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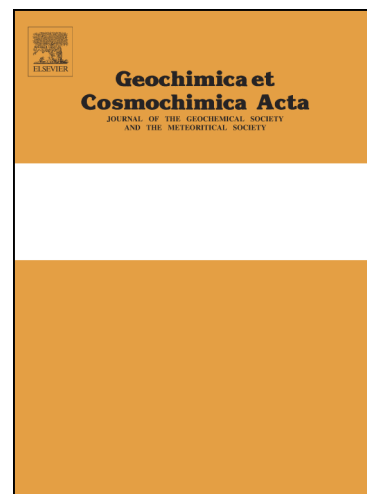
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Community calcification in Lizard Island, Great Barrier

Reef: A 33 year perspective

J. Silverman^{1*}, K. Schneider¹, D. I. Kline^{2,3}, T. Rivlin^{4,5}, A. Rivlin⁴, S. Hamylton⁶, B. Lazar⁵, J. Erez⁵, K. Caldeira¹

¹ Carnegie Institution for Science, Department of Global Ecology, Stanford, CA, USA

² Scripps Institution of Oceanography, University of California San Diego, La Jolla, CA, USA, 92037-0218

³ Global Change Institute, Coral Reef Ecosystems Lab, The University of Queensland, St. Lucia, QLD, Australia, 4072

⁴ The Interuniversity Institute for Marine Sciences, Eilat, The H. Steinitz Marine Biology Laboratory, The Hebrew University of Jerusalem, Eilat, Israel

⁵ The Fredy and Nadine Herrman Institute of Earth Sciences, The Hebrew University of Jerusalem, Edmond J. Safra Campus, Jerusalem, Israel, 91904

⁶ The School of Earth and Environmental Sciences, University of Wollongong, NSW, Australia, 2522

*Present address: Institute for Oceanographic and Limnological Research, Haifa, Israel
Corresponding author: jacobs1@ocean.org.il

Abstract

Measurements of community calcification (G_{net}) were made during September 2008 and October 2009 on a reef flat in Lizard Island, Great Barrier Reef, Australia, 33 years after the first measurements were made there by the LIMER expedition in 1975. In 2008 and 2009 we measured $G_{net} = 61 \pm 12$ and 54 ± 13 mmol $\text{CaCO}_3 \cdot \text{m}^{-2} \cdot \text{day}^{-1}$, respectively. These rates are 27%-49% lower than those measured during the same season in 1975-76. These rates agree well with those estimated from the measured temperature and degree of aragonite saturation using a reef calcification rate equation developed from observations in a Red Sea coral reef. Community structure surveys across the Lizard Island reef flat during our study using the same methods employed in 1978 showed that live coral coverage had not changed significantly ($\sim 8\%$). However, it should be noted that the uncertainty in the live coral coverage estimates in this study and in 1978 were fairly large and inherent to this methodology. Using the reef calcification rate equation while assuming that seawater above the reef was at equilibrium with atmospheric PCO_2 and given that live coral cover had not changed G_{net} should have declined by $30 \pm 8\%$ since the LIMER study as indeed observed. We note, however, that the error in estimated G_{net} decrease relative to the 1970's could be much larger due to the uncertainties in the coral coverage measurements. Nonetheless, The similarity between the predicted and the measured decrease in G_{net} suggests that ocean acidification may be the primary cause for the lower CaCO_3 precipitation rate on the Lizard Island reef flat.

Keywords: Coral Reefs, Community Calcification and Dissolution, Ocean Acidification

Introduction

Since the beginning of the industrial revolution nearly half of the anthropogenic CO_2 emitted to the atmosphere has been absorbed by the oceans (Sabine *et al.*, 2004). As a result pH and the carbonate ion (CO_3^{2-}) concentration have already decreased (Kleypas *et al.*, 2006) and are expected to continue decreasing with increasing levels of atmospheric CO_2 (Ocean Acidification – OA, Caldeira and Wickett, 2003). The decrease in CO_3^{2-} , which is often expressed in terms of aragonite saturation state (Ω_{arag}) (aragonite is the CaCO_3 mineral precipitated by corals), has been shown in lab and field studies to be potentially harmful to the well being and integrity of coral reefs (Kleypas *et al.*, 1999; Ohde and van-Woesik, 1999; Langdon and Atkinson, 2005;

Gattuso *et al.*, 1998; Schneider and Erez, 2006; Silverman *et al.*, 2007; Silverman *et al.*, 2009; Derse-Crook *et al.*, 2013). Where, calcification rates of reef building corals and coral communities are positively correlated with ambient seawater Ω_{arag} . Thus, the ability of coral reefs to accumulate $CaCO_3$ at a rate greater or equal to the sum of mechanically, biologically and chemically mediated erosion rates will and may already be severely compromised as a result of ocean acidification.

Silverman *et al.* (2007) combined observed values of seasonally varying G_{net} , Ω_{arag} and temperature in a Red Sea coral reef (Fig. 1) with laboratory experiment results of inorganic aragonite precipitation kinetics (Burton and Walter, 1987) and formulated a reef community rate equation:

$$G_{net} = A_c \cdot K_r \cdot K \cdot (\Omega_{arag} - 1)^n - D \quad (3)$$

Where, A_c is the fraction of live coral coverage in the reef; K_r is the three-dimensional to planar conversion factor for reef surfaces actively precipitating $CaCO_3$; both the rate coefficient K and the order of reaction n are temperature dependent (Burton and Walter, 1987) and formulated in Silverman *et al.* (2007); D is the diurnal average dissolution rate, estimated from the mean nighttime $CaCO_3$ loss. If K_r , A_c and D remain constant then changes in G_{net} are proportional to the changes in the inorganic component of equation (3), *i.e.*

$$G_i = K \cdot (\Omega_{arag} - 1)^n \quad (4)$$

Using equation 4 we predicted that calcification in reefs of the Great Barrier Reef (GBR), Australia, would decrease due to OA by 20-40% from their pre-industrial rates, at atmospheric PCO_2 level of 450 ppm (Fig. 2 in Silverman *et al.*, 2009).

