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Seasonal coupling and de-coupling of net calcification rates from coral reef metabolism and carbonate chemistry at Ningaloo Reef, Western Australia

James L. Falter,^{1,2,3} Ryan J. Lowe,^{1,3} Marlin J. Atkinson,⁴ and Pascale Cuet⁵

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[1] Rates of net production, net calcification, and nutrient uptake were measured in a coral-dominated reef flat community on Ningaloo Reef in northwestern Australia under seasonally minimum and maximum light levels. Daily integrated light decreased twofold while water temperatures remained relatively constant increasing by only 1°C on average from summer to winter. Rates of daily community gross primary production (*GPP*) were only 33% ± 9% higher in summer than in winter (1400 ± 70 versus 1050 ± 60 mmol C m⁻² d⁻¹), far less than the twofold seasonal changes reported for most shallow reef communities. Rates of daily community net calcification (*G_{net}*) were not significantly different between seasons (190 ± 40 mmol CaCO₃ m⁻² d⁻¹ in summer versus 200 ± 10 mmol CaCO₃ m⁻² d⁻¹ in winter). The average rate of total nitrogen uptake (dissolved + particulate) was also not significantly different between summer and winter (8.3 ± 3.8 versus 6.6 ± 3.4 mmol N m⁻² d⁻¹, respectively), despite evidence of sporadically high nitrate uptake in both seasons. In summer, rates of hourly net calcification (*g_{net}*) were linearly correlated with diurnal changes in net production, pH, and aragonite saturation state (Ω_{ar}); and were mostly correlated with light except at mid-day under heavy cloud cover. However, in winter, *g_{net}* was independent of diurnal changes in light, net production, pH, and Ω_{ar} indicating that the reef flat community had possibly reached a threshold above which rates of net calcification were insensitive to diurnal changes in their environment.

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1. Introduction

[2] Calcification is the core process driving the long-term growth of scleractinian coral and the overall rate of coral reef accretion. Early work showed that rates of calcification were much higher in the light than in the dark, a phenomena referred to as ‘light-enhanced calcification’ [Barnes and Taylor, 1973; Chalker and Taylor, 1975, 1978; Goreau and Goreau, 1960]. These results, along with subsequent work, indicated that rates of calcification were being driven largely by light via net photosynthesis [Allemand *et al.*, 2004; Gattuso *et al.*, 1999]. However, more recent evidence from both field studies and controlled laboratory

experiments indicate that changes in ambient carbonate chemistry can also affect rates of calcification; i.e., decreasing seawater aragonite saturation state (Ω_{ar}) and/or pH can cause rates of coral calcification to decline [e.g., Gattuso *et al.*, 1998; Langdon *et al.*, 2000; Marubini *et al.*, 2008; Schneider and Erez, 2006]. Such observations have caused wide-spread concern over the negative impact that rising levels of atmospheric CO₂ will have on rates of coral growth and reef accretion through a process known as ‘ocean acidification’ [Hoegh-Guldberg *et al.*, 2007; Kleypas *et al.*, 1999; Silverman *et al.*, 2009]. However, there are still other variables that influence rates of calcification as well. Rates of coral calcification can respond negatively to rapid changes in temperature on time scales of weeks or less due to thermal stress [Jokiel and Coles, 1977; Reynaud *et al.*, 2003], or more gradually due to seasonal changes in water temperature [Marshall and Clode, 2004]. Finally, the response of calcification to nutrients is particularly ambiguous; increasing rates of nutrient uptake can either enhance or diminish rates of calcification [Ferrier-Pagès *et al.*, 2000; Koop *et al.*, 2001; Shinn, 1966; Tanaka *et al.*, 2007]. Furthermore, higher rates of nutrient uptake have been found to reduce the sensitivity of calcification rates to changes in Ω_{ar} ; a less direct but nonetheless important effect [Langdon and

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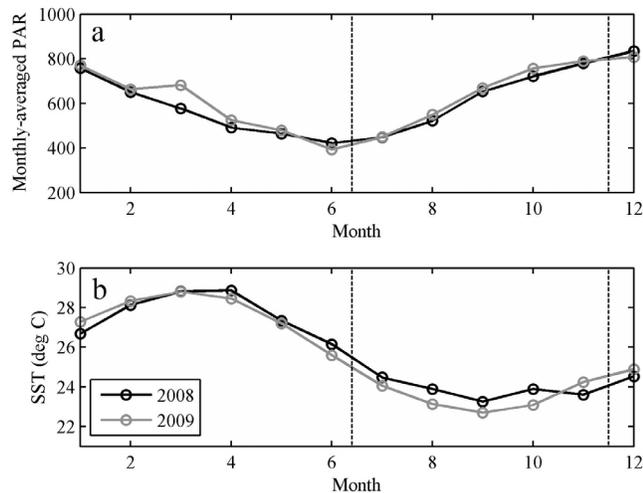


Figure 1. (a) Monthly averaged downwelling PAR irradiance in $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$ and (b) sea surface temperature at Ningaloo for all of 2008 and 2009, as measured by moderate resolution imaging spectroradiometer (MODIS) daily averaged raw Terra and Aqua data for a $1 \text{ km} \times 1 \text{ km}$ pixel near the coast of Sandy Bay (<http://oceancolor.gsfc.nasa.gov>). The vertical dashed lines indicate the two seasonal periods when measurements were made.

Atkinson, 2005; Silverman *et al.*, 2007b; Atkinson and Cuet, 2008; Cohen and Holcomb, 2009].

[3] Given the number of interacting physical and chemical factors that influence rates of calcification, it is thus not surprising that in situ rates vary by an order of magnitude across reef communities worldwide ($30\text{--}270 \text{ mmol CaCO}_3 \text{ m}^{-2} \text{ d}^{-1}$) [Atkinson and Falter, 2003]. It is also not surprising that predictions of how much coral calcification rates will decline in response to rising levels of CO_2 vary widely in the literature as well (0 to 85%) [Kleypas *et al.*, 2006]. Many of these predictions were derived from controlled experiments that spanned a broad range of technical and conceptual designs. Though highly informative in their own right, it is necessary to test these results against in situ observations from natural reef systems in order to properly interpret their significance within a fully realistic environmental context. Furthermore, oceanic and atmospheric forcing of key physical and chemical variables driving the growth and metabolism of reef communities can vary considerably from one oceanic province to the next. Therefore, it is essential to compare experimental results against real reef systems from different regions across the globe.

[4] While much current interest has focused on the anticipated decline in reef calcification rates over the coming decades (up to 85%), superimposed on these longer-term trends will be seasonal variations in reef metabolism that are at least comparable in magnitude (up to 100% or more). Thus, discrimination of these seasonal cycles is essential for the identification of longer-term trends. Early studies of reef community metabolism from the 1970s and 1980s found that daily rates of community photosynthesis, respiration, and calcification were generally around a factor of 2 higher in summer than in winter, and that such seasonality appeared to be independent of latitude [Kinsey, 1985]. Unfortunately, most of these earlier studies lacked the necessary ancillary

data on light, temperature, carbonate chemistry, water motion, and/or nutrient uptake rates to properly evaluate the reported metabolic rates within the context of their physical and chemical environment. More recent studies have considered the role that these factors may play on in situ rates of calcification within the context of particular reef systems [e.g., Bates *et al.*, 2010; Silverman *et al.*, 2007a]. For many reef systems; however, influential environmental variables such as light, temperature, and Ω_{ar} co-vary with both time of day and season (i.e.; high at mid-day and in summer, low at night and in winter) making it difficult to isolate their individual effects from even the most comprehensive data sets [De'ath *et al.*, 2009; Lough and Barnes, 2000].

[5] Seasonal changes in temperature on Ningaloo Reef in the southeast Indian Ocean lag seasonal changes in light by roughly 3 months (Figure 1). We used this phase lag to compare rates of production and calcification under entirely different seasonal light conditions but at similar water temperatures; thus allowing us to eliminate variation in at least one key physical parameter (temperature) while exploiting the maximum changes in another (light). Seasonal variation in pelagic productivity on the Ningaloo shelf causes seasonal fluctuations in the uptake of particulate nutrients [Wyatt *et al.*, 2010, 2012; Rousseaux *et al.*, 2012] while physical mechanisms such as upwelling can cause sporadically high dissolved nutrient concentrations [Feng and Wild-Allen, 2008]. The carbonate chemistry of the waters on and off Ningaloo Reef (e.g., Ω_{ar} , pH, etc.), however, remains largely unknown and uncharacterized. The goal of the present study was to compare differences in community photosynthesis and calcification, not only within the context of changes in light with temperature constant, but with changes in nutrient uptake and carbonate chemistry as well.

2. Methods

2.1. Study Site and Measurements

[6] The Ningaloo Reef tract is a fringing reef that stretches roughly 300 km from north of Shark Bay to the North West Cape on the northwestern Australian coast (Figure 2). Our research focused on the reef flat off Sandy Bay (22.23°S , 113.83°E), located approximately 50 km south of the North West Cape in the Cape Range National Park (Figure 2). The Cape Range region is considered arid receiving only 200–300 mm of precipitation per year. The dominant oceanic feature on the northwest shelf is the Leeuwin Current that brings warm, oligotrophic water from the northeast tropical Indian Ocean poleward along the west coast of Australia [Feng and Wild-Allen, 2008; Smith *et al.*, 1991]. This highly stratified current provides conditions favorable for the growth of coral reefs inshore; while at the same time limiting the upwelling of deeper, colder water that normally inhibits the growth of tropical coral at similar latitudes on the west coasts of the Americas and Africa. Offshore significant wave heights (H_{sig}) along the west coast of Australia typically vary from 1 to 4 m and are highest in summer with a median annual height of ~ 2 m. Waves incident to the reef at Sandy Bay break on the reef crest, driving flow across the shallow reef flat (1–2 m) and into the deeper lagoon (3–4 m) before exiting the channel just to the south [Taebi *et al.*, 2011]. The tides at Sandy Bay are semi-diurnal and vary within a range of roughly 0.5 to 1 m.

