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Net loss of CaCO_3 from coral reef communities due to human induced seawater acidification

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Received: 31 December 2008 – Accepted: 8 January 2009 – Published: 23 February 2009

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Published by Copernicus Publications on behalf of the European Geosciences Union.

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Abstract

Acidification of seawater owing to oceanic uptake of atmospheric CO₂ originating from human activities such as burning of fossil fuels and land-use changes has raised serious concerns for its adverse effects on corals, coral reefs and carbonate communities in general. Here we demonstrate a transition from net accumulation towards net loss of calcium carbonate (CaCO₃) material owing to decreased calcification and increased carbonate dissolution from replicated subtropical coral reef communities (*n*=3) incubated in continuous-flow mesocosms subject to present and future seawater conditions. The calcifying community was dominated by the coral *Montipora capitata*. Daily average community calcification or Net Ecosystem Calcification (NEC = CaCO₃ production – dissolution) was positive at 4.5 mmol CaCO₃ m⁻² h⁻¹ under ambient seawater pCO₂ conditions as opposed to negative at -0.1 mmol CaCO₃ m⁻² h⁻¹ under seawater conditions of double the ambient pCO₂. These experimental results provide support for the conclusion that some net calcifying communities could become subject to net dissolution in response to anthropogenic ocean acidification within this century.

1 Introduction

A substantial fraction of the CO₂ released to the atmosphere from human activities is taken up by the ocean (e.g., Mackenzie et al., 2001; Sabine et al., 2004). CO₂ in solution produces carbonic acid (H₂CO₃), which is a weak acid and results in a decrease in seawater pH (increasing acidity) and removal of carbonate ions (CO₃²⁻). A decrease of CO₃²⁻ produces a drop in the seawater saturation state with respect to carbonate minerals (Ω), which is the quotient of the product of the seawater concentration of calcium and carbonate ions and an experimentally determined stoichiometric solubility product ($\Omega = [\text{Ca}^{2+}][\text{CO}_3^{2-}]/K_{sp}^*$). Simplified, the seawater carbonate saturation state index can provide information on the rates at which marine calcifiers can deposit skeletons and shells of CaCO₃, or the opposite, the rates of dissolution and disinte-

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gration of these phases. Based on thermodynamic principles, precipitation of CaCO_3 is expected when $\Omega > 1$ and dissolution when $\Omega < 1$. Future model projections indicate that surface seawater pH will decrease 0.5–0.7 pH units relative to pre-industrial conditions in the next couple of centuries under a Business-As-Usual (BAU) CO_2 emission scenario (Caldeira and Wickett, 2003). Simultaneously, seawater saturation state with respect to carbonate minerals will decrease and seawater could become undersaturated in many environments with respect to high Mg-calcite minerals and even aragonite (Andersson et al., 2005; Orr et al., 2005). As a result, the ability to calcify and the rates of calcification among marine calcifiers are expected to decrease significantly. Additionally, the dissolution of carbonate sediments, structures, and even individual organisms could increase. These changes could be drastic and sufficiently large so that coral reef communities and carbonate ecosystems in general could become subject to a net loss of CaCO_3 material as a result of anthropogenic ocean acidification (Kleypas et al., 1999; Andersson et al., 2005, 2007; Yates and Halley, 2006; Hoegh-Guldberg et al., 2007). The effect of ocean acidification on carbonate dissolution has received relatively little attention compared to the effect of this process on organisms' ability to calcify despite the fact that it is more or less certain carbonate dissolution will increase in response to ocean acidification.

In the present study, we investigate the effects of future seawater conditions anticipated by the end of the present century and beyond on the community calcification (G) or what also has been referred to as the Net Ecosystem Calcification ($\text{NEC} = \text{CaCO}_3$ production – dissolution) (e.g., Andersson et al., 2005) of a typical subtropical coral reef community including its sediments incubated in mesocosms over a complete, 24-h, diel cycle.