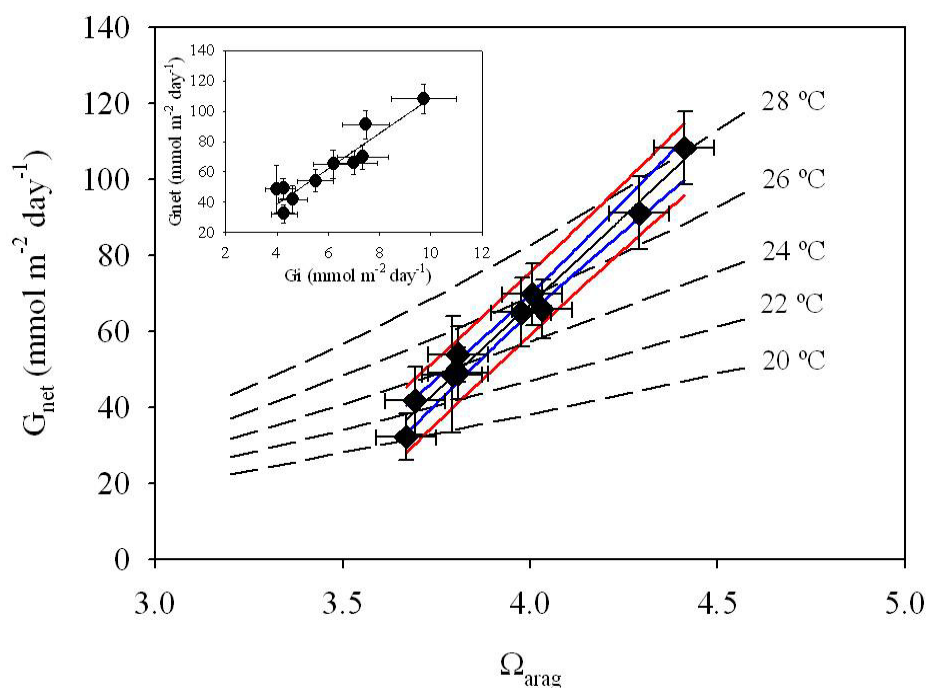


Figure 1. Diel average G_{net} of a fringing reef in the Gulf of Aqaba, northern Red Sea measured at different times of the year during the period 1997-2002 (Silverman *et al.*, 2007), plotted against corresponding values of the diel average reef water Ω_{arag} . Contours of constant temperature in the observed range are calculated according to Equation 3 and fit parameters from (Silverman *et al.*, 2007). Blue and red lines indicate the 95% confidence and prediction bands, respectively. The insert plot demonstrates the excellent correlation between reef G_{net} and the precipitation rates of inorganic aragonite ($G_i = K \cdot (\Omega_{arag} - I)^n$) calculated according to (Burton and Walter, 1987) with the corresponding diel average Ω_{arag} and temperature of the reef ($R^2 = 0.89$, $n = 10$).

Recent studies showed a reduction in individual coral growth from the Great Barrier Reef, southern Thailand and the central Red Sea of 13 to 24% over the last 20-30 years (Cooper *et al.*, 2008; De'ath *et al.*, 2009; Tanzil *et al.*, 2009; Cantin *et al.*, 2010). However, the lack of well characterized carbonate chemistry trends at these sites prevented the establishment of direct causality between OA and coral growth decline.

During the 1970's a number of community metabolism studies were conducted on coral reefs in the Indo-Pacific using the alkalinity depletion method (Smith, 1973). According to this approach

precipitation of 1 mol CaCO_3 in the reef water will lower the total alkalinity (A_T) by 2 moles, and vice versa for CaCO_3 dissolution. Thus, the rate of A_T depletion between two or more points along the flow's trajectory over wide areas of a coral reef is twice the net rate of CaCO_3 precipitated or dissolved by the benthic community (G_{net}).

In 1975-76 measurements of community calcification were made using the alkalinity anomaly technique on the South Island reef flat, Lizard Island (14°40'S, 145°30'E), northern GBR, Australia (Fig. 2) (LIMER 1975, 1976; Kinsey, 1979). The goal of the current study was to repeat these measurements more than three decades later and determine if a decline in reef calcification had occurred and if this decline was caused by OA.

Materials and methods

In September 2008 and in October–November 2009 we measured G_{net} at stations between South Island and Bird Island reef flats (Fig. 2). Water samples were collected at SIRM01 every 2 hours for 24 hours and were analyzed for A_T , dissolved inorganic carbon (C_T), nitrate (NO_3^{-1}), nitrite (NO_2^{-1}) and ammonia + ammonium ($\text{NH}_{3\text{-tot}}$). Samples were also collected several times during daytime at SIRM02 and SIRM03 in order to assess the spatial variability of G_{net} . Water samples were also collected a number of times in the open water off the reef throughout the entire study period. Automated measurements of salinity, temperature and depth were recorded with a SBE-19 deployed on the reef flat at SIRM01-02-03 every 10 minutes throughout the sampling periods. Current speed and direction were recorded with Interocean Ltd S4 fluxgate current meters every 10 minutes, which were deployed on tripods that held them ca. 0.2-0.5 m above the reef flat at SIRM01-02-03 throughout the sampling periods. Weather data (including precipitation) were recorded at 10 minute intervals throughout the study periods at a station on Lizard Island shoreline ca. 10 m above the water surface.

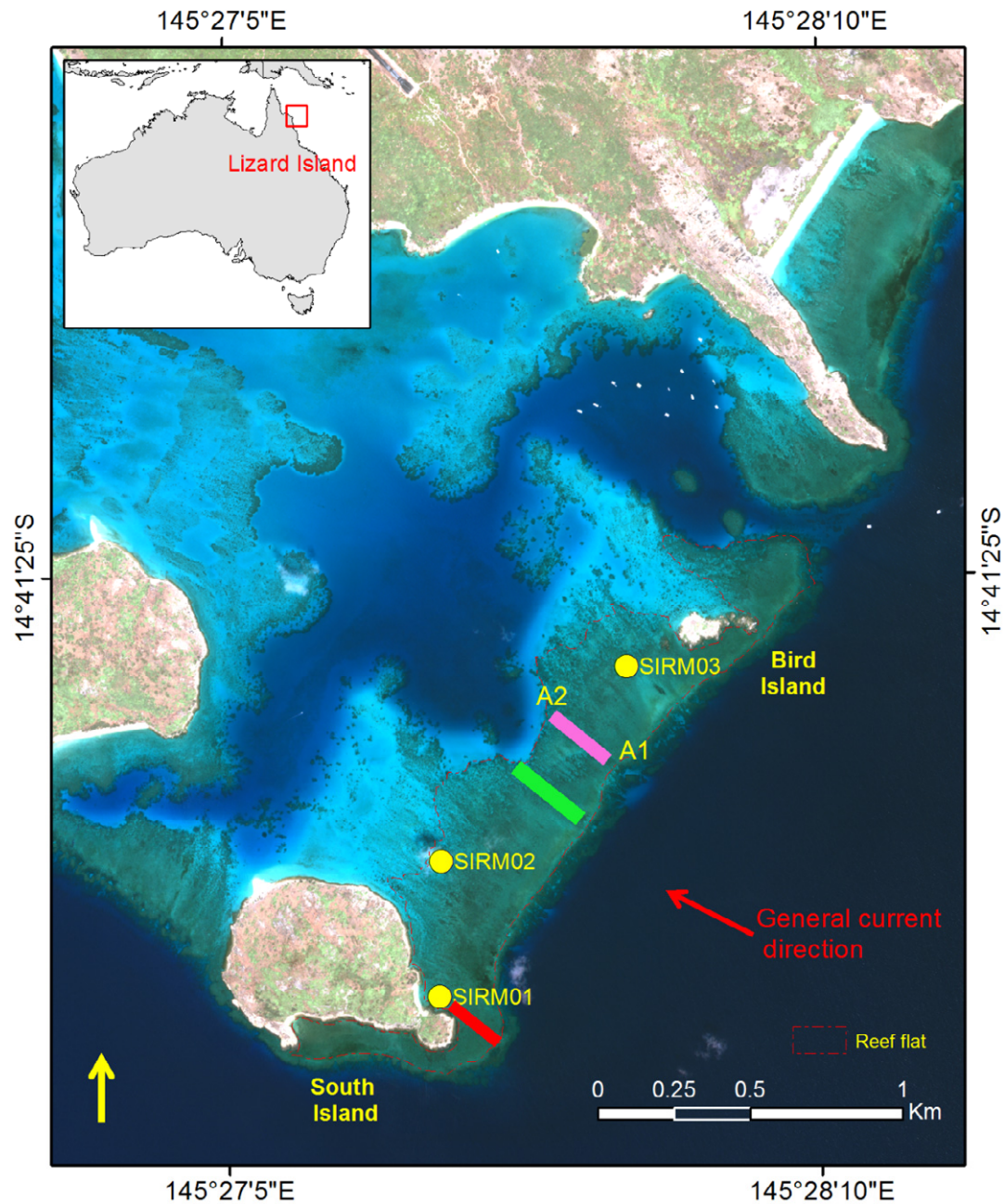


Figure 2. Location map and aerial photo of Lizard Island and South Island reef flat study site. During 1975-76 transect measurements were made along lines A1 and A2 (LIMER 1975, 1976). In this study G_{net} was measured at SIRM01 (2008-09), SIRM02 (2008) and SIRM03 (2009). Benthic community surveys were conducted along the red line and green line, which is also in the region of the reef surveyed by Pichon and Morrisey in 1979 (1981). The red dashed line outlines the reef flat as defined by the IKONOS image classification.

