Reviewer #1: We thank you very much for your helpful review. Below are responses to your comments and specific questions.

One problem with TA anomaly when looking at bioerosion is that it measures only the "chemical dissolution". The breaking of CaCO3 structure is also important and it would have been nice to do buoyant weight measurements to quantify the overall decrease in weight of rubbles (i.e. how much is dissolved vs how much is broken in smaller pieces).
This is an important point. Using the TA anomaly method, we can only address the impacts of climate stress on chemical dissolution and not the breakdown of $CaCO_3$ into smaller pieces (e.g., the production of sponge chips). We have added text to section 2.3 Experimental Design in the revision to clarify this limitation. Note that, because the rubble communities had both secondary calcifiers and bioeroders, the distinction between chemical and mechanical breakdown could not be distinguished using buoyant weight: the change in weight includes both the addition of $CaCO_3$ by secondary calcifiers and the breakdown of $CaCO_3$ by eroders. Additionally, it would have been challenging to obtain an accurate estimate of change in buoyant weight given the short duration of the experiment and, therefore, the small magnitude of weight changes relative to the weight of the rubble pieces (1748 g, on average). Nonetheless, we have highlighted this limitation of the TA anomaly method and noted that it is an important distinction for future studies to address.

Specific points:

P12804: What were the flow rates in the mesocosms?
Flow rates were 115 ± 1 (SD) ml min^{-1}, as reported in section 2.4 – Mesocosm Set-up

P12804-l-19: Please provide _ sizes of the rubbles. How was the homogeneity of the rubbles determined? I guess dissolution of old rubbles would be different than the one of "young" rubbles?
There was approximately 1.2L of rubble in each tank, as reported in the third paragraph of section 2.3 – Experimental Design. In response to the reviewer's question, we have added some additional information describing the characteristics of the rubble (3-4 pieces of average weight 499 ± 148 g , average skeletal density of 1.53 ± 0.1 g cm^{-3} (mean ± SD, n=85)) to give the reader a better sense of the volume and homogeneity of rubble pieces. To keep rubble consistent among aquaria, we kept the volume, weight, and skeletal density of individual rubble pieces consistent and put a similar total volume of rubble in each aquarium. In addition, NEC and NCP rates were normalized to the surface area of rubble in each aquarium. We agree with the reviewer that the age of the rubble could be relevant to the dissolution rate. However, the age of the collected rubble is unknown. We accounted for this in two ways: we controlled for rubble density (expecting that rubble density may be a proxy for rubble age), and we randomized rubble pieces across treatments (so that variation in age adds noise, but not systematic bias, across treatments).

P12804-l-19: Why were the incubations not replicated? 24h incubations are easy to replicates and could have inform on temporal changes.
This manuscript reports the experiment as it was performed. Limitations of facility time and sample cost prevented us from repeating the 24-hour incubations. Despite this limitation, we believe that the results of this experiment give important insights into community calcification processes and will be of interest to Biogeosciences readers.

P12805-l-10. I guess the TA changes in the mesocosms were very limited. Were the errors associated with measurements small enough to be sure to detect a change in calcification? Maybe you should provide the range of TA changes during incubations.

We have added information on the magnitude of TA changes during the day and the night to the methods text in 2.5.1 – Total Alkalinity, the same section where the accuracy and precision of the TA measurements are reported: "The accuracy of the titrator never deviated more than ±0.8% from the standard, and TA measurements were corrected for these deviations. The precision was 3.55µEq (measured as standard deviation of the duplicate water samples).During the 24-hour control experiment, the average changes in TA were 37µEq over the day and 20µEq over the night (day and night TA changes were of larger magnitude in the treatment experiments): these are measurable changes given the precision and accuracy of the TA measurements." In addition, the regression analysis indicates that the systematic differences due to treatment effects exceeded the variability due to error, including measurement error.

P12808-l-5: What do you mean by normalized to DIN? Do you mean that TA was corrected for the changes in NH4+ etc? Please clarify.

TA was corrected for changes in the concentration of nitrate, nitrite, ammonium, and phosphate. We have changed the wording in section 2.6 Measuring Net Ecosystem Calcification and added a citation. It now says "TA was normalized to a constant salinity (35 psu) to account for changes due to evaporation and then corrected for dissolved inorganic nitrogen and phosphate to account for their small contributions to the acid-base system (Wolf-Gladrow et al., 2007)."

P12808-l-11: A change in TA in mmolCaCO3 m-2 h-1? Reformulate this sentence.

Sentence changed to read, "F_{TAin} is the rate of TA flowing into an aquarium (= average TA in the header tank times the flow rate), F_{TAout} is the rate of TA flowing out of an aquarium (= average TA in the aquarium times the flow rate), and , $\frac{d\mathrm{TA}}{dt}$ is the change in TA in an aquarium during the measurement period (change in TA normalized to the volume of water and the surface area of the rubble). The rates are measured in mmol $CaCO_3$ m^{-2} hr^{-1} (specific calculations are given in the supplemental material)."

P12808-l-11: Rates are normalized in mmol CaCO3 m-2 h-1, does m-2 represents the surface of the mesocosms, surface of the rubble, etc? Clarify.

Data are normalized to the surface area of the rubble. This was stated in the original MS on page 12805 line 14 : "… and normalized all our calculations to the surface area of the rubble in each tank". For clarity, we added "change in TA normalized to the surface area of the rubble" to section 2.6 Measuring Net Ecosystem Calcification and included this detail in the description of the calculations in the appendix.

P12809-l-10: What about the exchanges with the atmosphere? Were the tanks sealed? If not, exchanges with the atmosphere could have lead to under/overestimations of photosynthesis and respiration.

The tanks were not sealed. Air-sea CO_2 flux is minimal for windspeeds less than 10 ms^{-1} (Wanninkhof 1992). In our indoor mesocosm system, the windspeed inside the mesocosm room was near zero. Therefore, we did not account for air-sea fluxes in our analysis.

P12811-l-14: Provide details on the response of NCP.

We have added data on the response of NCP to the results section in the text and in a new table and an extended figure in the main text and in the supplement. Table 3 now includes the regression results for standardized climate change vs NCP, and Figure 3 now has an additional panel showing the relationship between Standardized Climate Change and NCP. Table A2 has the

regression analysis for NCP and Figure A4 shows the means and standard error bars for NCP by treatment.

P12812-l-12: Are the normalization the same? If in the present study the rates are normalized by the actual surface of the rubbles (which needs to be clarified, see above) it might be different than the study of Yates and Halley who normalized by planar surface...

Added this sentence for clarification, "It is important to note that we normalized our rates to the surface area of the rubble while Yates and Halley (2006) normalized their rates to planar surface area." to the discussion.

P12813-l-2-14: I am really not convinced by this explanation for two reasons. – What was the importance of the CCA? Most of the photosynthesis was likely due to turf algae and not to calcify algae. - In addition the authors mention themselves later "non-photosynthesizing invertebrates in the community (such as bivalves) might be dominating the calcification signal in these conditions." In contrast I think that the second hypothesis makes much more sense and should be developed.

We expanded on this point in the discussion. We also added a thermally-induced metabolic response as a possible mechanism. This paragraph now reads as follows:

"1) Some calcifiers can maintain and even increase their calcification rates in acidic conditions (Kamenos et al., 2013;Findlay et al., 2011;Rodolfo-Metalpa et al., 2011;Martin et al., 2013) by either modifying their local pH environment (Hurd et al., 2011) or partitioning their energetic resources towards calcification (Kamenos et al., 2013). For example, in low, stable pH conditions the coralline algae, *Lithothamnion glaciale*, increased its calcification rate relative to a control treatment but, did not concurrently increase its rate of photosynthesis (Kamenos et al., 2013). Kamenos et al (2013) suggest that the up-regulation of calcification may limit photosynthetic efficiency. In the present study, the increase in G_{day} coincided with a decrease in net photosynthesis (Figure 3a,b). Photosynthesizing calcifiers in the community may be partitioning their energetic resources more towards calcification and away from photosynthesis in order to maintain a positive calcification rate (Kamenos et al., 2013). Notably, turf algae likely have a major control over the NCP in this community which would not have any impact on calcification. 2) An alternative hypothesis is that the calcifiers may be adapted or acclimatized to high pCO_2 conditions (Johnson et al., 2014) and have not yet reached their threshold because the rubble was collected from a naturally high and variable pCO_2 environment (Guadayol et al., 2014; Silbiger et al. 2014). 3) In this study, the calcifiers experienced a combined increase in both pCO_2 and temperature and, thus, the non-linear response in G_{day} may also be due a metabolic response. In a typical thermal performance curve, organisms increase their metabolism until they have reached a thermal maximum and then rapidly decline (Huey and Kingsolver, 1989; Pörtner et al., 2006), and we see this response in our results. A recent study found a similar nonlinear response to temperature and pCO_2 in the coral *Siderastrea sidera* (Castillo et al. 2014). While they attribute the pCO_2 response to photosynthesis being neutralized (we did not see this response in our non-coral community), they suggest that the thermal response is due to both changes in metabolism and thermally-driven changes in aragonite saturation state (Castillo et al. 2014). "

-P12814-l-7-15: I agree with this paragraph but it would be important to specify that this is true for an ecosystem dominated by rubbles. In an ecosystems with very high coral cover, the story would likely not be the same...

We clarified that this generalization is specific to our rubble community. This sentence now reads, "Standardized Climate Change explained more of the variance in dissolution than

in calcification in our rubble community: ($R^2_{G_{night}} = 0.64 > R^2_{G_{day}} = 0.33$; Table 2) this result is not surprising"

Reviewer 2: We thank you very much for your helpful review. Below are responses to your comments and specific questions.