2 Methods

The present diel investigation (21–22 June 2006) was a part of a longer term ocean acidification experiment conducted at the Hawaii Institute of Marine Biology (HIMB)

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at Moku O Loe (Coconut Island), Kaneohe Bay, Hawaii (21.4° N, 157.8° W) between 31 October 2005 and 8 August 2006 (Jokiel et al., 2008; Kuffner et al., 2008). Six 1×1×0.5-m fiberglass mesocosm tanks (Fig. 1) located in full sunlight were continuously supplied with flowing seawater pumped from approximately 2 m depth at the edge of the coral reef at a rate of approximately 7 to 8 l min⁻¹ per mesocosm (turnover rate ~1 h). Three mesocosms were randomly chosen to be maintained at an ambient chemical state with respect to seawater $p\text{CO}_2$, pH, $[\text{CO}_3^{2-}]$, and Ω . The remaining three mesocosms were maintained at a chemical state with respect to these parameters anticipated under a doubling of ambient seawater $p\text{CO}_2$ conditions. The carbonic-acid system was manipulated by constant addition of HCl (1.1 N) using a 205CA Watson Marlow multi-channel peristaltic pump at a rate of ~1.3 ml min⁻¹. This produced a decrease in the seawater total alkalinity (TA) and a subsequent shift in the distribution of dissolved inorganic carbon species similar to that resulting from uptake of anthropogenic CO₂ (e.g., Langdon and Atkinson, 2005). Maintaining seawater flow and acid addition at constant rates ensured that natural fluctuations in seawater chemistry on both diel and seasonal cycles were preserved throughout the duration of the experiment (Kayanne et al., 1995; Ohde and van Woessik, 1999; Bates, 2002). Control mesocosms received plain tap water at the same rate acid was added to the treatment mesocosms.

Environmental and chemical parameters were measured in each mesocosm at least weekly in the long-term experiment to ensure that the desired treatment conditions were effective (Jokiel et al., 2008; Kuffner et al., 2008). During the diel experiment, in situ measurements were made and seawater samples collected every 2 and 4 h, respectively, in each mesocosm and also in the seawater intake lines for a duration of 24 h. Measured parameters included temperature and salinity (YSI 30 salinity/conductivity/temperature; ±0.1°C; ±0.1 ppt), dissolved oxygen (YSI 95 Dissolved Oxygen Microelectrode Array Model; ±0.2 mg L⁻¹), $p\text{H}_{\text{NBS}}$ (Accumet AP72 pH/mV/temperature meter and Oakton fully enclosed Ag/AgCl combination electrode; ±0.01 pH units), TA and nutrients (PO_4^{3-} , NO_2^- , NO_3^- , NH_4 , $\text{Si}(\text{OH})_4$; all data are

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presented in supplementary Table S1, <http://www.biogeosciences-discuss.net/6/2163/2009/bgd-6-2163-2009-supplement.pdf>). TA samples were collected in 200 ml Kimax brand glass sample bottles and fixed with 100 μ L saturated HgCl_2 solution. Nutrient samples were filtered using 0.45 μ m Millipore filters, stored in 60 ml opaque amber plastic bottles and kept frozen until analysis. Nutrient analyses were conducted by the Marine Chemistry Laboratory at the University of Washington using an autoanalyzer (Technicon Model AAII). TA was determined by potentiometric acid titration similar to the procedures described by Grashoff et al. (1983) and DOE (1994) using a Brinkmann Methrohm Dosimat and an Orion Expandable Ion Analyzer EA920 with an Accumet calomel combination electrode. The acid (~ 0.1 N HCl with an ionic strength of 0.7) was standardized against certified reference material (CRM) prepared in the laboratory of Andrew Dickson at Scripps Institute of Oceanography. CRMs were analyzed every 7 samples to ensure accuracy and precision of the titration system. The 1σ precision of TA analysis was 0.11% (~ 2.5 $\mu\text{mol kg}^{-1}$; $n=14$). Seawater dissolved inorganic carbon parameters and saturation state with respect to carbonate minerals were calculated based on pH_{NBS} and TA using the program CO2SYS (Lewis and Wallace, 1998) and stoichiometric dissociation constants defined by Mehrbach et al. (1973) and refit by Dickson and Millero (1987). Constants were redefined on the NBS scale. Although pH_{NBS} measurements are not ideal for calculating the carbonic acid system in seawater, calculated ambient $p\text{CO}_2$ levels agreed well with independent measurements by a NOAA PMEL $p\text{CO}_2$ buoy located near the seawater intake line (see supplemental information of Kuffner et al., 2008). Furthermore, it is the relative difference between treatment and control mesocosms that is most important in the present case. This difference is little affected by the shortcomings of the pH measurements.

