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Title: Environmental drivers of coral reef carbonate production and bioerosion: a multi-scale analysis

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ABSTRACT

The resilience of coral reefs depends on the balance between reef growth and reef breakdown, and their responses to changing environmental conditions. Across the 2500 km Hawaiian Archipelago, we quantified rates of carbonate production, bioerosion, and net accretion at regional, island, site, and within-site spatial scales and tested how carbonate production,

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bioerosion, and net accretion rates respond to environmental conditions across different spatial scales. Overall, there were four major outcomes from this study: 1) bioerosion rates were generally higher in the populated Main Hawaiian Islands (MHI) than the remote, protected Northwestern Hawaiian Islands (NWHI), while carbonate production rates did not vary significantly between the two regions; 2) variability in carbonate production, bioerosion, and net accretion rates was greatest at the smallest within-reef spatial scale; 3) carbonate production and bioerosion rates were associated with distinct sets of environmental parameters; and 4) the strongest correlates of carbonate production, bioerosion, and net accretion rates were different between the MHI region and the NWHI region: in the MHI, the dominant correlates were % cover of macroalgae and herbivorous fish biomass for carbonate production and bioerosion, respectively, whereas in the NWHI, the top correlates were total alkalinity and benthic cover. This study highlights the need to understand accretion and erosion processes as well as local environmental conditions to predict net coral reef responses to future environmental changes.

Keywords: Spatial scale, coral reefs, net accretion, bioerosion, carbonate production, local variability, latitudinal gradients, pH, multiple stressors

1. INTRODUCTION

Worldwide, declines in coral cover and shifts in coral reef community composition have raised concerns about reef persistence and the shifting balance between reef accretion and net bioerosion (e.g., Gardner et al. 2003, Bruno and Selig 2007, Kennedy et al. 2013). Corals and other calcifiers (e.g. non-coral encrusting invertebrates and crustose coralline algae (CCA)) build reefs through the production of calcium carbonate ($CaCO_3$) skeletons, while a diverse community of organisms bioerode reefs through grazing on (e.g., urchins, parrotfish) and boring into (e.g., boring sponges, sipunculids, and polychaetes) $CaCO_3$ reef substrate (e.g., Hutchings 2011, Tribollet and Golubic 2011). Anthropogenic stressors affect the accretion-erosion balance of coral reefs at a range of spatial scales from global ocean acidification (e.g., Hoegh-Guldberg et al. 2007, Silbiger and Donahue 2015) to regional overfishing (e.g., Brown-Saracino et al. 2007, Kennedy et al. 2013) and local eutrophication (e.g., Fabricius 2005, Hutchings et al. 2005,

Le Grand and Fabricius 2011). These stressors threaten to shift reefs from a state of net accretion to net erosion. Experimental studies on bioerosion have increased in recent years, especially those focused on the impacts of rising temperature and ocean acidification on bioerosion rates (see, Tribollet et al. 2009, Wisshak et al. 2012, 2013, Enochs et al. 2015, Silbiger and Donahue 2015). To predict how reefs may shift under future ocean conditions, experimental studies must be contextualized with measurements of *in-situ* accretion-erosion rates and across a range of environmental conditions. Three major factors influence accretion-erosion rates on coral reefs: the chemical environment, the physical environment, and biological interactions. Here, we address how each of these factors influences accretion-erosion rates across different spatial scales.

Shifts in environmental conditions can alter bioerosion rates through changes in the physiology and metabolic pathways of bioeroders. Seawater pH (and related carbonate parameters) and nutrients are the two groups of chemical drivers that have received the most attention on coral reefs. For example, both experimental (Tribollet et al. 2009, Wisshak et al. 2012, Fang et al. 2013, Reyes-Nivia et al. 2013, Wisshak et al. 2013, Enochs et al. 2015, Silbiger and Donahue 2015) and correlative (Silbiger et al. 2014, DeCarlo et al. 2015, Enochs et al. 2016, Silbiger et al. 2016) studies have demonstrated that decreasing pH increases bioerosion. Many studies have also demonstrated that decreasing pH reduces calcification in corals and crustose coralline algae (e.g., Hoegh-Guldberg et al. 2007, Jokiel et al. 2008, Diaz-Pulido et al. 2012, Johnson and Carpenter 2012, Comeau et al. 2013). In several field studies, bioerosion increased in eutrophic relative to oligotrophic conditions (e.g., Le Grand and Fabricius 2011, DeCarlo et al. 2015), likely due to increased food availability to filter feeding bioeroders. Field studies that examined the simultaneous impact of nutrients and ocean acidity on bioerosion have found different responses over different spatial scales (DeCarlo et al. 2015, Silbiger et al. 2016). In a within-reef study (~30m) (Silbiger et al. 2014, Silbiger et al. 2016), ocean acidity was the best predictor of reef bioerosion when compared to nutrients, chlorophyll, temperature, depth, and distance from shore. At a large-scale (~16,000 km) comparison across the Pacific Basin (DeCarlo et al. 2015), the positive relationship between bioerosion rates and ocean acidity was more pronounced at sites with higher nutrient concentrations.

