p < 0.05$).

Figure 6. Linear extension calculated for the 08TNT (black circles), 08BND (blue circles), 13TNT (black squares), and 13BND Sr/Ca data (blue squares). Linear extension was measured for the 12 months from July to June of each year (i.e., centered on January) by measuring the distance between Sr/Ca maxima's (SST minima's) for each of the core records. For the overlapping section of the 08BND and 13BND cores, the later 13BND showed reduced extension rates (by a factor of 1.3 on average). Thus, to enable comparisons of extension rates between the two Bundegi cores, we generated an adjusted 13BND linear extension record (red squares) by multiplying all the 13BND extension values by a factor of 1.3.

4. Discussion

4.1. Absence of Thermal Stress Signatures at Tantabiddi

In comparison to the Bundegi core records, the Tantabiddi records showed no significant short-term variability in either Sr/Ca-SST or Mg/Ca-SST regressions or abrupt declines in annual linear extension corresponding with the timing of the 2010/2011 warming event

at Ningaloo Reef. This suggests that thermal stress during the summer of 2010/2011 was much lower (or not present) at Tantabiddi relative to Bundegi; results consistent with in situ observations of bleaching made throughout the Ningaloo Peninsula following this regional warming episode [Moore *et al.*, 2012]. During the peak of the 2010/2011 heat wave in January 2011, maximum weekly averaged temperatures reached 31.8°C (in situ) at Bundegi [Depczynski *et al.*, 2013], or 3.6°C above the highest 7 year average monthly maximum for the reef site (28.2°C from 2003 to 2010). Thus, it was not surprising that ~90% of the coral bleached [Depczynski *et al.*, 2013]. In comparison, maximum weekly average temperatures for January 2011 at Tantabiddi reached 28.9°C, which was only 1.0°C above the highest 7 year average monthly maximum for the reef site (27.9°C); thus, explaining why only moderate coral bleaching (~20%) was observed at the site [Moore *et al.*, 2012]. As such, where the peak temperature anomaly at Tantabiddi only just reached the coral bleaching threshold for the site (i.e., 28.9°C) [Fitt *et al.*, 2001], this was probably insufficient to result in significant stress of the sampled *Porites* sp. colony. We suspect that coral bleaching at Tantabiddi was probably largely confined to the more thermally sensitive branching coral species (e.g., *Acropora* sp. [Guest *et al.*, 2012]). These sensitive coral species are also more abundant in the shallower and more shoreward reef habitats [Collins *et al.*, 2003; Cassata and Collins, 2008] that are more susceptible to reef-scale temperature anomalies [Falter *et al.*, 2014] than the deeper channel at Tantabiddi where the sampled *Porites* corals were located.

Although no signs of thermal stress were observed in the Tantabiddi 13TNT core record, we did observe a significant shift in the Sr/Ca-SST regression where there was a prominent change in the direction of the coral growth axis along the sampling transect (around the year 2008, Figure 1). If these differences in Sr/Ca-SST regressions were unaccounted for, this could produce a bias in temperature reconstructions of up to ~2°C for predicted temperature minima and ~0.5°C for predicted temperature maxima. Thus, these results are consistent with the findings of Alibert and McCulloch [1997] and Delong *et al.* [2013] in showing how off-axis sampling of coral slices can lead to significant deviations in derived Sr/Ca-SST calibrations.

4.2. Impact of Thermal Stress on Trace Element Chemistry at Bundegi

The anomalous increase in Sr/Ca ratios and decrease in Mg/Ca ratios recorded from November 2010 to June 2011 in the 13BND record was consistent with the timing of the regional marine heat wave along the western coastline of Australia during the summer of 2010/2011 [Feng *et al.*, 2013] as well as the onset of severe coral bleaching observed at Bundegi reef [Depczynski *et al.*, 2013]. These anomalous trace element ratios were further accompanied by a strong decline in the linear extension rate (Figure 6) and an apparent high-density stress band in the 13BND record, both of which provide additional compelling evidence for acute thermal stress impacting the reef site and, in particular, the sampled coral colony during the summer of 2010/2011.

