Reefs shift from net accretion to net erosion along a natural environmental gradient

Nyssa J. Silbiger1,*, Óscar Guadayol1,2, Florence I. M. Thomas1, Megan J. Donahue1

1University of Hawai‘i at Mānoa, Hawai‘i Institute of Marine Biology, PO Box 1346, Kāne‘ohe, Hawai‘i 96744, USA
2Present address: University of Lincoln, School of Life Sciences, Joseph Banks Laboratories, Green Lane, Lincoln LN6 7DL, UK

ABSTRACT: Coral reefs persist in an accretion-erosion balance and ocean acidification resulting from anthropogenic CO2 emissions threatens to shift this balance in favor of net reef erosion. Corals and calcifying algae, largely responsible for reef accretion, are vulnerable to environmental changes associated with ocean acidification, but the direct effects of lower pH on reef erosion has received less attention, particularly in the context of known drivers of bioerosion and natural variability. This study examines the balance between reef accretion and erosion along a well-characterized natural environmental gradient in Kāne‘ohe Bay, Hawai‘i using experimental blocks of coral skeleton. Comparing before and after micro-computed tomography (µCT) scans to quantify net accretion and erosion, we show that, at the small spatial scale of this study (tens of meters), pH was a better predictor of the accretion-erosion balance than environmental drivers suggested by prior studies, including resource availability, temperature, distance from shore, or depth. In addition, this study highlights the fine-scale variation of pH in coastal systems and the importance of microhabitat variation for reef accretion and erosion processes. We demonstrate significant changes in both the mean and variance of pH on the order of meters, providing a local perspective on global increases in pCO2. Our findings suggest that increases in reef erosion, combined with expected decreases in calcification, will accelerate the shift of coral reefs to an erosion-dominated system in a high-CO2 world. This shift will make reefs increasingly susceptible to storm damage and sea-level rise, threatening the maintenance of the ecosystem services that coral reefs provide.

KEY WORDS: Coral reefs · pH · Bioerosion · Accretion-erosion balance · Environmental variability · Ocean acidification

INTRODUCTION

Ocean acidification is threatening the persistence of coral reef ecosystems (Hoegh-Guldberg et al. 2007). The oceans have absorbed ~30% of the anthropogenic increase in carbon dioxide (CO2), resulting in a decrease in the pH of ocean water (‘ocean acidification’) and a shift in the chemical equilibrium towards dissolution (Caldeira & Wickett 2003, Feely et al. 2004, Sabine et al. 2004). Current IPCC models predict changes in pH for the open ocean, but these mean predictions are problematic for coral reefs, which are embedded in highly variable coastal ecosystems (Gagliano et al. 2010, Hofmann et al. 2011) where restricted water motion, terrestrial influences, and feedbacks between benthic productivity and calcification strongly influence the physicochemical environment (Yates et al. 2007, Drupp et al. 2011, Massaro et al. 2012, Duarte et al. 2013, Smith et al. 2013). In this variable coastal environment, coral reef organisms experience biologically-relevant daily variation in pH (Price et al. 2012) and the magnitude of this variation changes over small spatial scales (meters to tens of meters) that are relevant to individ-
ual organisms (Guadayol et al. 2014). This natural spatial and temporal variation can exceed the 0.07 to 0.33 pH unit increase predicted for the global oceans in the 21st century (Bopp et al. 2013), demonstrating the need to study reef processes on finer spatial and temporal scales than prior studies and presenting an opportunity to examine ecological responses to environmental variation in situ. Here, we take advantage of the high spatial variability in lagoon reef systems and directly measure net reef accretion and erosion in experimental blocks of coral skeleton along a natural environmental gradient.

Coral reef ecosystems persist in a balance between accretion and erosion; this balance is vulnerable to observed and predicted changes in ocean carbonate chemistry. While the response of calcifying organisms to ocean acidification is variable (Ries et al. 2009), calcification rates for most tropical coral species and other reef calcifiers decline with increasing pCO2 (Kroeker et al. 2010, Pandolfi et al. 2011). However, these demonstrated declines may underestimate the impact of ocean acidification because net reef accretion, or growth, depends not only on the constructive process of reef calcification, but also the destructive processes of reef dissolution and bioerosion, i.e. the removal of lithic substrate by bioeroding organisms (Neumann 1966). For reefs to persist, reef accretion must exceed erosion. Reef erosion by a diverse community of grazers (fish and urchins) and internal eroders (sponges, marine worms, bivalves, and microboring flora) plays a major role in the calcium carbonate (CaCO3) budget (reviewed in Hutchings 1986). Reef eroders are responsible for 90% of coral reef sediment production and just over half of these sediments are re-incorporated back into the coral framework (Hubbard et al. 1990). In addition, bioerosion increases the porosity of the coral reef framework, which provides shelter for cryptic organisms (Moran & Reaka 1988) but also reduces mechanical stability (Scott & Risk 1988).