Along with a changing chemical environment, physical parameters can affect the reef carbonate budget. For example, water movement can enhance growth of corals and other

calcifiers through transport and removal of nutrients and metabolic wastes (Hearn et al. 2001) or enhance erosion through dislodgement and abrasion (Madin and Connolly 2006). A study at Lizard Island, a relatively protected set of islands in the Great Barrier Reef approximately 5 km across, found that CCA and live coral cover was positively correlated with wave energy (Hamylton et al. 2013). Conversely, in a Pacific-wide study (~8000 km) that incorporated several exposed reef systems, coral cover declined with increasing wave energy (Williams et al. 2015). The chemical and physical environment can also interact as water residence times influence pH variability (Jury et al. 2013). These studies highlight the complex chemical and physical interactions influencing the accretion-erosion balance at different spatial scales.

Overlaid on a landscape of chemical and physical drivers, biological interactions also influence reef accretion-erosion rates. For example, grazers can influence bioerosion directly by incidentally removing $CaCO_3$ substrate while grazing for algae (e.g., Bellwood 1995, Ong and Holland 2010) and can influence calcification indirectly by removing fleshy algae and relieving competitive interactions with CCA (Cebrian and Uriz 2006, Cebrian 2010, O'Leary and McClanahan 2010, González-Rivero et al. 2012). Benthic cover can also be a major factor affecting accretion-erosion rates. The amount of dead substrate on a reef is directly related to reef bioerosion rates, as bioeroders prefer dead substrate over live reef (Highsmith 1981b, Hutchings 1986). Therefore, events that negatively impact live coral, such as large storms and bleaching events, can indirectly impact bioeroders.

While there have been several *in situ* studies focused on understanding controls on bioerosion rates and associated macroborer communities—chiefly at sites in Australia (e.g., Davies and Hutchings 1983, Risk et al. 1995, Tribollet et al. 2002, Hutchings et al. 2005, Tribollet and Golubic 2005), the Caribbean (e.g., Neumann 1966, Rützler 1975, Perry et al. 2012), and the Eastern Tropical Pacific (e.g., Scott and Risk 1988)—there have been no broad scale studies on accretion-erosion rates in the Hawaiian Archipelago; existing studies in Hawai‘i have focused mainly on Kāne‘ohe Bay (White 1980, Tribollet et al. 2006, Silbiger et al. 2014, Silbiger et al. 2016). Here, we examine the patterns of carbonate production, bioerosion, and net accretion rates over multiple spatial scales at 29 sites across the Hawaiian Archipelago (~2500km). There were three goals for this study: 1) describe spatial patterns in rates of carbonate production (primarily from the settlement of crustose coralline algae), bioerosion, and net accretion on experimental blocks of dead coral substrate, 2) relate these patterns to chemical,

physical, and biological data from long-term monitoring and remote sensing data, and 3) test if the relationships between accretion-erosion rates and environmental drivers are consistent across spatial scales. We use a newly developed µCT methodology (Silbiger et al. 2014, Silbiger et al. 2016) to measure *in situ* rates of carbonate production, bioerosion, and net accretion (calculated as percent change in volume) from experimental blocks of $CaCO_3$ deployed across the Hawaiian Archipelago. In the first large scale application of this µCT method, we calculate carbonate production rates primarily from crustose coralline algae, and bioerosion rates from borers and grazers from an early successional community after a one-year deployment period.

2. MATERIALS AND METHODS

2.1 Study Sites: This study was conducted at 29 forereef sites (8-16 m depth) across six islands/atolls in the Hawaiian Archipelago (Fig. 1, S1, Table S1). Kure Atoll (KUR), Pearl and Hermes Atoll (PHR), Lisianski Atoll (LIS), and French Frigate Shoals (FFS) are atolls in the Northwestern Hawaiian Islands (NWHI) and protected by the Papahānaumokuākea Marine National Monument (PMNM), one of the largest and most remote marine protected areas in the world. O‘ahu and Maui are populated volcanic islands in the Main Hawaiian Islands (MHI). Twenty-seven of these sites were co-located with long-term monitoring sites maintained by the NOAA Coral Reef Ecosystem Program (CREP) to take advantage of pre-existing environmental data and research cruise logistics. The remaining two sites, O‘ahu-KBay and Maui-A27, were selected with similar depth and exposure characteristics. Maui-A27 was co-located with a long-term monitoring site maintained by the Hawai‘i Division of Aquatic Resources; O‘ahu-KBay is accessible from the Hawai‘i Institute of Marine Biology. The experimental design was explicitly hierarchical with n=5 replicates per site, 4-5 sites per island/atoll, and 2 (MHI) or 4 (NWHI) sites per region.

2.2 Carbonate Production, Bioerosion, and Net Accretion: Five blocks (5 x 5 x 2.5 cm) cut from dead *Porites lobata* Dana 1846, collected above the high tide mark on O‘ahu, were deployed at each site for approximately one year (Fig. S2a, Table S1). Each block was carefully inspected and any block with obvious pre-existing boreholes was discarded. Blocks were then soaked in freshwater and autoclaved to sterilize the substrate. Two holes were drilled into each block for cable ties. At each site, one block was attached to each of five rebar stakes installed on the reef within a 5 m x 5 m area. Blocks were attached using cable ties and oriented vertically, such that the end of the block was in contact with the substrate (Fig. S2a). Because of the