Filtered (0.45 μm Sartorius filter) replicate A_T samples (~ 20 g) were measured within a few days of sampling by titration with 0.05 N HCl using the Gran method with a precision of better than ± 2 $\mu\text{mol/kg}$. The acid was calibrated with a seawater Certified Reference Material (CRM) from A. Dickson's laboratory before each titration session. Samples for C_T analysis were stored in 30 ml glass bottles sealed with rubber stoppers and crimped with tin caps after adding 15 μl (0.05% v/v) saturated HgCl_2 solution (Dickson *et al.*, 2007). Analysis was conducted about 2 months after sampling by acidifying with phosphoric acid (H_3PO_4 , 5%) and extracted CO_2 with an extractor and delivery system (D. Mucciarone, EESS, Stanford) using a high grade nitrogen carrier gas to a LiCor 7000 $\text{CO}_2/\text{H}_2\text{O}$ analyzer, based on the Bandstra *et al.* design (2006). C_T measurements were calibrated using seawater CRMs from A. Dickson's laboratory. Every sample was measured in triplicate. The repeatability (mean \pm SD) of the measurements was 1.3 ± 0.9 $\mu\text{mol/L}$. NO_2^{-1} and NO_3^{-1} were measured with a colorimetric method (Grasshoff *et al.*, 1999) using a Flow Injection Autoanalyzer (Lachat Instruments Model QuickChem 8000) with a precision of ± 0.02 $\mu\text{mol/L}$. $\text{NH}_{3\text{-tot}}$ was determined by a fluorometric method modified from protocol A of Holmes *et al.* (1999).

Values of Ω_{rag} were calculated as a function of salinity, temperature, A_T , C_T and atmospheric PCO_2 from the Mauna Loa record for 1975, 2008 and 2009, using the CO2sys.exe program (Lewis and Wallace, 1998). We used the dissociation constants of Roy *et al.* (1993) for the total hydrogen scale for both A_T/C_T and A_T/PCO_2 combinations, and the apparent aragonite solubility constant of Mucci (1983) for calculating Ω_{rag} . The assigned error in Ω_{rag} is ± 0.08 following Milero (1979).

Benthic community structure surveys were conducted along four 30 meter replicate transects every 50 m from the reef crest to SIRM01 and from the reef crest to the back reef in the same site surveyed by Pichon and Morrissey (1981) and using their method (Fig. 2). Where, the measured diameter of corals was used to calculate the percentage of coral coverage. It should be noted that the expressed goal of the Pichon and Morrissey study was to provide a community structure context to compliment the community calcification rates measured during LIMER (LIMER 1975, 1976). In order to compare the measurements made in 1975-76 with those made in 2008-09, it was necessary to establish that the benthic cover types across the reef flat were consistent to account for the different locations of the sampling stations. To determine the spatial

variation in benthic cover types across the reef flat, two analyses were performed on a multi spectral IKONOS satellite image with a spatial resolution of 3.2 m acquired in 2005 (Fig. 2). Initially, a supervised classification was applied to the satellite data, which has been pre-processed to remove the influence of the atmospheric effects as well as light absorption and scattering in the water column. Half of a field dataset of 107 benthic cover reference points was used to calibrate the classifier, while the other half was used to validate the classification. The maximum likelihood classification assigned each pixel of the image to the most likely benthic cover class on the basis of the training statistics (Mather and Koch, 2011). The proportion of points classified correctly when compared to the map (Congalton, 1991) was 81%. Finally, reflectance data from 3034 pixels were extracted from the areas coinciding with the 1975-76 and 2008-09 sampling stations and the statistical significance of the difference in the reflective properties of these two groups of exported pixels (which itself indicated benthic cover type) was assessed using a one-way ANOVA test.

G_{net} for each sampling time was calculated according to Equation 5, where: \bar{Z}_τ is the average depth of water over the reef flat during its transit from the reef crest to the reef flat sampling stations derived from a detailed bathymetric survey of the reef flat study site using a graded pole, a single beam echo sounder and GPS; ΔA_T is The difference between A_T measured in the open water off the reef and the reef flat sampling stations; τ is the estimated transit time of water from the reef crest to the reef flat sampling stations, which was determined from the current measurements at each station by plotting the reverse trajectory of the current on the map of the reef (Fig. 2) from the sampling station until it crossed the reef crest similar to the method used by Falter *et al.* (2012). However, because the reef crest does not follow a straight line in the vicinity of SIRM01 (Fig. 2), we did not plot only the component of the current aligned with the diagonal to the reef crest and therefore the trajectory of the cumulative vector did not follow the same path for each transit time estimate and its length varied accordingly.

$$G_{net} = \frac{\bar{Z}_\tau}{\tau} \cdot \frac{\Delta A_T}{2} \quad (5)$$

The error in G_{net} (ΔG_{net}) was estimated using the first differential method of error analysis (Topping, 1972). The assigned errors for the transit time $\Delta t = \pm 10$ min, for the average depth $\overline{\Delta Z}_\tau = \pm 0.1$ m and for the difference in alkalinity $\Delta A_T = \pm 2$ $\mu\text{mol/kg}$.

Results

Sampling at SIRM01 was conducted during neap tide and relatively calmer winds when there were no breakers on the reef crest. Sampling at SIRM02-03 was conducted under stronger wind conditions when there were breakers on the reef crest and the current was stronger (Table 1). The current direction over the reef flat during both studies was nearly constant towards the NW, in roughly the same direction as the prevailing winds (Table 1, Fig. 3) similar to those reported for this season in 1975-76 (LIMER 1975, 1976; Kinsey, 1979). In 2008 and 2009 τ for SIRM01 was 2-3 times longer on average than τ for SIRM02 and SIRM03. This difference reflects the effect of South Island on the current as well as the relatively calmer weather conditions and tidal range of the measuring period at SIRM01 relative to SIRM02 and SIRM03 (Table 1). During the sampling periods the sky was partly cloudy to clear with occasional light rains before daybreak. The ranges of ΔA_T for SIRM01 were very similar in 2008 and 2009 (Table 1). The negative ΔA_T observed only during the night at SIRM01 (no nighttime data for SIRM02-03) indicates CaCO_3 dissolution. In both studies changes in $\text{NH}_3\text{-tot}$, NO_3^{-1} between the reef crest and the sampling stations were < 0.5 $\mu\text{mol}\cdot\text{l}^{-1}$, and hence had negligible effect on ΔA_T . The differences between salinities at the reef crest and SIRM01 were calculated as a function of the evaporation rate, which was calculated using the simplified version of Fairall *et al* (1996) TOGA/COARE code using the `hfbulktc.m` matlab function in the `airsea` toolbox (ver. 2.0, 1999), developed by Pawlowicz and Anis (<http://www.eos.ubc.ca/about/faculty/R.Pawlowicz.html>). Wind speed, dry and wet bulb air temperature, and air pressure, required for this function were measured on the southern shore of Lizard Island, ca. 10 m above sea level, at 10 min intervals. These calculations yielded an average evaporation rate of 2.1 ± 0.6 and 5.3 ± 0.9 mm/day during the 24 hour sampling cycle at SIRM01 in 2008 and 2009, respectively. The resulting average difference in salinity was 0.008 ± 0.002 and 0.019 ± 0.004 , respectively. The effect of these changes in salinity on total alkalinity were 0.5 and 1.3 $\mu\text{mole/kg}$, respectively. These changes are both well within the analytical error for total alkalinity, and therefore were considered negligible. Furthermore, it

should be noted that measurements of alkalinity on the reef during the 1970's were not normalized to changes in salinity.