Reef bioerosion rates respond strongly to eutrophication (e.g. Rose & Risk 1985, Edinger et al. 2000, Holmes 2000, Holmes et al. 2000, Le Grand & Fabricius 2011) and substrate type (Highsmith 1981, Risk et al. 1995, Edinger & Risk 1996, Perry 1998, Schönberg 2002). Distance from shore (Risk et al. 1995, Tribollet et al. 2002) and depth (Perry 1998, Le Grand & Fabricius 2011, Schmidt & Richter 2013) are also common correlates of bioerosion rates. However, the in situ response of erosion rates to pH and temperature—the variables most relevant to climate change—remains poorly characterized. Recent reviews suggest that reef erosion will increase in a high CO2 world (Hoegh-Guldberg et al. 2007, Guinotte & Fabry 2008, Andersson & Gledhill 2013) and that reefs may shift from an accretion-dominated to an erosion-dominated state (Silverman et al. 2009), making them more susceptible to storm damage and sea-level rise (Hutchings 1986). Yet, there is little field data testing a pH-driven shift from accretion to erosion in situ. Laboratory studies of bioerosion response to ocean acidification have focused on specific eroding groups and shown increases in the penetration depth and erosion rates of microboring flora (Tribollet et al. 2009, Reyes-Nivia et al. 2013), under elevated pCO2 conditions. Field studies have been indirect or strongly confounded by other environmental variables: Fabricius et al. (2011) showed that the density of externally visible borer orifices in live Porites sp. were higher in closer proximity to CO2 seeps in Papua New Guinea (Fabricius et al. 2011). Manzello et al. (2008) compared 3 sites in the eastern tropical Pacific and found that erosion rates were higher at sites with frequent upwelling of water with a low aragonite saturation state (Manzello et al. 2008), but these upwelling sites also had high nutrients and low temperature; temperature and nutrients are both known drivers of bioerosion (Le Grand & Fabricius 2011, Davidson et al. 2013).

In this study, we took advantage of the natural pH variation in coral reef ecosystems emphasized by recent studies (Gagliano et al. 2010, Hofmann et al. 2011, Guadayol et al. 2014) and directly measured net reef accretion and erosion using experimental blocks of coral skeleton in response to natural pH variation. This experimental approach integrated a natural, early successional community of bioeroders (including internal eroders and external grazers) and reef calcifiers, but excluded accretion by corals. To calculate net reef accretion and erosion, we used micro-computed tomography (µCT) to create high resolution (100 µm), 3-dimensional (3D) density profiles of experimental CaCO3 blocks before and after deployment (see Fig. 2 below). Previous studies have used µCT to visualize bioerosion by sponges (Schönberg & Shields 2008) and to examine coral skeletal morphology (Roche et al. 2011); we applied this technology in a novel way to quantify net accretion and erosion more precisely than buoyant weight methods. Using a model-comparison framework, we compared pH with other known drivers and correlates of the accretion-erosion balance, including resource availability for filter feeding bioeroders, temperature, depth, and distance from shore.
**MATERIALS AND METHODS**

**Study site and experimental design**

**Study site.** The study site is located in Kāne‘ohe Bay, O‘ahu on the windward (eastern) side of Moku o Lo‘e (Coconut Island), adjacent to the Hawai‘i Institute of Marine Biology (21° 25.98’ N, 157° 47.18’ N) (Fig. S1 in Supplement 1 at www.int-res.com/articles/suppl/m515p033_supp/). This fringing reef is dominated by *Porites compressa* and *Montipora capitata*, with occasional colonies of *Pocillopora damicornis*, *Fungia scutaria*, and *Porites lobata*. Kāne‘ohe Bay is a protected, semi-enclosed embayment; the residence time can be >1 mo in the protected southern portion of Kāne‘ohe Bay, where our study was located (Lowe et al. 2009a). Wave action is low (Smith et al. 1981, Lowe et al. 2009b,a), and currents are moderate (5 cm s\(^{-1}\) maximum) and tidally driven (mean and maximum tidal ranges are 0.7 and 1.1 m, respectively) (Lowe et al. 2009a,b). Daily averages in pH, temperature, and O\(_2\) in the Kāne‘ohe Bay waters just offshore our site ranged from 7.83 to 8.03, 21.84 to 27.86°C, and 5.82 to 7.81 mg l\(^{-1}\), respectively, during our study period (Guadayol et al. 2014; data for the entire transect is presented in Table S1 in Supplement 1).