remoteness of our field sites, all blocks were deployed and retrieved on NOAA ships with pre-determined cruise schedules. Blocks were deployed at FFS, LIS, and PHR sites in July/August 2011 on NOAA cruise HA1103 and retrieved in August 2012 on NOAA cruise HA1204; at KUR sites in August 2012 on NOAA cruise HA1204 and retrieved in July 2013 on NOAA cruise SE1305; and at O‘ahu and Maui sites in September/October 2012 on NOAA cruise SE1207 and retrieved September/October 2013 with small boat operations (Table S1). While deploying blocks during different years is not ideal because recruitment of bioeroders can vary over time (e.g., Hutchings et al. 1992, Hutchings 2011), the remoteness of our sites and pre-determined cruise schedules and logistics made it unavoidable. All blocks were deployed on the reef for a full year and thus the substrate was available to bioeroders and calcifiers during all four seasons; all blocks were deployed between late July and early October. We recovered 143 of 145 deployed experimental blocks; 122 blocks had before and after µCT scans of adequate quality for data analysis.

Carbonate production, bioerosion, and net accretion rates were calculated for each block by comparing before and after µCT scans of the entire blocks (Silbiger et al. 2014, Silbiger et al. 2016). µCT is an X-ray technology that non-destructively images the external and internal structures of solid objects, resulting in a three-dimensional array of object densities. We used an eXplore CT120 µCT (GE Healthcare Xradia, Inc) at the Cornell University Imaging Multiscale CT Facility to scan blocks before and after deployment (voltage = 100kV, current = 50mA). The µCT was calibrated with a phantom (density standard) prior to running each batch of samples. A three-dimensional array of isotropic voxels at 50 μm^3 resolution was generated using the GE Console Software and the voxels were averaged to 100 μm^3 for data analysis. We used a threshold of 200 Hounsfield Units to separate coral from air (Silbiger et al. 2014). The number of voxels exceeding this threshold was multiplied by the voxel size $(100\ \mu m)^3$ to give the total volume of $CaCO_3$ for pre- and post-deployment blocks. The pre- and post-deployment scans were then aligned using an intensity-based registration technique from the MATLAB R2014b Image Processing Toolbox, converted to binary, and subtracted from one another resulting in a matrix of 0’s, 1’s, and -1’s. All positive values were new pixels added to the post-deployment scan, which indicate carbonate production, negative values were pixels that were lost and indicate bioerosion, and zeros meant there was no change at that pixel between the two scans. All

values were summed and multiplied by the resolution of the scan to obtain the volume lost (bioerosion) or gained per block (carbonate production) (Fig. S2b,c).

Prior studies highlighted the need to analyze both carbonate production and bioerosion independently (Silbiger and Donahue 2015, Silbiger et al. 2016), but net accretion rates are also necessary for understanding long-term reef sustainability (Silbiger et al. 2014). Here, we calculated carbonate production, bioerosion, and net accretion rates (the percent change in volume of experimental blocks) over the one-year deployment time. In the literature, carbonate production rates on calcium carbonate blocks are typically presented as layer thickness in mm yr^{-1} (e.g, Payri 1995, Tribollet et al. 2006), and bioerosion rates are presented as mass loss in kg m^{-2} yr^{-1} (e.g., Tribollet and Golubic 2005, Wisshak et al. 2012). To align our rates with literature data, these conversions were followed, but, in order to make them comparable to each other and to enable the calculation of a net rate, we used percent change in volume of the block to determine whether blocks were net accreting (positive change) or net eroding (negative change). Bioerosion and carbonate production rates were calculated using the following equations (Silbiger et al. 2016):

$$\text{Bioerosion rate (kg m}^{-2}\text{ yr}^{-1}) = (\Delta Vol_i \times \rho_i)/(SA_i \times Time) \quad (1)$$

$$\text{Carbonate production rate (mm yr}^{-1}) = 1000 \times (\Delta Vol_i)/(SA_i \times Time) \quad (2)$$

where i represents an individual block, ΔVol_i is the volume lost (bioerosion) or gained (carbonate production) in m^3, SA_i is the surface area of the pre-deployment blocks (m^2), ρ_i is the skeletal density of the pre-deployment block (kg m^{-3}), and $Time$ is the deployment time (years). Carbonate production rates were multiplied by 1000 to convert from m to mm yr^{-1}. Surface area was calculated from the µCT scans following methods by Legland et al. (2011). Skeletal density of the blocks was calculated by converting intensity values from the µCT scans to bulk skeletal density following methods in DeCarlo et al. (2015). Net accretion rates were calculated as percent change in volume per year (Silbiger et al. 2014):

$$\text{Net accretion (\% y}^{-1}) = 100 \times (Vol_{post,t2} - Vol_{pre,t1})/(Vol_{pre,t1} \times Time), \quad (3)$$

where $Vol_{post,t2}$ and $Vol_{pre,t1}$ were the post-deployment and pre-deployment volumes of the blocks, respectively. Note that this change in total volume does not depend on the alignment of pre- and post-scans.

2.3 Environmental Data: We compiled 23 variables describing the chemical, physical, and biological characteristics of each site (Table 1) from NOAA CREP

(https://www.pifsc.noaa.gov/cred/), Hawai‘i Department of Aquatic Resources (DAR), NOAA satellite data, NOAA global wave models (WaveWatch III), and *in situ* sampling. Detailed methods and collection protocols are described in the supplemental material.

