

8-1-2013

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Ashly McMahon, Isaac R. Santos, Tyler Cyronak, and Bradley D. Eyre. 2013. Hysteresis Between Coral Reef Calcification and the Seawater Aragonite Saturation State. *Geophysical Research Letters*, (17) : 4675 -4679. https://nsuworks.nova.edu/occ_facarticles/1038.

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Hysteresis between coral reef calcification and the seawater aragonite saturation state

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Received 20 June 2013; revised 29 July 2013; accepted 30 July 2013; published 10 September 2013.

[1] Some predictions of how ocean acidification (OA) will affect coral reefs assume a linear functional relationship between the ambient seawater aragonite saturation state (Ω_a) and net ecosystem calcification (NEC). We quantified NEC in a healthy coral reef lagoon in the Great Barrier Reef during different times of the day. Our observations revealed a diel hysteresis pattern in the NEC versus Ω_a relationship, with peak NEC rates occurring before the Ω_a peak and relatively steady nighttime NEC in spite of variable Ω_a . Net ecosystem production had stronger correlations with NEC than light, temperature, nutrients, pH, and Ω_a . The observed hysteresis may represent an overlooked challenge for predicting the effects of OA on coral reefs. If widespread, the hysteresis could prevent the use of a linear extrapolation to determine critical Ω_a threshold levels required to shift coral reefs from a net calcifying to a net dissolving state. **Citation:** McMahon, A., I. R. Santos, T. Cyronak, and B. D. Eyre (2013), Hysteresis between coral reef calcification and the seawater aragonite saturation state, *Geophys. Res. Lett.*, 40, 4675–4679, doi:10.1002/grl.50802.

1. Introduction

[2] The global seawater pH is predicted to drop ~ 0.3 units by 2100, and the associated drop in aragonite saturation state (Ω_a) is expected to result in lower coral calcification [Doney *et al.*, 2009]. For example, a 14% reduction in calcification has been detected over a 40 year time period in a system on the Great Barrier Reef [Silverman *et al.*, 2012]. A major implication of ocean acidification (OA) is that coral reefs may experience a transition from net CaCO_3 production to net dissolution [Andersson and Gledhill, 2013]. An understanding of the chemical thresholds required to shift coral reefs to a net erosive state are fundamental for developing predictions of how OA will impact reef survival. The carbonate chemistry of coral reefs is highly dynamic, and multiple biogeochemical interactions within coral reefs may drive feedbacks to OA on a local scale [Shaw *et al.*, 2012]. For example, primary production can shift Ω_a over the short and long terms,

potentially masking the local impacts of OA [Anthony *et al.*, 2011].

[3] A number of mesocosm [Andersson *et al.*, 2009; Langdon and Atkinson, 2005; Langdon *et al.*, 2003] and field studies [Ohde and van Woerik, 1999; Shamberger *et al.*, 2011; Shaw *et al.*, 2012] have found decreasing net ecosystem calcification (NEC) rates in coral reefs as Ω_a decreases. A recent review relied on theoretical considerations and hypothetical reactions to highlight that the Ω_a versus NEC relationship may not represent a functional relationship [Andersson and Gledhill, 2013]. Here, we further develop this hypothesis by describing detailed NEC observations in a healthy coral reef lagoon during different times of the day.

2. Material and Methods

[4] This study was performed at Heron Island in the Great Barrier Reef, Australia (23°27'S, 151°55'E). The reef covers 26.2 km² and has an average depth of 1.7 m. The lagoon benthos is approximately 85% CaCO_3 sand with scattered coral clusters [Santos *et al.*, 2010, and references therein]. The lagoon is at a higher level than the open ocean during low tide periods. Tidal isolation is a convenient feature widespread in reef lagoons that allows for flux rates to be calculated during times when mixing with offshore waters is negligible. Here, samples were taken at a designated site 10 m off the beach at low tide in the lagoon adjacent to the Heron Island Research Station. All samples were taken approximately 1–2 h each side of the low tide. Three to five samples were collected per low tide (every 30–40 min) dependent on the length of the tide. We report the results of a total of 47 tides sampled in the autumn (April 2012).