**Experimental design.** Twenty-one experimental blocks were deployed along a 32 m transect perpendicular to the shore, stratified between reef flat and reef slope (Fig. 1e). Blocks were cable-tied to D-rings that were epoxied to the substrate and deployed from March 31, 2011 to April 10, 2012 (Fig. S2 in Supplement 1). Water samples for nutrients, chlorophyll \(a\), total alkalinity (TA), and pH \(T\) (i.e. pH on the total scale, hereafter ‘pH’) were collected directly above each block 4 times within 24 h in September, December, and April in order to capture both diel and seasonal variability in the environment. In addition to discrete water samples, we measured high frequency (0.1 min\(^{-1}\)) variation in temperature and depth using a continuous sensor stationed over each block for a minimum of 2 wk. These short time series were nor-

---

**Fig. 1.** Environmental parameters measured at 21 points along a coral reef transect in Kāne‘ohe Bay, Hawai‘i, where experimental blocks of dead coral were sampled to compare pH with other known drivers and correlates of the accretion-erosion balance: (a) relative temperature anomalies; (b) pH (total scale); (c) chlorophyll \(a\) (µg l\(^{-1}\)); (d) DIN:DIP; (e) the depth and distance from shore of each experimental block. In panels (a) to (d), circles and error bars show means and standard deviations of the variable at each point along the transect. The x-axes indicate position (m) on the the transect with 0 being closest to shore, and colors represent depth (m) as shown in the color bar.
malized to a continuous time series from a permanent station positioned adjacent to the transect, allowing comparison of the micro-environments at each block (Guadayol et al. 2014). Spatial variation in the mean and variance of environmental parameters across the transect allowed comparison of potential drivers of the accretion-erosion balance (Fig. 1, Figs. S3 & S4 in Supplement 1, Table 1).

Experimental blocks. Blocks were cut from dead pieces of massive Porites sp. skeleton collected above the high-tide mark from beaches around O’ahu (Fig. S2). Only coral pieces with obvious calices and no visible external borings were selected. Coral pieces were cut into 5 × 5 × 2 cm blocks, soaked in fresh water, and then autoclaved to remove any living organisms. Because substrate skeletal density can influence reef bioerosion rates (Highsmith 1981, Schönberg 2002), we used blocks with similar skeletal densities. The average (±SD) skeletal density of each coral block was 1.57 ± 0.07 g cm⁻³. The skeletal density of Porites lobata ranges from 1.27 to 1.66 g cm⁻³ on O’ahu and from 1.15 to 1.95 g cm⁻³ across the Hawaiian Archipelago (Grigg 1982).

Micro-computed tomography (µCT). Net accretion and erosion rates were calculated using µCT, an X-ray technology that non-destructively images the external and internal structures of solid objects, resulting in a 3D array of object densities (Fig. 2). Previous studies have used single CT scans to analyze bioerosion (Becker & Reaka-Kudla 1996, Beuck et al. 2007, Schönberg & Shields 2008, Crook et al. 2013). We used µCT in a novel way by comparing pre- and post-deployment scans. This technique allowed us to calculate a very accurate rate for net accretion-erosion and to account for and digitally remove the effect of any pre-existing borings in the experimental substrate. Further, we were able to visualize new erosion scars by external and internal eroders and new growth by secondary calcifiers in 3 dimensions, information that cannot be acquired.

Table 1. Model selection for comparison of pH with other known drivers and correlates of the accretion-erosion balance on 21 experimental blocks of dead coral sampled along a transect in Kāne‘ohe Bay, Hawai‘i. k: number of parameters in the model; −log(L): negative log likelihood of the model; AICc: the corrected Aikake Information Criterion; ΔAICc: difference from the lowest AICc value; R²: proportion of total variance explained by the model; Rank: rank of the model, with 1 being the best fit. See Table S5 in Supplement 1 at www.int-res.com/articles/suppl/m515p033_supp/ for a list of environmental parameters considered and their ranges. Each model is a linear regression of net reef erosion versus the means (X̄) and variances (Var(X)) or covariances (Covar) of each parameter. The Resource Availability Model includes the ratio of dissolved inorganic nitrogen to dissolved inorganic phosphate (DIN:DIP) and chlorophyll a concentration. The Full Model includes means and variances for all listed environmental parameters. The upper table (a) shows a model comparison for all measured environmental parameters (which include both means and variances of each parameter) and the lower table (b) shows the model selection for only pH mean versus variance.