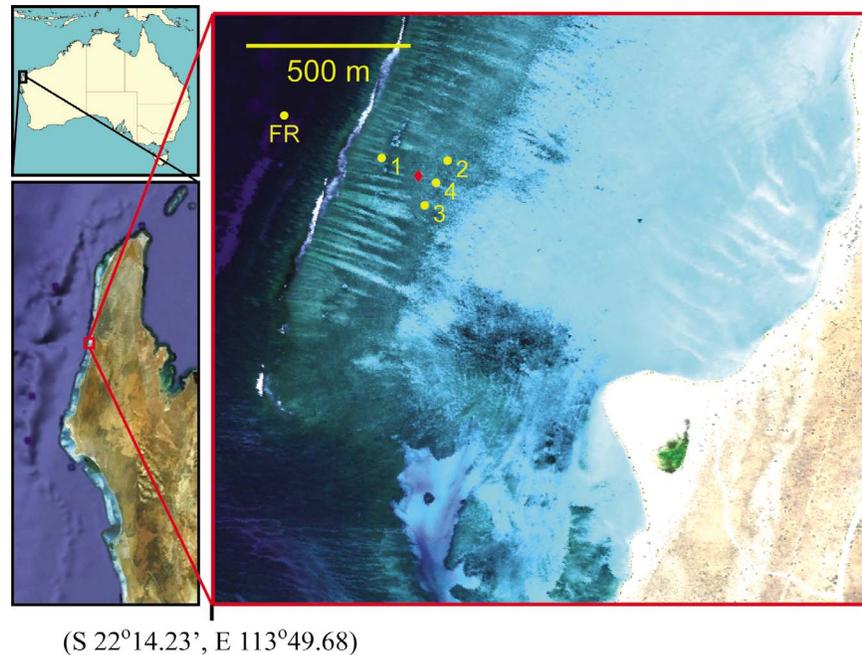


Figure 2. Location of the study site within the Sandy Bay area of the Ningaloo Reef on the northwest coast of Australia. Dissolved oxygen was measured at sites 1, 2, and 3. Nutrient and carbonate chemistry measurements were made at sites 1 and 4. The location of the ADP and light sensor is shown by the red diamond. Site FR represents a fore reef site where wave heights were measured. The exact location of site 1 is S 22°13.495', E 113°49.970'.

[7] All measurements were made within a triangular study area (or ‘control volume’) ~ 200 m long in the cross-reef direction and ~ 200 m wide at its base on the reef flat off Sandy Bay (Figure 2). Coral cover within the control volume varied from around 90% at the apex (nearest the reef crest) to around 50% at the rear [Cassata and Collins, 2008; Wyatt *et al.*, 2010]. We made initial measurements of light, temperature, currents, and water chemistry on this area of the reef flat in Nov 2007 (summer); however, we did not make extensive measurements of net production, calcification, or nutrient uptake within the study area until between 8 and 22 Nov 2008 (summer) and between 10 and 14 Jun 2009 (winter). We then returned briefly to the same site in the first week of Sep 2010 (late winter) to determine the representativeness of the physical and chemical measurements made in the prior winter (Jun 2009) as part of a regional-scale study of waters on the adjacent continental shelf. During the more extensive Nov 2008 and Jun 2009 surveys, continuous measurements of dissolved oxygen were made at each vertex of the control volume while continuous measurements of light, temperature, and vertical current profiles were made at the center according to the approach developed by Falter *et al.* [2008]. Both spatial and temporal changes in oxygen concentration were used to calculate the net production of oxygen within the study area, and therefore the net production of organic carbon by proxy. Periodic water samples were collected at the apex of the control volume (#1) and the base of the control volume (#4) for measurement of pH on the total hydrogen ion concentration scale (pH_T), total alkalinity (TA), dissolved reactive phosphorus (herein referred to as ‘phosphate’) and nitrate plus nitrite (herein

referred to as ‘nitrate’). The definitions for all important physical and biogeochemical variables are provided in Table 1.

[8] Downwelling planar PAR irradiance ($\pm 5\%$ in $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$) was measured on the reef bottom using a LiCor 192A cosine PAR sensor logging into an RBR XRT400+PAR logger, which was also recording water temperature ($\pm 0.05^\circ\text{C}$). The light sensor was wiped every day with a soft sponge to prevent biofouling of the sensor surface. Prior surveys of surface waters on the fore reef and reef flat in 2007, 2008, and later in 2010 indicated that variation in salinity was minimal in both seasons (34.8 to 35.0); therefore we did not make continuous measurements of salinity throughout each study period. However, we did make periodic measurements of salinity on and around the Sandy Bay section of Ningaloo Reef during each survey and each time found them to lie within this defined range. Vertical profiles of current speed and direction were measured with a 2 MHz Nortek Aquadopp Profiler (Nortek AS) continuously sampling at 10-cm intervals every 5 min. These profiles were used to calculate the vertically integrated two-dimensional (2D) volume transport ($\pm 0.02 \text{ m}^2 \text{ s}^{-1}$) and direction ($\pm 2^\circ$). Dissolved oxygen was measured at the vertices of the control volume using In Situ Troll 9000 loggers equipped with Aanderaa RDO dissolved oxygen optodes sampling every 5 min. Before deployment, all three oxygen sensors were calibrated in seawater ($\pm 2 \mu\text{M O}_2$) with Winkler titrations ($\pm 0.5 \mu\text{M O}_2$) over a range of 20 to 350 $\mu\text{M O}_2$ at 25°C . To correct for sensor drift, duplicate 300-mL water samples were collected next to each dissolved oxygen sensor each day in the field and analyzed by Winkler titration.

Table 1. Definition of Physical and Biogeochemical Variables Used in This Paper^a

Variable	Units	Description
E_d	$\mu\text{mol m}^{-2} \text{s}^{-1}$	Instantaneous downwelling planar PAR irradiance
ΣE_d	$\text{mol m}^{-2} \text{d}^{-1}$	Daily integrated downwelling planar PAR irradiance
T	$^{\circ}\text{C}$	Temperature
h	m	Depth of the reef
q_x	$\text{m}^2 \text{s}^{-1}$	Depth-integrated cross-reef transport
\bar{U}_z	m s^{-1}	Depth-averaged current
θ_U	deg	Depth-averaged current direction clockwise from north
τ	min	Transit time of water through the control volume
pH _T	–	pH (total hydrogen ion scale)
TA	$\mu\text{eq kg}^{-1}$	Total alkalinity
Ω_{ar}	–	Saturation state of aragonite in seawater
$p\text{CO}_2$	μatm	Partial pressure of dissolved carbon dioxide
DIC	$\mu\text{mol kg}^{-1}$	Dissolved inorganic carbon
DIN	$\mu\text{mol kg}^{-1}$	Dissolved inorganic nitrogen
gp	$\text{mmol C m}^{-2} \text{hr}^{-1}$	Hourly gross photosynthesis
np	$\text{mmol C m}^{-2} \text{hr}^{-1}$	Hourly net production
g_{net}	$\text{mmol C m}^{-2} \text{hr}^{-1}$	Hourly net calcification
GPP	$\text{mmol C m}^{-2} \text{d}^{-1}$	Daily community gross primary production
R	$\text{mmol C m}^{-2} \text{d}^{-1}$	Daily community respiration
G_{net}	$\text{mmol C m}^{-2} \text{d}^{-1}$	Daily community net calcification
$J_{\text{NO}_3^-}$	$\text{mmol N m}^{-2} \text{d}^{-1}$	Daily net uptake of nitrate
J_{Npart}	$\text{mmol N m}^{-2} \text{d}^{-1}$	Daily particulate nitrogen uptake
J_{Total}	$\text{mmol N m}^{-2} \text{d}^{-1}$	Daily total nitrogen uptake ($J_{\text{NO}_3^-} + J_{\text{part}}$)

^aFor all carbon fluxes lowercase variables represent hourly rates while uppercase variables represent daily integrated rates.