The calcifying community of each mesocosm consisted of an identical number of corals (*Pocillopora damicornis* and *Montipora capitata*) and rhodoliths (i.e., crustose coralline algae; e.g., *Lithophyllum* cf. *pallascens*, *Hydrolithon* sp., and *Porolithon* sp.) introduced to the mesocosms well before the present diel study (2 weeks to 8 months). In addition, crustose coralline algae (CCA), mussels, vermetids, barnacles and other

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calcifiers were also present in each mesocosm as a result of natural settlement of larvae from the continuous flowing seawater (Jokiel et al., 2008; Kuffner et al., 2008). Other non-calcifying organisms, including various algae, diatoms, cyanobacteria and sea hares, were also able to colonize the mesocosms in this manner. Nevertheless, forty colonies of *M. capitata* (Fig. 2) were by far the most important calcifying component of each mesocosm. Furthermore, a thin sediment layer of a few millimeters thickness comprised of very fine-grained carbonate material and organic debris was present at the bottom of each mesocosm. Some of this material came in through the seawater intake lines and settled out in the mesocosms, and some was produced in situ by the mechanical disintegration and as detritus from epiphytic borings of substrates of the biological community in the mesocosms.

NEC was calculated according to the procedure outlined in Fig. 3 (see also supplementary Table S2, <http://www.biogeosciences-discuss.net/6/2163/2009/bgd-6-2163-2009-supplement.pdf>). Statistical analysis of measured parameters was conducted using two-way analysis of variance (ANOVA) with mesocosms and time as fixed factors. Tukey's 1-degree of freedom test for non-additivity was used to evaluate interactions between the fixed factors. A priori contrasts of control and treatment mesocosms were used to evaluate the effects of treatment and formed the basis of the main statistical results reported here.

3 Results and discussion

Acidification of seawater in the treatment mesocosms resulted in a shift in the distribution of dissolved inorganic carbon parameters and produced conditions in the seawater with respect to $p\text{CO}_2$, pH, CO_3^{2-} and carbonate saturation state that could become reality by the end of this century and beyond as a result of continued anthropogenic emissions of CO_2 (Table 1; Fig. 4a, b). All these parameters were statistically significantly different between treatment and control mesocosms. Because of natural changes in seawater chemistry on diel time scales owing to metabolic pro-

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cesses (Kayanne et al., 1995; Ohde and van Woelik, 1999; Bates, 2002), neither control nor treatment chemical conditions were maintained at constant levels, but as anticipated varied significantly throughout a diel cycle. Both control and treatment mesocosms were subject to $p\text{CO}_2$ levels significantly higher than the current atmospheric $p\text{CO}_2$ and a doubling of the current level, respectively. However, it is important to realize that many coral reef environments are subject to surface seawater $p\text{CO}_2$ s much higher than the overlying atmosphere owing to processes such as calcification and remineralization of organic matter. For example, measurements in Kaneohe Bay made by E. DeCarlo and colleagues at the University of Hawaii and NOAA PMEL have on occasion shown surface seawater $p\text{CO}_2$ exceeding $1000 \mu\text{atm}$ at present time (http://www.pmel.noaa.gov/co2/coastal/kbay/CRIMP2_all.htm). In the present study, the absolute difference between treatment and control mesocosms appeared greater at night than during the day, but the relative difference remained essentially constant throughout the 24-h period. On average, $p\text{CO}_2$ in the treatment mesocosms exceeded control mesocosms by $104 \pm 11\%$, pH was lower by $3.6 \pm 0.2\%$, and $[\text{CO}_3^{2-}]$ and aragonite saturation state were both lower by $46 \pm 3\%$. Thus, the treatment effect represented a doubling of ambient conditions with respect to $p\text{CO}_2$. The observed daytime and nighttime $p\text{CO}_2$ in treatment mesocosms roughly correspond to equilibrium levels with the atmosphere projected for year 2100 under emission scenarios B1 and A1FI, respectively (IPCC, 2001). The seawater saturation state with respect to aragonite was supersaturated in both control ($\Omega_{\text{arag}} \sim 3.6$) and treatment ($\Omega_{\text{arag}} \sim 2.1$) mesocosms during daytime. While control mesocosms remained supersaturated at night with respect to this mineral phase ($\Omega_{\text{arag}} \sim 2$), treatment mesocosms reached values close to equilibrium ($\Omega_{\text{arag}} = 1.0$). Consequently, the seawater was undersaturated with respect to carbonate minerals more soluble than aragonite, such as high Mg-calcite phases, at this time and potentially subject to dissolution.