2.4 Statistical Analysis:

To compare means at each level, we used a nested analysis of variance (ANOVA) with a Tukey Honestly Significant Difference (HSD) *post-hoc*, where site, island, and region were all fixed effects. To evaluate the contribution of variance at each spatial scale (sites within islands within regions) to rates of carbonate production, bioerosion, and net accretion, we used a variance components analysis, where site, island, and region were hierarchical random effects. Carbonate production and bioerosion rates were both log-transformed to meet assumptions of normality for all analyses. We used a simple linear regression to test the relationship between block skeleton density and bioerosion rates, as small differences in skeletal density on the blocks could impact bioerosion rates (Highsmith 1981a), but found no effect ($F_{1,120} = 0.06$, $p = 0.84$).

To determine environmental drivers of accretion-erosion rates, we used a model selection approach by ranking Akaike Information Criterion (AIC) weights from simple linear models in which the environmental predictors were the independent variables, and carbonate production, bioerosion, and net accretion rates were the dependent variables. All environmental data that did not meet the assumption of normality were transformed (Table 1). While it is common to find non-linear relationships in field data, we did not find any evidence of non-linearity in our dataset. AIC weights can be interpreted as a relative probability, where the model with the highest weight is the most probable of the candidate models (Wagenmakers and Farrell 2004). To test if the relationship between the environmental predictors and accretion-erosion values are consistent between regions, we constructed individual models by region and compared the highest-ranking models between regions (MHI and NWHI). A principal components analysis (PCA) was used to visualize the spatial structure of the 23 environmental parameters.

3. RESULTS

3.1 Environmental drivers:

The biological, chemical, and physical drivers all varied widely throughout the Hawaiian Archipelago (Fig. 2), and there were distinct patterns in environmental conditions across islands (Fig. 3).

3.1.1 Biological Divers: Herbivorous fish biomass ranged from 0.4 to 22.8 g m^{-2} with the highest herbivorous fish biomass on Kure in the protected Papahānaumokuākea Marine National Monument and lowest biomass on O'ahu (Figure 2a), an island with substantial fishing pressure (Williams et al. 2008). The benthic community also fluctuated widely throughout the Hawaiian Archipelago with coral cover varying from 1.3 – 56% across the 29 sites with the lowest coral cover also on the island of O'ahu (Fig. 2a).

3.1.2. Chemical Drivers: PO, N+N, and Si ranged from 0.008 – 0.18, 0.066 – 1.79, and 0.83 – 2.45 µmol L^{-1} (Fig. 2c), respectively, and TA, DIC, pH, and Ω_{arag} ranged from 2197 – 2387 µmol kg^{-1}, 1985 - 2065 µmol kg^{-1}, 7.81 – 8.05, and 2.27 – 3.73, respectively, throughout the Archipelago (Fig. 2d,e). Lisianksi, the site with the most distinct chemical environment, had the highest N+N and lowest TA, DIC, pH, and Ω_{arag} values.

3.1.3 Physical Drivers: Average wave energy ranged from 22.3 – 45.0 kW m^{-2} with the highest wave energy in the northernmost sites (Fig.2b). The northernmost sites also had the lowest and most variable temperatures across the archipelago with mean and standard deviation in temperature ranging from 23.4 - 25.5 ºC and 0.83 - 5.25 ºC, respectively (Fig.2b).

3.2 Carbonate production, bioerosion, and net accretion rates:

3.2.1 Spatial patterns in carbonate production, bioerosion and net accretion:

Carbonate production, bioerosion, and net accretion rates had distinct spatial patterns throughout the Hawaiian Archipelago. At the regional scale, bioerosion rates were 39% higher at the MHI sites than at the NWHI sites (Table 2, Fig. 4b), while carbonate production rates were similar between regions (Table 2, Fig 4a); average net accretion was 2.2 times higher in the NWHI than in the MHI, but the difference was not significant (Fig. 4e and Table 2). At the island scale, however, there was significant variation in carbonate production rates, driven primarily by exceptionally high carbonate production at Lisianski (nearly double the rate of other NWHI sites; Table 2, Fig. 4d); net accretion also varied by island, with a similar pattern for Lisianski (Fig. 4f). In contrast, differences in bioerosion rate at the island scale were marginal but non-significant (Table 2, Fig. 4d). Lisianski had the highest average net accretion rate, the highest carbonate production rate, and second lowest bioerosion rate. O'ahu, the island with the highest population density and the most direct anthropogenic impacts, had the most blocks that were net eroded (46%) and the lowest average net accretion, coupled with the second lowest carbonate production rate and highest bioerosion rate (Table S2). Lastly, site-level variation was

significant for all rates (Fig. 4g-i, and Table 2, S3). MauiA27 (Kahekili, Maui), a site impacted by wastewater effluent (Dailer et al. 2012), had the highest average bioerosion rate (0.35 kg m^{-2} y^{-1} ± 0.03) and the lowest net accretion rate (-8.2% ±1.97), while LIS18 had the highest carbonate production rate (3.68 ± 0.57 mm y^{-1}) (Fig. 4g-i, S2 and Table S3).