General comments:

As a more general question though I wondered the following: since the organisms being studied here are described as "secondary calcifiers" how do their responses impact coral reefs directly, which I'm assuming is thought of in this context as "primary calcification"?

While secondary calcification contributes significantly less to the overall growth of coral reefs than primary calcifiers (such as corals), secondary calcifiers still play several key ecological roles on coral reef ecosystems. For example, they help to cement the reef together which maintains reef stability, and they produce chemical cues that induce the settlement of many types of invertebrate larvae (including corals). I have added this information to the introduction.

Specific points:

1. (12802, 20) – Is it "increase to 557 ppm by the year 2100" (rather than "increase by 557 ppm the year 2100")?

The increase actually is "by 557", not "to". RCP 8.5 is a high-emissions scenario, but one that we are currently tracking. Meinshausen et al., 2011 states that under the RCP8.5/ECP8.5 scenario pCO_2 is predicted to be 936ppm by 2100, which is 557ppm above current levels (379ppm).

2. (12804, 9) – How long were the aquaria monitored without rubble to establish the stability conditions in Table 1? How many measurements were made to determine the mean values in this table?

The data presented in Table 1 are from one 24 hour cycle: each aquarium was measured in the light and then, again, in the dark. Each entry in the table is the average of 12 measurements: day samples and night samples for each of the six aquaria. This is now clarified in the text and the table caption. We have also changed the wording to reflect that these measurements demonstrate the consistency of the treatments within each rack between day and night, but not temporal stability, persay. The temporal stability of the mesocosm system was measured over a 26 day period and is reported in Putnam (2012). We have added this citation to the ms.

3. (12807, 2) - Is there a reference for the technique used to determine pH?

Yes, the reference is Dickson, A. G., Sabine, C. L., and Christian, J. R.: Guide to best practices for ocean CO2 measurements, 2007. This was referenced later in the paragraph, but we have added it to the end of line 3 for clarity.

4. (12808, 5) – I think there must be some words missing here in this description of how things were normalized to DIN.

This sentence now reads, "TA was normalized to a constant salinity (35 psu) to account for changes due to evaporation and then corrected for dissolved inorganic nitrogen and phosphate to account for their small contributions to the acid-base system (Wolf-Gladrow et al., 2007)."

5. (Eqn. 1) - I think a little more detail is needed for how the 3 measurements made per experiment (12805, 7-11) were specifically used in this equation (i.e., which values were used to determine the F values, and which were used for dTA/dt). The same is true for Eqn. 2 although I assume the same general approach was used in both cases.

We added some additional text to describe the equation. "F_{TAin} is the rate of TA flowing into an aquarium (= average TA in the header tank times the flow rate), F_{TAout} is the rate of TA flowing out of an aquarium (= average TA in the aquarium times the flow rate), and , $\frac{d\mathrm{TA}}{dt}$ is the change in TA in an aquarium during the measurement period (change in TA normalized to the volume of water and the surface area of the rubble). The rates are measured in mmol $CaCO_3$ m^{-2} hr^{-1} (specific calculations are given in the supplemental material)."

Additionally, we added the specific calculation for F_{TAin}, F_{TAout} , and $\frac{d\mathrm{TA}}{dt}$ to the supplemental files. These calculations follow Andersson et al. 2009, as referenced in the text.

6. (12810, 5) – I'm not sure I understand why a simple product of temperature and pCO2 was used as the independent variable (i.e., the one sentence explanation here seems inadequate to me).

We agree with the reviewer that a simple product of pCO_2 and temperature was not straightforward to interpret. We have revised the manuscript so that the Standardized Climate Change (SCC) axis is a simple linear combination of ΔpCO2 and ΔTemperature that puts ΔpCO_2 and ΔTemperature on the same scale. The results and interpretations of our study are the same with this new axis (indeed, any of several choices of synthetic axes produced similar results). Further, we added figures to the supplement showing G and NCP versus ΔpCO_2 and versus ΔTemperature to show that the relationships between G and NCP versus ΔpCO_2 and ΔTemperature are similar to the relationships using the combined axis (Standardized Climate Change). Here is the explanation of our new version of the SCC axis in the text:

"Although we imposed four discrete temperature-pCO_2 scenario treatments on each tank (Table 1), random variation between treatments and the feedback between the rubble communities and the water chemistry resulted in near-continuous variation in temperature-pCO_2 treatments across aquaria (Figures 2 and A1). To capture this continuous variation in temperature-pCO_2 in the analysis, we used the measured temperature-pCO_2 seawater condition as a continuous independent variable in a regression rather than the four categorical treatment conditions in an ANOVA (an analysis of G and NCP using the ANOVA approach is included in Figures A3, A4 and Tables A1, A2). The regression approach allowed us to better capture the quantitative relationships between net calcification (G) or NCP and the temperature-pCO_2 treatment. We created a single, continuous variable, Standardized Climate Change (SCC), from a linear combination of temperature and pCO_2 values in each aquarium. A simple linear combination was used because pCO_2 increased linearly with temperature (Figure 2), as imposed by our treatments. We first calculated the relationship between ΔTemp (Eq 3) and ΔpCO_2 (Eq 4) using linear regression. The coefficients from this regression (slope: α = 0.0031; y-intercept: β = -0.078) were used to combine pCO_2 and temperature onto the same scale, as a measure of Standardized Climate Change (Eq 5):

$$\Delta Temp_i = Temp_{trt,i} - Temp_{cont,i} \quad \text{Eq. 3}$$

$$\Delta pCO_{2_i} = pCO_{2_{trt,i}} - pCO_{2_{cont,}} \quad \text{Eq. 4}$$

$$SCC_i = \Delta Temp_i + \alpha * \Delta pCO_{2_i} + \beta \quad \text{Eq. 5}$$

This synthetic temperature-pCO_2 axis, SCC, is centered on the ambient (control) conditions such that a value of 0 corresponds to present day Kāne'ohe Bay conditions, a negative value corresponds to water that is colder and less acidic (pre-industrial) and a positive value corresponds to water that is warmer and more acidic (future conditions) compared to background seawater. (The independent relationships between G and NCP with ΔTemp and ΔpCO_2 are shown in Figures A5 and A6 and are similar to the relationship with SCC.)'

7. It also occurred to me that if calcification rates vary differently in response to changes in temperature versus changes in pCO2, then this might explain the non linear response seen in Fig. 3A. I would think that this might be considered a bit more explicitly in the discussion starting on line 24, p. 12812.

Yes, we agree. We have added a section to the discussion about the impact of temperature on daytime calcification, specifically focusing on metabolic response.

8. (12811,15) – Which G values were used in Figs. 4 and 3A? Since Gnet = Gday + Gnight, using Gnet here (along with Gday and Gnight) would seem to be "doubledipping" with the data.

G_{net} is the sum of G_{day} and G_{night}. We thought that it was critical to show our readership the response of net calcification over a 24 hour cycle. Figure 3e highlights the aquaria that were net calcifying or net dissolving over the entire experiment. It is difficult to elucidate this from figures 3a and c alone. We added a line at the zero point in 3e to futher highlight that there is a shift from net calcification to net dissolution over the 24 hour cycle. The data shown in Figure 4 are simply the day (squares) and night (circles) data. The figure legend reads: "Squares are data collected during the light (day) conditions and circles represent data collected during dark (night) conditions".

"Double dipping" typically refers to an iterative analysis where initial analyses or preprocessing of data guides subsequent analyses and increases the likelihood that the subsequent analyses are signficant. Here, the separate and planned analyses of day, night, and net are critical because each analysis gives distinct information to the reader about the community response to climate change when (day) photosynthesizers are active and (night) when all members of the community are respiring, and (net) whether there is net calcification or net erosion over a diel cycle. Although G_{net} is not statistically independent of G_{night} and G_{day}, it is still appropriate to analyze the sum separately from the components: for example, consider if G_{day} had a positive relationship with SCC and G_{night} had a negative relationship with SCC and, when summed, G_{net} had no significant relationship with SCC. Each of these results would tell us something different and important about the relationship between calcification and SCC (daytime calcification increases with SCC, nighttime calcification decreases with SCC, and daily net calficifation is unaffected by SCC). Although the actual results of this study are somewhat more complex, all three analyses must be presented for the reader to understand the dynamics of the system.

9. (12811, 21) –Maybe I'm getting caught up in semantics but referring to changes in carbonate system parameters due to calcificiation, dissolution, photosynthesis and respiration as "feedbacks" seems to imply a bit more complexity than is really occurring. I'm not sure I would use this word here and throughout the manuscript to describe how these biological processes affect carbonate chemistry.

We disagree. As CO_2 is added to the water it impacts the biology of the organisms, and those biological responses then also change the water chemistry. For example, increased pCO_2 decreases pH which may result in increased erosion/dissolution, or increased pCO_2 may enhance photosynthesis, which could increase erosion/dissolution by autotrophic microborers (Tribollet et al. 2009). The enhanced photosynthesis then also alters the seawater chemistry. This interaction between the biology and chemistry causes a feedback loop. The term "Feedbacks" has been used in the literature (e.g., Jury et al 2011, Anthony et al 2011) to describe the interaction between increased CO_2 from the atmosphere and biological responses (e.g. calcification, dissolution, respiration, and photosynthesis) in altering the chemistry of the seawater. In our study, we saw a positive relationship between the amount of CO_2 that we added to the mesocosms and the deviation in CO_2 from the intended concentration (Figure A1). If there were no feedbacks, then the relationship between pCO_2 with rubble and pCO_2 without rubble from each aquarium would

have a slope of one with a fixed offset (change in y-intercept) due to increased respiration by the organisms. With feedbacks, we would expect that as pCO_2 increases, feedbacks would increase resulting in deviations from the 1:1 slope. During the day, we saw a slope of 1.1 while during the night, the slope was much greater than one (slope = 1.4, Figure A1b). This relationship suggests that there were feedbacks in our mesocosms. We added regression lines to Figure A1 to better illustrate these feedbacks.