Daily average temperature, salinity and dissolved oxygen were close to identical in all mesocosms (Table 1). Nitrate and nitrite concentrations were statistically not different between treatment and control mesocosms, but concentrations of ammonium,

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phosphate and silicate were significantly different based on two-way ANOVA and a priori contrasts (Table 1). It is not clear whether the observed differences in these cases were due to the seawater acidification treatment or to other factors that were not accounted for. For example, average ammonium concentration was higher in the control relative to the treatment mesocosms. This was possibly due to nitrogen fixation by extensive mats of cyanobacteria observed on the mesocosm walls in two of the three control mesocosms. These mats reoccurred throughout the long-term experiment, and were observed in both control and treatment mesocosms with no obvious distinguishable pattern in their dynamics. Increases in ammonium concentration during incubations containing cyanobacteria have been observed and reported in other incubation studies (Kuffner and Paul, 2001). The reasons for the statistically significant differences in phosphate and silicate concentrations are unknown, but because the observed differences are small and the natural variability large (Table 1), there is little reason to suspect that these differences had any major direct or indirect effect on the observed TA and NEC.

The calculated NEC in control mesocosms consistently exceeded NEC in treatment mesocosms and the difference was statistically different (Table 1). Net calcification, i.e., net accumulation of CaCO_3 , was observed in both treatment and control mesocosms during daytime hours (Fig. 1). The highest daytime rate ($\pm 1\text{std}$) of calcification was $9.7(6.2) \text{ mmol m}^{-2} \text{ h}^{-1}$ in the control mesocosms and $4.0(1.4) \text{ mmol m}^{-2} \text{ h}^{-1}$ in the treatment mesocosms. Net dissolution, i.e., net loss of CaCO_3 , was observed in both control and treatment mesocosms during nighttime. The highest dissolution rate ($\pm 1\text{std}$) was $-3.1(1.8) \text{ mmol m}^{-2} \text{ h}^{-1}$ in the control mesocosms and $-5.0(2.5) \text{ mmol m}^{-2} \text{ h}^{-1}$ in the treatment mesocosms. Marginal positive calcification was observed during one measurement interval at night (0000–0400) in the control mesocosms, but the associated error suggests that these mesocosms could just as well have been subject to marginal dissolution during this time interval. Regardless, the two processes appeared closely balanced at this time. Daily average NEC and CaCO_3 accumulation were equal to $4.5 \text{ mmol CaCO}_3 \text{ m}^{-2} \text{ h}^{-1}$ or $11 \text{ g CaCO}_3 \text{ m}^{-2} \text{ day}^{-1}$

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in the control mesocosms. In contrast, daily average dissolution exceeded calcification in the treatment mesocosms and gave rise to a loss of $-0.1 \text{ mmol m}^{-2} \text{ h}^{-1}$ or $-0.2 \text{ g CaCO}_3 \text{ m}^{-2} \text{ day}^{-1}$. These results are the net of living community metabolism as well as carbonate dissolution occurring in the thin sediment layer that accumulated at the bottom of the mesocosms. For a number of different studies investigating community calcification either in situ or in mesocosms for a range of different coral reef communities, substratum types, and CO_2 conditions, daily average net calcification rates range from $-1 \text{ g CaCO}_3 \text{ m}^{-2} \text{ day}^{-1}$ to $25 \text{ g CaCO}_3 \text{ m}^{-2} \text{ day}^{-1}$ (e.g., Gattuso et al., 1996; Boucher et al., 1998; Langdon et al., 2000; Leclercq et al., 2002; Yates and Halley, 2006; Silverman et al., 2007). However, because of the large differences in experimental settings and conditions, it is not informative to make direct comparisons of results between these studies. Nevertheless, studies investigating the effect of rising levels of CO_2 and decreasing Ω showed a consistent decrease in the rate of community calcification concurrent with changes in these parameters (Langdon et al., 2000; Leclercq et al., 2002; Yates and Halley, 2006; Silverman et al., 2007).