<table>
<thead>
<tr>
<th>Model parameters</th>
<th>k</th>
<th>−log(L)</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>R²</th>
<th>Rank</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a) Model selection comparing pH and other environmental parameters</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>pH Y ~ pH + Var(pH)</td>
<td>4</td>
<td>−30.46</td>
<td>68.42</td>
<td>0.00</td>
<td>0.64</td>
<td>1</td>
</tr>
<tr>
<td>Depth Y ~ Depth</td>
<td>3</td>
<td>−40.01</td>
<td>84.73</td>
<td>16.30</td>
<td>0.06</td>
<td>2</td>
</tr>
<tr>
<td>Distance Y ~ Distance</td>
<td>3</td>
<td>−40.40</td>
<td>85.50</td>
<td>17.08</td>
<td>0.02</td>
<td>3</td>
</tr>
<tr>
<td>Temperature Y ~ Temp + Covar(Temp)</td>
<td>4</td>
<td>−40.42</td>
<td>88.33</td>
<td>19.91</td>
<td>0.03</td>
<td>4</td>
</tr>
<tr>
<td>Resource availability Y ~ Chl + Var(Chl) + N:P + Var(N:P)</td>
<td>6</td>
<td>−38.91</td>
<td>92.11</td>
<td>23.68</td>
<td>0.18</td>
<td>5</td>
</tr>
<tr>
<td>Full model Y ~ pH + Var(pH) + Temp + Covar(Temp) + Chl + Var(Chl) + N:P + Var(N:P) + Depth + Distance</td>
<td>12</td>
<td>−25.92</td>
<td>106.84</td>
<td>38.42</td>
<td>0.82</td>
<td>6</td>
</tr>
<tr>
<td>(b) Model selection considering only pH mean and variance</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>pH mean Y ~ pH</td>
<td>3</td>
<td>−30.41</td>
<td>65.52</td>
<td>0.00</td>
<td>0.64</td>
<td>1</td>
</tr>
<tr>
<td>pH mean and variance Y ~ pH + Var(pH)</td>
<td>4</td>
<td>−30.46</td>
<td>68.42</td>
<td>2.90</td>
<td>0.64</td>
<td>2</td>
</tr>
<tr>
<td>pH variance Y ~ Var(pH)</td>
<td>3</td>
<td>−39.34</td>
<td>83.39</td>
<td>17.87</td>
<td>0.12</td>
<td>3</td>
</tr>
</tbody>
</table>
Silbiger et al.: Reef accretion-erosion balance from traditional buoyant weight techniques. We used an eXplore CT120 µCT (GE Healthcare Xradia) at the Cornell University Imaging Multiscale CT Facility to scan blocks before and after deployment (voltage = 100 kV, current = 50 mA). Angular projections were acquired in a full 360° rotation in 0.5° increments; 2 images at each angle were acquired and averaged. A 3D array of isotropic voxels at 50 µm resolution was generated using the GE Console Software. These 50 µm voxels were averaged to 100 µm for data analysis. The intensity value in each voxel is directly related to the density of the object at that voxel. A global threshold value of 200 Hounsfield Units (HU) was used to separate CaCO3 from air and remove any effects of partial volume averaging at the coral block-air interface (Roche et al. 2010). The number of voxels exceeding this threshold was multiplied by the voxel size (100 µm)³ to give the total volume of CaCO3. We measured net accretion-erosion as the change in volume of CaCO3 from before and after scans. Note that this volumetric analysis measures changes at the voxel scale of 50 µm, which was then averaged to 100 µm, and may, therefore, underestimate erosion by microborers, which make erosion scars between 1 and 100 µm (Tribollet 2008). The values were square-root transformed to meet model assumptions of normality, and 1 block with a large aggregation of oysters was excluded from the analysis.

Environmental parameters: potential predictors and correlates of net reef erosion

Sampling technique. Previous studies have identified nutrient concentration (e.g. Rose & Risk 1985, Edinger et al. 2000, Holmes 2000, Holmes et al. 2000, Le Grand & Fabricius 2011), temperature (Davidson et al. 2013), pH (Tribollet et al. 2009, Wisshak et al. 2012, 2013, Reyes-Nivia et al. 2013, Fang et al. 2013) and depth (Perry 1998, Le Grand & Fabricius 2011, Schmidt & Richter 2013) as possible drivers of the accretion-erosion balance. This study compared the effect of these environmental parameters on net accretion-erosion using data obtained from discrete water samples (pH, TA, nitrate (NO3⁻), nitrite (NO2⁻), ammonium (NH4⁺), phosphate (PO4³⁻), and chlorophyll a) and from continuous sensors (temperature and depth) along the transect. The discrete water samples were collected directly above each block within 2 d of spring tide at 08:00, 14:00, 20:00 h, and 02:00 h on September 10−11, 2011, December 12−13, 2011, and April 4−5, 2012. All discrete water samples were collected using snorkel or SCUBA using 60 and 120 ml plastic syringes. Syringes and storage vials were all pre-cleaned in a 10% HCl bath for 24 h and rinsed 3 times with MilliQ water; during sample collection and processing they were rinsed 3 times with sample water. The environment was sampled more continuously for temperature and depth (sampling rate of ~0.1 min⁻¹) using 1 permanent and 2 mobile monitoring stations. Two mobile stations were deployed at a time, one on the reef flat and one on the reef slope, to get simultaneous measurements at 2 different blocks on the transect. Mobile stations (Sonde 600XLM, YSI) were positioned 5 to 10 cm above each block for a 2-wk period between May 2011 and March 2012. Blocks were sampled in ran-
dom order, ensuring that the spatial gradient along the transect was not systematically confounded by temporal trends or seasonality (Guadayol et al. 2014). The permanent monitoring station (Sonde 6600-V2-4, YSI) was mounted on a pole a few meters away from the transect, downward facing at 1.7 m depth over a 3 m deep bottom, with sensors for temperature, depth, conductivity, pH, and O2 to characterize the background water column conditions for the duration of the experiment. All multi-parametric probes were calibrated periodically using standard procedures and calibration solutions. The permanent station was recovered, cleaned, calibrated, and re-deployed 3 times during the study, and the mobile station probes were calibrated 7 times. Pre-calibration measurements of commercial standard solutions were conducted to detect sensor drift, although none was found for the period of study. The background water column data are reported in Guadayol et al. (2014).