[9] Water samples collected for the analysis of dissolved nutrients and TA were immediately filtered in the field using GF/F glass fiber filters, collected in Nalgene HDPE bottles, and stored in the dark on ice. Dissolved phosphate ($\pm 0.02 \text{ mmol m}^{-3}$) and nitrate ($\pm 0.03 \text{ mmol m}^{-3}$) were measured using standard spectrophotometric techniques [Parsons *et al.*, 1984]. Total alkalinity was analyzed by a potentiometric Gran titration [Dickson, 1993] with an accuracy of ± 2 to $3 \mu\text{eq kg}^{-1}$ based on the analyses of duplicate samples with a titrant calibrated against an alkalinity standard prepared in artificial seawater [Dickson and Goyet, 1994] in 2008 and 2009 and against seawater certified reference materials provided by Andrew Dickson at the Scripps Institute of Oceanography in 2007 and 2010 (batches #79 and #105). The pH_T was measured in the field using a Methrom 826 field pH meter equipped with a Primatrode electrode from Nov 2007 to Jun 2009 and a Schott Handylab pH 12 m equipped with a BlueLine 24 pH electrode in Sep 2010. All electrodes were calibrated against a ‘Tris’ buffer according to the Dickson and Goyet [1994] protocols. We measured pH_T in the field and therefore report it at in situ temperatures rather than at a standard reference temperature (25°C). Absolute differences between calibration temperatures and sample temperatures in the field averaged $\sim 2^{\circ}\text{C}$ (range: 0 to 3°C) resulting in corrections to pH_T of 0.014 on average. Given uncertainties in (1) the pH_T the Tris buffer (± 0.002) [Nemzer and Dickson, 2005] correcting for differences between sample and calibration temperature (± 0.008), (2) the slope of voltage versus pH_T

(± 0.001), and (3) in the pH meter itself (± 0.004); we estimate the accuracy of our pH_T measurements to be around ± 0.01 . Finally, Dissolved Inorganic Carbon (DIC), $p\text{CO}_2$, bicarbonate, carbonate, and Ω_{ar} were calculated from measured temperature, pH_T, and total alkalinity assuming an average salinity of 34.9 ± 0.1 (see above) using the CO2SYS program provided by Lewis and Wallace [1998] with the carbonate species dissociation constants of Mehrbach *et al.* [1973] as re-fit by Dickson and Millero [1987], the borate and sulfate dissociation constants of Dickson [1990a, 1990b], and the aragonite solubility constants of Mucci [1983]. Uncertainties in calculated DIC, $p\text{CO}_2$, bicarbonate, carbonate, and Ω_{ar} were estimated by Monte-Carlo simulation to be $\pm 11 \mu\text{mol kg}^{-1}$, $\pm 11 \mu\text{atm}$, $\pm 12 \mu\text{mol kg}^{-1}$, $\pm 4 \mu\text{mol kg}^{-1}$, and ± 0.06 , respectively assuming the errors in TA, pH_T, temperature, and salinity reported above.

2.2. Metabolic Rates

[10] Dissolved oxygen time series were used in conjunction with records of vertical current profiles to generate continuous records of hourly net production (np in $\text{mmol C m}^{-2} \text{hr}^{-1}$) for the reef community using the Eulerian approach of Falter *et al.* [2008] assuming a photosynthetic quotient equal to one [Carpenter and Williams, 2007; Gattuso *et al.*, 1996; Smith and Marsh, 1973]

$$np = h \frac{\partial C_{O_2}}{\partial t} + \underbrace{q_x \frac{\partial C_{O_2}}{\partial x}}_{\text{cross-reef}} + \underbrace{q_y \frac{\partial C_{O_2}}{\partial y}}_{\text{along-reef}} - J_{\text{gas}}, \quad (1)$$

where h is the water depth (m), C_{O_2} is the concentration of dissolved oxygen (mmol m^{-3}), q_x is the volume transport per meter width in the cross-reef direction ($\text{m}^2 \text{s}^{-1}$), q_y is the volume transport in the along-reef direction ($\text{m}^2 \text{s}^{-1}$), and J_{gas} is the flux across the air-sea interface ($\text{mmol O}_2 \text{ m}^{-2} \text{hr}^{-1}$). Equation (1) shows how the total flux of dissolved oxygen is comprised of a local time-dependent term, an advective term representing the movement of water across gradients in O_2 in the cross-reef and along-reef directions, and a gas term representing the flux of O_2 across the air-sea interface. J_{gas} was calculated according to Ho *et al.* [2006] from in situ measurements of temperature and dissolved oxygen and assuming a salinity of 34.9 and an average gas exchange velocity of 4 m d^{-1} , which corresponds to an average wind speed of $\sim 30 \text{ km hr}^{-1}$ or 7.5 m s^{-1} based upon measurements from a weather station maintained by the Australian Institute of Marine Science at Milyering $\sim 20 \text{ km}$ north of the study site. Preliminary analysis showed that the gas flux term contributed less than 1% of the total variance in benthic net production in this system, thus justifying our simplifying assumption of a constant gas transfer velocity. Daily community respiration (R in $\text{mmol C m}^{-2} \text{d}^{-1}$) for a given day was calculated as the average of nighttime respiration ($-np$) from the preceding and following nights. Hourly rates of gross primary production (gp in $\text{mmol C m}^{-2} \text{hr}^{-1}$) were calculated by adding hourly net community photosynthesis to daily community respiration ($np + R/24$). Daily gross primary production (GPP in $\text{mmol C m}^{-2} \text{d}^{-1}$) was calculated from integrating gp between sunrise and sunset [Falter *et al.*, 2001].

Table 2. Key Physical and Biogeochemical Parameters Recorded at the Most Seaward Location on the Ningaloo Reef Flat (#1, Figure 2) Corresponding With the Measurements of Community Metabolic Rates Reported Here^a

Parameter	Units	Summer (Nov 2008)		Winter (Jun 2009)	
		Average	Std. Err.	Average	Std. Err.
ΣE_d	$\text{mol m}^{-2} \text{d}^{-1}$	40.9	± 3.1	20.3	± 0.8
T	$^{\circ}\text{C}$	23.7	< 0.1	24.7	< 0.1
nitrate	mmol m^{-3}	0.52	± 0.10	0.48	± 0.09
phosphate	mmol m^{-3}	0.08	± 0.01	0.07	0.01
pH_T	–	8.08	± 0.01	8.16	± 0.01
TA	$\mu\text{eq kg}^{-1}$	2284	± 5	2272	± 4
Ω_{ar}	–	3.44	± 0.09	4.03	± 0.06
CO_3^{2-}	$\mu\text{mol kg}^{-1}$	221	± 5	254	± 4
HCO_3^-	$\mu\text{mol kg}^{-1}$	1740	± 12	1644	± 9
pCO_2	μatm	359	± 13	287	± 8
DIC	$\mu\text{mol kg}^{-1}$	1973	± 12	1907	± 6

^aData shown represents the average (\pm std. err.) for each survey period.

[11] Previous detailed hydrodynamic studies of this same Sandy Bay study site have shown that the flow across the control volume is consistently directed shoreward across the reef year-round, driven by wave-driven currents that deviate minimally due to the weak tides [Wyatt *et al.*, 2010; Taebi *et al.*, 2011]. During the experiments, the currents measured by the ADP at the center of the control volume also confirmed that the flow was consistently aligned with the cross-reef axis (toward $\sim 120^{\circ}$), deviating by around 30° at most throughout the study (see Results). As a result, we calculated hourly net calcification rates (g_{net} in $\text{mmol CaCO}_3 \text{ m}^{-2} \text{ hr}^{-1}$) by multiplying one-half the differences in total alkalinity across the control volume by the cross-reef component of the depth-integrated volume transport (q_x)

$$g_{\text{net}} = \frac{1}{2} q_x \frac{\Delta \text{TA}}{\Delta x}, \quad (2)$$

where Δx is the distance between sites 1 and #4 (Figure 2), q_x is related to the depth (h), the depth-averaged current (\bar{U}_z), and the direction of the depth-averaged current (θ_U) relative to the cross-reef direction

$$q_x = h \bar{U}_z \cos(\theta_U - 120^{\circ}). \quad (3)$$

[12] Net calcification rates represent the sum of contributions from both calcification and dissolution. Net nutrient uptake rates were similarly calculated by multiplying measured spatial gradients in phosphate and nitrate concentrations across the control volume by the cross reef transport ($J_{\text{net}} = q_x \frac{\Delta C}{\Delta x}$). We were able to sample station #4 within ~ 20 min of sampling station #1 for nutrients, total alkalinity and pH. These simplified equations assume that the cross-reef advection term is the single most dominant term describing the non-conservative behavior of metabolites across the reef flat (equation (1)). We will later justify this simplifying assumption through a comparative analysis of the benthic net production calculated from just the cross-reef advection term versus using all the terms shown in equation (1). In addition to checking our full Eulerian calculations in this way, we also

calculated discrete rates of net production from our in situ measurements of TA and pH according to

$$np_{\text{DIC}} = q_x \frac{(\Delta \text{DIC})}{\Delta x} - g_{\text{net}} \quad (4)$$

as a further check of our data as well as to check the robustness of our assumption about the photosynthetic quotient being close to one.