The observed diel trend in NEC agrees with expectations based on theoretical and observational considerations. During daytime, primary production consumes CO_2 at a greater rate than respiration and microbial decomposition of organic matter produce CO_2 . This raises the seawater saturation state with respect to carbonate minerals and consequently favors more rapid calcification (e.g., Gattuso et al., 1999; Marubini et al., 2003; Langdon and Atkinson, 2005). Furthermore, photosynthesizing symbiotic algae provide their hosts, e.g., corals, with substantial amounts of energy that can be utilized for mechanisms such as the calcium-ATPase pump to control the chemistry of their internal calcifying fluid and thus enhance calcification (e.g., Cohen and McConnaughey, 2003). Corals calcify 3–5 times faster in light compared to dark conditions, which attests to the important coupling of this process to photosynthesis in these organisms (Gattuso et al., 1999). At nighttime, in the absence of photosynthesis, production of CO_2 from respiration lowers seawater saturation state with respect to carbonate minerals, which then could become subject to dissolution if the seawater becomes under-

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saturated with respect to a particular carbonate mineral phase. In the present case, the seawater of the treatment mesocosms was at times undersaturated with respect to all Mg-calcite minerals more soluble than aragonite; thus, these mineral phases potentially were subject to dissolution. In addition, chemical conditions in microenvironments were most likely even more corrosive to carbonate minerals owing to the metabolic activity of microbes, but also due to endolithic microorganisms known to colonize and actively penetrate carbonate substrates, i.e., bioerosion (e.g., Tribollet, 2008). Evidence of physical dissolution was observed in Mg-calcite producing rhodoliths that lost mass throughout the long-term experiment in the treatment mesocosms (Jokiel et al., 2008). Similarly, recruitment of crustose coralline algae depositing Mg-calcite containing 13–14 mol% MgCO₃ was significantly reduced by as much as 85% under treatment conditions (Jokiel et al., 2008; Kuffner et al., 2008). Physical and biological dissolution and disintegration processes probably produced much of the thin sediment layer that accumulated in the bottom of the tanks. This material is very fine-grained and thus has a high specific surface area making it very susceptible to dissolution. Despite the transition from net accumulation of CaCO₃ towards net dissolution under the current treatment conditions, the majority of individual coral colonies appeared healthy and gained mass throughout the long-term experiment, although at a slower rate relative to coral colonies in control mesocosms (Jokiel et al., 2008).

The observed change in NEC between ambient and future seawater conditions is consistent with what we might expect as a result of lower seawater Ω , i.e., slower calcification and faster dissolution. However, the fact that the daily average NEC reached negative values under the prevailing chemical conditions of the treatment mesocosms has important implications for the oceanic inorganic carbon cycle, and the function and role of coral reefs and carbonate environments in the cycling of carbon should these conditions mimicking ocean acidification materialize in the natural environment. Since the seawater low stand of the last glacial maximum (~18 000 years before present) and concurrent with the rise in sea level and the evolution of the present coastal ocean, significant accumulations of biologically produced CaCO₃ have occurred throughout

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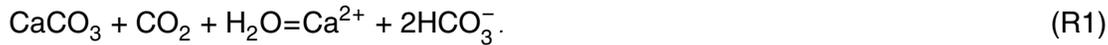
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shallow-water ocean environments worldwide (Milliman, 1993). Thus, the transition from net accumulation of CaCO_3 to a net loss represents a major reversal of a process that has been in effect for thousands of years. Interestingly, the transition to negative NEC acts as a weak negative feedback to rising anthropogenic CO_2 and ocean acidification since dissolution of calcium carbonate minerals consumes CO_2 through the reaction:



Furthermore, this reaction increases alkalinity which further increases the capacity of the seawater to absorb more CO_2 . However, this process is slow relative to the rate at which human activities are changing the chemistry of surface seawater. It has been demonstrated that it will not produce sufficient alkalinity to produce a significant buffer effect on time scales of decades to centuries either on a global or a regional scale (e.g., Andersson et al., 2005).

Other investigators have attempted to define a critical threshold value with respect to either $p\text{CO}_2$ or $[\text{CO}_3^{2-}]$ when dissolution will exceed calcification in different tropical and subtropical coral reef environments (Yates and Halley, 2006). However, such threshold values will vary significantly from environment to environment as a result of a myriad of factors that are difficult to account for accurately and depend on the temporal and spatial scale being considered. What is important in this context is the current trend and the relatively small changes in seawater chemistry required to reverse the net effect of marine calcification and carbonate dissolution. Some subtropical coral reef ecosystems, such as the coral reefs of Bermuda, may be subject to a net loss in CaCO_3 much sooner than ecosystems located at more tropical latitudes because of lower average seawater $[\text{CO}_3^{2-}]$ and Ω (e.g., Kleypas et al., 1999). Intermediate, high latitude environments and associated cold water bioherms are even at greater risk since many of these environments currently exist at conditions close to equilibrium with aragonite (Orr et al., 2005; Guinotte et al., 2006).