**Nutrients and chlorophyll.** Water samples collected for nutrients were immediately filtered through combusted 25 mm glass fiber filters (GF/F 0.7 µm) and transferred into 50 ml plastic centrifuge tubes. Nutrient samples were frozen and later analyzed for NO3−, NO2−, NH4+, and PO43− on a Seal Analytical AA3 HR Nutrient Analyzer at the University of Hawai'i SOEST Laboratory for Analytical Biochemistry (Table S2 in Supplement 1). GF/F filters were folded in half, wrapped in aluminum foil, and frozen for chlorophyll a analysis using a Turner Designs 10AU Benchtop Fluorometer (Table S2). The ratio of dissolved inorganic nitrogen to dissolved inorganic phosphate (DIN:DIP) was used as a proxy for resource quality available to filter feeders (Hauss et al. 2012), assuming that elemental composition of planktonic prey will be influenced by elemental composition of the water column, and was calculated from ([NO3−] + [NO2−] + [NH4+]):[PO43−]).

**pH and total alkalinity (TA).** Mean and variance in pH at each block was calculated from water samples along the transect. Water samples for pH were immediately transferred into 25 ml borosilicate glass vials, brought to a constant temperature of 25°C in a water bath, and immediately analyzed using an m-cresol dye addition spectrophotometric technique and calibrated against a Tris buffer of known pH from Andrew Dickson's Laboratory at Scripps Institution of Oceanography (Table S2). TA was fixed with 100 µl of HgCl2 and analyzed using open cell potentiometric titrations on a Mettler T50 autotitrator and calibrated against a Certified Reference Material following Dickson et al. (2007) protocols. In situ pH and all other carbonate parameters (see Table S1) were estimated using CO2SYS (van Heuven et al. 2011) with the following parameters: pH, TA, temperature, and salinity. The K1K2 dissociation constants were from Mehrbach (1973) (refit by Dickson & Millero 1987) and HSO4− dissociation constants were taken from Uppström (1974) and Dickson (1990). Accuracy for TA and pH was better than 0.8 and 0.04%, respectively, and the precision was 3.55 µEq and 0.004 pH units.

**Temperature.** Temperature sensors (YSI 6560) were thermistors with manufacturer-reported accuracy of ±0.15°C and resolution of 0.01°C (YSI Incorporated). Average differences in temperature along the transect were small and measured as a relative anomaly from the permanent station: \( \Delta \text{temperature} = (x_{\text{mobile}} - x_{\text{permanent}})/x_{\text{permanent}} \). To measure relative variability in temperature across the transect, we calculated the covariance in temperature between the mobile and permanent sensor arrays over a 2 wk period and compared this covariance across the transect.

**Depth and distance from shore.** Depth is the average depth measured at each block over the 2 wk deployment of the mobile station. Distance from shore is the along-transect distance (Fig. 1e).

**Model selection.** Our goal was to compare pH with other known drivers and correlates of the accretion-erosion balance. In a model selection framework, we used Aikake Information Criterion (AIC) values to rank candidate models, accounting for both fit and complexity. Carefully constructed model selection avoids problems associated with multiple hypothesis testing that are common in stepwise regression, such as arbitrary α levels and uninterpretable functional relationships (Johnson & Omland 2004, Anderson 2008). Here, we used the corrected AIC (AICc), which is recommended for sample sizes <30 (Anderson 2008). While the model with the smallest AICc value \( (\Delta \text{AICc} = 0) \) is the ‘best’ of the models considered, models with an \( \Delta \text{AICc} \) value of <4 have some empirical support. Models with a \( \Delta \text{AICc} \) value greater than 10 to 12 are less plausible (Anderson 2008).