3. Results

[13] Light incident to the reef benthos was approximately twice as high in summer as in winter (41 versus 20 $\text{mol quanta m}^{-2} \text{d}^{-1}$, Table 2 and Figures 3a and 3b). The arid climate of the northwest Australian coast provided conditions that generally favored clear skies and, therefore, smooth quasi-sinusoidal diurnal light curves. Nonetheless, heavy cloud cover at the end of the Nov 2008 survey substantially reduced the amount of sunlight to less than half the mean of the previous 2 days (15.3 versus 45.1 $\text{mol quanta m}^{-2} \text{d}^{-1}$). Water temperatures on the reef flat were similar in summer and winter due to the seasonal lag between light and temperature (23.7°C in Nov versus 24.7°C in Jun, Table 2 and Figures 3c and 3d); however, they ranged by roughly $\pm 1.5^{\circ}\text{C}$ over the course of all sampling periods. Depth-averaged currents on the reef flat averaged 10.7 ± 4.0 cm s^{-1} (\pm std. dev.) in magnitude and $125^{\circ} \pm 5^{\circ}$ in direction during the Nov 2008 survey and 9.5 ± 3.7 cm s^{-1} in magnitude and $134^{\circ} \pm 18^{\circ}$ in direction during the Jun 2009 survey based on the complete data records measured continuously by the ADP. In both seasons, the current directions were typically very close to the direction of the cross-reef axis (120°); results consistent with similar measurements made in prior seasons [Wyatt *et al.*, 2010]. More importantly, current directions differed from the cross-reef direction by less than 20° on average when all water samples

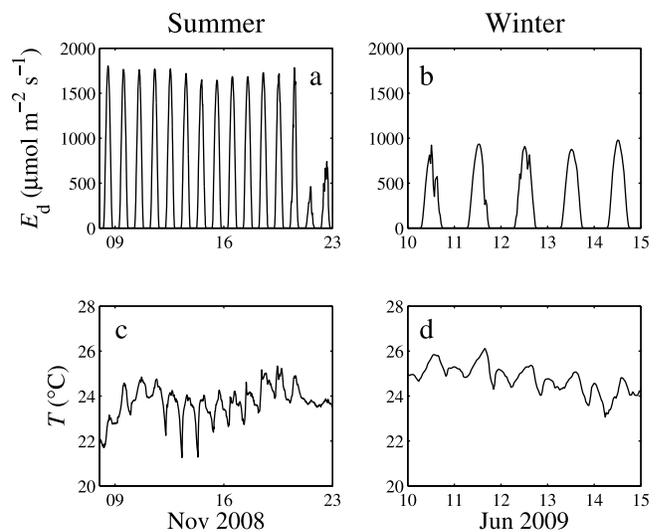


Figure 3. (a and b) Downwelling planar PAR irradiance and (c and d) water temperature on the reef flat at Sandy Bay in Nov 2008 (Figures 3a and 3c) and in Jun 2009 (Figures 3b and 3d).

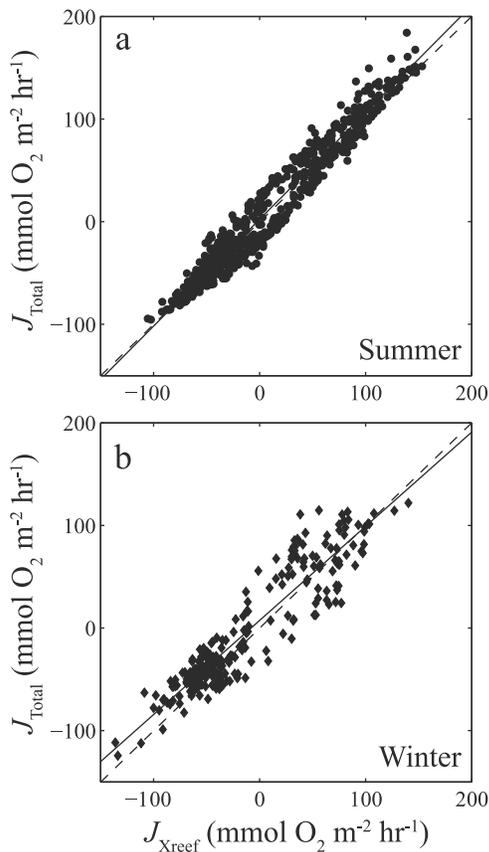


Figure 4. Net benthic oxygen fluxes calculated from the cross-reef gradient in oxygen concentration along versus fluxes calculated from all the terms shown in equation (1) for (a) summer and (b) winter. Solid lines represent the best fit regressions for summer ($y = 0.94x - 2.3$, $r^2 = 0.96$, and $n = 806$) and winter ($y = 0.93x - 8.7$, $r^2 = 0.88$, and $n = 249$). The dashed lines represent a perfect 1:1 relationship. The root mean square difference between the two fluxes is $12 \text{ mmol m}^{-2} \text{ hr}^{-1}$ for the summer and $21 \text{ mmol m}^{-2} \text{ hr}^{-1}$ for the winter.

were collected, in both seasons. Thus, q_x was on average 97% of the total cross-reef transport in summer and 91% of the cross-reef transport in winter. Differences between dissolved oxygen measured with the optodes and those measured by Winkler titration were generally less than 5 mmol m^{-3} in the beginning of each survey and less than 10 mmol m^{-3} near the end of each survey period. More importantly, benthic oxygen fluxes calculated using just the cross-reef term were highly correlated with rates calculated using all the terms in equation (1) and comparable in magnitude ($r^2 = 0.96$ in summer and 0.88 in winter, Figure 4). The root mean square difference between the two oxygen fluxes was $12 \text{ mmol m}^{-2} \text{ hr}^{-1}$ in the summer and $21 \text{ mmol m}^{-2} \text{ hr}^{-1}$ in the winter. Finally, there was generally good agreement between estimates of net production derived from the dissolved oxygen time series and those derived from the pH and TA data confirming that the ratio of oxygen release to DIC uptake for this system was not significantly different from one in both seasons (Figure 5).

[14] The pH_T of waters just inside the reef crest (site #1) were on average 0.08 lower in summer than in winter ($p < 0.05$)

whereas TA did not differ substantially between seasons (Table 2). The pH_T and TA reported near the reef crest during summer of 2008 and winter of 2009 were consistent with measurements of these same parameters made in the summer of 2007 and the late winter of 2010, respectively (Table 3). As a result of these seasonal differences in carbonate chemistry, Ω_{ar} was on average lower in summer than in winter (3.5 versus 4.0 , $p < 0.05$, Table 2) while the average pCO_2 was higher (360 versus 290 , $p < 0.05$, Table 2). TA typically decreased by 10 to $20 \mu\text{eq kg}^{-1}$ across the reef flat during the day due to net calcification (Tables 4 and 5).

[15] A more detailed analysis of nutrient uptake rates for the present reef community during the summer of 2008 as well as for earlier seasons (2007 and 2008) is provided by Wyatt *et al.* [2012]. Nutrient uptake rates for the winter of 2009 have not yet been published elsewhere so we will report those additional data for the first time here. To summarize all data sets, we found that net nitrate uptake rates

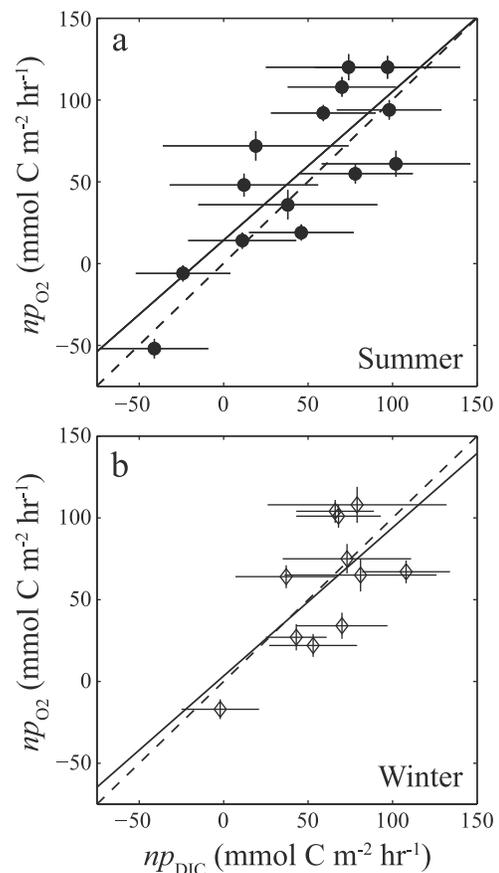


Figure 5. Hourly rates of net production calculated from the dissolved oxygen time series using the control volume approach versus discrete measurements of net production derived from in situ measurements of total alkalinity and pH for (a) summer and (b) winter. Solid lines represent the best fit regressions for summer ($y = 0.9x + 14$, $r^2 = 0.67$, and $n = 14$) and winter ($y = 0.9x + 3$, $r^2 = 0.44$, and $n = 11$). The dashed lines represent a perfect 1:1 relationship. In both seasons the slopes are not significantly different from one.

Table 3. Key Physical and Biogeochemical Parameters Recorded at the Most Seaward Location on the Ningaloo Reef Flat (#1) From a Summer Reconnaissance Survey Done Before and From a Late Winter Survey Done After Field Measurements of Carbon Metabolism and Nutrient Uptake Rates Reported in This Paper^a

Parameter	Units	Summer (Nov 2007)		Winter (Sep 2010)	
		Average	Std. Err.	Average	Std. Err.
ΣE_d	$\text{mol m}^{-2} \text{d}^{-1}$	41.4	± 0.4	29.5	± 3.0
T	$^{\circ}\text{C}$	23.7	< 0.1	22.8	< 0.1
nitrate	mmol m^{-3}	0.67	± 0.06	0.29	± 0.08
phosphate	mmol m^{-3}	0.13	± 0.01	0.10	± 0.02
pH_T	–	8.09	± 0.01	8.15	± 0.01
TA	$\mu\text{eq kg}^{-1}$	2280	± 6	2294	± 1
Ω_{ar}	–	3.55	± 0.06	3.80	± 0.10
CO_3^{2-}	$\mu\text{mol kg}^{-1}$	223	± 4	241	± 4
HCO_3^-	$\mu\text{mol kg}^{-1}$	1729	± 12	1698	± 13
$p\text{CO}_2$	μatm	345	± 9	298	± 8
DIC	$\mu\text{mol kg}^{-1}$	1963	± 8	1949	± 8

^aSee also Table 2. Data shown represents the average (\pm std. err.) for each survey period.