The anomalous increase in Sr/Ca ratios during the 2010/2011 thermal stress event for the Bundegi colony is consistent with previous research that has suggested that the ability of *Porites* sp. to pump calcium from the ambient seawater into the calcifying fluid via the Ca^{2+} ATPase transport enzyme can become impaired during periods of thermal stress [Marshall and McCulloch, 2002; Sinclair, 2005]. Although still an unresolved issue, if it is assumed that the Ca^{2+} ATPase enzyme is specific for Ca^{2+} [e.g., Tanaka *et al.*, 2015], then inhibition of the enzyme would result in reduced concentrations of Ca^{2+} in the calcifying fluid relative to other ions transported to the calcifying fluid via passive seawater pathways (e.g., Sr^{2+} and Mg^{2+}) [Sinclair, 2005]. As Sr^{2+} directly substitutes for Ca^{2+} in coralline aragonite [Speer, 1983], reduced concentrations of Ca^{2+} in the calcifying fluid would therefore lead to increases in skeletal Sr/Ca ratios [Sinclair, 2005]; thus, potentially explaining the anomalously high Sr/Ca ratios observed in the Bundegi core record during the 2010/2011 warming event.

Although a disruption of the Ca^{2+} ATPase enzyme could occur via direct temperature effects, that is the enzyme is forced to operate at suboptimal temperatures that result in a reduced ability to transport calcium across the calicoblastic layer [Cossins and Bowler, 1987; Marshall and Clode, 2004; Al-Horani, 2005], it is also possible that a reduction in calcium pumping could occur due to reduction in the supply of the energy needed to drive the molecular pump [e.g., Fang *et al.*, 1991]. Given that symbiotic algae provide the principle source of energy supporting calcification by the coral host [Muscatine, 1990], some reduction in the supply of metabolic energy (in the form of ATP) to the coral host during periods of thermal stress could be expected [Fang *et al.*, 1991; Jones *et al.*, 1998]. This, in turn, could lead to a reduction in the activity of the Ca^{2+} ATPase enzyme during periods of thermal stress that is similar to what has been shown to occur

during nighttime calcification when active Ca^{2+} transport is reduced compared to during the day [Al-Horani *et al.*, 2003]. Interestingly, we observed that the decline in slope of the Sr/Ca-SST calibration for the Bundegi coral during the 2010/2011 thermal stress event ($\sim 70\%$) was similar to the differences in slopes observed between day and nighttime skeletal deposits ($\sim 80\%$) for *Porites lutea* [Cohen *et al.*, 2001]. Thus, the reduction in the slope of the Sr/Ca-SST regression could suggest that the chemical conditions of the calcifying fluid of the Bundegi coral during the 2010/2011 warming event were more similar to that of nighttime and thus ambient seawater conditions due to a reduction in the activity of the Ca^{2+} ATPase enzyme. This idea is further supported by the decline in linear extension and hence calcification [Lough and Barnes, 2000] observed in the Bundegi record corresponding with the timing of the 2010/2011 event. The removal of two H^+ ions in exchange for the addition of Ca^{2+} by the Ca^{2+} ATPase enzyme plays a crucial role in the elevation of pH and aragonite saturation state of the calcifying fluid [Tambuttè *et al.*, 2011; McCulloch *et al.*, 2012], which in turn, permits the rapid deposition of coral skeleton [Gattuso *et al.*, 1998; Al-Horani *et al.*, 2003; Tambuttè *et al.*, 2011]. Therefore, both the decline in slope of the Sr/Ca-SST regression and the decrease in calcification observed during the 2010/2011 event provide strong evidence for reduced activity of the Ca^{2+} ATPase enzyme due to thermal stress of the sampled *Porites* colony.