[5] Water analysis was carried out within 20 min of sampling. Total alkalinity (TA) and pH were measured using a high-precision titration unit (Metrohm Titrando). TA was estimated by Gran Titration using 0.01 M prestandardized HCl and certified against Dickson's reference material (Batch 111). Calibration of the pH probe (Metrohm Electrode Plus) was done using Oakton National Bureau of Standards (buffers pH 4, 7, and 10). Alkalinity replicates were obtained for each sample and an average of replicates was used ($<0.2\%$). A Hydrolab DSX5 data logger was used to monitor photosynthetically active radiation (PAR) ($\pm 5\%$), salinity ($\pm 0.5\%$), dissolved oxygen (DO) ($\pm 1\%$), and temperature ($\pm 0.5\%$) every 15 min. Samples for dissolved ammonium, nitrate, and nitrite (NO_x) and orthophosphate were filtered through a 0.45 μm cellulose acetate syringe filter before the sample was frozen for later analysis by a Lachat Flow Injection Analysis Unit ($\pm 5\%$) [Eyre and Ferguson, 2005]. Dissolved inorganic carbon (DIC) concentrations were estimated using the Excel macro CO2SYS [Lewis *et al.*, 1998]

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0094-8276/13/10.1002/grl.50802

with temperature, pH, and TA inputs measured during the titrations and a constant salinity of 35 g kg^{-1} . Settings in CO2SYS were set to the NBS pH scale and the constants from *Dickson and Millero* [1987] as cited in *Lewis et al.* [1998].

[6] Net ecosystem calcification (NEC) rates were determined by the alkalinity anomaly technique [*Chisholm and Gattuso*, 1991] using the average depth of the lagoon (1.7 m). This technique captures only net calcification or dissolution (NEC or G_{net}) and does not separate the relative contribution of gross calcification and dissolution to each individual NEC rate. Net ecosystem production (NEP) was calculated from the change in DIC corrected for changes in alkalinity [*Silverman et al.*, 2012]. Wind speed measurements were taken using a Davis Vantage Pro2 weather station. Calculations of $f\text{CO}_2$ and Ω_a were done with the CO2SYS program, using inputs of temperature, salinity, alkalinity, and pH (constants from *Dickson and Millero* [1987] and piston velocities from *Wanninkhof* [1992] as cited in *Lewis et al.* [1998]).

3. Results and Discussion

3.1. Diel Trends

[7] There were clear diel trends in DO, pH, TA, and DIC, as expected for coral reefs (Figure 1). For example, DO increased from a minimum of 68% saturation just before sunrise to a maximum of 190% saturation towards late afternoon. Alkalinity increased during the night and was consumed during the day (range from 2185 to $2322 \mu\text{mol L}^{-1}$). Metabolic rates (NEC and NEP) steadily increased from sunrise to a peak in the mid-afternoon (15:00), about 3 h after the peak in PAR (Figure 2). The 15:00 peak was followed by a sharp decline in both NEC and NEP. NEP was lowest just before sunset and was less variable at night than during the day. On a few occasions, net calcification was observed during the night, even at low Ω_a and pH. Integrating the hourly rates over a full diel cycle yielded an overall NEC rate of $2.4 \text{ mmol CaCO}_3 \text{ m}^{-2} \text{ h}^{-1}$. The overall NEC daytime rate was $8.5 \text{ mmol CaCO}_3 \text{ m}^{-2} \text{ h}^{-1}$, and the nighttime rate was $-3.7 \text{ mmol CaCO}_3 \text{ m}^{-2} \text{ h}^{-1}$. NEP rates revealed a nighttime respiration rate of $-27.4 \text{ mmol C m}^{-2} \text{ h}^{-1}$ and daytime production of $38.4 \text{ mmol C m}^{-2} \text{ h}^{-1}$. Overall, the system was net productive at a rate of $5.5 \text{ mmol C m}^{-2} \text{ h}^{-1}$, which was about threefold higher than NEC rates. The dynamic NEC and NEP rates demonstrate the need for intensive sampling during all times of the day to characterize coral reef metabolic rates.