Good inference from multivariate analyses is confounded by collinearity among environmental variables. Many of the environmental variables were collinear along the transect (Fig. S5 in Supplement 1); thus, we removed collinearity by using the residuals of a regression of each environmental variable against depth and distance from shore. Correlation coefficients for raw environmental data and the residual environmental data are shown in Fig. S5. Model selection with all raw data is presented in Table S3 in Supplement 1.
We compared models for 5 specific hypotheses about the accretion-erosion balance (carbonate chemistry, resource availability, temperature, depth, and distance from shore) to test which of these drivers had the strongest relationship to net accretion-erosion (Table 1). Because recent studies have demonstrated that pH variability correlates with calcification rates on coral reefs (Price et al. 2012), we measured spatial variation in both the mean and temporal variability of each environmental parameter. We used pH to test how carbonate chemistry influenced net accretion-erosion rates. Carbonate chemistry parameters are inherently correlated, and pH had the strongest relationship of the carbonate chemistry parameters (Table S4 in Supplement 1). The pH model includes both the mean and variance of the discrete pH samples from each block. The resource availability model includes the means and variances of DIN:DIP ratios (a proxy for resource quality) and chlorophyll \(a\) (a measure of resource quantity) from the discrete water samples. The temperature model included the mean relative temperature anomaly of each block from the permanent station and temperature covariance between the mobile and permanent stations. The final 2 models were individual models for depth and distance from shore. These linear models were compared to a full model that includes the means and variances of every parameter stated above (Table 1). Environmental data that did not meet the assumptions of normality were log-transformed and net erosion data were square-root transformed.

RESULTS

There were considerable differences in both the mean and variance of pH and nutrients across the 32 m transect. Mean pH increased from 7.84 to 7.91 and the coefficient of variation decreased from 0.013 to 0.0032 from onshore to offshore (Fig. 1b, Tables S1 & S5 in Supplement 1). Mean DIN:DIP decreased from 87.5 to 42.4 and the coefficient of variation increased from 0.36 to 0.59 (Fig. 1d, Table S5) from onshore to offshore. Chlorophyll \(a\) and temperature remained relatively constant across the spatial gradient (Fig. 1a,c, Table S5).

We compared models of pH, resource availability, temperature, depth, and distance from shore as drivers of net accretion and erosion (Table 1, Figs. S3 & S4). The pH model best explained patterns in the accretion-erosion balance along the transect in both the residual and raw data models (Tables 1 & S3, Fig. 3). Accretion was higher on the deeper reef slope, where pH is higher and less variable (Fig. 1, Figs. S6 & S7 in Supplement 1). Removing the effects of depth and distance from shore, pH was an even better predictor of the accretion-erosion balance (Figs. 3 & S3), particularly on the reef flat, and it explains 64% of the variation in net accretion-erosion over a one year deployment (Table 1). The second best model, the depth model (\(\Delta AIC_c = 16.30\)), explained only 6% of the variance (Table 1, Fig. S7), followed by the distance model which explained only 2% of the variance. While the resource availability model described 18% of the variance in the data, it also had a larger number of parameters (6, including mean and variance for both DIN:DIP and chlorophyll \(a\)) and, therefore, ranked sixth in model parsimony.

We also tested whether the mean or variance in pH was a better predictor of net accretion-erosion. Mean pH was the best model, explaining 64% of the vari-
ance (Table 1) and had a strong negative relationship with net accretion-erosion (Fig. 3). pH was also a better predictor of net accretion-erosion than TA, pCO$_2$, and DIC, but these highly collinear carbonate chemistry parameters did have some empirical support and explained between 42 and 58% of the variance in net accretion-erosion (Table S4).

DISCUSSION

Spatial and temporal variation in pH across the transect

Across the transect, pH had a range of 0.33 pH units at the most variable site and 0.08 pH units at the least variable site over the year (Table S1). The organisms at these sites experience a natural variation in pH that is within the range that mean pH is predicted to decrease for the 21st century (Bopp et al. 2013). Indeed, this pH range is not unique to our transect, but is typical of other shallow coral reef sites in the Pacific. For example, pH at the CRIMP2 buoy, a slightly deeper (~3 m) nearby reef site located in central Kāne‘ohe Bay, ranged from 7.90 to 8.13 over a 2.5 yr study (Drupp et al. 2013). On a Palmyra reef terrace, pH ranged from 7.85 to 8.10 (Hofmann et al. 2011) and pH spanned 0.39 units in a study examining the spatial variability in microhabitats on the Great Barrier Reef (Gagliano et al. 2010). Additionally, Gagliano et al. (2010) found a similar inshore-offshore pattern: mean pH was lower and more variable inshore compared to offshore sites, though their study was conducted over a much larger spatial scale. The patterns in the means and variances here and in other studies arise from both physical and biological processes including: tidal mixing with offshore waters, photosynthesis/respiration (P/R) cycles, and reef metabolism (Hurd et al. 2011, Kleypas et al. 2011), upwelling events (Leichter et al. 2003, Manzello et al. 2008), and porewater advection from permeable sediments (Santos et al. 2011). We saw a very strong correlation between pH variance and distance from shore (Fig. S6), suggesting that tidal mixing was an important contributor to the spatial variation in pH, although we did not specifically test this hypothesis. Using the residual values that remove the effect of distance and depth from pH eliminates the impact of this large-scale mixing, leaving the effect of small-scale processes (such as local P/R and turbulent mixing) on pH. The raw pH data model explained 48% of the variance in net accretion-erosion (Table S3), but the residual model was an even better fit (Table 1), suggesting that small-scale physicochemical differences in microhabitats may strongly influence the patterns of accretion and erosion on coral reefs. The results of this study suggest that differences in microhabitat variability may be more important to the accretion-erosion balance than larger-scale processes. A better characterization of microhabitat variability (see Guadayol et al. 2014) and how this microhabitat variation impacts reefs will help predict reef responses to climate change in the context of natural variability.