In contrast to the Sr/Ca data, the decrease in Mg/Ca ratios observed in the 13BND record during the 2010/2011 heatwave could appear to contradict the idea that a reduction in active Ca^{2+} transport to the calcifying fluid occurs when corals are exposed to high levels of thermal stress. However, given the strong decrease in calcification observed in the Bundegi record during the 2010/2011 event, a decrease in the precipitation efficiency (i.e., the mass fraction of aragonite precipitated from a given batch of calcifying fluid) of the coral during this time could be expected [Gaetani and Cohen, 2006]. As such, the opposite response of Sr/Ca and Mg/Ca ratios observed during this period probably reflects the differential effect of decreased Rayleigh fractionation on the incorporation of Sr and Mg into the growing aragonite skeleton [Cohen and Gaetani, 2010]. Strong differences between the aragonite-seawater exchange coefficients (K_D) for Sr/Ca ($K_D^{\text{Sr/Ca}} = \sim 1.2$) and Mg/Ca ($K_D^{\text{Mg/Ca}} = \sim 0.001$) [Cohen and Gaetani, 2010] indicate that precipitating skeletal aragonite will have lower Mg/Ca ratios and higher Sr/Ca ratios relative to the calcifying fluid [Rimstidt *et al.*, 1998]. Thus, as calcification progresses (assuming a semienclosed calcification environment), the calcifying fluid would become progressively enriched in Mg and depleted in Sr, leading to increasing Mg/Ca ratios and decreasing Sr/Ca ratios in the precipitating coral skeleton [Cohen and Gaetani, 2010]. A reduction in the precipitation efficiency of the coral would therefore act to lower skeletal Mg/Ca ratios and increase Sr/Ca ratios and could explain the opposite behavior observed for these two trace element ratios from November 2010 to April 2011 in the 13BND record. This idea is supported by the observed differences in magnitude between the Sr/Ca and Mg/Ca anomalies in the 13BND record during the 2010/2011 event (i.e., $+2.5$ versus 10% , respectively). Where the magnitude of the Mg/Ca anomaly was 5 times larger than the Sr/Ca anomaly, this was observed to be consistent with previous research showing modeled precipitation efficiency related changes being ~ 6 times larger for Mg/Ca ratios than for Sr/Ca ratios in *Diploria* corals [Gaetani and Cohen, 2006]. Furthermore, the combined effect of a decrease in active Ca^{2+} transport to the calcifying fluid and a decrease in Rayleigh fractionation could also explain why the slope of the Sr/Ca-SST calibration observed during the 2010/2011 event decreased below that of experimentally precipitated abiogenic aragonite precipitated from seawater ($-0.038 \pm 0.004 \text{ mmol mol}^{-1} \text{ } ^\circ\text{C}^{-1}$ [Gaetani and Cohen, 2006]).

In addition to changes in precipitation efficiency, we also note that the incorporation of Mg into the coral skeleton can be further complicated by other mechanisms. For example, Mg is probably trapped (incorporated) in lattice defects [Amiel *et al.*, 1973; Cross and Cross, 1983; Watanabe *et al.*, 2001; Montagna *et al.*, 2014] and slower calcification rates lead to reduced rates of defect occurrence in coral skeleton, which can thereby also lower skeletal Mg/Ca ratios [Sinclair, 2005; Gaetani and Cohen, 2006]. Furthermore, the concentration of Mg is heterogeneous in coral skeleton with enrichments observed in the centers of calcification (COC) relative to the adjacent fibers [Meibom *et al.*, 2006; Holcomb *et al.*, 2009]. Diurnal variations in the aragonite saturation state of the cf are thought to control the formation of these two distinct skeletal components, with COCs deposited during the day (high aragonite saturation states) and fibers deposited during the night (lower saturation states) [Holcomb *et al.*, 2009]. Therefore, a decrease in the number of COCs per mass of aragonite could also have contributed to the observed decrease in Mg/Ca ratios in the Bundegi record during the summer of 2010/2011 as suggested by the strong decline in calcification rates observed during this time.