in summer were highly variable but significantly different from zero all of the time ($p < 0.1$), and averaged $7.3 \pm 3.8 \text{ mmol m}^{-2} \text{d}^{-1}$ (mean \pm std. dev.). Much of this variation was the result of nitrate concentrations ranging by more than a factor of 6 across the reef flat (0.17 to 1.12 mmol m^{-3}). Rates of net nitrate uptake in winter were comparably variable to those in summer but averaged just $2.5 \pm 3 \text{ mmol m}^{-2} \text{d}^{-1}$ (mean \pm std. dev.) while nitrate concentrations across the reef flat ranged by a factor of 5 (0.28 to 1.34 mmol m^{-3}). In contrast, changes in phosphate concentration across the reef flat, and therefore net phosphate fluxes, were significantly different from zero ($p < 0.1$) less than 20% of the time in either season. Although we did not measure the uptake of particles in this study, Wyatt *et al.* [2010, 2012] found that the average daily rates of winter particulate nitrogen uptake (J_{part}) for this same reef flat community were lower in summer 2008 than in winter 2007 and winter 2008 (1.0 ± 0.3 versus $4.1 \pm 1.0 \text{ mmol N m}^{-2} \text{d}^{-1}$). This implies that the average daily rates of total nitrogen uptake ($J_{\text{Total}} = J_{\text{NO}_3^-} + J_{\text{part}}$) were nonetheless comparable between summer and

winter for the present study (8.3 ± 3.8 versus $6.6 \pm 3.4 \text{ mmol N m}^{-2} \text{d}^{-1}$, Table 6). Although not recorded in the present study, prior measurements in May 2007 and Nov 2007 indicated that changes in ammonium concentrations across the reef flat were rarely significant and averaged 0.15 ± 0.01 and $0.20 \pm 0.02 \text{ mmol m}^{-3}$, respectively. This would imply that maximum rates of total dissolved inorganic nitrogen uptake allowed by the limits of convective mass transfer were between 6 and 7 $\text{mmol N m}^{-2} \text{d}^{-1}$ in both seasons, based on a mass transfer limited uptake rate coefficient of $\sim 10 \text{ m d}^{-1}$ for this particular reef flat under the observed wave conditions [Wyatt *et al.*, 2012; Zhang *et al.*, 2011].

[16] Hourly net production varied from between -60 to $150 \text{ mmol m}^{-2} \text{hr}^{-1}$ in summer and from around -50 to $110 \text{ mmol m}^{-2} \text{hr}^{-1}$ in winter (Figure 6). In both summer and winter, hourly rates of gross photosynthesis (gp) were significantly correlated with light and never appeared to reach saturation (Figure 7, $r^2 = 0.90$, and $n = 94$ for Nov 2008; $r^2 = 0.91$, and $n = 53$ for Jun 2009). Although differences in predictions from the nonlinear regressions of gp versus E_d were not significant between seasons ($p > 0.25$), photosynthetic light-use efficiency calculated from ratios of daily integrated community gross primary production to daily integrated light ($GPP/\Sigma E_d$) was significantly higher in winter than in summer ($5.1 \pm 0.3\%$ versus $3.5 \pm 0.3\%$, $p < 0.01$). Calculating light-use efficiencies in this way averages many measurements of gp and E_d resulting in a much lower relative uncertainty as compared with the uncertainty in gp at a given E_d (Figure 7). As a result of this apparent seasonal photoacclimation (i.e., higher light-use efficiency in winter), average daily gross community production was just 25% lower in winter than in summer (1050 versus $1400 \text{ mmol C m}^{-2} \text{d}^{-1}$, Table 6) even though average daily incident light was 50% lower (Table 2). Finally, daily integrated community respiration (R) was not significantly different from GPP in both winter and summer (Table 6).

[17] In summer, rates of hourly net calcification (g_{net}) were highly correlated with diurnal changes in E_d with the exception of two measurements made on 21 and 22 Nov 2008 (Figure 8a). These two particular measurements were

Table 4. Key Physical and Chemical Parameters Measured Within and Across the Control Volume in Summer (Nov 2008)^a

Day	Time (LT)	Physical					Chemical			
		T ($^{\circ}\text{C}$)	E_d ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	h (m)	θ_U (deg)	τ (min)	pH_T #1	pH_T #4	TA #1 ($\mu\text{eq kg}^{-1}$)	TA #4 ($\mu\text{eq kg}^{-1}$)
8	17:30	23.0	660	1.65	135	25	8.10	8.11	2321	2312
9	11:15	24.1	1520	1.42	134	27	8.14	8.18	2308	2294
10	12:00	24.4	1630	1.49	123	25	8.14	8.16	2302	2291
11	12:00	24.3	1650	1.52	124	39	8.08	8.14	2292	2281
19	21:00	24.3	0	1.45	127	36	8.07	8.05	2271	2271
20	8:20	23.9	280	1.26	132	32	8.01	8.05	2287	2282
20	11:01	24.5	1150	1.14	120	30	8.07	8.11	2264	2255
20	12:27	24.8	1670	1.30	119	33	8.13	8.16	2287	2259
20	16:10	24.7	690	1.77	119	42	8.09	8.13	2282	2273
20	17:55	24.5	140	1.74	117	50	8.10	8.07	2249	2247
21	10:40	23.7	230	1.24	127	31	8.01	8.01	2273	2267
21	12:45	23.7	320	1.30	129	24	8.00	8.00	2263	2252
22	13:15	23.8	660	1.38	123	20	8.10	8.10	2294	2281
22	15:47	23.7	670	1.63	123	30	8.02	8.08	2285	2281

^aPhysical parameters include temperature (T in $^{\circ}\text{C}$), light (E_d in $\mu\text{mol m}^{-2} \text{s}^{-1}$), depth (h in m), direction of the depth-averaged current (θ_U measured as degrees clockwise from North), and the estimated transit time of water through the control volume (τ) which was calculated from the depth-averaged cross-reef current. All other variables and their associated units are defined as in Table 1.

Table 5. Key Physical and Biogeochemical Parameters Measured Within and Across the Control Volume in Winter (Jun 2009)^a

Day	Time (LT)	T (°C)	Physical				Chemical			
			E_d ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	h (m)	θ_U (deg)	τ (min)	pH _r #1	pH _r #4	TA #1 ($\mu\text{eq kg}^{-1}$)	TA #4 ($\mu\text{eq kg}^{-1}$)
10	8:15	25.7	280	1.15	151	51	8.14	8.17	2245	2217
11	9:50	25.3	580	1.88	96	50	8.09	8.11	2280	2264
12	11:00	25.0	770	1.93	132	35	8.13	8.16	2270	2260
12	16:40	25.1	280	1.26	135	39	8.15	8.18	2253	2230
12	17:25	24.8	70	1.11	131	39	8.14	8.13	2257	2233
13	13:10	24.9	860	1.94	120	29	8.18	8.21	2284	2273
13	14:00	25.0	770	1.87	124	39	8.19	8.22	2280	2268
13	15:15	24.9	670	1.72	152	52	8.19	8.23	2280	2259
14	12:10	24.4	970	1.74	152	61	8.17	8.21	2283	2265
14	13:00	24.6	950	1.82	152	59	8.17	8.22	2276	2260
14	14:15	24.8	820	1.79	141	55	8.18	8.24	2287	2249

^aAll variables and units are the same as in Table 4.

made on days with unusually high cloud cover; when light incident to the benthos was substantially lower than in the prior 2 weeks (Figure 3a). If these two calcification rates are re-plotted against the average E_d for the same times of day from the prior 13 days, they follow the same linear relationship with E_d as did data collected in the prior 13 days. When comparing g_{net} against np , these same points follow a similar trend with respect to the other data (Figure 8b). Although we only made one measurement of nighttime g_{net} , it was not significantly different from zero (0.2 ± 4.1 mmol $\text{CaCO}_3 \text{ m}^{-2} \text{ hr}^{-1}$ at 21:00). Furthermore, the regression in Figure 8a indicates that g_{net} was likely not substantial at night (~ 2 mmol $\text{CaCO}_3 \text{ m}^{-2} \text{ hr}^{-1}$). Both these results are consistent with the literature which indicates rates of nighttime net calcification are minimal, or between -3 and $+3$ mmol $\text{CaCO}_3 \text{ m}^{-2} \text{ hr}^{-1}$ [Barnes and Devereux, 1984; Gattuso et al., 1996; Kraines et al., 1997; Smith, 1973, 1981]. Assuming that $g_{\text{net}} \approx 0$ at night in Nov 2008, we estimated an average daily community net calcification rate (G_{net}) of 190 ± 40 mmol $\text{CaCO}_3 \text{ m}^{-2} \text{ d}^{-1}$ for summer, or 14% of GPP (Table 6); however, the uncertainty in nighttime g_{net} of ± 3 mmol $\text{CaCO}_3 \text{ m}^{-2} \text{ hr}^{-1}$ as taken from the literature translates into an equivalent uncertainty in G_{net} of up to ± 40 mmol $\text{CaCO}_3 \text{ m}^{-2} \text{ d}^{-1}$ ($\pm 3 \times 12 = \pm 36$).