Implications for the accretion-erosion balance of coral reefs

Our results show that differences in the seawater chemistry on the scale of meters can have a substantial influence on the accretion-erosion balance. The majority of the blocks with mean pH <7.88 were net eroding (Fig. S3); this pH value is likely to become more prevalent with the predicted 0.3 to 0.4 pH unit reduction in oceanic waters (Orr et al. 2005, Bopp et al. 2013). Previous studies on coral reefs have shown shifts from net accretion to erosion after major disturbances, such as El Niño-Southern Oscillation (ENSO) events or hurricanes (Perry et al. 2008). Our data indicate that pH is a significant driver of net reef erosion and that, as mean pH decreases, erosion rates will increase. The pH model ranked higher than the distance, depth, and resource availability models; prior studies where depth, distance, and resource availability were stronger predictors of bioerosion were performed on much larger spatial scales and covered a greater range of values (e.g. Perry 1998, Holmes et al. 2000, Tribollet et al. 2002, Le Grand & Fabricius 2011, Schmidt & Richter 2013). For instance, a prior study showing a strong response of bioerosion to resource availability had mean chlorophyll a values ranging from 0.25 to 1.24 µg l$^{-1}$ across their comparison sites (Holmes et al. 2000), compared to a range of only 0.14 to 0.31 µg l$^{-1}$ in this study (Fig. 1). Results from the current study are in agreement with recent laboratory (Tribollet et al. 2009, Wisshak et al. 2012, 2013, Fang et al. 2013, Reyes-Nivia et al. 2013) and field experiments (Manzello et al. 2008, Fabricius et al. 2011, Crook et al. 2013) suggesting that erosion rates will increase with ocean acidification. However, this is the first study to directly test the relationship between the accretion-erosion balance and pH using a natural pH gradient, and to compare this relationship to other known drivers and correlates of reef accretion and erosion.
The bioeroder community is diverse and has a number of mechanisms for boring, including chemical dissolution and mechanical erosion. Individual species respond differently to environmental parameters and, thus, influence the accretion-erosion balance through changes in individual bioerosion rates and in community composition. For example, previous studies have found that boring sponges and bivalves respond positively to eutrophication, while the response of polychaetes is more variable (Le Grand & Fabricius 2011). Filter feeding sponges and bivalves are positively correlated with eutrophic sites in the Bahamas (Rose & Risk 1985), Barbados (Holmes et al. 2000), the Red Sea (Kleemann 2001), the Great Barrier Reef (Osorno et al. 2005, Tribollet & Golubic 2005) and the eastern Pacific (Fonseca et al. 2006); bivalve abundances are also correlated with high water velocity (Cantera et al. 2003, Londono-Cruz et al. 2003). In contrast, deposit feeding polychaetes in the Great Barrier Reef are more abundant at eutrophic sites (Osorno et al. 2005), while suspension feeding polychaetes are more abundant in oligotrophic sites (Le Bris et al. 1998). In addition, there are strong successional dynamics in these communities, and patterns of succession are location specific. In the Great Barrier Reef, microborers and polychaetes are the initial colonizers; these are followed by sipunculans, bivalves, and then sponges (Hutchings 1986); it may take up to 3 yr for sponges to fully colonize dead substrate (Tribollet & Golubic 2005). In the Caribbean, the suggested successional pattern of bioeroders is algae, fungi, clionid sponges, polychaetes, bivalves, barnacles, and then sipunculans (Risk & MacGeachy 1978). In Hawai‘i, an 18 mo study in Kāne‘ohe Bay found no obvious successional patterns (White 1980), but likely captured only the initial successional stages. Our study highlights the influence of pH on the accretion-erosion balance after 1 yr, i.e. during the early-successional stage of this community, and future studies should include multi-year comparisons to test if this pattern holds. In a previous Kāne‘ohe Bay study that used similar blocks, the most abundant organisms after a 1 yr deployment were polychaetes (Spionidae were the most abundant and largest polychaete borers) and sipunculans (White 1980). These were the most common taxa in our study as well. Parrotfish erosion was also evident on our blocks. Common secondary calcifiers in our community were crustose coralline algae (Hydrolithon spp.), barnacles, and the oyster Crassostrea gigas.