10. (12811,17) - I think it would help if the data described here as "exceptions" were explicitly indicated on Figs. 4 and 3A (perhaps circled on the figure ?). This concern is also relevant to discussions on p. 12813, line 24 ['This hypothesis . . .].)
We have changed the text to explicitly call out the points in the upper left quadrant with the points in the upper right and lower left quadrants of Figure 4. We have also added y = 0 lines to Figure 3 to make it easier for the reader to identify the net positive versus net negative values. We have shied away from circling these specific points on the graph so as not to distract readers from their own interpretations of patterns in the data. However, we have called out these points much more descriptively and specifically in the text to help orient the reader to the plots – thank you for highlighting the need for this direction.

11. In section 4.2, please don't switch flux units. Mixing 'per day' flux units with 'per hour' flux units makes it very difficult on the reader. If necessary, convert data from the literature to the units you wish to use in the manuscript.
We switched the units to mmol m^{-2} d^{-1} in the text.

12. (12813,10) – "In the present study . . .". Where is this shown? Is "net photosynthesis" actually NCP?
We added a panel with the NCP data to figure 3 and associated references, in the text; we also changed "photosynthesis" to "NCP".

13. (12813,18) – 'We saw a decline . . .". Again, where is this shown?
We added a citation to Figure 3 after this sentence.

14. (12814, 7) – How exactly is "strongly affected" defined here?
We changed the wording to be more precise: "Standardized Climate Change explained more of the variance in dissolution than in calcification in our rubble community: ($R^2_{G_{night}} = 0.64 > R^2_{G_{day}} = 0.33$; Table 2) this result is not surprising"

15. (12814, 15) – Talking about "distinct" responses here seems a little vague.
We added ": G_{day} had a non-linear response while G_{night} declined linearly with Standardized Climate change" for clarification.

16. Figure 4 – Why is the color scale for standardized climate change multiplied by 10^4?
This has been corrected in the revised manuscript using the new Standardized Climate Change axis.

17. Figure A3 – Is the y-intercept listed here (0.0016) correct? Also, it might be worth mentioning somewhere that you would expect the slope here to be roughly 2x that of the slope in Fig. 4 (which is what is actually seen), based on the way G and NCP are defined.

Figure A3b has now been added to the main text as Figure 4b. The y-intercept is 1557.4, and this has been changed in the text. We also note in the Figure 4b caption, "As expected, the slope of TA versus DIC (0.31) is approximately twice that of G versus NCP (0.14). "

Discussion Comment from G. Diaz Pulida

We thank you for commenting on our discussion paper and for your suggestion to add the importance of live tissue in mediating calcification and dissolution. You bring up a very interesting point, and we have expanded on it and cited your paper in the discussion.

Secondary calcification and dissolution respond differently to future ocean conditions.

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Abstract

Climate change threatens both the accretion and erosion processes that sustain coral reefs. Secondary calcification, bioerosion, and reef dissolution are integral to the structural complexity and long-term persistence of coral reefs, yet these processes have received less research attention than reef accretion by corals. In this study, we use climate scenarios from ~~RCP8~~RCP 8.5 to examine the combined effects of rising ocean acidity and SST on both secondary calcification and dissolution rates of a natural coral rubble community using a flow-through aquarium system. We found that secondary reef calcification and dissolution responded differently to the combined effect of pCO_2 and temperature. Calcification had a non-linear response to the combined effect of pCO_2-temperature: the highest calcification rate occurred slightly above ambient conditions and the lowest calcification rate was in the highest pCO_2-temperature condition. In contrast, dissolution increased linearly with pCO_2-temperature. The rubble community switched from net calcification to net dissolution at +~~272~~271 µatm pCO_2 and 0.~~84~~75° C above ambient conditions, suggesting that rubble reefs may shift from net calcification to net

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dissolution before the end of the century. Our results indicate that (i) dissolution may be more sensitive to climate change than calcification~~,~~ and (i) that calcification and dissolution have different functional responses to climate stressors~~, highlighting~~; this highlights the need to study the effects of climate stressors on both calcification and dissolution to predict future changes in coral reefs.

1 Introduction

In 2013, atmospheric carbon dioxide ($CO_{2(atm)}$) reached an unprecedented milestone of 400 ppm (Tans and Keeling, 2013), and this rising $CO_{2(atm)}$ is increasing sea-surface temperature (SST) and ocean acidity (Caldeira and Wickett, 2003;Cubasch et al., 2013;Feely et al., 2004). Global SST has increased by 0.78°C since pre-industrial times (Cubasch et al., 2013), and it is predicted to increase by another 0.8-5.7°C by the end of this century (Meinshausen et al., 2011;Van Vuuren et al., 2008;Rogelj et al., 2012). The Hawai`i Ocean Time-series detected a 0.075 decrease in mean annual pH at Station ALOHA over the past 20 years (Doney et al., 2009) and there have been similar trends at stations around the world including the Bermuda Atlantic Time-series and the European Station for Time-series Observations in the ocean (~~Dropp~~Solomon et al~~., 2013~~. 2007). pH is expected to drop by an additional 0.14-0.35 pH units by the end of the 21st century (Bopp et al., 2013). All marine ecosystems are at risk from rising SST and decreasing pH (Doney et al., 2009;Hoegh-Guldberg et al., 2007;Hoegh-Guldberg and Bruno, 2010), but coral reefs are particularly vulnerable to these stressors (reviewed in Hoegh-Guldberg et al., 2007).

Corals create the structurally complex calcium carbonate ($CaCO_3$) foundation of coral reef ecosystems. This structural complexity is at risk from climate-driven shifts from high-complexity, branched coral species to mounding and encrusting growth forms (Fabricius et al., 2011) and from increases in the natural processes of reef destruction, including bioerosion and dissolution (Wisshak et al., 2012, 2013;Tribollet et al., 2006). While substantial research attention has focused on the response of reef-building corals to climate change (reviewed in Hoegh-Guldberg et al., 2007;Fabricius, 2005;Pandolfi et al., 2011), secondary calcification (calcification by non-coral invertebrates and calcareous algae), bioerosion, and reef dissolution that are integral to maintaining the structural complexity and net growth of coral reefs has received less attention (Andersson and Gledhill, 2013;Andersson et al., 2011;Andersson and Mackenzie, 2012). Bioerosion and dissolution breakdown the reef framework while secondary calcification helps maintain reef stability by cementing the reef together (Adey, 1998; Camoin and Montaggioni, 1994; Littler, 1973) and producing chemical cues that induce settlement of many invertebrate larvae including several species of corals (Harrington et al. 2004; Price 2010). Coral reefs will only persist if constructive reef processes (growth by corals and secondary calcifiers) exceed destructive reef processes (bioerosion and dissolution). In this study, we examine the combined effects of rising ocean acidity and SST on both calcification and dissolution rates of a natural community of secondary calcifiers and bioeroders.

Recent laboratory experiments have focused on the response of individual taxa of bioeroders or secondary calcifiers to climate stressors. For example, studies have specifically addressed the effects of rising ocean acidity and/or temperature on bioerosion

by a *Clionid* sponge (Wisshak et al., 2012, 2013;Fang et al., 2013) and a community of photosynthesizing microborers (Tribollet et al., 2009;Reyes-Nivia et al., 2013). These studies found that bioerosion increased under future climate change scenarios. Several studies have focused on tropical calcifying algae and have found decreased calcification (Semesi et al., 2009; Johnson et al., 2014; Comeau et al., 2013;Jokiel et al., 2008;Kleypas and Langdon, 2006) and increased dissolution (Diaz-Pulido et al., 2012) with increasing ocean acidity and/or SST. However, the bioeroding community is extremely diverse and can interact with the surrounding community of secondary calcifiers: for example, crustose coralline algae (CCA) can inhibit internal bioerosion (White, 1980;Tribollet and Payri, 2001). To understand the combined response of bioeroders and secondary calcifiers, we take a community perspective~~. We~~ and examine the synergistic effects of rising SST and ocean acidity~~, modeled after the Representative Concentration Pathway (RCP) 8.5 climate scenario (Van Vuuren et al., 2011;Meinshausen et al., 2011),~~ on a natural community of secondary calcifiers and bioeroders. Using the total alkalinity anomaly technique, we test for net changes in calcification during the day and dissolution (most of which is caused by bioeroders; ~~(~~Andersson and Gledhill, 2013~~)),~~) at night. ~~RCP scenarios~~Our climate change treatments are modelled after the Representative Concentration Pathway (RCP) 8.5 climate scenario (Van Vuuren et al., 2011;Meinshausen et al., 2011), one of the high emissions scenarios ~~that were~~ used in the most recent Intergovernmental Panel on Climate Change (IPCC) report (Cubasch et al., 2013). The ~~RCP8~~RCP 8.5 scenario predicts ~~that~~an increase in temperature ~~will likely increase by~~of 3.8 – 5.7°C (Rogelj et al., 2012) and an increase in atmospheric CO_2 ~~will increase by~~of 557 ppm by the year 2100 (Meinshausen et al., 2011). We ~~chose to~~ use the

RCP8RCP 8.5 scenario because the current CO_2 concentrations are tracking just above what this scenario predicts (Sanford et al., 2014). While prior studies have focused on the contributions of individual community members, to increased temperature and CO_2; here, we testexamine the community response to the predicted RCP8RCP 8.5 climate scenario and measure both calcification and, dissolution, and net community production rates.