The variance components analysis revealed that the highest amount of variance in all three rates were at the finest spatial scales (Table 2). Regional-scale differences contributed to 17.5% of the variance in bioerosion, but were negligible for carbonate production and net accretion rates whereas island-scale differences contributed to 14.5% of the variance in carbonate production, but only 2.5% in net accretion and <0.1% in bioerosion (Table 2). Site-level differences contributed to substantially more of the variance in each rate explaining 14.9%, 34.9%, and 32.1% of the variance in carbonate production, bioerosion, and net accretion rates, respectively (Table 2). However, the highest portion of variance in the data was attributed to the smallest (within sites) spatial scale, explaining 70.6%, 47.6% and 65.3% of the variance for carbonate production, bioerosion, and net accretion, respectively (Table 2).

3.2.2 Environmental drivers of carbonate production, bioerosion and net accretion:

Carbonate production and bioerosion rates always had different top-ranking models indicating that they respond differently to environmental conditions (Fig. 5 and Tables S4 and S5). Additionally, the environmental drivers differed between regions for all three rates (Fig. 5 and Tables S4-S6). For carbonate production, the top three models for the NWHI region were carbonate chemistry parameters; total alkalinity ranked highest and was negatively related to carbonate production (AIC_w = 0.40, R^2 = 0.25, Fig. 5b, Table S4). Aragonite saturation state and pH had similar AIC weights and R^2 values (Ω_{arag}: AIC_w = 0.31, R^2 = 0.24, pH: AIC_w = 0.28, R^2 = 0.24, Fig. 5b, Table S4) and both had a surprising negative association with carbonate production. For carbonate production in the MHI, physical and biological parameters were most parsimonious, with macroalgae ranked highest and positively associated with carbonate production (AIC_w = 0.30, R^2 = 0.14, Fig. 5a, Table S4). For bioerosion, biological parameters were the top models in both the MHI and NWHI regions (Fig. 5c,d and Table S5); herbivore biomass was the highest-ranking model for the MHI (AIC_w = 0.75, R^2 = 0.28, Fig 5c and Table S5), while benthic cover (% other: mainly bare substrate, cyanobacteria, and sessile invertebrates) ranked highest in the NWHI (AIC_w = 0.59, R^2 = 0.11; Fig. 5c and Table S5). Lastly, for net accretion, a combination of biological and chemical models was most informative

in both the MHI and NWHI (Fig. 5e, f and Table S6). All had relatively equal and low weights (0.16 – 0.24) and ΔAIC values of < 4. Models ranking environmental parameters across the entire Hawaiian Archipelago are listed in Supplemental Fig 3**.**

4 DISCUSSION

4.1 Spatial patterns in carbonate production, bioerosion, and net accretion rates along the Hawaiian Archipelago

The persistence of coral reefs depends on the balance between carbonate production and net reef erosion. While several studies have examined carbonate production (or calcification) and bioerosion rates independently, this is a broad-scale study that assesses patterns in carbonate production, bioerosion, and net accretion rates in concert and compare these rates to chemical, physical, and biological drivers across spatial scales.

Carbonate production and bioerosion rates were associated with different drivers at both regional and archipelagic scales. Prior studies have also found distinct drivers of carbonate production and erosion: for example, a fine-scale *in situ* study showed that bioerosion was most correlated with pH while carbonate production was most correlated with distance from shore (Silbiger et al. 2016). Further, carbonate production and erosion have been shown to have different responses to the same environmental parameters, chiefly pH, in both field (Barkley et al. 2015, Enochs et al. 2016, Silbiger et al. 2016) and laboratory (Silbiger and Donahue 2015) studies. Net accretion was driven by a combination of the dominant drivers for carbonate production and bioerosion, which is expected as net accretion is a composite of carbonate production and bioerosion.

We were surprised that this broad-scale study did not show a strong relationship between carbonate chemistry parameters and bioerosion, as several studies show a clear relationship between pH and bioerosion (Tribollet et al. 2009, Wisshak et al. 2012, Fang et al. 2013, Reyes-Nivia et al. 2013, Wisshak et al. 2013, Silbiger et al. 2014, Barkley et al. 2015, DeCarlo et al. 2015, Silbiger and Donahue 2015). Carbonate chemistry parameters were in the top-ranking models for carbonate production in the NWHI, but they also had a surprising negative relationship for both pH and Ω_{arag}: opposite of what is expected based on prior studies (e.g., Hoegh-Guldberg et al. 2007). In addition, nutrients were not in the top-ranking models for bioerosion, although nutrients are an important driver of reef bioerosion (e.g., Carreiro-Silva et al. 2005, DeCarlo et al. 2015). Silica, however, was in the top three models for bioerosion in

both regions. Excavating sponges have a siliceous skeleton; thus, sponge bioerosion rates could be sensitive to silica concentrations. There are a few possible explanations for these surprising results in the chemical parameters. 1) It is likely other, unmeasured collinear parameters are driving the negative relationship between carbonate production and pH. 2) All reef sites for which we had nutrient data were oligotrophic (0.066 - 1.8 μmol L^{-1}); thus, the range of nitrate was inadequate to elicit a nutrient response in bioerosion. 3) Nutrient data was unavailable for site with the highest bioerosion rates (Kahekili, Maui – Maui A27); a site known to be impacted by wastewater effluent (Dailer et al. 2012) and likely with high nutrient concentrations. 4) The chemistry data had low replication (1-3 points) collected between spring and summer during daylight hours which ignores the high temporal variability in water chemistry on coral reefs (e.g., Guadayol et al. 2014). Prior studies have shown that diel variability in carbonate chemistry is an important driver of carbonate production on coral reefs (Price et al. 2012). This low replication reflects the only data publicly available for these very remote sites. However, a previous study over broad spatial scales used similarly sparse *in situ* chemistry data and found significant relationships between bioerosion and water chemistry (DeCarlo et al. 2015). 5) The strong direct and indirect effects of herbivore grazing may be swamping or interacting with the effects carbonate chemistry and nutrients on bioerosion rates. Overall, the drivers of accretion-erosion rates were multifactorial, highlighting the many interacting factors that influence accretion-erosion rates of coral reefs.