Table 1. Summary of physical and chemical data measured on the South Island Reef Flat, Lizard Island during September 2008 and October 2009.

Station ID	SIRM01		SIRM02	SIRM03
Date	9/6-7/2008	10/28-29/2009	9/8-11/2008	10/28 – 11/4/2009
Wind Speed \pm 1STD (m/sec)	7.4 \pm 1.4	8.2 \pm 2.1	8.3 \pm 1.9	11.2 \pm 2
Wind direction \pm 1STD (°)	163 \pm 10	151 \pm 8	148 \pm 8	153 \pm 5
Current direction \pm 1STD (°)	311 \pm 22	332 \pm 51	340 \pm 16	309 \pm 41
τ (min)*	130 – 290	100 – 300	40 – 120	20 – 190
Open sea A_T ($\mu\text{mol/kg}$)	2278	2256-2268	2278	2256-2297
ΔA_T ($\mu\text{mol/kg}$)* ^a	-13 – 71	-10 – 71	1 – 65	6 – 20
Daytime ^b G_{net} range ($\text{mmol}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$)	16 – 472	47 – 439	3 – 418	36 – 436
Nighttime ^b G_{net} range ($\text{mmol}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$)	-19 – 11	-57 – 38	---	---

^a Minimum and maximum differences in A_T between open sea surface water and the reef flat sampling stations ($A_{T(\text{open-sea})} - A_{T(\text{reef})}$) with positive and negative values during the daytime and nighttime, respectively.

^b Daytime (06:00 – 18:00), nighttime (18:00 – 06:00).

* The errors assigned to τ and ΔA_T for calculation of calcification rates according to Equation 4 are ± 10 min and $\pm 2 \mu\text{mol}\cdot\text{kg}^{-1}$, respectively.

Diel G_{net} cycles at SIRM01 in 2008 and 2009 were very similar both in absolute values and pattern (Fig. 3c). Because of the large diel range in G_{net} (e.g. Fig. 3, Table 1), and the lack of semi continuous data from SIRM02-03 it was not possible to calculate diel integrated values for these sections of the reef. However, the ranges and timing of daytime G_{net} extremes at SIRM02-03 are similar to those measured at SIRM01 (Table 1), indicating that calcification is uniform along the reef flat.

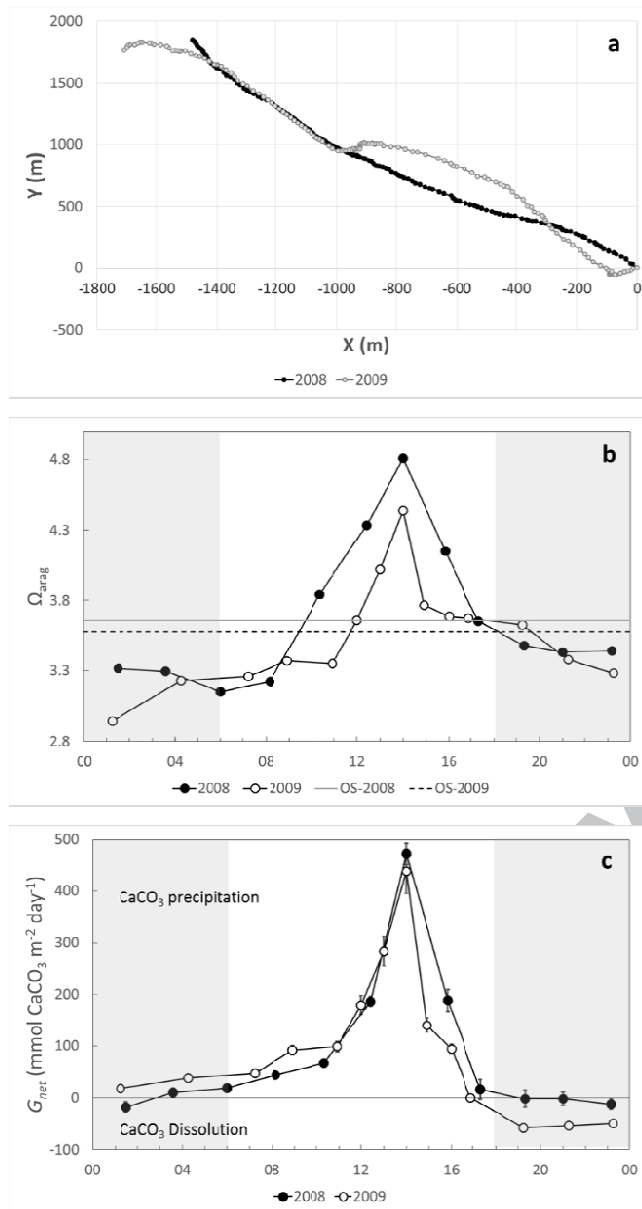


Figure 3. a) Cumulative vector diagrams of current measurements made during 6-7 of September 2008 and 28-29 of October 2009 using an S4 Interocean ltd. current meter deployed 0.4 m above the reef at SIRM01 during 6-7 of September 2008 and 28-29 of October 2009. b) Diel cycles of Ω_{arag} (b) and G_{net} (c) measured at SIRM01 during 6-7 of September 2008 and 28-29 of October 2009. Ω_{arag} were calculated as a function of C_T , A_T , T and S measured at SIRM01 and the open sea values (OS) were calculated as a function of C_T and A_T measured in the open sea together with diel average temperature and salinity measured at SIRM01. The shaded areas in b and c indicate approximately the nighttime periods in both studies.

The live coral cover measured across the two reef flat transects (Fig. 2) was $8.3\% \pm 3.2\%$ and $7.1\% \pm 1.5\%$ ($\pm 1SD$). Both values are nearly identical (Wilcoxon rank sum test, $p=0.82$) to that of Pichon and Morrissey (1981) who reported a hard coral cover of $8.0\% \pm 5.6\%$ ($\pm 1SD$). The live coral coverage reported by LIMER along A1 (Fig. 2) was described as very low with 0% coverage on the algal flat adjacent to the reef crest and 10% -15% in the coral – algal zone toward the back reef along transect A2 (LIMER 1975, 1976; Kinsey, 1979). No details of the methods used in the benthic coverage surveys were given. However, given that the transect lengths are approximately the same then the coral coverage, which was likely to have been very low and could be calculated as the average, i.e. 5-7.5%. This value is also very similar to the values measured by Pichon and Morrissey, who also reported a higher coverage toward the back reef suggesting that the coral coverage of the South Island reef flat was relatively homogenous. In addition, these values are also similar to measurements made during the mid 1990s (Chisholm and Barnes, 1998) suggesting that the benthic community was stable throughout the last three decades.

The satellite image analysis revealed an internally consistent benthic cover class composed of coral and algae across the South Island reef flat. The one-way ANOVA of reflectance values extracted from the sampling stations near South Island and near Bird island indicated that these areas were not statistically different (F statistic was below the statistical distribution at $p=0.05$). These results suggest that the benthic coverage across the reef flat was uniform during this study and comparison of the diurnal average G_{net} values measured at SIRM01 and G_{net} measured near Bird Island in 1975-76 is valid.