Based on the current global socio-economic situation, it is highly unlikely that anthropogenic CO_2 emissions to the atmosphere will decrease significantly in the next

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several decades. Regardless of the effect of this additional CO₂ accumulating in the atmosphere on the magnitude of change of future global average temperature, which is still debated, the oceans will continue to absorb a significant fraction of this gas causing increasing acidity and all the potential ecological consequences associated with this major change in seawater chemistry.

Acknowledgements. This work was partially supported by NSF (Grants ATM 04-39051, EAR 02-23509, and OCE 07-49401, FTM), USGS Terrestrial, Freshwater and Marine Ecosystem program and the USGS Coastal and Marine Geology program (IBK), EPA Star (R832224-010) and NOAA National Ocean Service (PLJ). FTM also gratefully acknowledges partial support from a grant from the FNRS of the Belgium-French community.

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Table 1. Average physical and chemical properties in control ($n=3$; white rows) and treatment mesocosms ($n=3$; gray rows) and results of statistical tests. Numbers in paranthesis represent 1 standard deviation. Δ is the average 24 h difference between control and treatment mesocosms relative to the former.

Time	12:00	16:00	20:00	0:00	4:00	8:00	12:00	MEAN [†]	Δ	$\Delta\%$	Two-way analysis of variance (ANOVA) by time (t) and mesocosm (m)		Tukey's 1-degree of freedom test for non-additivity		A priori contrast between treatment and control mesocosms		
											F	P	F	P	t	P	
T (°C)	27.8(0.1)	27.0(0.1)	26.3(0.1)	25.9(0.1)	25.8(0.1)	26.0(0.1)	27.7(0.1)	26.5(0.1)	-0.1	0	t						
	27.8(0.1)	26.9(0.1)	26.3(0.1)	26.0(0.1)	25.8(0.1)	26.0(0.1)	27.6(0.1)	26.4(0.1)			m	variability smaller or equal to analytical precision of instrument					
S	35.0(0.1)	35.2(0.1)	35.2(0.0)	35.2(0.0)	35.3(0.1)	35.2(0.1)	35.2(0.1)	35.2(0.0)	0	0	t						
	35.1(0.1)	35.2(0.1)	35.3(0.0)	35.3(0.0)	35.3(0.0)	35.3(0.0)	35.2(0.1)	35.2(0.1)			m	variability smaller or equal to analytical precision of instrument					
DO ($\mu\text{mol kg}^{-1}$)	272(8)	235(19)	250(32)	239(24)	256(37)	241(25)	254(35)	249(24)			t	95.21	<0.0001				
	249(7)	272(6)	235(19)	250(32)	239(24)	256(37)	241(25)	250(21)	1	0	m	0.2	=0.9574	43.8	<0.0001	-0.84	=0.4069
[NO ₂] ($\mu\text{mol kg}^{-1}$)	0.03(0.00)	0.03(0.00)	0.06(0.00)	0.03(0.00)	0.06(0.01)	0.05(0.00)	0.03(0.00)	0.05(0.00)	-0.01	-20	t	27.66	<0.0001				
	0.05(0.02)	0.03(0.02)	0.06(0.02)	0.03(0.02)	0.05(0.02)	0.05(0.02)	0.03(0.02)	0.04(0.02)			m	27.05	<0.0001	0.0	=0.9603	-0.45	=0.6545
[NO ₃] ($\mu\text{mol kg}^{-1}$)	0.17(0.07)	0.19(0.06)	0.49(0.04)	0.25(0.06)	0.44(0.09)	0.41(0.02)	0.18(0.07)	0.32(0.06)	-0.02	-6	t	19.05	<0.0001				
	0.20(0.04)	0.24(0.05)	0.38(0.06)	0.23(0.10)	0.36(0.04)	0.38(0.05)	0.16(0.08)	0.30(0.06)			m	1.39	=0.2627	2.32	=0.1411	-1.34	=0.1920