2 Materials and Methods

2.1 Collection Site

All collections were made on the windward side of Moku o Loʻe (Coconut Island) in Kāneʻohe Bay, Hawaiʻi adjacent to the Hawaiʻi Institute of Marine Biology. This fringing reef is dominated by *Porites compressa* and *Montipora capitata*, with occasional colonies of *Pocillopora damicornis*, *Fungia scutaria*, and *Porites lobata*. Kāneʻohe Bay is a protected, semi-enclosed embayment; the residence time can be >1 month long in the protected southern portion of the Bay (Lowe et al., 2009a;Lowe et al., 2009b) that is coupled with a high daily variance in pH (Guadayol et al., 2014). The wave action is minimal (Smith et al., 1981;Lowe et al., 2009a;Lowe et al., 2009b) and currents are relatively slow (5cm s^{-1} maximum) and wind-driven (Lowe et al., 2009a;Lowe et al., 2009b).

2.2 Sample Collection

We collected pieces of dead *Porites compressa* coral skeleton (hereafter, referred to as rubble) as representative communities of bioeroders and secondary calcifiers. Rubble was collected with a hammer and chisel from a shallow reef flat (~1m depth) in November, 2012. Only pieces of rubble without any live coral were collected. The average (±SE)

~~skeletal density of the rubble was 1.53 ± 0.012 g cm^{-3} (n=85).~~ The rubble community in Kāne‘ohe Bay is comprised of secondary calcifiers, including CCA from the genera *Hydrolithon*, *Sporolithon*, and *Peyssonnelia* and non-coral calcifying invertebrates (e.g. boring bivalves (*Lithophaga fasciola* and *Barbatia divaricate*), oysters (*Crassostrea gigas*), and small crustaceans); filamentous and turf algae; and internal bioeroders, including boring bivalves (*L. fasciola* and *B.divaricate*), sipunculids (*Aspidosiphon elegans*, *Lithacrosiphon cristatus*, *Phascolosoma perlucens*, and *Phascolosoma stephensoni*), phoronids (*Phoronis ovalis*), sponges (*Cliona* spp.) and a diverse assemblage of polychaetes (White, 1980). All rubble ~~was~~pieces were combined after collection and maintained in a 100L flow-through tank with ambient seawater from Kāne‘ohe Bay until random assignment to treatments.

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2.3. Experimental Design

The Hawai‘i Institute of Marine Biology (HIMB) hosts a mesocosm facility with flow-through seawater from Kāne‘ohe Bay and controls for light, temperature, pCO_2, and flow rate. The facility is comprised of 24 experimental aquaria split between four racks; each rack has ~~a150L~~a 150L header tank which feeds 6 experimental aquaria, each 50L in volume (Figure 1).

Before adding rubble to the experimental aquaria, we collected day and night samples of pH, total alkalinity (TA), temperature, and salinity from ~~each aquarium during light and dark conditions~~ all aquaria to demonstrate the ~~stability of the system~~ consistency of water conditions across aquaria without any rubble present (Table 1). The long-term temporal stability of the mesocosm system is reported in Putnam (2012). We

then conducted "control" and "treatment" experiments to determine how ~~RCP8~~RCP 8.5 predictions affect daytime calcification and nighttime dissolution rates in a natural rubble community. The first "control experiment" characterized baseline calcification and dissolution in each aquarium caused by differences in rubble communities. In the second "treatment experiment", we manipulated pCO_2 and temperature to simulate four climate scenarios (pre-industrial, present day, 2050, and 2100) and tested the response of calcification~~ and dissolution.~~ , dissolution, and net community production. Each experiment used the TA anomaly method (Smith and Key, 1975; Andersson et al., 2009). This method calculates net calcification from changes in total alkalinity, and calculates net community production from changes in total dissolved inorganic carbon adjusted for changes in carbon due to calcificaiton. Because estimates of calcification are based on changes in total alkalinity, this method does not account for mechanical erosion (e.g., small chips of $CaCO_3$ produced by sponge erosion). However, given the short duration of the experiment and the types of bioeroders present, we expect that chemical dissolution captured a significant proportion of the erosion in the system.

Approximately 1.2L of rubble (3-~~4~~ ~~5~~ pieces of ~~approximately equal size)~~weight 499 ± 148 g and skeletal density 1.53 ± 0.1 g cm^{-3} (mean ± SD, n=85)) were placed in each of the 24 experimental aquaria and acclimated to tank conditions in ambient seawater for three days. On the fourth day, we performed the control experiment, calculating daytime calcification and nighttime dissolution for rubble in ~~the~~ ambient seawater conditions using the TA anomaly technique ~~(Smith and Key, 1975).~~. The next day we manipulated seawater pCO_2 and temperature to replicate four climate scenarios for the treatment experiment ~~(Table 1):~~: pre-industrial (-1±0.057°C and -205±11.9 µatm),

present day (natural Kāneʻohe Bay seawater 24.8±0.09 °C, 614±15.6 µatm), 2050 (+1.4±0.09 °C and +255±31 µatm), and 2100 (+2.4±0.08 and +433±40 µatm). Note that all changes in temperature and pCO_2 were made relative to present day Kāneʻohe Bay seawater conditions: pCO_2 in Kāneʻohe Bay is consistently high relative to the open ocean and can range from 196-976 µatm in southern Kāneʻohe bay depending on conditions (Drupp et al., 2013). The yearly average pCO_2 at our collection site ranged from 565-675 µatm (Silbiger et al., ~~*in review*~~2014). After an acclimation time of seven days, we sampled the treatment experiment, calculating daytime calcification and nighttime dissolution over a 24 hour period.

During both experiments, TA, pH, salinity, temperature, and dissolved inorganic nutrient (DIN) samples were collected every 12 hours over a 24 hour period ~~(total of three times):~~: just before lights-on in the morning (time 1) and just before lights-off at night (time 2) to capture light conditions, and then again before lights-on the next morning (time 3) to capture dark conditions. Flow into each aquarium was monitored and adjusted every three hours to ensure a consistent flow rate over the 24 hour experiment. We calculated net ecosystem calcification ~~and~~, dissolution, and net community production using a simple box model (Andersson et al., 2009) and normalized all our calculations to the surface area of the rubble in each tank. Surface area of the rubble was calculated using the wax dipping technique (Stimson and Kinzie III, 1991) at the end of the experiment.

2.4 ~~Laboratory~~Mesocosm Set-up

The mesocosm facility (Figure 1) is supplied with ambient seawater from Kāne‘ohe Bay, which is filtered through a sand filter, passed through a water chiller (Aqualogic Multi Temp MT-1 Model # 2TTB3024A1000AA), and then fed into one of the four header tanks. pCO_2 was manipulated using a CO_2 gas blending system (see Fangue et al., 2010; Johnson and Carpenter, 2012). Each target pCO_2 concentration was created by mixing CO_2-free atmospheric air with pure CO_2 using mass flow controllers (C100L Sierra Instruments). Output pCO_2 was analyzed using a calibrated infrared CO_2 analyzer (A151, Qubit Systems). CO_2 mixtures were then bubbled into one of the four header tanks and water from each individual header tank fed into the six individual treatment aquaria (Figure 1). The pCO_2 in each treatment aquarium was estimated with CO2SYS (Van Heuven et al., 2009) using pH and TA as the parameters.

Temperature was manipulated in each treatment aquarium using dual-stage temperature controllers (Aqualogic TR115DN). The temperature was continuously monitored with temperature loggers (TidbiT v2 Water Temperature Data Logger, sampling every 20 min) and point measurements were taken during every sampling period with a handheld digital thermometer (Traceable Digital Thermometer, Thermo Fisher Scientific; precision = 0.001 °C). Light was controlled by positioning an oscillating pendant metal-halide light (250 W) over a set of three aquaria and was programmed to emit an equal amount of light to each tank (~500µE of light). Lights were set to a 12:12 hour photoperiod and were monitored using a LI-COR spherical quantum PAR sensor. Flow rate was maintained at 115±1 ml min^{-1}, resulting in a residence time of

7.3±0.07 hours per tank. Each aquarium was equipped with a submersible powerhead pump (Sedra KSP-7000 powerhead) to ensure that the tank was well-mixed.

2.5 Seawater Chemistry

All sample collection and storage vials were cleaned in a 10% HCl bath for 24 hours and rinsed three times with MilliQ water before use and rinsed three times with sample water during sample collection and processing.

2.5.1 Total Alkalinity

Duplicate TA samples were collected in 300 ml borosilicate sample containers with glass stoppers. Each sample was preserved with 100µL of 50% saturated $HgCl_2$ and analyzed within 3 days using open cell potentiometric titrations on a Mettler T50 autotitrator (Dickson et al., 2007). A Certified Reference Material (CRM - Reference Material for Oceanic CO_2 Measurements, A. Dickson, Scripps Institution of Oceanography) was run at the beginning of each sample set ~~to ensure the~~. The accuracy of the titrator~~. Our accuracy was better~~ never deviated more than ±0.8~~%,~~% from the standard, and ~~our~~TA measurements were corrected for these deviations. The precision was 3.55µEq (measured as standard deviation of the duplicate water samples). During the 24-hour control experiment the average changes in TA were 37µEq over the day and 20µEq over the night (day and night TA changes were of larger magnitude in the treatment experiments): these are measurable changes given the precision and accuracy of the TA measurements.