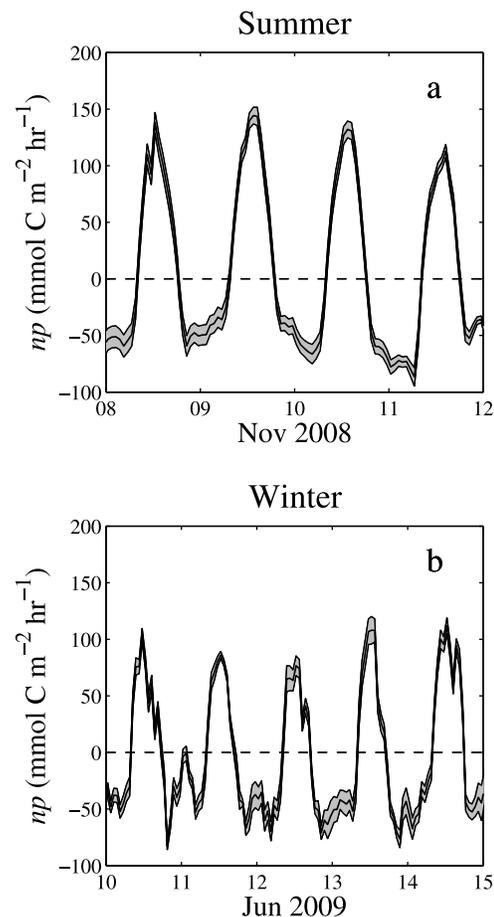
[18] In contrast to the summer data, g_{net} was independent of E_d and np in winter (mean \pm std. err. = 18.2 ± 0.8 mmol $\text{CaCO}_3 \text{ m}^{-2} \text{ hr}^{-1}$, Figures 8c and 8d). We did not measure nighttime rates of net calcification in Jun 2009; however,

Table 6. Key Rates of Daily Carbon Metabolism and Nitrogen Uptake for the Sandy Bay Reef Flat Community in Summer and Winter^a

	Summer		Winter	
	Average	Std. Err.	Average	Std. Err.
GPP	1400	± 70	1050	± 60
R	1290	± 60	1070	± 60
G_{Net}	190	± 40	200	± 10
$J_{\text{NO}_3^-}$	7.3	± 3.8	2.5	± 3.2
J_{Npart}	1.0	± 0.3	4.1	± 1.0
J_{Total}	8.3	± 3.8	6.6	± 3.4

^aSee Table 1 for definitions. Data shown represents the average for each study period (\pm std. err) in mmol C or N $\text{m}^{-2} \text{ d}^{-1}$. Particulate nitrogen fluxes (J_{Npart}) were estimated from Wyatt et al. [2010, 2012]. Total nitrogen fluxes (J_{Total}) were estimated as the sum of $J_{\text{NO}_3^-}$ and J_{Npart} .

the independence of g_{net} with light and np during this period suggests that nighttime rates could have been significantly greater than zero. For purposes of simplicity we estimate G_{net} in Jun 2009 to have been 200 ± 10 mmol $\text{CaCO}_3 \text{ m}^{-2} \text{ d}^{-1}$ or 18% of gross primary production assuming that $g_{\text{net}} \approx 0$ for the present reef community at night; however, we recognize that this estimate is conservative and could be underestimating true G_{net} by up to 20% or ± 40 mmol

**Figure 6.** Time series of net production (np , heavy line) in (a) summer and (b) winter. Gray regions represent ± 1 standard error while the dashed lines indicate $np = 0$.

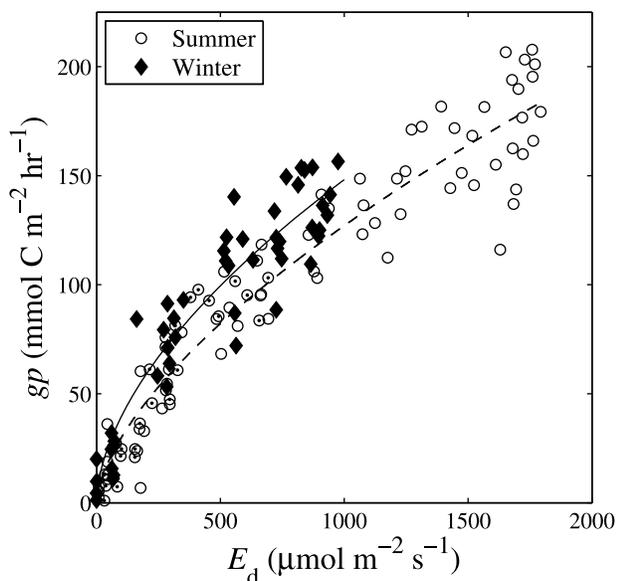


Figure 7. Hourly rates of gross photosynthesis versus downwelling PAR irradiance in summer (open circles) and winter (solid diamonds). Open circles with dots represent data from 21 and 22 of Nov 2008 when mid-day light levels were anomalously low. Also shown are the best fit nonlinear regressions of the form $gp = aE_d^b$ for summer (dashed line) and winter 2009 (solid line) where the regression parameter values (\pm std. err.) are $a = 1.64 \pm 0.34$, $b = 0.63 \pm 0.03$, $r^2 = 0.90$, and $n = 94$ for summer; and $a = 2.80 \pm 0.94$, $b = 0.57 \pm 0.05$, $r^2 = 0.91$, and $n = 53$ for winter.

$\text{CaCO}_3 \text{ m}^{-2} \text{ d}^{-1}$. Regardless, our data indicate that G_{net} was not significantly lower in winter than it was in summer. Finally, diurnal changes in g_{net} were correlated with changes in Ω_{ar} ($r^2 = 0.55$) and pH_{T} ($r^2 = 0.57$) in summer but not in winter (Figure 9).

4. Discussion

[19] Light incident to the Sandy Bay reef flat community was twice as high in summer as it was in winter while water temperatures were very similar between seasons; results consistent with long-term averages available from satellite data (Figure 1). Seasonal differences in planar light fluxes at Sandy Bay were also consistent with measurements from other shallow reef systems at similar latitudes (e.g., $\sim 17.5^\circ$) [Gattuso *et al.*, 1996]. Average concentrations of nitrate, ammonium, and phosphate observed on this reef community (around 0.4, 0.2, and 0.1 mmol m^{-3} ; respectively) were typical of coral reef systems worldwide [Atkinson and Falter, 2003]. Furthermore, rates of total nitrogen uptake for the present community did not appear to differ much between seasons and were comparable to those reported for other shallow reef communities (6.3 $\text{mmol N m}^{-2} \text{ d}^{-1}$ in the present study versus 4.7 $\text{mmol N m}^{-2} \text{ d}^{-1}$ from Falter *et al.* [2004] and 6.9 $\text{mmol N m}^{-2} \text{ d}^{-1}$ from Cuet *et al.* [2011]). Seasonal differences in the carbonate chemistry of waters incident to the reef flat were primarily of the result of $p\text{CO}_2$ being $\sim 70 \mu\text{atm}$ lower in winter than in summer while TA were effectively unchanged ($\pm 0.5\%$, Table 2). While some

of this disparity could be due to lower cross-reef transport in winter, there is recent evidence of strong phytoplankton blooms and high rates of pelagic primary production in late autumn and winter offshore of Ningaloo Reef [Rousseaux *et al.*, 2012]. We suggest that these blooms may have caused a significant drawdown of CO_2 from the water column resulting in undersaturation with respect to aqueous $p\text{CO}_2$ in waters incident to the reef during winter and thus elevated pH and Ω_{ar} relative to summer; however, this is only a hypothesis since we do not have corresponding data on shelf pelagic production during the reef sampling periods. Nonetheless, we have observed consistently depressed $p\text{CO}_2$ of around $60 \mu\text{atm}$ below atmospheric equilibrium in surface waters extending up to $\sim 13 \text{ km}$ offshore from cross-shelf transects taken in the same section of Ningaloo Reef in Sep 2010 ($325 \pm 6 \mu\text{atm}$, mean \pm s.d., $n = 24$), thus indicating the regional scale of this low- $p\text{CO}_2$ signature.

[20] For the present reef flat community, rates of benthic net production calculated using only the cross-reef advection term were very similar to rates calculated using the local, advective, and gas flux terms (Figure 4). Thus, the non-conservative behavior of metabolites on this reef flat was overwhelmingly dominated by the advection of water in the cross-reef direction. This was likely due to the fact that (1) water moved across the reef in a very consistent direction close to that of the cross-reef axis thus minimizing the impact of any along reef gradients, (2) the transit time across the control volume was very short (20 to 50 min), and (3) the cross-reef gradients in water chemistry were large given the shallow depth and high rates of community metabolism. The similarity between our estimates of net production made using both the dissolved oxygen data as well as the pH and TA data further confirm the validity of our simplified flux calculations despite the fact that changes in pH across the reef flat were generally not much greater than the precision in their measurement (0.03 versus 0.01, respectively). We are therefore confident that our two-point estimates of net dissolved nutrient uptake rates and calcification rates are robust. This may not be the case for other shallow reef environments where more variable circulation patterns require a more two-dimensional approach [Falter *et al.*, 2008].