Biological parameters ranked highest in five out of the six model selection analyses. Specifically, herbivorous fish was the highest-ranking model in the MHI for bioerosion, and benthic cover descriptors ranked highest for carbonate production in the MHI, bioerosion in the NWHI, and net accretion in both regions. Benthic cover, specifically the amount of dead substrate on a reef, could influence bioerosion rates, as bioeroders prefer dead substrate over live reef (Highsmith 1981b, Hutchings 1986). Herbivorous fish can directly influence bioerosion by removing $CaCO_3$ substrate while grazing for algae (e.g., Bellwood 1995, Ong and Holland 2010), and they can indirectly influence settlement and growth of calcifiers by removing fleshy algae and relieving competitive interactions with CCA (Cebrian and Uriz 2006, Cebrian 2010, O'Leary and McClanahan 2010, González-Rivero et al. 2012). Further, the interaction between benthic community composition and herbivorous fish can influence bioerosion rates because the presence of secondary calcifiers, mainly CCA, can inhibit the settlement of bioeroders by sealing

363 off the substrate and making it difficult for borers to penetrate (White 1980, Tribollet and Payri
364 2001). A prior field study suggested that grazer abundance could mediate the relationship
365 between accretion and pH as they saw a positive relationship between pH and accretion at one
366 CO_2 vent site and no relationship at a site with higher grazer abundance (Enochs et al. 2016).
367 Our results suggest that herbivorous fish have a negative indirect effect on bioerosion rates:
368 bioerosion rates decreased with increasing herbivorous fish biomass. The strong negative effect
369 of herbivorous fish biomass on bioerosion rates is important for coral reef managers: managing
370 for herbivorous fish could mitigate excessive bioerosion.
371 Among the physical parameters, mean and maximum SST were in the top-ranking
372 models for carbonate production in the MHI. Carbonate production can vary as a function of
373 temperature due to its effects on both chemical and biological processes (Mutti and Hallock
374 2003). Across all models, the top five highest-ranking models often had ΔAIC values of <4
375 (Table S4-S6), indicating empirical support for several of the environmental parameters and,
376 thus, evidence for multiple factors interacting to affect the accretion-erosion balance of coral
377 reefs.
378 In addition to different drivers between carbonate production and erosion rates, the
379 dominant drivers for carbonate production, bioerosion, and net accretion were always different
380 between the two regions. There are several possible explanations for these differences. First,
381 there are different ranges in the environmental parameters due to varying oceanographic
382 conditions and human-influences between the two regions. For example, there was a much larger
383 range in the carbonate chemistry in the NWHI than in the MHI which was mostly driven by
384 Lisianksi Island (Fig. 2d,e, 3a). Interestingly, Lisianski also had a substantially higher carbonate
385 production rate than the five other islands/atolls (Fig, 4a). Unlike other atolls in the NWHI,
386 Lisianski is an open atoll with reticulate reef separating lagoon and forereefs; this unique
387 geomorphology may underlie the distinct physicochemical environment (Fig 3a) and carbonate
388 production rates (Fig 4b) at Lisianski. There were considerable differences in fish biomass
389 between the two regions due to varying fishing pressure (Williams et al. 2008, Williams et al.
390 2010), likely driving the difference in the relative importance of herbivorous fish between the
391 MHI and NWHI. Prior studies have also found dissimilar relationships between environmental
392 drivers and coral reef processes between regions. For example, a Pacific Basin study
393 demonstrated that the relationship between environmental models and reef characteristics (coral,

CCA, and macroalgal cover) were not consistent across space (Williams et al. 2015). Williams et al. (2015) split sites between populated and unpopulated islands, found that biophysical parameters had higher explanatory power at unpopulated islands, and concluded that local human impacts decouple biophysical relationships on coral reefs. The MHI versus NWHI comparison is similarly populated versus unpopulated, and differences between sites could be driven by local human impacts; however, there are also several other major differences between these regions that may be more directly related (e.g., high vs low islands, benthic habitat differences, etc.).

Variability in carbonate production, bioerosion, and net accretion were all highest at the local scale. For all factors investigated here, the smallest scale of variation (within sites) contributed much more variance than any other spatial scale in this study, indicating that individual blocks within a site were more different than blocks 2500 km apart. It is important to note that the site scale is the residual variance and, therefore, includes all block-to-block variability within a site, including both spatial variability within each site and any differences between the blocks themselves. While our rate calculations normalized for differences between blocks in volume and surface area, and we found no effect of skeletal density, other differences between blocks, such as differences in surface roughness, or variability in the µCT measurements, would also contribute to within-site variability. Prior studies have also seen exceptionally high within-site variability in bioerosion rates. A recent study in Kāneʻohe Bay, Hawaiʻi saw a nearly 2 order of magnitude change in bioerosion rates across a short 34-m transect (Silbiger et al. 2016) – variability that was greater than a study comparing bioerosion rates across the Pacific (DeCarlo et al. 2015). Further, the low explanatory power of all environmental models (highest R^2 value was 0.28) reflect a response to the high local variability in accretion-erosion data. Prior studies examining within site environmental variability and accretion-erosion rates had markedly higher explanatory power between accretion-erosion rates and environmental parameters (Silbiger et al. 2014, Silbiger et al. 2016). While both broad and local scale gradients in biological and physicochemical drivers clearly interact to shape patterns in the accretion-erosion balance, this study provides compelling evidence that local variability is particularly important.