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2.5.2 pH_t (total scale)

Duplicate pH_t samples were collected in 20ml borosilicate glass vials, brought to a constant temperature of 25ºC in a water bath, and immediately analyzed using an m-

cresol dye addition spectrophotometric technique~~.~~ (Dickson et al., 2007). Accuracy of the pH was tested against a Tris buffer of known pH_t from the Dickson Lab at Scripps Institution of Oceanography (Dickson et al., 2007). Our accuracy was better than ±0.04~~%~~%, and the precision was 0.004 pH units (measured as standard deviation of the duplicate water samples). *In situ* pH and the remaining carbonate parameters were calculated using CO2SYS (Van Heuven et al., 2009) with the following measured parameters: pH_t, TA, temperature, and salinity. The K1K2 apparent equilibrium constants were from Mehrbach (1973) and refit by Dickson & Millero (1987) and HSO_4^- dissociation constants were taken from Uppström (1974) and Dickson (1990).

2.5.3 Salinity

Duplicate salinity samples were analyzed on a Portasal 8410 portable salinometer ~~which was~~ calibrated with an OSIL IAPSO standard (accuracy = ±0.003 psu, precision = ±0.0003 psu).

2.5.4 Nutrients

Nutrient samples were collected with 60ml plastic syringes and immediately filtered through combusted 25mm glass fiber filters (GF/F 0.7µm) and transferred into 50ml plastic centrifuge tubes. Nutrient samples were frozen and later analyzed for $Si(OH)_4$, NO_3^-, NO_2^-, NH_4^+, and PO_4^{3-} on a Seal Analytical AA3 HR Nutrient Analyzer at the UH SOEST Lab for Analytical Chemistry.

2.6 Measuring Net Ecosystem Calcification

We assumed that the mesocosms were well mixed systems; thus, we calculated net ecosystem calcification and net communtity photosynthesis following the simple box model presented in Andersson et al. (2009). TA was ~~first~~ normalized to a constant

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246 salinity (35 psu) ~~and to [DIN]~~ to account for changes ~~in TA~~ due to evaporation and
247 ~~photosynthesis/respiration, respectively.~~then corrected for dissolved inorganic nitrogen
248 and phosphate to account for their small contributions to the acid-base system (Wolf-
249 Gladrow et al., 2007). Net ecosystem calcification, or G, was calculated using the
250 following equation:

251

$$G = \left[F_{TAin} - F_{TAout} - \frac{d\mathrm{TA}}{dt}\right]/2 \qquad \text{Eq. 1}$$

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252 where F_{TAin} is the rate of TA flowing into an aquarium (= average TA in the ~~aquaria,~~
253 ~~F_{TAout}~~header tank times the inflow rate). F_{TAout} is the rate of TA flowing out of ~~the~~
254 ~~aquaria,~~an aquarium (= average TA in the aquarium times the outflow rate), and ,
255 ~~$\frac{dTA}{dt}$~~ $\frac{\mathrm{dTA}}{\mathrm{dt}}$ is the change in TA in ~~the aquaria per unit time in mmol $CaCO_3$ m^{-2} hr^{-1}~~an
256 aquarium during the measurement period (change in TA normalized to the volume of
257 water and the surface area of the rubble); specific calculations are given in the
258 supplemental material. The equation is divided by two because one mole of $CaCO_3$ is
259 precipitated or dissolved for every two moles of TA removed or added to the water
260 column. Here, G represents the sum of all the calcification processes minus the sum of all
261 the dissolution processes in mmol $CaCO_3$ m^{-2} hr^{-1}; thus, all positive numbers are net
262 calcification, and all negative numbers are negative net calcification (i.e., net dissolution).
263 Net daytime calcification (G_{day}) is calculated from the first 12 hour sampling period in
264 the light, net nightime dissolution (G_{night}) is calculated from the second 12 hour sampling
265 period in the dark, and total net calcification (G_{net}) is calculated from the full 24 hour

cycle (G_{day} + G_{night}). ~~All rates are~~G_{day}, G_{night}, and G_{net} are converted from hourly to daily rates and presented as mmol $CaCO_3$ m^{-2} d^{-1}.

2.7 Measuring Net Community Production and Respiration

Net community production (NCP) was calculated by measuring changes in DIC (Gattuso et al., 1999). DIC was normalized to a constant salinity (35 psu) to account for any evaporation over the 24 hour period. We used a simple box model to calculate NCP:

$$NCP = \left[F_{\mathrm{DIC}in} - F_{\mathrm{DIC}out} - \frac{d\mathrm{DIC}}{dt}\right] - G \quad \text{Eq. 2}$$

$F_{\mathrm{DIC}in}$, $F_{\mathrm{DIC}out}$, and $\frac{d\mathrm{DIC}}{dt}$ are the rates of DIC flowing into the aquaria, flowing out of the aquaria, and the change in DIC in the aquaria per unit time in mmol C m^{-2} hr^{-1}, respectively. To measure NCP, we subtract G to remove any change in carbon due to inorganic processes. NCP represents the sum of all the photynthetic processes minus the sum of all the respiration processes, thus all positive numbers are net photosynthesis and all negative numbers are negative net photosynthesis (i.e., net respiration). Net daytime NCP (NCP_{day}) is calculated from the first 12 hour sampling period in the light, net nighttime NCP (NCP_{night}) is calculated from the second 12 hour sampling period in the dark, and total NCP (NCP_{net}) is calculated from the full 24 hour cycle (NCP_{day} + NCP_{night}). All rates are presented as mmol C m^{-2} d^{-1}.

2.8 Statistical Analysis

Each aquarium contained a slightly different rubble community because of the randomization of rubble pieces to each treatment. To ensure there were no systematic differences in rubble communities between racks (rack effects) before the experimental

treatments were applied, we tested for differences in ~~G_{day}, G_{night},~~ calcification and ~~G_{net}~~ NCP between racks in the control experiment using an ANOVA~~.~~ (Figure A2).

In the treatment experiment, we first tested for feedbacks in carbonate chemistry due to the presence of rubble: using a paired t-test, we compared the day-night difference in measured pCO_2 in each aquarium with rubble, $\left(pCO_{2,day} - pCO_{2,night}\right)_{rubble}$, and without rubble, $\left(pCO_{2,day} - pCO_{2,night}\right)_{no\ rubble}$. ~~Because of~~

Although we imposed four discrete temperature-pCO_2 scenario treatments on each tank (Table 1), random variation between treatments and the feedback between the rubble communities and the water chemistry resulted in near-continuous variation in ~~pCO_2 and~~ temperature-pCO_2 treatments across ~~treatments and the significant feedbacks in the water chemistry due to the presence of rubble~~ aquaria (Figures 2 and A1~~), a regression using the actual~~). To capture this continuous variation in temperature-pCO_2 in the analysis, we used the measured temperature-pCO_2 seawater condition ~~was more informative than an ANOVA using the imposed seawater condition in testing~~as a continuous independent variable in a regression rather than the four categorical treatment conditions in an ANOVA (an analysis of G and NCP using the ANOVA approach is included in Figures A3, A4 and Tables A1, A2). The regression approach allowed us to better capture the quantitative relationships between net calcification (G) ~~and treatment. Therefore, we used a regression to test for linear and non-linear relationships between day, night,~~or NCP and ~~net calcification (G_{day}, G_{night}, and G_{net}) and our independent variable: change in pCO_2 × temperature from background seawater conditions (hereafter, referred to as~~ the temperature-pCO_2 treatment. We created a single, continuous variable,

Standardized Climate Change~~). (Results using an ANOVA design are included as supplemental materials: Figure A2, Table A1). Standardized Climate Change was calculated as (~~ (SCC), from a linear combination of temperature and pCO_2 values in each~~Treatment~~ ~~Experiment $pCO_{2,i}$ × Temperature$_i$) – (Control Experiment $pCO_{2,i}$ × Temperature$_i$), where *i* represents an individual~~ aquarium. A simple ~~product~~linear combination was used because pCO_2 increased linearly with temperature (Figure 2~~). We~~), as imposed by our treatments. We first calculated the relationship between ΔTemp (Eq 3) and ΔpCO_2 (Eq 4) using linear regression. The coefficients from this regression (slope: α = 0.0031; y-intercept: β = - 0.078) were used to combine pCO_2 and temperature onto the same scale, as a measure of Standardized Climate Change (Eq 5):

$$\Delta Temp_i = Temp_{trt,i} - Temp_{cont,i} \quad \text{Eq. 3}$$

$$\Delta pCO_{2_i} = pCO_{2_{trt,i}} - pCO_{2_{cont,}} \quad \text{Eq. 4}$$

$$SCC_i = \Delta Temp_i + \alpha * \Delta pCO_{2_i} + \beta \quad \text{Eq. 5}$$

This synthetic temperature-pCO_2 axis, SCC, is centered ~~the data around~~on the ambient (control) conditions such that a value of 0~~ in the independent variable (Standardized Climate Change)~~ corresponds to present day Kāne‘ohe Bay conditions, a negative value corresponds to water that is colder and less acidic (pre-industrial) and a positive value corresponds to water that is warmer and more acidic (future conditions) compared to background seawater. (The independent relationships between G and NCP with ΔTemp and ΔpCO_2 are shown in Figures A5 and A6 and are similar to the relationship with SCC.)