[21] The average daily community gross primary production in summer was close to the observed limit for coral reef communities (1400 versus 1700 $\text{mmol C m}^{-2} \text{ d}^{-1}$) [Kinsey, 1985], and far above the global average (580 $\text{mmol C m}^{-2} \text{ d}^{-1}$) [Kinsey, 1985]. Similarly, the average daily net calcification rate was roughly double the 'standard' global value for coral reef flat communities in both summer and winter (200 versus 110 $\text{mmol CaCO}_3 \text{ m}^{-2} \text{ d}^{-1}$) [Kinsey, 1985], yet still below the observed upper limit for coral reef communities (280 $\text{mmol CaCO}_3 \text{ m}^{-2} \text{ d}^{-1}$) [Kinsey, 1985]. Thus, the production, respiration, and net calcification of the Ningaloo reef flat community at Sandy Bay is high relative to most other shallow reef communities worldwide, but not anomalously so. The higher rates of metabolism we measure here could be because coral cover for the present reef community is probably higher than the more expansive reef flat communities studied and reviewed by Kinsey [1985]. We specifically located our control volume within a 200-m section of reef flat whose cover by coral and algae on hard bottom was higher than toward the back of the reef flat to maximize the measured metabolic signature. Despite the higher-than-

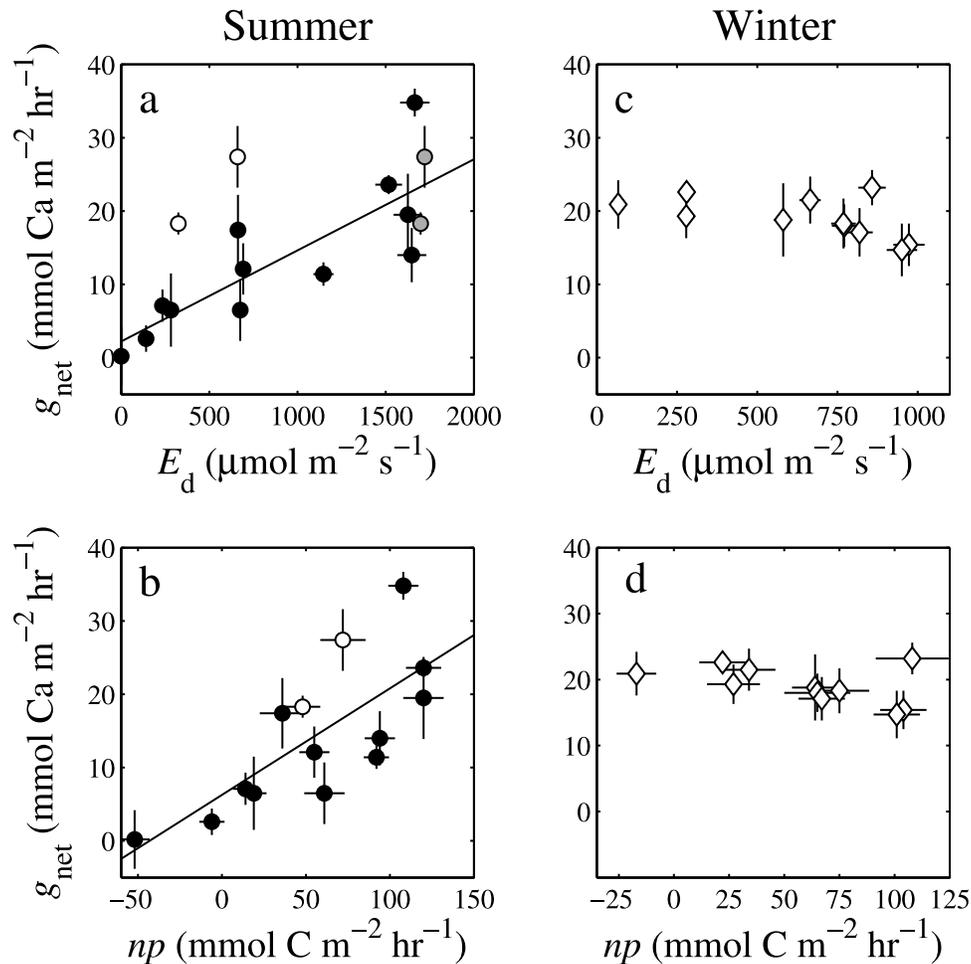


Figure 8. Hourly net community calcification rates (g_{net}) versus (a and c) incident light and (b and d) net production in summer (Figures 8a and 8b) and winter (Figures 8c and 8d). The open circles in Figure 8a represent net calcification rates at observed light levels that were re-plotted against light levels at the same time of day as recorded on prior days (gray circles). The regression shown in Figure 8a is $g_{\text{net}} = 0.0124E_d + 2.2$, $r^2 = 0.70$, and $n = 14$. The regression shown in Figure 8b is $g_{\text{net}} = 0.14np + 6.7$, $r^2 = 0.53$, and $n = 14$. Error bars shown represent \pm std. err. and were calculated using a Monte Carlo approach.

average metabolism, the ratio of GPP to R was not significantly different from one in either summer or winter (Table 6), results also consistent with many other coral-dominated communities [see *Atkinson and Falter*, 2003; *Kinsey*, 1985]. Furthermore, the ratio of G_{net} to GPP for the reef flat community at Sandy Bay in summer (14%) and winter (18%) were similar to the ratio of 20% for the ‘standard’ Indo-Pacific reef flat community [*Kinsey*, 1985]. While the absence of seasonality in daily net calcification deviates from the ‘standard’ model, a similar lack of seasonality in daily net calcification has been observed in select reef communities from the Red Sea [*Silverman et al.*, 2007b] and the Southeast Pacific [*Gattuso et al.*, 1996].

[22] Although in practice it is generally only possible to measure net calcification rates, we can still estimate gross calcification rates based on the broader data reported in the literature. A review by *Gattuso et al.* [1999] found that nighttime rates of calcification in reef coral were roughly one-third of maximum daytime rates. For the present reef community this would imply that nighttime rates of gross calcification were around 6 to 7 $\text{mmol CaCO}_3 \text{ m}^{-2} \text{ hr}^{-1}$.

Assuming that nighttime rates of net calcification are ~ 0 , then rates of community dissolution would therefore have to be around 6 to 7 $\text{mmol CaCO}_3 \text{ m}^{-2} \text{ hr}^{-1}$; values consistent with independent estimates of community dissolution (1.5 to 7 $\text{mmol CaCO}_3 \text{ m}^{-2} \text{ hr}^{-1}$) [*Kleypas et al.*, 2006]. Taken in tandem, these results would imply that rates of daily gross calcification for the Sandy Bay reef flat community were as high as 350 $\text{mmol CaCO}_3 \text{ m}^{-2} \text{ d}^{-1}$ in summer and in winter.

[23] Daily gross primary production was $33 \pm 9\%$ higher in summer than in winter; far less than the factor of two changes typically reported for shallow reef communities worldwide [*Kinsey*, 1985]. The more modest seasonal changes in gross primary production for the present reef community could be attributed to photo-acclimation under reduced winter light levels; however, it is highly likely that such photo-acclimation also occurs in other reef communities which demonstrate more typical seasonality in their rates of gross primary production. A more likely explanation would be the similar water temperatures between the two study periods (Table 2). Hypothetically, if seasonal changes in water temperature were in phase with seasonal changes in

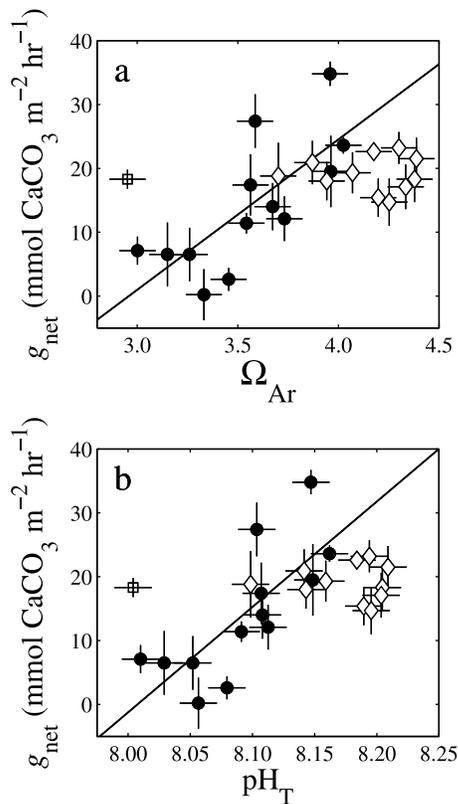


Figure 9. Hourly net calcification in summer (solid circles) and winter (open diamonds) versus average (a) aragonite saturation state and (b) pH over the entire reef flat. There are significant correlations between g_{net} and Ω_{ar} ($r^2 = 0.55$, $n = 13$, $p < 0.01$) as well as between g_{net} and pH_T ($r^2 = 0.57$, $n = 13$, $p < 0.01$) in summer, but not in winter. The open square represents a summer measurement excluded from the calculated correlations. Error bars shown represent \pm std. err. and were calculated using a Monte Carlo approach.

light, then the difference in temperature between the two study periods would have been $\sim 6^\circ\text{C}$ (Figure 1b). Assuming rates of gross photosynthesis depend on temperature according to $gp(T + \Delta T) = gp(T) \cdot Q_{10}^{\Delta T/10}$ where $Q_{10} \approx 2$ [Eppley, 1972; Iglesias-Prieto et al., 1992], then GPP would have been $\sim 50\%$ higher in summer than winter due to the effects of increasing temperature alone. If we were to then combine these hypothetical temperature-driven changes in metabolism with the observed 33% increase in GPP due to seasonal changes in light, the result would have been a more commonly observed twofold increase in GPP from winter to summer ($1.3 \times 1.5 = 2$). While some phase lag between seasonal light and temperature is present in most reef systems, our results nonetheless suggest that temperature could be as important a variable as light in driving seasonal changes in gross primary production as it is for calcification [Marshall and Clode, 2004].