3.2. The Ω_a and NEC Relationship

[8] At first glance, our observations revealed a significant positive, linear relationship between Ω_a and NEC in spite of some scatter (Figure 3 and Table 1). In most similar studies (Table 1), a linear relationship was used to predict the Ω_a value required for corals to shift from a net calcifying to a net erosive state (i.e., Ω_a for $\text{NEC}=0$). Interestingly, mesocosm experiments found a lower threshold value for Ω_a than in situ studies. Controlled experiments showed that the bulk of reef carbonates may dissolve at a Ω_a of 3.5–3.8, while high Mg calcites dissolve at 3.0 to 3.2 [*Yamamoto et al.*, 2012], though it is unclear how these Ω_a thresholds relate to sediments subjected to metabolic dissolution and pore water flow [*Cyronak et al.*, 2013]. In Heron Island, using a linear relationship leads to the interpretation

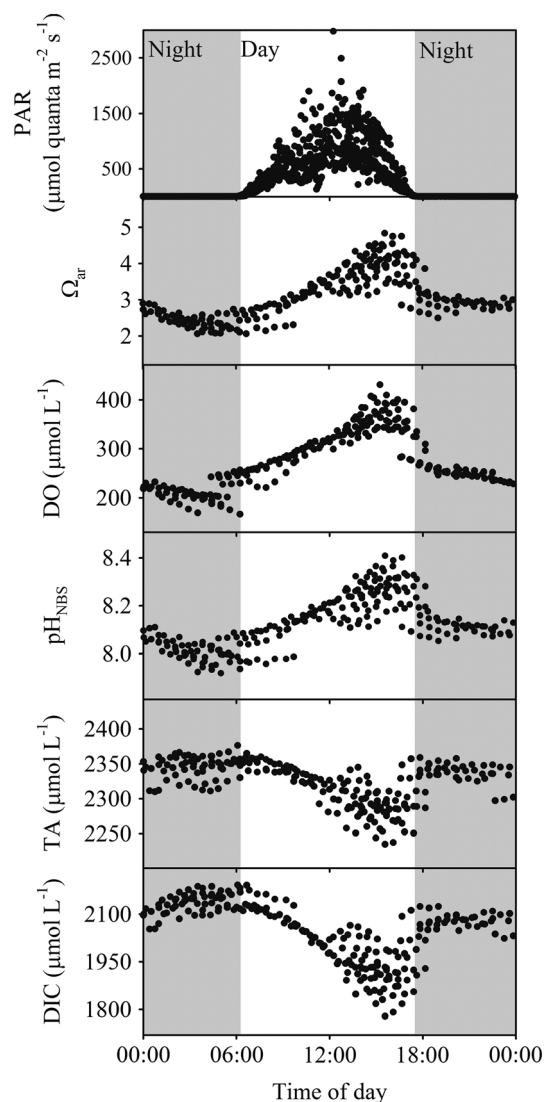


Figure 1. Diel cycle of major biogeochemical parameters in the Heron Island Lagoon. Samples were taken from a total of 47 low tides. Because each low tide occurred at a different time of the day, our observations covered a full 24 h cycle. Nutrient concentrations did not have a clear diel trend (not shown).

that at $\Omega_a=2.64$, the reef lagoon would shift from net calcifying to net dissolving. Calculations of Ω_a at $p\text{CO}_2$ levels predicted for the year 2100 (660–790 μatm) show that 100% of coral reefs will have a $\Omega_a < 3.25$ [*Cao and Caldeira*, 2008]. Therefore, it would be reasonable to expect that many reefs will shift to net dissolution by the end of this century.

[9] However, we cannot make this prediction using this approach if the assumption that there is a linear functional relationship between NEC and Ω_a is not valid. When grouping our data by night, morning, and afternoon time periods, the linear correlation becomes much less apparent and a diel hysteresis emerges in the Ω_a versus NEC relationship (Figure 3). We suggest that this hysteresis may invalidate the application of a simple linear correlation to predict coral reef dissolution threshold levels using field data obtained

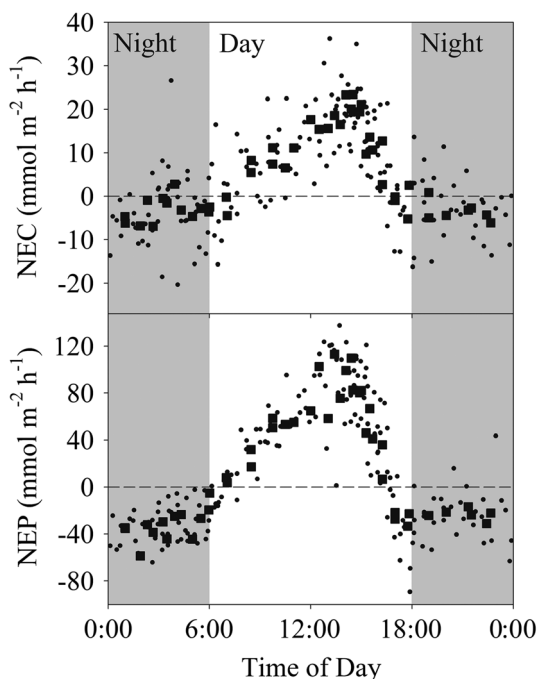


Figure 2. NEC and NEP rates during different times of the day. The small black dots represent rates estimated from two consecutive samples, while the large black squares represent rates estimated from the slope of all of the three to five samples taken at each low tide. The use of several samples from each low tide smoothed the data and revealed a peak in NEC and NEP at about 3:00 P.M.