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With SCC as a continuous, independent variable, we used a regression to test for linear and non-linear relationships between day, night, and net calcification (G_{day}, G_{night}, and G_{net}) and NCP (NCP_{day}, NCP_{night}, and NCP_{net}) versus SCC. For a simple test of nonlinearity in the response of calcification to ~~standardized climate change~~SCC, we included a quadratic term ~~((Standardized Climate Change)^2~~(SCC^2) in the model. For G_{day}, we used weighted regression (~~Fair, 1974)~~ weight function: $w_i=1/(1+|r_i|)$, where w_i = weight and r_i = residual~~;)~~, Fair, 1974) to account for heteroscedasticity. All other data met assumptions for a linear regression. Lastly, we used a linear regression to test the relationship between G and NCP.

3 Results

3.1 Control Experiment

For rubble in ambient seawater conditions, the average G_{day}, G_{night}, and G_{net} in the control experiment were 3.4±0.16 mmol m^{-2} d^{-1}, -2.4±0.15 mmol m^{-2} d^{-1}, and 0.96±0.20 mmol m^{-2} d^{-1}, respectively. There was no significant difference in G_{day} ($F_{3,23}$=0.68, p=0.58), G_{night} ($F_{3,23}$=1.52, p=0.24), or G_{net} ($F_{3,23}$=1.38, p=0.28) between racks in the control experiment (Figure A2). NCP rates also did not show any racks effects. Average NCP rates were 23.2±1.4 mmol m^{-2} d^{-1} ($F_{3,23}$=0.07, p=0.94) during the day, -20.7±1.9 mmol m^{-2} d^{-1} ($F_{3,23}$=1.95, p=0.15) during the night, and 2.5±2.1 mmol m^{-2} d^{-1} ($F_{3,23}$=1.5, p=0.25) over the entire 24 hour period.

3.2 Treatment Experiment

The rubble communities significantly altered the seawater chemistry, with higher pCO_2 than the applied pCO_2 manipulation, particularly at night (Figure A1). The mean difference between day and night pCO_2 for all treatments was 134.4 ± 39 µatm without rubble and was 438.5 ± 163.9 µatm when rubble was present (t_{23}= -7.23, p<0.0001; Figure 2).

Standardized Climate Change was a significant predictor for G_{day}, G_{night}, and G_{net} (Table 2; Figure 3). G_{day} had a non-linear relationship with Standardized Climate Change (Table 2, Figure 3a), increasing to a threshold and then rapidly declining. G_{night}, however, had a strong linear relationship with Standardized Climate Change (Table 2; Figure ~~3b~~3c), suggesting that joint increases in ocean pCO_2 and temperature will increase ~~night time~~nighttime dissolution of coral rubble. Lastly, G_{net} had a strong negative relationship with Standardized Climate Change (Table 2; Figure ~~3c~~3e) and the rubble community switched from net calcification to net dissolution at an increase in pCO_2 and temperature of 271~~.6~~ µatm and 0.~~84~~75° C, respectively. Standardized Climate Change was also a significant predictor of NCP: Day, night, and net NCP rates all declined with standardized climate change (Table 2; Figure 3b,d,f; Figure3).

~~G and NCP were significantly correlated (~~Net ecosystem calcification increased with net community production ($F_{1,46}$ = 260, p<0.0001, R^2=0.85; Figure 4~~ and Figure A3~~). In general, ~~rubble that was~~communities were net photosynthesizing ~~was also~~and net calcifying ~~and rubble that was~~during the day (Figure 4a: squares in the upper right quadrant) and were net respiring ~~was also~~and net dissolving~~.~~ at night (Figure 4a: circles

in the lower left quadrant). The exception was ~~rubble experiencing~~communities in the most extreme temperature-pCO_2 treatment~~, which was~~: these communities were net respiring during the day while ~~still~~ holding a positive, yet very low, calcification rate~~.~~ (Figure 4a: squares in the upper left quadrant).

4 Discussion

4.1 Carbonate Chemistry Feedbacks

The rubble communities in the aquaria significantly altered the seawater chemistry, particularly at night (t_{23}= -7.23, p<0.0001; Figure 2, Figure A1). This day-night difference in seawater chemistry increased under more extreme climate scenarios, as predicted by Jury *et al.* (2013). This large diel swing in pCO_2 is not uncommon on shallow coral reef environments. pCO_2 ranged from 480 to 975µatm over 24 hours on a shallow reef flat adjacent to our collection site (Silbiger et al ~~*in review*),~~. 2014) and ~~pCO_2~~ ~~ranged~~ from 450 to 742 µatm on a Moloka'i reef flat dominated by coral rubble (Yates and Halley, 2006). Here, pCO_2 had an average difference of 438 µatm between day and night with a range of 412 µatm in the pre-industrial treatment to 854 µatm in the most extreme ~~pCO_2 ×~~ temperature-pCO_2 treatments (Figure 2). In our study, we incorporated these feedbacks into the statistical analysis by using the actual, sampled pCO_2 (and temperature) in each aquaria (Figure 3) rather than using the intended pCO_2 (and temperature) treatments in an ANOVA (~~Table~~Tables A1, ~~Figure~~A2 and Figures A3, A4), better reflecting the pCO_2 experienced by organisms in each aquarium.

4.2 Calcification ~~and~~, Dissolution, and Net Community Production in a High CO_2 and Temperature Environment

Our results suggest that as pCO_2 and temperature increase over time, rubble reefs may shift from net calcification to net dissolution. In our study, this tipping point occurred at a pCO_2 and temperature increase of 271~~.6~~ µatm and 0.~~84~~75° C. Further, our results showed that G_{day} and G_{night} in a natural coral rubble community have different functional responses to changing pCO_2 and temperature (Figure 3). The ranges in G_{day} and G_{night} in our aquaria were similar to *in situ* rates on Hawaiian rubble reefs. Yates & Halley (2006) saw G_{day} values between ~~0.26~~3.3 to ~~0.98~~11.7 mmol $CaCO_3$ m^{-2} ~~hr~~d^{-1} and G_{night} values between -~~0.~~2.4 to -~~3.0~~24 mmol $CaCO_3$ m^{-2} ~~hr~~d^{-1} on a Moloka'i reef flat with only coral rubble~~.~~ (Note that Yates and Halley calculated G over a 4 hour timeframes and the data was multiplied by 3 here to show G in mmol m^{-2} d^{-1}. Also note that we normalized our rates to the surface area of the rubble while Yates and Halley (2006) normalized their rates to planar surface area.). G_{day} and G_{night} in our experiment ranged from ~~0.16~~1.9 to ~~0.78~~9.4 and ~~-0.~~-1.3 to -10~~ to -0.87~~.5 mmol $CaCO_3$ m^{-2} ~~hr~~d^{-1}, respectively, across all treatment conditions. The higher dissolution rates in the *in situ* study by Yates and Halley (2006) are likely due to dissolution in the sediment, which was not present in our study.

G_{day} had a non-linear response to Standardized Climate Change. G_{day} increased with ~~pCO_2 ×~~ temperature-pCO_2 until slightly above ambient conditions, and then decreased under more extreme climate conditions (Figure 3a). This mixed response, increasing and then decreasing with Standardized Climate Change, is reflected in prior experiments. We suggest ~~two~~three possible mechanisms to explain why calcification

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increases in slightly higher ~~$pCO_2 \times$~~ temperature-pCO_2 than ambient conditions. 1) Some calcifiers can maintain and even increase their calcification rates in acidic conditions (Kamenos et al., 2013;Findlay et al., 2011;Rodolfo-Metalpa et al., 2011;Martin et al., 2013) by either modifying their local pH environment (Hurd et al., 2011) or partitioning their energetic resources towards calcification (Kamenos et al., 2013). For example, in low, stable pH conditions the coralline algae, *Lithothamnion glaciale*, increased its calcification rate relative to a control treatment but, did not concurrently increase its rate of photosynthesis (Kamenos et al., 2013). Kamenos et al (2013) suggest that the up-regulation of calcification may limit photosynthetic efficiency. In the present study, the increase in G_{day} coincided with a decrease in net photosynthesis. (Figure 3a,b). Photosynthesizing calcifiers in the community may be partitioning their energetic resources more towards calcification and away from photosynthesis in order to maintain a positive calcification rate (Kamenos et al., 2013). Notably, turf algae likely have a major control over the NCP in this community which would not have any impact on calcification. 2) An alternative hypothesis is that the calcifiers may be adapted or acclimatized to high pCO_2 conditions (Johnson et al., 2014) and have not yet reached their threshold because the rubble was collected from a naturally high and variable pCO_2 environment (Guadayol et al., 2014~~).~~; Silbiger et al. 2014). 3) In this study, the calcifiers experienced a combined increase in both pCO_2 and temperature and, thus, the non-linear response in G_{day} may also be due a metabolic response. In a typical thermal performance curve, organisms increase their metabolism until they have reached a thermal maximum and then rapidly decline (Huey and Kingsolver, 1989; Pörtner et al., 2006), and we see this response in our results. A recent study found a similar nonlinear response to

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temperature and pCO_2 in the coral *Siderastrea sidera* (Castillo et al. 2014). While they attribute the pCO_2 response to photosynthesis being neutralized (we did not see this response in our non-coral community), they suggest that the thermal response is due to both changes in metabolism and thermally-driven changes in aragonite saturation state (Castillo et al. 2014).