[NH ₄] ($\mu\text{mol kg}^{-1}$)	0.51(0.13)	0.40(0.11)	0.45(0.14)	0.40(0.13)	0.46(0.19)	0.39(0.10)	0.45(0.10)	0.44(0.13)	-0.16	-36	t	10.3	<0.0001				
	0.39(0.03)	0.27(0.05)	0.26(0.03)	0.23(0.02)	0.24(0.02)	0.28(0.04)	0.33(0.02)	0.28(0.03)			m	65.38	<0.0001	0.37	=0.5461	-12.83	<0.0001
[PO ₄] ($\mu\text{mol kg}^{-1}$)	0.11(0.02)	0.10(0.00)	0.13(0.01)	0.11(0.01)	0.11(0.01)	0.12(0.01)	0.11(0.02)	0.11(0.01)	0.02	18	t	5.22	=0.0020				
	0.14(0.05)	0.12(0.04)	0.14(0.02)	0.11(0.02)	0.12(0.02)	0.12(0.01)	0.12(0.02)	0.13(0.03)			m	13.63	<0.0001	1.2	=0.2845	3.23	=0.0035
[Si(OH) ₄] ($\mu\text{mol kg}^{-1}$)	7.94(0.35)	7.39(0.23)	7.20(0.28)	6.78(0.34)	7.06(0.18)	7.34(0.18)	7.71(0.26)	7.28(0.26)	-0.25	-3	t	16.59	<0.0001				
	8.25(0.36)	7.11(0.21)	6.88(0.24)	6.42(0.38)	6.29(0.36)	7.23(0.04)	7.45(0.16)	7.03(0.26)			m	1.36	=0.2728	22.39	=0.0001	-2.34	=0.0274
pH _{nas}	8.23(0.05)	8.18(0.03)	7.99(0.01)	7.95(0.03)	7.91(0.03)	8.05(0.01)	8.24(0.04)	8.08(0.03)	-0.32	-4	t	203.82	<0.0001				
	7.95(0.10)	7.86(0.10)	7.69(0.08)	7.67(0.09)	7.62(0.08)	7.77(0.09)	7.97(0.10)	7.76(0.09)			m	354.5	<0.0001	0.31	=0.5828	-39.71	<0.0001
TA ($\mu\text{mol kg}^{-1}$)	2107(5)	2149(28)	2177(11)	2212(6)	2202(8)	2172(4)	2153(9)	2170(10)	-140	-6	t	41.11	<0.0001				
	1977(37)	2025(44)	2027(40)	2058(47)	2036(28)	2036(36)	2014(36)	2030(39)			m	234.03	<0.0001	3.36	=0.0794	-32.63	<0.0001
pCO ₂ (μatm)	317(42)	379(32)	634(12)	730(60)	806(66)	541(14)	317(39)	568(38)	579	109	t	45.1	<0.0001				
	657(154)	854(184)	1319(240)	1394(258)	1588(285)	1072(214)	638(149)	1147(223)			m	73.49	<0.0001	151.12	<0.0001	17.53	<0.0001
[HCO ₃] ($\mu\text{mol kg}^{-1}$)	1538(47)	1633(44)	1811(13)	1876(25)	1894(25)	1768(6)	1567(46)	1753(27)	32	2	t	57.33	<0.0001				
	1650(39)	1752(17)	1839(3)	1875(8)	1896(10)	1813(10)	1670(37)	1785(18)			m	3.53	=0.0150	54.6	<0.0001	4.07	<0.0001
[CO ₃] ($\mu\text{mol kg}^{-1}$)	227(17)	207(6)	147(1)	136(8)	125(7)	163(3)	235(14)	177(8)	-80	-45	t	49.56	<0.0001				
	130(27)	109(25)	75(15)	73(16)	65(13)	89(19)	136(29)	97(21)			m	89.76	<0.0001	60.58	<0.0001	-20.37	<0.0001
$\Omega_{aragonite}$	3.6(0.3)	3.3(0.1)	2.3(0.0)	2.2(0.1)	2.0(0.1)	2.6(0.1)	3.8(0.2)	2.8(0.1)	-1.4	-50	t	50.07	<0.0001				
	2.1(0.4)	1.7(0.4)	1.2(0.2)	1.2(0.3)	1.0(0.2)	1.4(0.3)	2.2(0.5)	1.4(0.3)			m	87.22	<0.0001	64.04	<0.0001	-20.08	<0.0001
NEC* ($\text{mmol m}^{-2} \text{h}^{-1}$)	-	9.7(6.7)	5.1(0.2)	-3.1(1.8)	0.3(1.7)	6.1(0.6)	8.9(2.0)	4.5(2.1)	-4.6	-105	t	33.14	<0.0001				
	-	1.6(1.1)	1.3(1.7)	-5.0(2.5)	-3.1(3.0)	0.9(1.8)	4.0(1.4)	-0.1(1.9)			m	12.25	<0.0001	11.36	=0.0025	-7.34	<0.0001

[†]Mean calculated based on data from 12:00 to 08:00

*Rank transformation applied to data to meet assumptions of ANOVA

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Fig. 1. Continuous-flow mesocosm facility at Hawaii Institute of Marine Biology (HIMB).