over diel time scales. This is consistent with recent theoretical predictions demonstrating that a correlation between Ω_a and NEC may not necessarily be interpreted as a functional relationship [Andersson and Gledhill, 2013]. It is also in line with the self-regulation hypothesis suggesting that corals can alter the carbonate chemistry within microenvironments and calcify at suboptimal seawater pH conditions [McCulloch *et al.*, 2012]. We speculate that similar hysteresis patterns may be hidden in other coral reef NEC data sets. Several previous studies relied on a small number of samples (Table 1) or seasonal sampling (not necessarily at the same time of the day), perhaps preventing complex relationships from emerging.

[10] Some pioneering controlled mesocosm studies were based on weekly NEC which may remove the short-term effect of light availability and thus better isolate the influence of Ω_a on NEC rates [Langdon *et al.*, 2000, 2003; Marubini *et al.*, 2001]. However, it is very difficult to perform such experiments in field conditions. As a result, recent field investigations attempting to replicate these earlier mesocosm observations are more likely to reflect a combination of multiple processes driving NEC rates. To better understand the influence of Ω_a on NEC, it may be necessary to separate out the processes of calcification and dissolution which is not possible using our data set. Other studies have shown that dissolution may be more sensitive to OA [Andersson *et al.*, 2009]. However, we observed stable net dissolution throughout the night despite a Ω_a drop. Long-term, high-resolution NEC, calcification, and dissolution observations in reefs with

contrasting $p\text{CO}_2$ levels may help to improve predictions of how OA will impact NEC.

3.3. Other Drivers of NEC

[11] Uncoupling the multiple drivers of NEC is difficult in field experiments. Coral calcification may be controlled by a complex combination of drivers that include light, nutrients, temperature, pH, and Ω_a . A linear relationship was apparent between light intensity and NEC in spite of the 2–3 h lag in the NEC peak relative to the PAR peak (Figure 4). Temperature and nitrate had weaker, but still significant, linear correlations with NEC. NEP had the strongest correlation with NEC indicating that NEP (not Ω_a) may be the strongest control over NEC. The relationship between NEC and NEP may be associated with photosynthesis creating microenvironments at coral calcification sites that are conducive to calcification. It is interesting that nighttime NEC rates were relatively constant in spite of an overall decrease in Ω_a during the night (Figure 1). This supports our suggestion that NEC is more closely related to NEP over a diel cycle than to the bulk Ω_a of the overlying seawater, similar to results from sediment chamber incubations at Heron Island [Cyronak *et al.*, 2013]. Therefore, the effect of OA on coral reef NEC rates could be masked by other processes that influence NEP (i.e., the input of nutrients, light, and temperature) [Shaw *et al.*, 2012].

[12] Several studies have demonstrated that light exerts a strong control on NEC rates [Marubini *et al.*, 2001]. The availability of PAR is potentially one of the main drivers of the observed hysteresis in the in situ NEC versus Ω_a relationship from Heron Island. To remove any effects of PAR on the Ω_a versus NEC relationship, we performed a linear regression using only the hours when PAR is saturating (10:00 to 14:00), similar to Langdon *et al.* [2003]. This approach revealed a significant linear trend ($p < 0.05$,

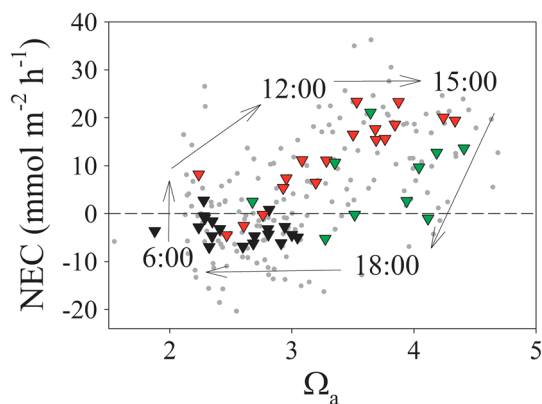


Figure 3. Net ecosystem calcification (NEC) rates as a function of Ω_a . The grey circles represent NEC rates estimated from every two consecutive samples, while the colored triangles represent NEC rates estimated from three to five samples taken at each low tide. The red triangles (06:00–15:00), green triangles (15:00–18:00), and black triangles (18:00–06:00) represent groups of samples taken during different time intervals. A clockwise diel hysteresis pattern emerged from the observations, as indicated by arrows.