Discussion

During late September and early October 1975 G_{net} of the South Island reef flat near Bird Island (Fig. 2) was measured over a two week period by the LIMER expedition by following the trajectory of a dye patch and drogue across the reef flat during the daytime and nighttime, respectively (LIMER 1975, 1976; Kinsey, 1979). According to these measurements G_{net} during this period varied between $9.5-10.5 \text{ g CaCO}_3 \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ or $95-105 \text{ mmol} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$, while the annual average rate reported by Smith and Kinsey (1976) varied between 3.6 and $3.8 \text{ kg CaCO}_3 \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ or $99-104 \text{ mmol} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$. In a later compilation, which included in total 38 daytime and 9 nighttime measurements of G_{net} made on the South Island reef flat near Bird

Island during September-October 1975-76, the diel integrated G_{net} was $1.0 \text{ g C}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ or $83 \text{ mmol}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ (Kinsey, 1979). Relative to the LIMER measurements (LIMER 1975, 1976), the G_{net} of the South Island reef flat in our study is 27%-49% less, and relative to the later compilation (Kinsey, 1979), it is 31% less on average. The decrease in G_{net} between 2008-09 and the mid 1970's is clearly not an artifact resulting from seasonal variability as both studies were conducted during the same season.

As stated previously the established horizontal homogeneity of cover type across the south Island reef flat (based on reflectance analysis) and the similar live coral coverage measured in our study and in 1978 may be used to justify the comparison of the calcification rates measured near Bird Island in the 1970's to those made at SIRM01 during this study. Therefore, it could be concluded that the apparent decrease in G_{net} is not caused by variations in live coral coverage and some other mechanism may be responsible for it assuming that corals do most of the CaCO_3 precipitation on the reef flat. However, while the measured coral coverage in this study is not significantly different from the coral coverage measured by Pichon and Morrissey, there is considerable uncertainty in the measurement of live coral cover ($\pm 20\text{-}40\%$ in this study and $\pm 70\%$ in Pichon and Morrissey) that could easily explain the apparent decrease in G_{net} making our conclusion less definitive.

An additional source of uncertainty is the possible effect of current flow rate across the reef flat at the different locations measured during the LIMER expedition and this study on G_{net} . In this study the current measurements clearly show that water flow across the reef flat was much faster nearer to Bird Island (SIRM02 and SIRM03) than near South Island (SIRM01, Table 1) by an average factor of 3.0 ± 2.3 (SIRM02/SIRM01) and 3.8 ± 3.9 (SIRM03/SIRM01) throughout the 2008 and 2009 study periods, respectively. Previous studies have demonstrated that photosynthesis and respiration of corals increase in response to increased flow rate as a result of increased mass transfer across their boundary layers (e.g. Dennison and Barnes, 1988; Patterson *et al.*, 1991; Mass *et al.*, 2010) with exception of Atkinson *et al.* (1994) Sebens *et al.* (2003) who showed that there was no correlation between current flow and respiration or photosynthesis, respectively. In their study on the effect of flow rate on the metabolism of *Acropora formosa dana* colonies from the GBR Dennison and Barnes (1988) showed that calcification decreased by 25% under no flow conditions (0 cm/sec) relative to flow condition (0-20 cm/sec). In contrast, Sebens *et al.* (2003) showed that growth rates in the branching scleractinian coral *Agaricia*

tenuifolia from Belize, which were incubated in respirometry chambers in-situ at a variety of depths (1-24 m) and reef habitats where flow rates varied between 0-30 cm/sec, were unaffected by flow rates. Similarly, Atkinson *et al.* (1994), showed that the community calcification rates of *Porites compressa dana* corals placed in a 10m flume were not correlated with water flow ranging from 1-57 cm/sec. In this study flow rates varied between 0-8.5 (avg. \pm STD = 2.9 ± 1.2) and 1.3-15.3 (avg. \pm STD = 6.5 ± 2.6) cm/sec at SIRM01 and SIRM02, respectively during September 2008, and between 0-13.9 (avg. \pm STD = 3.6 ± 2.1) and 0.2-33.8 (avg. \pm STD = 13.4 ± 9.1) cm/sec at SIRM01 and SIRM03, respectively during October – November 2009. Despite these significant differences in flow rate across the reef flat at these sites the ranges of daytime calcification at SIRM01-02-03 were similar in agreement with the Sebens *et al.* (2003) study.

During the 1970's the rate of nighttime CaCO_3 dissolution was $-0.01\pm 0.08 \text{ g C}\cdot\text{m}^{-2}\cdot\text{hr}^{-1}$ (average \pm 1STD) or $-20\pm 160 \text{ mmol}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ (Kinsey, 1979), while the nighttime dissolution rates (D) measured in our studies were -5 ± 4 and $-10\pm 5 \text{ mmol}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ (Table 2). It should be noted that the error in D values reported for our study are the analytical error unlike the error reported by Kinsey which is the standard deviation of all nighttime measurements ($n=9$) made during September and October 1975-76. Thus, calculation of the standard deviation of all nighttime measurements made in this study yields a value of $45 \text{ mmol}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ ($n=11$).

Nighttime calcification rates in crustose coralline algae measured on Lizard Island during March-July 1986 varied between $-5 - 4 \text{ mmol}\cdot\text{m}^{-2}\cdot\text{hr}^{-1}$ or $-120 - 106 \text{ mmol}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ for different species incubated between 0 and 18 m water depth (Chisholm, 2000). Calculating the average of the nighttime calcification rates for all species and depths (Table 2 in Chisholm (2000)) yielded a daily average value of $-5\pm 20 \text{ mmol}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ (\pm average of the standard deviations of nighttime measurements for each species and incubation depth tested), which is remarkably similar to the rates measured in this study. It should be noted that the different species of algae samples tested in the study by Chisholm were sampled together with a substantial layer of reef substrate below them (10-15 mm thickness, Op. Cit.). Therefore, it is very likely that the measured nighttime dissolution rates may actually represent the activity of endolythic flora and fauna as well as that of the algae, and therefore the comparison with the results of this study seems reasonably valid. Finally, in an experimental study of bioerosion rates in CaCO_3 blocks transplanted into the Lizard Island reef (NW of the main Island at 9 m depth (Tribollet *et al.*, 2002)) it was shown that

after 3 years of deployment the total bioerosion was 2.26 ± 0.26 kg CaCO_3 or 21 ± 2 $\text{mmol} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ (Tribollet and Golubic, 2005). Considering that nearly 50% of the erosion was caused by grazers, which was estimated from the gouge marks in the blocks, and the rest by micro and macro endolythic flora and fauna, we estimate from rates in Table 2 from Tribollet and Golubic (2005) that the bioerosion activity primarily associated with changes in the alkalinity budget of the reef was 12 ± 2 $\text{mmol} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$, which is again remarkably similar to the rates measured in this study. These observations suggest that rates of nighttime CaCO_3 dissolution in the South Island reef flat have not changed significantly since the 1970's and are comparable to bioerosion rates measured over long periods of time using a completely independent method.

During the period 1975-2009 atmospheric PCO_2 increased by 55 ppm (Keeling *et al.*, 2009). If it is assumed that total alkalinity of the surface water at Lizard Island remained constant over the same period then a corresponding change in the PCO_2 of surface seawater at Lizard Island (55 ppm) assuming that it is at atmospheric equilibrium would cause a 14% decrease in Ω_{ag} (Table 2). It is noted that both assumptions regarding PCO_2 and total alkalinity are unrealistic and are only meant to provide an estimate of the potential change in the carbonate system due to increasing atmospheric PCO_2 without taking into consideration any other possible feedbacks. Thus, according to equation 4 the potential decline in G_i with Ω_{ag} is 30 ± 8 %, which is remarkably very similar to the apparent decrease in G_{net} . However, according to the meta-analysis conducted by Chan and Connolly (2012) of numerous (n=25) experimental studies testing the effect of ocean acidification on the growth of individual corals using the alkalinity anomaly technique (n=9) there is an average linear decrease of 25% per unit Ω_{arag} . Thus, the potential decrease in coral growth on the south Island reef flat in 2008-09 relative to 1975 is 12 ± 2 %, which is substantially lower than the measured decrease in G_{net} . It should be noted however that the range of responses is considerable and varies between 32.0 ± 5.6 % and 3.9 ± 0.6 % potential decrease. It is particularly interesting to note that one of the high end responses based on measurements by Langdon *et al.* (2000) in a mesocosm over a 3.8 yr period was 31.5 ± 5.5 % potential decrease, which is similar to the potential decrease in G_i calculated from the Red Sea rate equation, while the rest of the studies were conducted over substantially shorter periods of time from 1.5 hrs to 1 month. This may suggest that a longer acclimation period is necessary in order to produce more realistic responses in these types of experimental studies.