4.3. Modeling of Trace Element Thermal Stress Induced Changes

To constrain the relative effects of changes in precipitation efficiency and active Ca^{2+} transport to the calcifying fluid on skeletal Mg/Ca and Sr/Ca ratios, a closed system, Rayleigh-type equation can be applied [Albarede and Bottinga, 1972; Gagnon et al., 2007; Cohen and Gaetani, 2010; Sinclair, 2015; Stewart et al., 2016]. Using the equation from Sinclair [2015] (see below), the observed and predicted Sr/Ca and Mg/Ca ratios for January 2011 in the 13BND record were modeled considering the effects of variations in the concentration of Ca^{2+} in the calcifying fluid or changes in P (Figure 7).

$$\left(\frac{\text{Me}}{\text{Ca}}\right)_{\text{coral}} = \left(\frac{\text{Me}}{\text{Ca}}\right)_i \frac{\left(1 - P^{K_D \frac{\text{Me}}{\text{Ca}}}\right)}{(1-P)} \quad (1)$$

where $\text{Me}/\text{Ca}_{\text{coral}}$ is the metal/calcium ratio (Sr/Ca or Mg/Ca) in the coral skeleton, Me/Ca_i is the initial metal/calcium in the calcifying fluid before precipitation begins, and P is the proportion of Ca remaining in a batch of cf after precipitation has ended (P). The changes in Ca_i can be considered to reflect changes in the activity of Ca^{2+} ATPase enzyme: its ability to pump the concentration of Ca^{2+} within the calcifying fluid above the seawater end member of ~ 10.28 mmol (no up-regulation) [Millero, 1979] while changes in P reflect changes in precipitation efficiency. The model confirms that the opposite response of Sr/Ca and Mg/Ca ratios observed in the Bundegi record for the summer of 2010/2011 could be explained by a decrease in precipitation efficiency of the coral (increase in P). However, the model suggests an increase in P alone could not account for the observed magnitude of both the Sr/Ca (+2.5%) and Mg/Ca (−10%) anomalies and, in order to obtain a single P value for both Sr/Ca and Mg/Ca, some decrease in Ca_i is also required. For example, the stress response observed in the BND coral Sr/Ca and Mg/Ca data during the summer of 2011 was able to be realistically matched (i.e., with a single P obtained for each of the pairs of the predicted and observed Sr/Ca and Mg/Ca ratios) by assuming an increase in P (reduction in precipitation efficiency) from 0.68 to 0.87 and a small reduction in Ca_i from 10.63 to 10.53 ($\sim 1\%$ decline). Regarding the latter, given previous estimates of coral Ca^{2+} up-regulation of ~ 0.5 mmol kg^{-1} above seawater values [Al-Horani et al., 2003; McCulloch et al., 2012], this small decline in Ca_i could be considered to represent an $\sim 20\%$ decline in active Ca^{2+} transport to the calcifying fluid although actual changes could vary substantially depending on

Figure 7. Modeled response of Sr/Ca and Mg/Ca ratios to variations in P (i.e., 0–1) and the concentration of Ca^{2+} in the calcifying fluid (i.e., 10.53 for “low Ca” versus 10.63 for “high-Ca”). Calculations were based on the Rayleigh fractionation definitions from Sinclair [2015] using a $K_{\text{DSr}} = e^{(-1.86 + 600/T)}$ from Gaetani and Cohen [2006] and $K_{\text{DMg}} = e^{(-12.9 + 1729/T)}$. It was assumed that the active transport to CF is specific only to Ca. The predicted and observed Sr/Ca and Mg/Ca ratios for January 2011 for the 13BND coral record are shown with the square markers (no fill = predicted, black/blue fill = observed). The predicted Sr/Ca and Mg/Ca ratios were determined from the long-term, pre-thermal stress calibrations (i.e., June 2005 to October 2010 calibrations, Figures 5a and 5b) for a temperature of 29.8°C.

slight variations in sensitive input parameters (e.g., $K_D^{Mg/Ca}$). We emphasize that this model does not accommodate active Ca^{2+} transport that occurs during calcification (i.e., closed system assumption); thus, the effect of reduced Ca^{2+} transport on skeletal Sr/Ca and Mg/Ca ratios could in reality be more complicated. Nonetheless, our data provide strong evidence for changes in Ca^{2+} ATPase and precipitation efficiency to account for the observed Sr/Ca and Mg/Ca anomalies observed in the Bundegi record during the summer of 2010/2011. As such, because no significant change in the slope of the Sr/Ca versus Mg/Ca linear regression was observed for the Bundegi coral during the 2010/2011 event (Figure 4), this provides strong evidence suggesting changes in coral precipitation efficiency are related, either directly or indirectly to changes in the activity of the Ca^{2+} ATPase enzyme.