Table 1. Summary of NEC Versus Ω_a Relationships in Different Coral Reef Communities Assuming a Linear Correlation to Predict Critical Ω_a Values Required to Shift a Coral Reef from a Net Calcifying to a Net Dissolving System (i.e., $NEC = 0$)^a

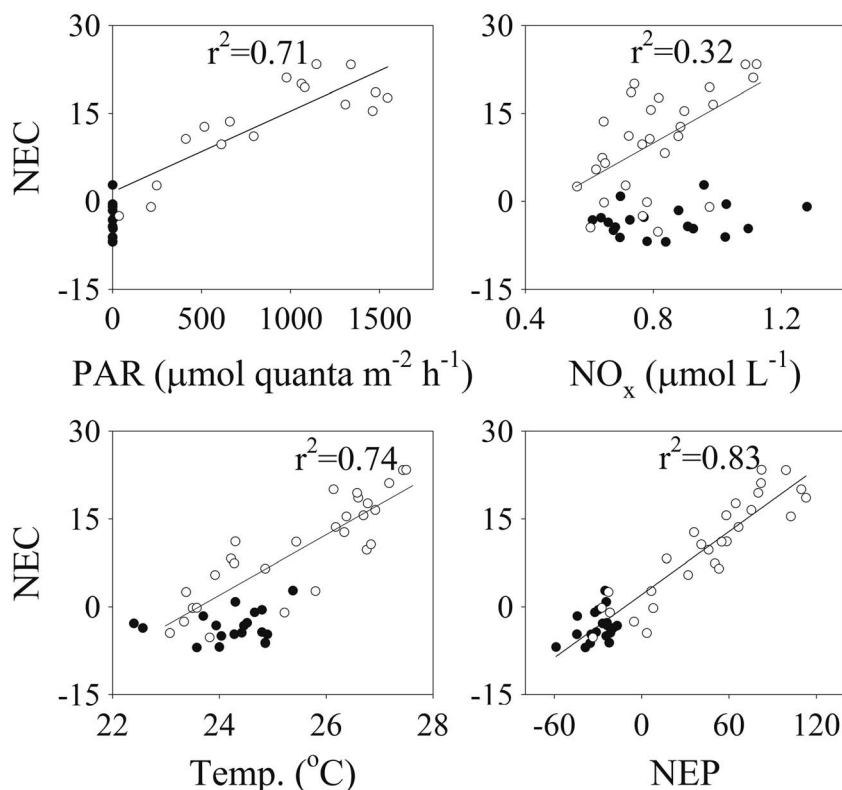
Location	Approach	Slope	Ω_a for $NEC = 0$	p Value	n	Reference
Kaneohe Bay	Mesocosm	187 ± 41	0.93 ± 0.61	0.0195	5	<i>Langdon and Atkinson [2005]</i>
Biosphere-2	Mesocosm	28 ± 3	1.50 ± 0.30	<0.0001	12	<i>Langdon et al. [2003]</i>
Kaneohe Bay	Mesocosm	78 ± 14	1.57 ± 0.32	0.0002	14	<i>Andersson et al. [2009]</i>
Hawaii	Flow respirometry	210 ± 98	1.65 ± 0.92	0.0841	7	<i>Shamberger et al. [2011]</i>
Lady Elliot Island	Slack water	85 ± 17	1.78 ± 0.41	<0.0001	56	<i>Shaw et al. [2012]</i>
Red Sea	Flow respirometry	80 ± 12	3.25 ± 0.24	<0.0001	14	<i>Silverman [2007]</i>
Ryukyu Islands	Slack water	190 ± 63	4.72 ± 0.52	0.0557	5	<i>Ohde and van Woessik [1999]</i>
Heron Island	Slack water	240 ± 26	2.64 ± 0.21	<0.0001	47	This study

^aOur observations revealed that a linear correlation assumption may not be valid because of a hysteretic behavior (Figure 3).