Despite the large difference in the measured diurnal average PCO_2 from atmospheric equilibrium and from each other during the 2008-09 studies (Table 2), their corresponding G_{net} and G_i values fall well within the confidence intervals of the linear trend, which was calculated from the available data measured in a number of Pacific Ocean and Red Sea reefs (Fig. 4). It is interesting to note that D values in this study are similar to those measured during the 1970's and to bioerosion rates measured during the 2000's (see above) suggesting that OA has not yet affected rates of $CaCO_3$ dissolution in the reef as expected perhaps from the results of experimental studies (Andersson *et al.*, 2009; Tribollet *et al.*, 2009). These studies showed that under conditions of the carbonate system in seawater anticipated by the end of the 21st century due to OA, nighttime $CaCO_3$ dissolution of a coral mesocosm after short term exposure (Andersson *et al.*, 2009) and bioerosion of $CaCO_3$ blocks after long term exposure (Tribollet *et al.*, 2009) would both increase substantially. In the Andersson *et al.* study the nighttime dissolution increased by a factor of ~ 3 on average for a decrease of 1 unit of Ω_{rag} from 2.1 to 1.1. For $3.5 < \Omega_{rag} < 4.5$, ratios of volume bored to volume of coral measured in coral cores sampled along a naturally occurring acidification gradient in the Eastern Pacific appear to be independent of Ω_{rag} (Derse-Crook *et al.*, 2013). However, this ratio increases exponentially below $\Omega_{rag} \sim 2$, where in the range $2 < \Omega_{rag} < 3.5$ there is no data. These data suggest that under low Ω_{rag} corals skeletons are more susceptible to bioerosion, however it should be noted that in the Derse-Crook *et al.* study low Ω_{rag} coincided with high nutrient levels (Crook *et al.*, 2012), which could also cause increased bioerosion (Glynn, 1997). On the other hand Tribollet *et al.* (2009) showed that coral blocks euendolithic micro-algae developed significantly under conditions of comparably low Ω_{rag} levels at low nutrient levels ($NH_4^+ = 0.4 \mu\text{mole/L}$ and $PO_4^{-3} = 0.1 \mu\text{mole/L}$). Therefore, it is reasonable to conclude that OA may not have impacted nighttime dissolution yet or are too small to measure as the Ω_{rag} may still be relatively high (see Table 2) as well as the associated uncertainty in the LIMER measurements. Supporting evidence for this conclusion can be found in the nighttime dissolution measurements we made on One Tree Island in 2009, which were three time greater than those measured at the same site during the 1970's (Silverman *et al.*, 2012). It was suggested that the increase in nighttime dissolution observed on One Tree Island may have been caused by ocean acidification (Op. Cit.). In that study the nighttime average and nighttime and minimum Ω_{arag} were 2.53 ± 0.46 (1STD) and 1.80, respectively, while on Lizard

Island the average values in 2008 and 2009 were 3.35 and 3.24, and the minimum values were 2.94 and 3.15, respectively. Therefore, it is possible that while at DK13 the threshold for exponentially increasing dissolution had been crossed, it hadn't on Lizard Island. It is also worth noting that the nighttime dissolution rate at DK13 during the 1970's was already 3 times greater than the dissolution rate measured on Lizard Island by Kinsey. So, perhaps even during the 1970's the saturation state was low enough to be in the range of the exponential increase in dissolution. Unfortunately, we do not have good carbonate chemistry measurements from the 1970's either on Lizard Island or on One Tree Island to test this hypothesis.

Table 2. G_i , G_{net} and D in the South Island reef flat during September – November 1975-76, September 2008 and October 2009 and their changes relative to 1975-76.

Study	LIMER 1975-1976	SIRM01-2008	SIRM01-2009
Atmospheric PCO_2 (ppm)	331	386	387
Reef water PCO_2 (ppm)*		393	455
T (°C)	26.7	24.9	26.4
Reef water Ω_{rag} with PCO_2 at atmospheric equilibrium**	4.33	3.76	3.93
Diel average reef water Ω_{rag} *		3.65	3.45
Open sea Ω_{rag} ***		3.66	3.58
Reduction in G_i relative to LIMER (%)		38 ± 12	22 ± 12
G_{net} (mmol·m ⁻² ·day ⁻¹)	83-105	61 ± 12	54 ± 13
Reduction in G_{net}		27-42	35-49

Relative to LIMER (%)			
D (mmol·m ⁻² ·day ⁻¹)	-20±160	-5 ± 4	-10 ± 5

* Calculated as a function of measured T , S , A_T and C_T at SIRM01.

** Calculated as a function of measured T , $S = 35$, $A_T = 2300$ $\mu\text{mol/kg}$ and assuming equilibrium with atmospheric PCO_2 .

*** Calculated as a function of the diurnal average salinity and temperature at SIRM01 with DIC and A_T values measured in the open water.

Chisholm and Barnes (Chisholm and Barnes, 1998) reported similarly low $G_{net} = 55$ mmol·m⁻²·day⁻¹ measured during March 1996 on the South Island reef flat using the pH-O₂ method. Their measurements were conducted immediately after 12 days of heavy rains leading to a significant reduction in salinity from ~35 to an average value of ~33 (Chisholm *et al.*, 1996), and as a result A_T and C_T would have been diluted by ~6% (a multiplicative factor of 0.94). At a temperature of 27°C (op. Cit.) and assuming that the initial A_T was 2300 $\mu\text{mol/kg}$ and seawater was at equilibrium with atmospheric PCO_2 prior to the rain event ($PCO_2 = 365$ ppm), we calculate that Ω_{rag} decreased from 3.97 to 3.77. In a later report it was stated that the heavy rainfall and low salinity caused substantial decomposition of organic matter on the reef flat (Chisholm and Barnes, 1998), which could easily explain an additional reduction in Ω_{rag} due to increasing respiratory CO_2 concentration in seawater. While the actual value of Ω_{rag} in March 1996 is unknown it is not inconceivable that it could have been as low as the measured Ω_{rag} in this study (diel average $\Omega_{rag} = 3.65$ and 3.45 in 2008 and 2009, respectively). Finally, seasonality may also play an important role in the carbonate budget of the reef as previously demonstrated (Silverman *et al.*, 2007; Bates *et al.*, 2010). However, past studies of reef metabolism on Lizard Island (Kinsey, 1979) did not define its calcification seasonality well enough to relate them to the present study.