[24] The general coherence between rates of net calcification and light in summer is consistent with numerous observations from across the globe including the Great Barrier Reef [Barnes and Devereux, 1984; Gattuso et al., 1996], the Red Sea [Mass et al., 2007; Schneider et al., 2009], the Southeast Pacific [Boucher et al., 1998; Gattuso

et al., 1996], the Indian Ocean [Cuet et al., 2011], and the Caribbean [Chalker and Taylor, 1978; Chalker, 1981]. Furthermore, because photosynthesis and respiration are also by far the dominant processes driving diurnal changes in pH, $p\text{CO}_2$, and Ω_{ar} in waters overlying shallow reef environments; rates of calcification in summer were expectedly correlated with diurnal changes in both pH and Ω_{ar} (Figure 9). Our data further indicate that rates of calcification in summer were more closely tied to net production than instantaneous light (Figure 8); results also consistent with prior reviews of field and experimental data [Allemand et al., 2004; Gattuso et al., 1999]. The episodic decoupling of calcification rates from diurnal changes in light in summer was most evident from our measurements made during mid-day on 21 and 22 Nov 2008. Despite anomalously low mid-day light levels (Figure 3a), gross photosynthesis was still responding to light the same as it had on prior cloudless days (Figure 7). In contrast, net calcification rates at mid-day on 21 and 22 Nov 2008 were very similar to mid-day values from prior cloudless days despite the lower mid-day light levels (Figure 8b). Thus, calcification rates appeared to follow the same diurnal rhythm independent of diurnal changes in light and light-driven photosynthesis. Moya et al. [2006] found that calcification in *Stylophora pistillata* responded only to changes in light intensity and displayed no apparent circadian rhythm when exposed to periods of constant light and constant darkness; whereas Al-Horani et al. [2007] found that *Galaxea fascicularis* exhibited more conventional diurnal variations in calcification (i.e., maximal at mid-day) despite being grown under constant light. Our results are thus more consistent with the results of Al-Horani et al. [2007] and indicate that calcification rates for entire reef communities can become decoupled from diurnal changes in light as they have for some species of coral. Regardless, the dependence or independence of diurnal changes in calcification rates on diurnal changes in light should be further explored through more controlled experimentation at time scales longer than a several hours to better explain this behavior.

[25] In contrast with summer, rates of net calcification in winter demonstrated an uncommon decoupling from diurnal changes in both light and net production (Figures 8c and 8d). Because photosynthesis and respiration are the primary factors driving diurnal changes in pH, $p\text{CO}_2$, and Ω_{ar} in waters overlying shallow reef environments; rates of calcification in winter were therefore not correlated with changes in pH or Ω_{ar} as they were in summer (Figure 9). Given that temperatures between the winter and summer surveys were so similar, the most likely factors causing this apparent decoupling in winter would be light, photosynthesis, carbonate chemistry, dissolution, and/or nutrient uptake. As expected, both light and gross primary production were substantially higher in summer than they were in winter (Tables 2 and 4; $p < 0.01$); thus, we doubt it was simply from differences in the gross supply of photosynthetic energy. While it is difficult to assess the influence of changing carbonate chemistry on net calcification rates independent of light and net production for natural reef communities because of their synoptic diurnal variation, the results of Chauvin et al. [2011] indicate that the ratio of net calcification to net production should have changed by at most $\pm 10\%$ over the course of a day given maximum diurnal

changes in Ω_{ar} of around 3.0 to 4.0. Thus, calcification rates were far more sensitive to diurnal changes in net production than ambient carbonate chemistry in the present reef flat community. The results of *Chauvin et al.* [2011] also indicate that the ratio of net calcification to net production should have seasonally increased by just 10% on average given the observed changes in Ω_{ar} of around 3.5 to 4.0 from summer to winter (Table 2). This projection is consistent with our measurements indicating that the ratios of maximum net calcification to maximum net production were approximately equal in summer and winter ($25/130 = 0.2$ in summer versus $20/100 = 0.2$ in winter, Figure 9); at least to within the errors of their respective calculation (± 0.05 or $\pm 25\%$). Therefore, it would appear that both diurnal and seasonal changes in carbonate chemistry had little influence on rates of net calcification for reef flat community at Sandy Bay. Unfortunately, we cannot explain how the same reef flat community maintained such high rates of net calcification while rates of net production decreased to negative values. Perhaps there is some threshold level of pH or Ω_{ar} above which rates of calcification become independent of light and net production the same way they can become independent of ambient pH or Ω_{ar} at high rates of net production and/or nutrient uptake [*Atkinson and Cuet*, 2008; *Cohen and Holcomb*, 2009; *Langdon and Atkinson*, 2005; *Ries et al.*, 2010].

[26] It is possible that rates of gross calcification were actually higher in winter than in summer even though rates of net calcification were not that different between seasons; however, this increase was being offset by simultaneously higher rates of dissolution due to the increased activity of particle-feeding macroborers in response to an increased supply of living particles. Thus, rates of gross calcification would have potentially followed a similar relationship to Ω_{ar} and pH in winter as they did in summer even if rates of net calcification did not. It is equally reasonable to assume that dissolution could have been higher in summer than winter due to the increased activity of photosynthetic microborers under seasonally higher light [*Tribollet et al.*, 2006]. Rates of bioerosion due to micro- and macroborers reported from reefs around the world average around 2 and 1.5 mmol $\text{CaCO}_3 \text{ m}^{-2} \text{ hr}^{-1}$, respectively [*Tribollet and Golubic*, 2011]. Given that rates of dissolution due to photo- and heterotrophic bioeroders are comparable in magnitude, are both much less than net and gross rates of community calcification which are roughly 10 to 40 mmol $\text{CaCO}_3 \text{ m}^{-2} \text{ hr}^{-1}$, and that the metabolic activity of these organisms should be seasonally out of phase; we doubt that seasonal changes in the activity of micro- and macroborers were enough to cause substantially higher rates of gross calcification in winter versus summer or in summer versus winter.

[27] It is also possible that greater particle feeding by the coral in winter could have facilitated rates of calcification that were more independent of photosynthetic production given that rates of total nitrogen uptake were similar between seasons (Table 6). The ability of coral to take up particles can be species dependent [*Palardy et al.*, 2008], and has been shown to influence rates of coral growth under controlled feeding [see *Houlbrèque and Ferrier-Pagès*, 2009]. For instance, *Houlbrèque et al.* [2004] found that rates of calcification for unfed corals living in aquaria declined by nearly one half in comparison with those fed *Artemia*

salina nauplii after 8 weeks of starvation. Most of the particle feeding by the present reef community is on small living phytoplankton [*Wyatt et al.*, 2010] and heterotrophic bacteria [*Patten et al.*, 2011] less than 5 μm in size whose C:N ratio should be around 10 [*Houlbrèque et al.*, 2006]. Thus, the maximum amount of particulate carbon that coral within this community could take up would be around 10 mmol $\text{C m}^{-2} \text{ d}^{-1}$ in summer and around 50 mmol $\text{C m}^{-2} \text{ d}^{-1}$ in winter assuming that rates of particle feeding by sponges, ascidians, bivalves, etc. were negligible by comparison (Table 6). These rates are about 2 orders of magnitude lower than gross rates of photosynthesis for this same community in either season (900 to 1500 mmol $\text{C m}^{-2} \text{ d}^{-1}$). Furthermore, prior studies have shown that passive suspension feeders such as coral are much poorer at removing particles from the water column than active filter feeders, especially when those particles are small [*Ribes et al.*, 2005]. At present, the primary biological sink for living particles on the reef flat at Sandy Bay has not yet been identified (e.g., coral, sponges, bivalves, ascidians, etc.); however, it is likely that a substantial fraction of the particle feeding in the present reef flat community is by heterotrophic organisms that are contributing little to community calcification rates. Thus, unless the transfer of photosynthetic energy from zooxanthellae to coral is particularly inefficient and particle feeding by active filter feeders and other heterotrophs in this community is unusually trivial, we doubt that particle feeding provided as large a source of metabolic energy to drive calcification as did photosynthesis. To the best of our knowledge, no direct measurements of particle feeding by the *Acropora* species dominating the present reef community have yet been made; especially on the small phytoplankton and heterotrophic bacteria which are being taken up by the reef. Unfortunately, it is still uncertain as to how much the growth and metabolism of coral depend on the uptake of particles under natural rather than experimental conditions.

5. Conclusions and Future Work

[28] Based on results from the present study and from the broader literature, we draw the following conclusions: First, we believe the more modest seasonal differences in daily gross primary production for the present reef community compared with most other Indo-Pacific communities was the result of similar temperatures between the summer and winter solstices. Second, although net production more directly influences rates of calcification than does light, light is still the primary environmental forcing variable for both photosynthesis and calcification and, therefore, still generally a good predictor of calcification rates if our results are interpreted within the broader context of the general reef literature. Nonetheless, our results also demonstrate that there are circumstances under which the relationships between calcification, light, and net production do not follow the conventional model. At present we cannot explicitly isolate the mechanisms responsible for the decoupling of calcification rates from diurnal variations in light and net production in winter; however, it appears as if the present reef community crossed some threshold in pH or Ω_{ar} close to pre-industrial levels at which point net calcification was no longer sensitive to diurnal changes in light or organic carbon metabolism. Any future investigations into the mechanisms responsible

for this behavior would be best conducted through more direct experimentation. At present we are also unable to identify how frequent or infrequent such decoupling of net calcification rates from light and photosynthesis are in natural reef communities without gathering longer-term records of key environmental variables, net production rates, and net calcification rates over multiple seasons and years. We hope the results of the present study will thus be useful for the strategic development of longer-term monitoring of reef growth and metabolism in the future.

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