4.4. Recovery of Bundegi Coral Following Thermal Stress

Following the summer of 2010/2011 in the Bundegi (13BND) record, the reestablishment of the original bulk Sr/Ca and Mg/Ca-SST relationships from May 2011 to May 2012 (see orange markers, Figures 5a and 5b) could be indicative of the return to “normal” calcification conditions for Bundegi coral. Previous research has shown that in some cases, it is possible for corals to recover from thermal stress and bleaching within a few months following acute warming events [e.g., Brown, 1997]; however, substantially longer recovery times, of up to several years, have also been reported for *Porites* sp. corals following major bleaching events on the Great Barrier Reef [D’Olivo et al., 2013; Cantin and Lough, 2014]. In this case, because linear extension rates for the Bundegi coral were observed to remain anomalously low for at least 2 years following the 2010/2011 thermal stress event (Figure 6), it is unlikely that the coral had experienced a complete recovery within such a short time frame. Nonetheless, the different recovery times between trace elements (months) and growth rates (years) suggest that while the basic physiology governing the chemistry of the calcifying fluid appeared to have returned to normal, the absolute rate at which the coral could precipitate its skeleton had clearly not.

5. Conclusions

Our results show that coral core geochemical records can provide a distinct signature of past environmental stress events making them useful for understanding the variable impacts of acute ocean-warming episodes within individual reef systems. The presence of Sr/Ca and Mg/Ca anomalies in the Bundegi core record during the 2010/2011 marine heat wave at Ningaloo, and the absence of any such anomalies in the Tantabiddi record, was consistent with the respective instrumental temperature records and contrasting reports of coral bleaching from the two reef sites (~20% bleaching at Tantabiddi versus ~90% at Bundegi) [Moore et al., 2012]. The anomalous increase in Sr/Ca ratios and decrease in Mg/Ca ratios observed during the summer of 2010/2011 in the Bundegi coral core record indicated that thermal stress can strongly influence the “vital” effects governing the incorporation of trace elements in the skeletons of *Porites* sp. corals resulting in significant short-term changes in coral Sr/Ca and Mg/Ca ratios and, thus, biased predictions of in situ temperature. We show that the increase in skeletal Sr/Ca ratios in *Porites* sp. could partially be explained by a reduction in active (Ca^{2+} ATPase) Ca^{2+} transport to the calcifying fluid during thermal stress events [Marshall and McCulloch, 2002]. However, the strong decline in skeletal Mg/Ca ratios recorded during this same period can only be explained by secondary growth effects (i.e., a decline in the precipitation efficiency and/or defect entrapment of Mg), that could have directly or indirectly resulted from a decline in active Ca^{2+} transport to the calcifying fluid.

Although short-term deviations in coral Sr/Ca-SST and Mg/Ca-SST relationships due to changing vital effects are a source of error for paleoclimate temperature reconstructions, they provide clear evidence of the significance of “vital” effects to modulate the climate signal preserved in coral core records. However, given that the geochemical signature of a stress event could appear as a reduction in the seasonal amplitude of Sr/Ca and Mg/Ca minima and maxima, distinguishing a past stress event from a cold year could prove difficult solely based on the information from these geochemical proxies. We therefore suggest future research investigate combining Sr/Ca and Mg/Ca analyses with additional trace element or isotopic proxies whose abundance may be unaffected by changes in calcification processes during thermal stress events (e.g., Li/Mg [Montagna et al., 2014]). This could potentially allow for historic stress events to be identified in coral core records without the need for overlapping temperature data.

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