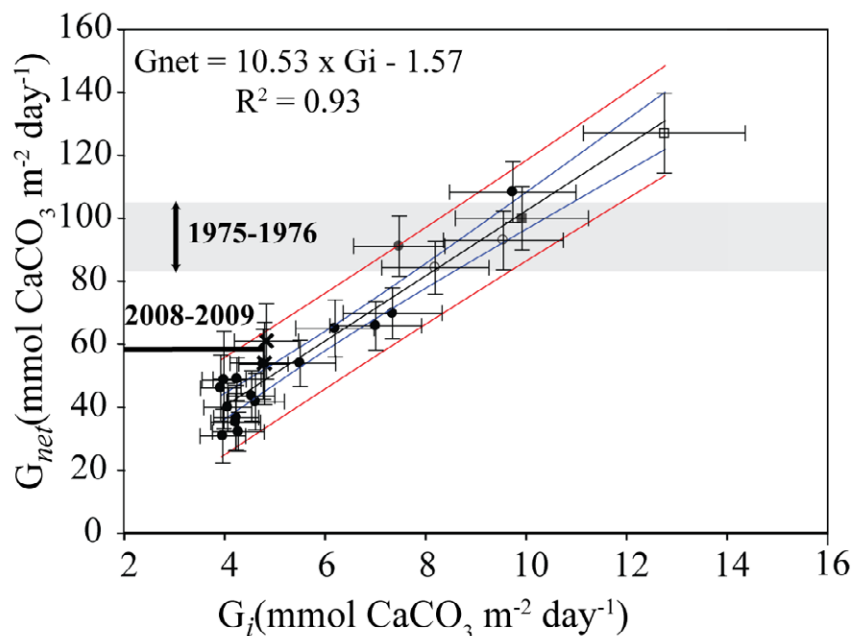


Figure 4. G_{net} at SIRM01 during the this study (\ast), \circ -Moorea (Gattuso *et al.*, 1996), \blacksquare -Enewetak (Smith, 1973), \square -Shiraho (Hata *et al.*, 2002); and \bullet -Red Sea, Eilat (Silverman *et al.*, 2007), plotted vs. G_i . In all studies the G_{net} was measured using the alkalinity depletion method. The G_i was calculated with the diel average temperature and Ω_{arag} measured at each study site. The black line indicates the linear fit through all of the data ($n = 24$). The blue and red lines indicate the 95% confidence and prediction bands, respectively. The grey shaded area indicates G_{net} measured on the South Island reef flat during September-November 1975-76 (LIMER 1975, 1976; Kinsey, 1979).

Summary and conclusions

In this study we measured the community calcification on a reef flat in Lizard Island during the spring of two 2008 and 2009 using similar methodology to the classical studies that were carried out on this reef during the 1970s. In both study periods the calcification rates were lower by 27-49% than those measured previously during the same season. This observed decline in calcification agrees well with the decline predicted for this region calculated from the Eilat reef community calcification rate equation (as a function of temperature and Ω_{arag}) assuming equilibrium with atmospheric PCO_2 . This statement relies on the measurements of live coral coverage during both periods, which are inherently associated with a large degree of uncertainty. Nonetheless, future estimates of G_{net} using Equation 3 show that it will become negative (net dissolution) by the time atmospheric CO_2 levels reach 750 ppm (assuming the same live coral

coverage). Such a scenario may ultimately lead to a net loss of reef framework and with it decline of the entire reef ecosystem. Routine measurements of net community calcification should be able to validate these predictions not only for Lizard Island but other reefs around the world in order to monitor their well-being in a high CO_2 world.

ACCEPTED MANUSCRIPT

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References

- Andersson A., Kuffner I.B., Mackenzie F.T., Jokiel P.L., Rodgers K.S. and Tan A. (2009) Net Loss of CaCO_3 from a subtropical calcifying community due to seawater acidification: mesocosm-scale experimental evidence. *Biogeosciences*, **6**:1811-1823.
- Atkinson M.J., Kotler E. and Newton P. (1994) Effects of water velocity on respiration, calcification and ammonium uptake in a *Porites compressa* community. *Pac. Sci.* 48:296–303.
- Bandstra L., Hales B. and Takahashi T. (2006) High-frequency measurements of total CO_2 : Method development and first oceanographic observations. *Mar. Chem.*, **100**:24–38, doi:10.1016/j.marchem.2005.10.009.
- Bates N.R., Amat A. and Andersson A.J. (2010) Feedbacks and responses of coral calcification on the Bermuda reef system to seasonal changes in biological processes and ocean acidification. *Biogeosciences*, **7**:2509-2530, doi:10.5194/bg-7-2509-2010.
- Burton E.A. and Walter L.M. (1987) Relative precipitation rates of aragonite and Mg calcite from seawater: Temperature or carbonate ion control? *Geology*, **15**:111-114.
- Caldeira K. and Wickett M.E. (2003) Anthropogenic carbon and ocean pH. *Nature*, **425**:365.
- Cantin N.E., Cohen A.L., Karnauskas K.B., Tarrant A.M. and McCorkle D.C. (2010) Ocean Warming Slows Coral Growth in the Central Red Sea. *Science*, **329**:322-325, doi:10.1126/science.1190182.
- Chisholm J.R.M. (2000) Calcification by crustose coralline algae on the northern Great Barrier Reef, Australia. *Limnol. Oceanogr.*, **45**(7):1476-1484.

- Chisholm J.R.M., Barnes D.J. and Devereux M.J. (1996) Measurement and Analysis of Reef Flat Community Metabolism at Lizard Island, Great Barrier Reef, Australia. *Australian Institute of Marine Science*, Report No. 857.
- Chisholm J.R.M. and Barnes D.J. (1998) Anomalies in coral reef community metabolism and their potential importance in the reef CO₂ source-sink debate. *Proc. Natl. Acad. Sc.*, **95**:6566-6569.
- Congalton R.A. (1991) Review of Assessing the Accuracy of Classifications of Remotely Sensed Data. *Remote Sensing of Environment*, **37**:35–46.
- Cooper T.F., De 'ath G., Fabricius K.E. and Lough J.M. (2008) Declining coral calcification in massive Porites in two nearshore regions of the northern Great Barrier Reef. *Global Change Biology*, **14**:529-538.
- Crook E.D., Potts M., Rebolledo-Vieyra L., Hernandez L. and Paytan A. (2012) Calcifying coral abundance near low-pH springs: Implications for future ocean acidification. *Coral Reefs*, **31**:239-245, DOI 10.1007/s00338-011-0839-y.
- De'ath G., Lough J.M. and Fabricius, K.E. (2009) Declining Coral Calcification on the Great Barrier Reef. *Science*, **323**:116-119, doi:10.1126/science.1165283.
- Dennison W.C. and Barnes D.J. (1988) Effect of water motion on coral photosynthesis and calcification. *J. Exp. Mar. Biol. Ecol.*, **115**(1):67-77.
- Derse-Crook E., Cohen A.L., Rebolledo-Vieyra M., Hernandez L. and Paytan A. (2013) Reduced calcification and lack of acclimatization by coral colonies growing in areas of persistent natural acidification. *Proc. Natl. Acad. Sc.*, **110**(27), 11044-11049. doi/10.1073/pnas.1301589110.
- Dickson A.G., Sabine C.L. and Christian J.R. (2007) Guide to Best Practices for Ocean CO₂ Measurements. PICES Special Publication 3, pp. 191.
- Fairall C.W., Bradley E.F., Rogers D.P., Edson J.B., Young G.S. (1996) Bulk parameterization of air-sea fluxes for tropical ocean-global atmosphere coupled-ocean atmosphere response experiment. *Jour. Geophys. Res.* **101**:3747–3764.
- Falter J.L., Lowe R.J., Atkinson M.J. and Cuet P. (2012) Seasonal coupling and de-coupling of net calcification rates from coral reef metabolism and carbonate chemistry at Ningaloo Reef, Western Australia. *Jour. Geophys. Res.*, **117**, C05003, doi:10.1029/2011JC007268.