There are some limitations to this study that should be considered when interpreting the results. First, the temporal scales of the environmental variables differ and, particularly in the

case of water chemistry, are disconnected from the block deployment period (Table S1 and S7). Second, the highest spatial resolution of the environmental data was at the site level, but the majority of the variance in the accretion-erosion data was within sites. Monitoring protocols are typically in place to track broad environmental trends; however, a better understanding of local-scale variability is necessary to predict how environmental change will impact the accretion-erosion balance. Third, because the blocks were deployed for one year, the results are based on an early successional community. Studies have shown that bioeroder community composition and bioerosion rates change over time in $CaCO_3$ block experiments (e.g., Hutchings et al. 1992, Tribollet and Golubic 2005). For example, several species of boring polychaetes have shown increased recruitment over a one to two-year deployment period followed by a decline, while eunicids, sipunculans, and bivalves continuously increased over a four-year period in Australia (Hutchings et al. 1992). Another study demonstrated that bioerosion rates on Lizard Island, Australia were 0.71, 0.11, and 0.32 kg m^{-2} y^{-1} after a one-year exposure for microborers, macroborers, and grazers, respectively. After 3 years of exposure, macrobioerosion rates were 3x higher (Tribollet and Golubic 2005). As bioeroding species respond differently to environmental conditions and erode at different rates (e.g., Hutchings 1986, Hutchings et al. 1992, Hutchings and Peyrot-Clausade 2002, Tribollet and Golubic 2005), the deployment length could have impacted the results of this study. Lastly, our analysis did not separate bioerosion rates by functional groups. Future studies should address the effect of multiple chemical, physical, and biological divers of bioerosion functional groups at multiple successional stages.

4.2 Conclusions

Despite the limitations, this is the highest resolution analysis that allows for the simultaneous measurement of carbonate production, bioerosion, and net accretion from the same experimental substrate and correlates these rates with a suite of chemical, physical, and biological parameters, and the first study to use µCT to quantify carbonate production, bioerosion and net accretion rates over large spatial scales. Our results and those from previous studies (Silbiger et al. 2014, Silbiger et al. 2016) provide compelling evidence that local-scale environmental variability is particularly important to the coral reef accretion-erosion balance. We also demonstrated that the relationships between explanatory and response variables are not consistent across space, as there were differences in the highest-ranking environmental models between the MHI and NWHI datasets. The differing relationships between environmental

variability and accretion-erosion data should be taken into consideration when interpreting those results and in future management decisions on coral reefs.

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644 **Data Accessibility**
645 Data are available on GitHub: https://doi.org/10.5281/zenodo.818093

Table 1: Environmental parameters: Environmental parameters grouped by (a) chemical, (b) physical, (c) and biological drivers. Parameters are parameter type, transformation is how the data were normalized, data source is the agency, satellite, or model source for the data, and method is collection method for each parameter.

	Parameters	Abbreviation	Transformation	Data Source	Method
(a) Chemical					
	PO_4^{3-}	PO	log(X)	CREP/Silbiger[1]	Water Sample
	Si	Si	log(X)	CREP/Silbiger[1]	Water Sample
	$NO_3^- + NO_2^-$	N+N	log(X)	CREP/Silbiger[1]	Water Sample
	Ω_{arag}	Ω_{arag}	log(X)	CREP/Silbiger[1]	CO2SYS
	pH	pH	log(X)	CREP/Silbiger[1]	CO2SYS
	Total Alkalinity (salinity normalized)	TA	log(X)	CREP/Silbiger[1]	Water Sample
	Dissolved Inorganic Carbon (salinity normalized)	DIC	log(X)	CREP/Silbiger[1]	Water Sample
(b) Physical					
	Depth	Depth	NA	CREP	Dive computer
	Mean Sea Surface Temperature	mean(SST)	NA	G1SST	Satellite
	Maximum Sea Surface Temperature	max(SST)	NA	G1SST	Satellite
	Minimum Sea Surface Temperature	min(SST)	NA	G1SST	Satellite
	Standard Deviation of Sea Surface Temperature	std(SST)	log(X)	G1SST	Satellite
	Mean Wave Energy	mean(energy)	log(X)	Wave Watch III	Satellite
	Maximum Wave Energy	max(energy)	log(X)	Wave Watch III	Satellite
	Sum of Wave Energy	sum(energy)	NA	Wave Watch III	Satellite
	Standard Deviation Wave Energy	std(energy)	log(X)	Wave Watch III	Satellite
(c) Biological					
	Fish herbivore biomass	Herb	log(X)	CREP/DAR[2]	BLT/nSPC
	% Coral cover	% Coral	log(X+1)	CREP/DAR[2]	LPI/Photoquad[3]