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Fig. 2. The calcifying community of each mesocosm was dominated by forty colonies of *Montipora capitata*.

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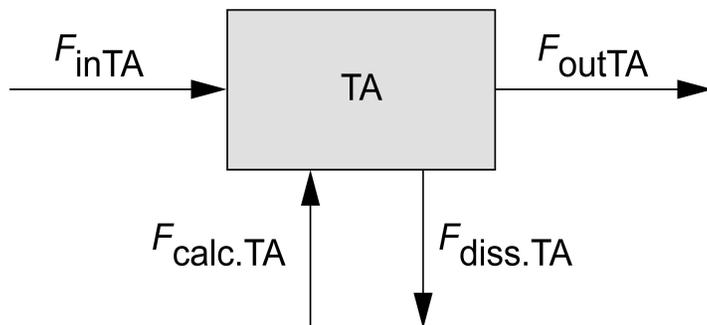
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$$\text{I. } 2\text{NEC} = F_{\text{calc.TA}} - F_{\text{diss.TA}}$$

$$\text{II. } d\text{TA}/dt = F_{\text{inTA}} - F_{\text{outTA}} - 2\text{NEC}$$

$$\text{III. } \text{NEC} = [F_{\text{inTA}} - F_{\text{outTA}} - d\text{TA}/dt]/2$$

Fig. 3. The mesocosms are well mixed systems and can be represented by a simple box model. Assuming that changes in total alkalinity (TA) are uniquely attributed to calcification or carbonate dissolution, the Net Ecosystem Calcification (NEC) can be easily calculated according to equations I. to III. by measuring the TA of the inflowing (F_{inTA}) and outflowing (F_{outTA}) seawater, and the change in TA per unit time ($d\text{TA}/dt$) of the seawater in the mesocosms between consecutive sampling times. The NEC is multiplied by 2 owing to the fact that for every 1 mol of CaCO_3 precipitated or dissolved, 2 mol of TA is produced or removed.

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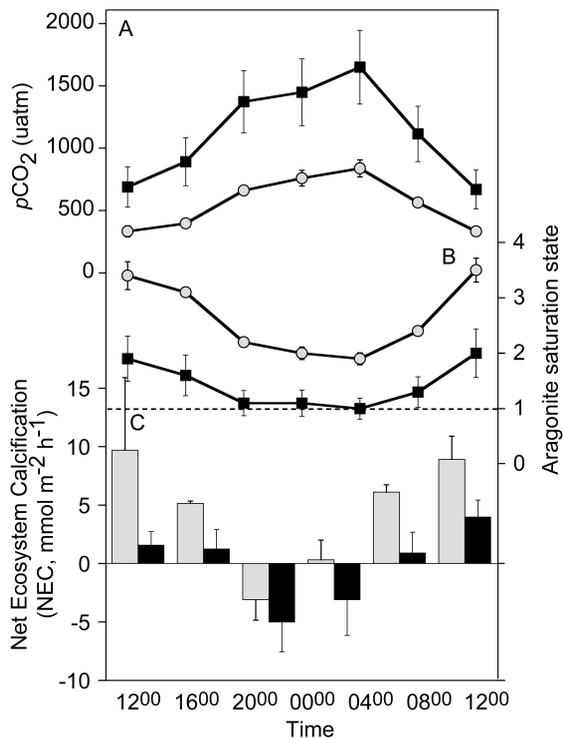


Fig. 4. (A) Seawater partial pressure of CO_2 ($p\text{CO}_2$) and (B), saturation state with respect to aragonite ($\Omega_{\text{aragonite}}$) in the control (gray) and treatment (black) mesocosms as a function of time. The dashed line represents seawater equilibrium with respect to aragonite ($\Omega=1$). (C) NEC in the control and treatment mesocosms during a complete diel cycle under the chemical conditions shown in (A) and (B). Positive values imply net calcification and negative values imply net dissolution. Error bars denote 1 standard deviation ($n=3$).

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