- Gattuso J.-P., Frankignoulle M., Bourge I., Romaine S. and Buddemeier R.W. (1998) Effect of calcium carbonate saturation of seawater on coral calcification. *Global. Planet. Change.*, **18**:37-46.
- Gattuso J.-P., Pichon M., Delesalle B., Canon C. and Frankignoulle M. (1996) Carbon fluxes in coral reefs .1. Lagrangian measurement of community metabolism and resulting air-sea CO₂ disequilibrium. *Mar. Ecol. Prog. Ser.*, **145**:109-121.
- Glynn P.W. (1997) Bioerosion and coral-reef growth: A dynamic balance, p. 68-94. In: Birkeland C. (Ed.), *Life and Death of coral reefs*. Chapman and Hall, New York.
- Grasshoff K., Kremling K. and Ehrhardt M. (Eds.)(1999) *Methods of Seawater Analysis*, 3rd ed., 600 pp., Wiley-VCH, Weinheim, doi:10.1002/9783527613984.
- Hata H., Kudo S., Yamano H., Kurano N. and Kayanne H. (2002) Organic carbon flux in Shiraho coral reef (Ishigaki Island, Japan). *Mar. Ecol. Prog. Ser.*, **232**:129-140.
- Holmes R.M., Aminot A., Kerouel R., Hooker B.A. and Peterson B.J. (1999) A simple and precise method for measuring ammonium in marine and freshwater ecosystems. *Can. J. Fish. Aquat. Sci.*, **56**(10):1801–1808, doi:10.1139/cjfas-56-10-1801.
- Keeling R.F., Piper S.C., Bollenbacher A.F. and Walker J.S. (2009) In *Trends: A Compendium of Data on Global Change*. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, U.S. Department of Energy, Oak Ridge, Tenn., U.S.A.
- Kinsey D.W. (1979) **CARBON TURNOVER AND ACCUMULATION BY CORAL REEFS**. PhD dissertation, University of Hawaii.
- Kleypas J.A., Buddemeier R.W., Archer D., Gattuso J.-P., Langdon C. and Opdyke B.N. (1999) Geochemical consequences of increased atmospheric carbon dioxide on coral reefs. *Science*, **284**:118-120.
- Kleypas J.A., Feely R.A., Fabry V.J., Langdon C., Sabine C.L. and Robbins L.L. (2006) *Impacts of Ocean Acidification on Coral Reefs and Other Marine Calcifiers: A Guide for Future Research*, report of a workshop held 18–20 April 2005, St. Petersburg, FL, sponsored by NSF, NOAA, and the U.S. Geological Survey, 88 pp.
- Langdon C. and Atkinson M.J. (2005) Effect of elevated pCO₂ on photosynthesis and calcification of corals and interactions with seasonal change in temperature/irradiance and nutrient enrichment. *J. Geophys. Res.*, **110**:C09S07.

- Lewis, E. and Wallace, D.W.R. (1998) In: ORNL/CDIAC-105 (Ed.), Program Developed for CO₂ System Calculations. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, U.S. Department of Energy, Oak Ridge, TN.
- LIMER 1975 Expedition Team (1976) Metabolic processes of coral reef communities at Lizard Island, Queensland. *Search*, **7**:463-468.
- Mass T., Genin A., Shavit U., Grinstein M. and Tchernov D. (2010) Flow enhances photosynthesis in marine benthic autotrophs by increasing the efflux of oxygen from the organism to the water. *Proc. Natl. Acad. Sc.*, **107**(6):2527-2531, doi:10.1073/pnas.0912348107.
- Mather P.M. and Koch M. (2011) *Computer Processing of Remotely-Sensed Images: An Introduction*, Fourth Edition, Chichester, UK: Wiley-Blackwell, pp. 504.
- Millero F.J. (1979) The thermodynamics of the carbonate system in seawater, *Geochim. Cosmochim. Acta*, **43**:1651– 1661.
- Mucci A. (1983) The solubility of calcite and aragonite in seawater at various salinities, temperatures, and one atmosphere total pressure. *Am. J. Sci.*, **283**:780 – 799.
- Ohde S. and van Woesik R. (1999) Carbon dioxide flux and metabolic processes of a coral reef, Okinawa. *Bulletin of Marine Science*, **65**:559-576.
- Patterson M.R., Sebens K.P. and Olson R.R. (1991) In situ measurement of flow effects on primary production and dark respiration in reef corals. *Limnol Oceanogr*, **36**:936–948.
- Pichon M. and Morrissey J. (1981) Benthic Zonation and Community Structure of South Island Reef, Lizard Island (Great Barrier Reef). *Bulletin of Marine Science*, **31**:581-593.
- Roy R.N., Roy L.N., Vogel K.M., Porter-Moore C., Pearson T., Good C.E., Millero F.J. and Campbell, D.M. (1993) The dissociation constants of carbonic acid in seawater at salinities 5 to 45 and temperature 0 to 45°C. *Mar. Chem.*, **44**:249 – 267.
- Sabine C.L., Feely R.A., Gruber N., Key R.M., Lee K., Bullister J.L., Wanninkhof R., Wong C.S., Wallace D.W.R., Tilbrook B., Millero F.J., Peng T.-H., Kozyr A., Ono T. and Tios A.F. (2004) The oceanic sink for anthropogenic CO₂. *Science*, **305**(5682):367-371.
- Schneider K. and Erez J. (2006) The effect of carbonate chemistry on calcification and photosynthesis in the hermatypic coral *Acropora eurystroma*. *Limnol. Oceanogr.*, **51**:1284-1293.

- Sebens K.P., Helmuth B., Carrington E. and Agius B. (2003) Effects of water flow on growth and energetics of the scleractinian coral *Agaricia tenuifolia* in Belize. *Coral Reefs*, 22:35-47.
- Silverman J., Lazar B. and Erez, J. (2007) Effect of aragonite saturation, temperature, and nutrients on the community calcification rate of a coral reef. *J. Geophys. Res.*, **112**:C05004, doi:10.1029/2006JC003770.
- Silverman J., Lazar B., Cao L., Caldeira K. and Erez, J. (2009) Coral reefs may start dissolving when atmospheric CO₂ doubles. *Geophys. Res. Lett.*, **36**:L05606, doi:10.1029/2008GL036282.
- Silverman J., Kline D., Johnson L., Rivlin T., Schneider K., Erez J., Lazar B., Caldeira K. (2012). Carbon turnover rates in the One Tree Island reef – A 40 year perspective. *J. Geophys. Res.*, VOL. 117, G03023, doi:10.1029/2012JG001974.
- Smith S.V. (1973) Carbon dioxide dynamics: a record of organic carbon production, respiration and calcification in the Eniwetok Reef flat community. *Limnol. Oceanogr.*, **18**:106-120.
- Smith S.V. and Kinsey D.W. (1976) Calcium carbonate production, coral reef growth and sea level change. *Science*, **194**:937-939.
- Tanzil J., Brown B., Tudhope A. and Dunne R. (2009) Decline in skeletal growth of the coral *Porites lutea* from the Andaman Sea, South Thailand between 1984 and 2005. *Coral Reefs*, **28**:519-528.
- Topping J. (1972) *Errors of Observation and Their Treatment*. Chapman and Hall, London.
- Tribollet A., Decherf G., Hutchings P.A. and Peyrot-Clausade M. (2002) Large-scale spatial variability in bioerosion of experimental coral substrates on the Great Barrier Reef (Australia): importance of microborers. *Coral Reefs*, 21:424-432, DOI 10.1007/s00338-002-0267-0.
- Tribollet A. and Golubic S. (2005) Cross-shelf differences in the pattern and pace of bioerosion of experimental carbonate substrates exposed for 3 years on the northern Great Barrier Reef, Australia. *Coral Reefs*, **24**:422-434, DOI 10.1007/s00338-005-0003-7.
- Tribollet A., Godinot C., Atkinson M. and Langdon C. (2009) Effects of elevated pCO₂ on dissolution of carbonates by microbial euendoliths. *Global Biogeochem. Cycles*, **23**: GB3008, doi:10.1029/2008GB003286.