	% Calcified algae	% Calg	log(X+1)	CREP/DAR[2]	LPI/Photoquad[3]
	% Macroalgae	% Malg	log(X+1)	CREP/DAR[2]	LPI/Photoquad[3]
	% Turf algae	% Talg	log(X+1)	CREP/DAR[2]	LPI/Photoquad[3]
	% Sand	% Sand	log(X+1)	CREP/DAR[2]	LPI/Photoquad[3]
	% Other	% Other	log(X+1)	CREP/DAR[2]	LPI/Photoquad[3]

[1.] Silbiger collected nutrient samples at all O‘ahu sites and carbonate chemistry samples at all Maui sites and OahuKB and OahuKN. All other data was collected by CREP. There is currently no nutrient data available for MauiA27

[2.] MauiA27 fish and benthic data was collected by DAR and all other data was collected by CREP

[3.] Data was collected using LPI at all sites except for OahuKBay, OahuKN, Oahu10, Oahu4, and MauiA27

Table 2: Hierarchical ANOVA for (a) carbonate production, (b) bioerosion, and (c) net accretion rates across regions, islands, and sites. DF is degrees of freedom, SS is sum of squares, Mean SS is mean sum of squares, F is the F-test, and p is the p-value. Percent variance is from a variance components analysis, where site, island, and region were hierarchical random effects. Bold values represent statistically significant differences.

Model	DF	SS	Mean SS	F	p	% Variance
a) Carbonate Production						
Region	1	0.025	0.25	1.26	0.27	<0.1%
Island:Region	4	5.48	1.37	7.03	**<0.001**	14.50%
Site:Island:Region	23	8.55	0.37	1.91	**0.01**	14.90%
Residuals/Within Site	93	18.11	0.19			70.60%
b) Bioerosion						

Region	1	7.15	7.15	20.18	**<0.001**	17.50%
Island:Region	4	3.41	0.85	2.4	0.055	<0.1%
Site:Island:Region	23	35.6	1.55	4.37	**<0.001**	34.90%
Residuals/Within Site	93	32.96	0.35			47.60%
c) Net Accretion						
Region	1	65.1	65.14	2.76	0.1	<0.1%
Island:Region	4	374.2	93.56	3.97	**0.005**	2.50%
Site:Island:Region	21	1641.7	71.38	3.03	**<0.001**	32.10%
Residuals/Within Site	93	2215.1	23.57			65.30%

Figure Legend:

Figure 1: Map of 29 forereef sites across the Hawaiian Archipelago. Top inset shows the extent of the Hawaiian Archipelago. Maui and O'ahu are in the Main Hawaiian Islands region and French Frigate Shoals, Lisianksi Atoll, Pearl and Hermes Atoll, and Kure Atoll are in the Northwestern Hawaiian Islands region in the Papāhanaumokuākea Marine National Monument. Green areas are land. Red dots are individual sites. Grey areas in maps are 0-40m bathymetry data from NOAA CREP.

Figure 2: Summary of environmental data for (a) biological, (b) physical, and (c-e) chemical drivers. (a) Benthic cover is the mean % cover of the benthic community for all data collected between 2010 – 2012 at each site. (a) Herbivore fish biomass (g m^{-2}) are the means ± SE for all available data between 2000 – 2014 at each site. In the physical data plot (b), black and red bars represent the ranges for temperature (ºC) and wave energy (kW m^{-2}), respectively, and the dots are the mean values. The chemistry plots show mean values for (c) PO, Si, and N+N in µmol L^{-1}, (d) TA (µEq kg^{-1}), DIC (µmol kg^{-1}), and Ω_{arag} (colors), and (e) pH for all data available between 2008 – 2014 at each site. The sites are ordered from south to north. All parameters and data sources are listed in Table 1.

Figure 3: Principal components analysis (PCA) of the environmental data. The PCA is a combination of all environmental parameters collected (Table 1). Panel (a) are the PC scores of each site and panel (b) are the loadings of each environmental parameter. The x-axis is the first principal component and y-axis is the second principal component. Numbers in parentheses are the percent of variance explained by each PC axis. Polygons outline data from individual islands.

Figure 4: Means ± SE for (a,d,g) carbonate production, (b,e,h) bioerosion, and (c,f,i) net accretion rates across (a,b,c) regions, (d,e,f) islands, and sites (g,h,i). For net accretion, positive values were net accreting while sites with negative values were net eroding over the deployment period. Sites are show in order of latitude. Data were log-transformed in the analysis and were back-transformed in this figure. ANOVA results for this figure are in Table 2. Letters are from pairwise comparisons from a TukeyHSD post-hoc test and means with different letters

are statistically different from each other (pairwise comparisons for site-level data are in Table S3).

Figure 5: AIC weights (AICw) for environmental parameters versus (a,b) carbonate production, (c,d) bioerosion, and (e,f) net accretion for (a,c,e) the MHI, and (d,b,f) the NWHI. Each inset shows the top three highest ranking models for each model selection with bars representing individual environmental models. Signs next to bars represent positive (+) or negative (-) relationships between environmental drivers and the accretion-erosion rates. Full model selections are available in Tables S3-S5. X-axes are the AICw values with 1 being the model with the highest weight. Bar colors represent environmental driver groups.