$R^2 = 0.80$) between Ω_a and NEC, with a similar x intercept ($\Omega_a = 2.62$ at $NEC = 0$) to that calculated when using all of the data (Table 1). A previous study demonstrated a hysteretic pattern in coral photosynthesis, with higher production rates observed in the afternoon than during the morning though the corals received similar levels of PAR [*Levy et al., 2004*]. Therefore, any hysteresis in coral NEP could drive the observed hysteresis in NEC rates. Interestingly, net dissolution was relatively stable during the evening and nighttime periods even though Ω_a decreased throughout the night due to respiration (Figure 3).

[13] At Heron Island, a DIC versus alkalinity plot (Figure 5) highlights that NEP is the major control on seawater Ω_a . While a linear relationship can be observed between DIC and TA ($R^2 = 0.73$), a closer inspection of the plot reveals a hysteresis pattern over a diel cycle as also observed for the NEC versus Ω_a plot. The current ratio of NEP to NEC in Heron Island is about 3. While NEC can account

for changes in both the TA and DIC concentrations, net ecosystem production (NEP) only changes DIC concentrations [*Langdon and Atkinson, 2005*]. Therefore, Ω_a is a function of the changes in carbonate chemistry due to both NEP and NEC, and any changes in DIC concentration relative to alkalinity will result in different influences on Ω_a . For example, in systems with high organic production relative to calcification (i.e., high DIC to TA consumption), Ω_a will increase due to a low uptake of TA and high uptake of CO_2 . Conversely, in systems with low organic production relative to calcification, Ω_a will decrease due to the uptake of TA [*Andersson and Gledhill, 2013*]. The reaction pathways shown in Figure 5 indicate that a decrease in calcification associated with an increase in organic production would increase Ω_a and potentially change the way NEC responds to OA. Therefore, any prediction of NEC based on ambient seawater Ω_a also needs to take into account the influence of NEP on both NEC and Ω_a .


Figure 4. Correlations between NEC and some potential drivers. The open circles represent daytime observations, while the closed circles represent nighttime observations. The correlation coefficients for the daytime observations are also shown.

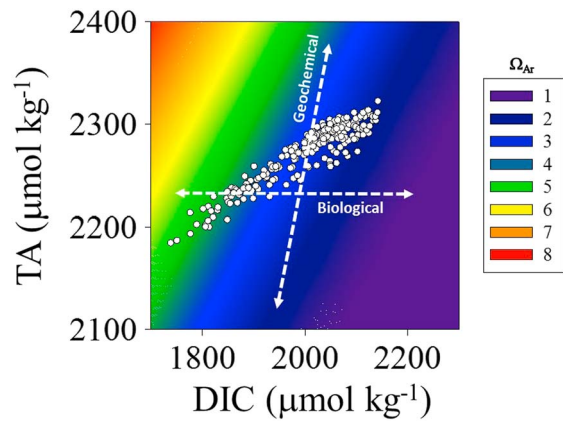


Figure 5. DIC and TA concentrations in the Heron Island lagoon along with the associated overlying seawater Ω_a calculated for constant temperature (25°C) and salinity (35 g kg^{-1}). The results demonstrate how changes in both DIC and TA may drive Ω_a .

4. Summary and Conclusions

[14] The ambient seawater Ω_a versus NEC relationship in coral reefs may be more complex than a simple linear trend. The observed hysteresis pattern demonstrates that we should exert caution when using the Ω_a versus NEC relationship from short-term observations over natural variations in carbonate chemistry to predict tipping points in coral reef calcification. Our field observations thus support theoretical considerations that question the use of Ω_a to predict NEC using short-term experimental observations [Andersson and Gledhill, 2013]. We hypothesize that the observed Ω_a versus NEC relationship in Heron Island and elsewhere are not necessarily functional. In fact, these correlations may be a casual effect of the way organic metabolism (i.e., photosynthesis and respiration) drives both Ω_a and calcification.

[15] **Acknowledgments.** This study was supported by an ARC grant (DP110103638). We thank the staff of the Heron Island Research Station for support in the field and Chris Langdon and Frank Sansone for helpful reviews.

[16] The Editor thanks F. J. Sansone and an anonymous reviewer for their assistance in evaluating this paper.

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