We saw a decline in both calcification and ~~photosynthesis~~NCP in the extreme ~~pCO_2 ×~~ temperature-pCO_2 condition~~.~~ (Figure 3). Calcification has been shown to decline with climate stressors and the magnitude of decline differs across species (Kroeker et al., 2010;Pandolfi et al., 2011;Ries et al., 2009;Kroeker et al., 2013). The concurrent decline in ~~photosynthesis~~NCP and calcification (Figure 3a,b & 4) suggests that non-photosynthesizing invertebrates in the community (such as bivalves) might be dominating the calcification signal in these conditions. This hypothesis would explain the pattern that we see in Figure 4, where communities in the most extreme pCO_2 and temperature conditions are net respiring during the day while still maintaining a small, positive calcification rate~~.~~ (Figure 4a: five points in the upper left quadrant).

G_{night} rates are more straightforward, decreasing linearly with pCO_2 and temperature (Figures ~~3b~~3c and 4). NCP_{night} rates also decreased linearly with pCO_2 and temperature (Figure 3d). Similarly, Andersson et al. (2009) saw an increase in dissolution under acidic conditions in a community of corals, sand, and CCA. Previous studies on individual bioeroder taxa have also found higher rates of bioerosion or dissolution in more acidic, higher temperature conditions (Wisshak et al., 2013;Fang et al., 2013;Reyes-Nivia et al., 2013;Tribollet et al., 2009;Wisshak et al., 2012). ~~Studies, including the present one, that focused on community-level responses~~There are several mechanisms

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that could be mediating the increased dissolution rates in the high temperature-pCO_2 treatments: 1) Higher temperatures could increase the metabolism of the bioeroder community, thus increasing borer activity (e.g., Davidson et al. 2013). 2) Because many boring organisms excrete acidic compounds to erode the skeletal structure (Hutchings 1986), reduced pH in the overlaying water column may reduce the metabolic cost to the organisms, making it easier for eroders to breakdown the $CaCO_3$. 3) Higher dissolution rates could be mediated by an increase in the proportion of dolomite in the skeletal structure of CCA on the rubble. A recent study found a 200% increase in dolomite in CCA that was exposed to high pCO_2 and temperature conditions; this increase in dolomite resulted in increased bioerosion by endolithic algae (Diaz-Pulido et al., 2014). However, it is unlikely that changes in the mineralogy of the CCA indirectly increased dissolution here given the short time-scale of our study. In the present study, we used the TA anomaly method to calculate chemical dissolution as a proxy for bioerosion. Future studies should also include measures of mechanical breakdown (e.g. the production of sponge chips) in addition to chemical dissolution for a more complete picture of the impacts of climate stress on reef breakdown. Studies, including the present one, which focused on community-level responses, have consistently found that ocean acidification will increase dissolution rates on coral reefs (Andersson and Gledhill, 2013).

~~Dissolution was more strongly affected by~~ Standardized Climate Change explained more of the variance in dissolution than in calcification~~:~~ in our rubble community: ($R^2_{G_{night}} = 0.64 > R^2_{G_{day}} = 0.33$; Table 2) this result is not surprising. Bioerosion, an important driver of dissolution, may be more sensitive to changes in ocean

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acidity than calcification, leading to net dissolution in high CO_2 waters. Many boring organisms excrete acidic compounds, which may be less metabolically costly in a low pH environment. Erez et al. (2011) hypothesize that increased dissolution, rather than decreased calcification, maybe be the reason that net coral reef calcification is sensitive to ocean acidification. The results of this study support this hypothesis. Although G_{net} declines linearly with pCO_2-temperature, calcification (G_{day}) and dissolution (G_{night}) have distinct responses to Standardized Climate Change~~.~~: G_{day} had a non-linear response while G_{night} declined linearly with Standardized Climate Change. Our results highlight the need to study the effects of climate stressors on both calcification and dissolution.

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Author contributions:

Conceived and designed the experiments: NJS MJD. Performed the experiments: NJS. Analyzed the data: NJS MJD. Wrote the paper: NJS MJD.

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Table 1: Means and standard errors of all measured parameters by rack. pCO_2, HCO_3^-, CO_3^{2-}, DIC, and Ω_{arag} were all calculated from the measured TA and pH samples using CO2SYS. Each table entry is the mean of 12 water samples: one daytime sample and one nighttime sample for six aquaria within a rack. Data are all from the imposed treatment conditions with no rubble inside the aquaria.

Rack	Pre-industrial	Present Day	2050 prediction	2100 prediction
Temp (°C)	23.8±0.07	24.8±0.08	26.2±0.06	27.2±0.08
Salinity(psu)	35.65±0.01	35.71±0.02	35.62±0.02	35.71±0.02
Total Alkalinity (µmol kg^{-1})	2137±1.7	2138±2.3	2139±2.0	2142±1.9
pH_t	8.02±0.02	7.87±0.01	7.74±0.02	7.67±0.02
pCO_2 (µatm)	409±20.0	614±15.6	868±33.0	1047±38.7
HCO_3^- (µmol kg^{-1})	1692±16.9	1815±7.3	1894±7.8	1939±6.6
CO_3^{2-} (µmol kg^{-1})	194.20±6.7	147.08±2.8	113.98±3.8	99.24±3.3
DIC (µmol kg^{-1})	1898±10.9	1980±5.1	2032±5.0	2067±4.5
Ω_{arag}	3.06±0.1	2.32±0.04	1.80±0.06	1.57±0.05
NO_2^- (µmol L^{-1})	0.082 ± 0.0028	0.078 ±0.0045	0.074 ± 0.0047	0.070 ± 0.0051
PO_4^{3-} (µmol L^{-1})	0.017 ±0.014	0.0097 ±0.0081	0.033 ±0.016	0.018±0.0061
$Si(OH)_4$ (µmol L^{-1})	3.60 ±0.58	3.64 ±0.61	3.88 ± 0.49	3.78 ± 0.52
NH_4^+ (µmol L^{-1})	0.45 ±0.30	0.19 ±0.067	0.23 ±0.15	0.34 ± 0.14
NO_3^-(µmol L^{-1})	2.13±0.20	2.25±0.21	2.55±0.10	2.48±0.11

Table 2: Regression results for the treatment experiments: G_{day}, G_{night}, and G_{net} versus Standardized Climate Change (Figure ~~3).~~3a,c,e) and NCP_{day}, NCP_{night}, and NCP_{net} versus Standardized Climate Change (Figure 3b,d,f). Bold values indicate a statistically significant p-value at an α <0.05.

	SS	df	F	p	R^2
G_{day}					
Standardized Climate Change	~~5.82~~3.79	1	1.~~97~~45	0.~~17~~06	
(Standardized Climate Change)^2	~~18.67~~23.	1	~~6.33~~	**0.~~02~~**	
Error	~~61.86~~	21	~~2.95~~		0.~~29~~
G_{night}					
Standardized Climate Change	~~73.60~~67.	1	~~50.09~~39.1	**<0.0001**	
Error	~~32.32~~	22			0.~~70~~
G_{net}					
Standardized Climate Change	~~89.79~~88.	1	~~20.25~~19.4	**<0.001**	
Error	~~97.57~~ ~~99.35~~	22	~~0.002~~		0.~~48~~ ~~47~~
NCP_{day}					
Standardized Climate Change	5687.2	1	57.36	**<0.0001**	
Error	2181.4	22			0.72
NCP_{night}					
Standardized Climate Change	3816.1	1	52.06	**<0.0001**	
Error	1612.6	22			0.70
NCP_{net}					
Standardized Climate Change	17925	1	121.47	**<0.0001**	
Error	3246.4	22			0.85

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Figure 1: A schematic of the mesocosm system at the Hawai‘i Institute of Marine Biology. Ambient seawater is pumped into the system from a nearby fringing reef in Kāne‘ohe Bay. The seawater is filtered with a sand trap filter, passed through a water chiller and then fed into one of four header tanks. pCO_2 is manipulated in each header tank by bubbling a mixture of CO_2-free air and pure CO_2 to the desired concentration. The water from one header tank flows into 6 aquaria (a rack). Light is controlled by rack with metal-halide lights. There are two metal-halide lights per rack with each light oscillating over a set of three aquaria. Flow and temperature are controlled in each individual aquarium with flow valves and aquarium heaters and coolers, respectively.

Figure 2: pCO_2 and temperature in each aquarium (a) without any rubble present and (b) with rubble present. Daily variability in pCO_2 was higher when rubble was present due to feedbacks from the rubble community (~~Note~~note the different x-axis scales in panels a and b). Panel (c) shows the mean difference between day and night pCO_2 with and without rubble present with observations paired by aquarium (error bars are standard error) (t_{23}= -7.23, $p<0.0001$).

Figure 3: Net ecosystem calcification~~:~~ ((a) G_{day}, (~~b~~c) G_{night}, (~~c~~e) and G_{net}) and net community production ((b) NCP_{day}, (d) NCP_{night}, and (f) NCP_{net}) versus Standardized Climate Change~~.~~ (SCC). Each point represents net ecosystem calcification (left panel) or net community production (right panel) calculated from an individual aquarium. Standardized Climate Change was centered around background seawater conditions such that a value of 0 indicated that there was no change in pCO_2 or temperature. Positive values indicate an elevated pCO_2 and temperature condition relative to background and negative values represent lower pCO_2 and temperature conditions. G_{day} had a non-linear relationship with Standardized Climate

Change (y = ~~-1.6×10^{-8}~~0.27 x^2 + ~~1.4×10^{-4}x~~0.59x+5.~~5~~7), while G_{night} (y=-~~1.~~0.63x - 3~~×10^{-4}x -~~ ~~3.4.~~6) and G_{net} (y=~~-~~=--0.76x + 1.~~7×10^{-4}x + 1.4~~) each had a negative linear relationship with Standardized Climate Change (Table 2). NCP_{day} (y=-7.01x +23.4), NCP_{night} (y=-35.76 – 4.74), and NCP_{net} (y=-12.07x – 10.85) all had significant negative relationships with Standardized Climate Change. Black lines are best fit lines for each model with 95% confidence intervals in gray. Greek letters on the top panel represent the imposed conditions for pre-industrial (α), Present Day (β), 2050 (γ), and 2100(δ). The black horizontal line in in panels (b), (e) and (f) shows the point where G and NCP = 0. Points above the line are net calcifying (e) or net photosynethsizing (f) and points below the line are net dissolving (e) or net respiring (f) over the entire 24 hour period.