Our results highlight the value of using of µCT as a tool to calculate accretion and erosion rates on coral reefs. µCT provides a more sensitive measure of net accretion-erosion in the field than previously published methods (e.g. Edinger & Risk 1996, Tribollet et al. 2009, Perry et al. 2012), and it is directly comparable across studies. Prior studies have used single CT scans to calculate skeletal density (Bosscher 1993), skeletal porosity (Roche et al. 2010), and linear extension (Crook et al. 2013); here, we used µCT in a novel way by comparing before and after images to calculate the precise volume of CaCO₃ removed or accreted. As reef erosion and coral growth are often decoupled on coral reefs (Edinger et al. 2000), quantification of net erosion must complement measures of coral growth for a more complete picture of coral reef health.

Although chemical dissolution will accelerate in future decades as tropical coral reefs shift to less saturated aragonite conditions (van Woesik et al. 2013), bioerosion is currently the main driver of reef loss (Andersson & Gledhill 2013). The mechanisms by which ocean acidification may enhance bioerosion rates include: (1) lower coral skeletal densities (Hoegh-Guldberg et al. 2007, Cooper et al. 2008), making it easier for bioeroders to penetrate the coral skeleton (Edinger & Risk 1996, Dumont et al. 2013), though this point is debated in the literature (Highsmith 1981, Schönberg 2002, Hernández-Ballesteros et al. 2013); (2) increased growth rates of photosynthesizing bioeroders (Tribollet et al. 2009); (3) declines in crustose coralline algae (Jokiel et al. 2008), which can inhibit settlement and growth of micro- and macroborers (Tribollet & Payri 2001); and (4) increased susceptibility of calcifiers to grazers (Johnson & Carpenter 2012). In addition, many boring organisms excrete acidic compounds, raising the possibility that a reduction in ocean pH could make it less metabolically costly to lower pH at the site of erosion.

The combination of slower coral growth (Hoegh-Guldberg et al. 2007, Kroeker et al. 2010, Pandolfi et al. 2011) and higher erosion rates with ocean acidification could act synergistically to hinder reef growth. In the Caribbean, erosion rates are highest in areas where coral cover is low (Perry et al. 2013), indicating that the same drivers that negatively impact corals may also promote erosion. Further, given the strong relationship between bioerosion and local anthropogenic impacts like sedimentation and nutrient runoff (Edinger et al. 2000, Le Grand & Fabricius 2011), the combined effect of these local impacts with decreases in pH in the global oceans could be devastating to reefs worldwide. This study portrays how coral reef ecosystems may change under pre-
dicted increases in ocean acidity: an existing community of reef secondary calcifiers and bioeroders showed a shift from net accretion to net erosion along a naturally occurring, within-reef gradient of high to low pH.

Acknowledgements. We are grateful to C.J. Bradley, J. Chen, R. Coleman, A. Copeland, K. DiPerna, M. Donovan, N. Griffith, K. Hurley, M. Iacchei, I. Iglesias, M. Siple, E.M. Sogin, M. Sudek, J. Sziklai, M. Walton, and the Point Lab for help with data collection. We thank M. Riccio and F. von Stein from the Cornell University mCT Facility for Imaging and Preclinical Research, R. Briggs from UH SOEST Laboratory for Analytical Biochemistry, and the UH lapidary facility. Funding for this project came from NOAA Office of National Marine Sanctuaries-HIMB partnership (MOA #2009-039/7932), National Science Foundation EPSCoR Hawai‘i, NOAA Dr. Nancy Foster Scholarship to N.J.S., Sigma-Xi GIAR to N.J.S., and by Hawai‘i Sea Grants #1889 to F.I.M.T and #1847 to M.J.D. and F.I.M.T. This paper is funded in part by a grant/cooperative agreement from the National Oceanic and Atmospheric Administration, Project No. R/IR-18, which is sponsored by the University of Hawaii’s Sea Grant College Program, School of Ocean and Earth Science and Technology, under Institutional Grant No. NA09OAR4170060 Office of Sea Grant, Department of Commerce. The views expressed herein are those of the author(s) and do not necessarily reflect the views of NOAA or any of its subagencies. Comments from H. Putnam, C. Jury, E. Wolkovich, and 3 anonymous reviewers improved this manuscript. This is HIMB contribution #1597, SOEST #9188, and SeaGrant #UNIHJ-SEAGRANT-JC-13-13.

LITERATURE CITED

Dickson AG (1990) Standard potential of the reaction: AgCl(s) + ½H2(g) = Ag(s) + HCl(aq), and the standard acidity constant of the ion HSO4− in synthetic sea water from 273.15 to 318.15 K. J Chem Thermodyn 22: 113–127


Meethach C (1973) Measurement of the apparent dissociation constants of carbonic acid in seawater at atmospheric pressure. Limnol Oceanogr 18:897–907


Editorial responsibility: Brian Helmuth, Nahant, Massachusetts, USA

Submitted: January 14, 2014; Accepted: August 17, 2014
Proofs received from author(s): October 27, 2014