Figure 4: (a) Calculated G and NCP rates for all treatment aquaria. ~~The color represents Standardized Climate Change.~~ Squares are data collected during ~~the~~ light (day) conditions and circles represent data collected during dark (night) conditions~~. All negative numbers are either net dissolution or net respiration while positive numbers are net calcification or net photosynthesis.~~, and the color represents Standardized Climate Change (color bar). There is a strong positive relationship between G and NCP (y = 0.14x + 1.9, p<0.0001, R^2=0.85). Negative and positive y-values are net dissolution and net calcification, respectively; negative and positive x-values are net respiration and net photosynthesis, respectively. (b) TA versus DIC: There is a strong positive relationship between TA and DIC (y = 0.31x + 1577.4, p<0.0001, R^2=0.85). Black and gray lines represent the best-fit line and 95% confidence intervals, respectively. ~~Supplementary Figure A3 is a similar plot with specific aquaria labeled.~~ As expected, the slope of TA versus DIC (0.31) is approximately twice that of G versus NCP (0.14).

792

~~**Appendix A:**~~

Supplemental Material:

Tables A1-A2

Figures A1-A46

Table A1: Analysis of ~~treatment experiment using ANOVA table (Figure A4)~~variance for G_{day}, G_{night}, and G_{net} ~~versus Standardized Climate Change. Bold values indicate a statistically significant p-value at an α <0.05.~~across the four climate scenario treatments (Figure A3).

	SS	df	MS	F	p
G_{day}					
Treatment~~Groups~~	28.83	3	9.81	3.65	**0.030**
Error	52.61	20	2.63		
Total	81.45	23			
G_{night}					
~~Groups~~	60.39	3	20.13	8.84	**<0.0001**
Error	45.53	20	2.28		
Total	105.92	23			
G_{net}					
~~Groups~~	104.31	3	34.77	8.37	**<0.0001**
Error	83.05	20	4.15		
Total	197.36	23			

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Table A2: Analysis of variance for NCP_{day}, NCP_{night}, and NCP_{net} versus climate scenario treatments (Figure A4).Climate Change.

	SS	df	MS	F	p
NCP_{day}					
Treatment	6265.3	3	2088.4	26.0	**<0.0001**
Error	1603.2	20	80.2		
Total	7868.6	23			
NCP_{night}					
Treatment	4145.2	3	1381.7	21.5	**<0.0001**
Error	1283.4	20	64.2		
Total	5428.6	23			
NCP_{net}					
Treatment	1936.8	3	6456.0	71.6	**<0.0001**
Error	1803.4	20	90.17		
Total	2117.1	23			

Figure A1: Feedbacks in seawater chemistry caused by the presence of rubble during the (a) day and (b) night. X-axis is pCO_2 in seawater without any rubble and y-axis is pCO_2 in seawater with rubble present. Color represents temperature. ~~The top panel is data collected during the day and the bottom panel is data collected at night.~~ The black dashed line is a 1:1 line~~.~~ and the blue line is a regression line. The pCO_2 conditions drift farther away from the manipulated conditions during the night. The slopes from each regression analysis were both greater than one (Day: $y = 1.12x + 19.83$, Night: $y = 1.43x + 44.54$) meaning that the

biological feedbacks were greater at more extreme treatments and greater during the night than the day.

Figure A2: Boxplots for G_{day} (~~A~~a), G_{night} (~~B~~b), and G_{net} (~~C~~c) for the control experiment~~,~~ separated by rack. We used an ANOVA to test for differences across racks and found no significant difference in G_{day} ($F_{3,23}$=0.68, p=0.58), G_{night} ($F_{3,23}$=1.52, p=0.24), or G_{net} ($F_{3,23}$=1.38, p=0.28~~) .~~).

Figure A3: ~~Panel A is G versus NCP rates numbered by tank. Data and best fit line are the same as Figure 4. Panel B is salinity normalized TA on the y axis and salinity normalized DIC on the x axis in µmol kg^{-1}. There is a strong positive relationship between TA and DIC ($y = 0.31x + 0.0016$, $p<0.0001$, $R^2=0.85$).~~

~~**Figure A4:**~~ Means and standard error bars for (a) G_{day}, (b) G_{night}, and (c) G_{net} in mmol m^{-2} d^{-1}~~.~~ ~~X axis represents~~ in the four climate scenario ~~treatments.~~treatment categories. There were significant differences ~~across~~between treatments for G_{day} (p=0.03), G_{night} (p<0.0001), and G_{net} (p<0.0001) (Table A1).

Figure A4: Means and standard error bars for (a) NCP_{day}, (b) NCP_{night}, and (c) NCP_{net} in mmol m^{-2} d^{-1} across .the four climate scenario treatments. There were significant differences across treatments for NCP_{day} (p<0.0001), NCP_{night} (p<0.0001), and NCP_{net} (p<0.0001) (Table A2).

Figure A5: Net ecosystem calcification (G_{day}, G_{night}, and G_{net}) versus ΔTemperature (left panel) and ΔpCO_2 (right panel). Lines are best fit lines. G_{day} has a significant non-linear relationship ΔpCO_2 ($p=0.04$) and ΔTemperature ($p=0.01$). G_{night}, (ΔTemp: $p<0.001$, ΔpCO_2: $p<0.001$) and G_{net} (ΔTemp: $p<0.001$, ΔpCO_2: $p<0.001$) both have significant linear relationships with ΔpCO_2 and ΔTemperature.

Figure A6: Net community production (NCP_{day}, NCP_{night}, and NCP_{net}) versus ΔTemperature (left panel) and ΔpCO_2 (right panel). Lines are best fit lines. NCP_{day} (ΔTemp: $p<0.001$, ΔpCO_2: $p<0.001$), NCP_{night}, (ΔTemp: $p<0.001$, ΔpCO_2: $p<0.001$) and NCP_{net} (ΔTemp: $p<0.001$, ΔpCO_2: $p<0.001$) all have significant linear relationships with ΔpCO_2 and ΔTemperature.

G and NCP calculations: Below are the specific calculations for G and NCP for Equations 1 and 2 in the text (in mmol C m^{-2} hr^{-1}). For comparisons with existing literature,. G and NCP were both multiplied by 12 hr/day to get mmol m^{-2} d^{-1}.

Equation 1 (equations modified from Andersson et al. 2009):

$$G = \left[F_{TAin} - F_{TAout} - \frac{d\mathrm{TA}}{dt}\right]/2 \quad \text{(A1)}$$

F_{TAin} is the rate of TA flowing into the aquaria in mmol $CaCO_3$ m^{-2} hr^{-1}:

$$F_{TAin} = ((TA_{H,t2} + TA_{H,t1})\frac{1}{2} * FlowRate_{aq})/1000 \quad \text{(A2)}$$

F_{TAout} is the rate of TA flowing out of the aquaria in mmol $CaCO_3$ m^{-2} hr^{-1}:

$$F_{TAout} = ((TA_{aq,t2} + TA_{aq,t1})\frac{1}{2} * FlowRate_{aq})/1000 \quad \text{(A3)}$$

$\frac{d\mathrm{TA}}{dt}$ is the change in TA in each aquaria in mmol $CaCO_3$ m^{-2} hr^{-1}:

$$\frac{d\mathrm{TA}}{dt} = \frac{\frac{TA_{aq,t2} - TA_{aq,t1}}{\Delta t * SA} * Vol * \rho}{1000} \quad \text{(A4)}$$

Each equation is divided by 1000 to convert from µmol of $CaCO_3$ to mmol of $CaCO_3$

Parameters:

$TA_{H,t1}$ = Total alkalinity in the header tank at the first sampling time point (µEq kg^{-1}).

$TA_{H,t2}$ = Total alkalinity in the header tank at the second sampling time point (µEq kg^{-1}).

$TA_{aq,t1}$ = Total alkalinity in the aquarium at the first sampling time point (µEq kg^{-1}).

$TA_{aq,t2}$ = Total alkalinity in the aquarium at the second sampling time point (µEq kg^{-1}).

Δt = time between first and second sampling time point (h)

SA = surface area of the rubble in the aquarium (m^{-2})

Vol= volume of water in the aquarium (L)

ρ = density of seawater (kg L^{-1})

$FlowRate_{aq}$ = Flow rate of the water coming into the aquarium in kg m^{-2} h^{-1} (equal to flow rate of the water leaving the aquarium)

NCP is net community production rate in mmol C m^{-2} d^{-1} :

$$NCP = \left[F_{\mathrm{DIC}in} - F_{\mathrm{DIC}out} - \frac{d\mathrm{DIC}}{dt}\right] - G \quad \text{(A5)}$$

$F_{\mathrm{DIC}in}$, $F_{\mathrm{DIC}out}$, $\frac{d\mathrm{DIC}}{dt}$ are calculated in the same way as F_{TAin}, F_{TAout}, and $\frac{d\mathrm{TA}}{dt}$ in Equations A2-A4), replacing Total Alkalinity with Dissolved Inorganic Carbon.

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