Impacts of multiple environmental stressors on coral reef erosion and secondary accretion

Nyssa J Silbiger, Òscar Guadayol, Florence I.M. Thomas, Megan J Donahue

Ocean acidification threatens to shift coral reefs from net accreting to net eroding. While corals build reefs through accretion of calcium carbonate (CaCO$_3$) skeletons, net reef growth depends on bioerosion by grazers and borers and on secondary calcification by crustose coralline algae and other calcifying invertebrates. Primary calcification, secondary calcification, and erosion processes respond differently to climate change stressors; therefore, the combined accretion-erosion response is uncertain. Using a new micro-computed tomography (µCT) method, we measured the simultaneous response of secondary accretion and bioerosion along an environmental gradient: bioerosion rates ranged from 0.02 to 0.91 kg m$^{-2}$ yr$^{-1}$ and secondary accretion rates ranged from 0.01 to 0.4 mm yr$^{-1}$ across a 32m transect. Co-located measures of secondary accretion and bioerosion had different environmental drivers: bioerosion rates were highly sensitive to ocean acidity while secondary accretion rates were most sensitive to physical drivers. These results suggest that bioerosion plays a significant role in the shift from net accretion to net erosion on coral reefs.
**Title:** Impacts of multiple environmental stressors on coral reef erosion and secondary accretion

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**KEYWORDS:** Ocean acidification, accretion, bioerosion, natural gradients, coral reefs

**ABSTRACT**

Ocean acidification threatens to shift coral reefs from net accreting to net eroding. While corals build reefs through accretion of calcium carbonate (CaCO₃) skeletons, net reef growth depends on bioerosion by grazers and borers and on secondary calcification by crustose coralline algae and other calcifying invertebrates. Primary calcification, secondary calcification, and erosion processes respond differently to climate change stressors; therefore, the combined accretion-erosion response is uncertain. Using a new micro-computed tomography (µCT) method, we measured the simultaneous response of secondary accretion and bioerosion along an environmental gradient: bioerosion rates ranged from 0.02 to 0.91 kg m⁻² yr⁻¹ and secondary accretion rates ranged from 0.01 to 0.4 mm yr⁻¹ across a 32m transect. Co-located measures of secondary accretion and bioerosion had different environmental drivers: bioerosion rates were highly sensitive to ocean acidity while secondary accretion rates were most sensitive to physical drivers. These results suggest that bioerosion plays a significant role in the shift from net accretion to net erosion on coral reefs.
INTRODUCTION

Human-induced changes in ocean chemistry (Hoegh-Guldberg et al., 2007; Andersson and Gledhill, 2013; DeCarlo et al., 2014; Silbiger et al., 2014; Silbiger and Donahue, 2015; Wisshak et al., 2012; Tribollet et al., 2009; Reyes-Nivia et al., 2013; Fang et al., 2013), temperature (Hoegh-Guldberg et al., 2007; Silbiger and Donahue, 2015; Davidson et al., 2013; Fang et al., 2013), and water quality (Fabricius, 2005; DeCarlo et al., 2014; Risk et al., 1995b; Holmes et al., 2000; Tribollet and Golubic, 2005; Edinger et al., 2000; Le Grand and Fabricius, 2011) are threatening coral reefs (Pandolfi et al., 2011; Hoegh-Guldberg et al., 2007; Fabricius, 2005). Predictions of reef response to changing ocean conditions are often based on the response of reef building corals alone (Silverman et al., 2009; Pandolfi et al., 2011); however, coral reef bioerosion from borers and grazers and secondary accretion from crustose coralline algae and other encrusting invertebrates are also critical processes for reef sustainability (Przeslawski et al., 2008). There are several gaps in our knowledge about the response of coral reefs to future ocean conditions and whether reef accretion will continue to exceed reef erosion. 1) Will primary accretion, secondary accretion, and reef erosion respond similarly to environmental drivers and will their responses combine to accelerate reef loss? Studies that examine accretion or erosion processes individually have found different responses to environmental stress. In a field experiment in Indonesia, coral calcification and bioerosion had different functional relationships with land-based pollution (Edinger et al., 2000). Laboratory experiments focusing on climate stressors (i.e. temperature and ocean acidity) have found that bioerosion is linearly related to ocean acidity and temperature (Silbiger and Donahue, 2015; Wisshak et al., 2012; Tribollet et al., 2009; Reyes-Nivia et al., 2013; Fang et al., 2013), but that calcification exhibits both linear (Pandolfi et al., 2011; Comeau et al., 2013) and non-linear (Castillo et al., 2014; Silbiger and Donahue, 2015; Comeau et al., 2013; Pandolfi et al., 2011) responses. These differential responses of primary and secondary accretion and bioerosion challenge our ability to predict the net response of coral reefs to environmental change. 2) How will multiple environmental stressors impact individual reef processes? Many environmental parameters interact to drive patterns in accretion and erosion, including ocean acidity (Hoegh-Guldberg et al., 2007; Andersson and Gledhill, 2013; DeCarlo et al., 2014; Silbiger et al., 2014; Silbiger and Donahue, 2015; Wisshak et al., 2012; Tribollet et al., 2009; Reyes-Nivia et al., 2013; Fang et al., 2013), temperature (Hoegh-Guldberg et al., 2007; Silbiger and Donahue, 2015; Davidson et al., 2013; Fang et al., 2013), nutrients (Fabricius, 2005; DeCarlo et al., 2014; Risk et al., 1995b; Holmes et al., 2000; Tribollet and Golubic, 2005), and gradients of human influence (e.g., chlorophyll, turbidity, sedimentation) (Edinger et al., 2000; Le Grand and Fabricius, 2011). This myriad of drivers complicates the predictions of reef response to climate change. 3) How does local, natural variability contextualize global changes in the accretion-erosion balance? Shallow coral reef ecosystems persist in highly variable physicochemical environments (Guadayol et al., 2014; Hofmann et al., 2011; Rivest and Gouhier, 2015) driven by tidal flushing, photosynthesis and respiration, ground-water inputs, and other benthic biological processes (Shamberger et al., 2014; Yates et al., 2007; Drupp et al., 2011; Massaro et al., 2012; Duarte et al., 2013; Smith et al., 2013). Little is known about how climate change
interacts with this naturally variable environment to drive patterns accretion and erosion. Here, we address each of these knowledge gaps by leveraging a natural environmental gradient in Kāne‘ohe Bay to rank the impact of multiple environmental stressors on simultaneous measures of secondary accretion and reef bioerosion.

The physicochemical variability of reefs in Kāne‘ohe Bay, Hawai‘i has been extensively investigated (Guadayol et al., 2014; Drupp et al., 2011; Lowe et al., 2009). Like many reefs around the globe (Hofmann et al., 2011; Rivest and Gouhier, 2015; Shamberger et al., 2014; Manzello et al., 2008; Crook et al., 2013), Kāne‘ohe Bay has persistent areas of natural acidification that reach the low open-ocean pH values expected by the end of the 21st century (Silbiger et al., 2014; Guadayol et al., 2014). Using a space-for-time framework, we can leverage this natural variability to understand how reefs will respond to ocean acidification in the context of a naturally variable environment. Our prior work in Kāne‘ohe Bay demonstrates that net reef erosion (calculated as the percent change in volume of experimental blocks) is driven by natural variation in pH and that reefs could shift from net accretion to net erosion with increasing ocean acidity (Silbiger et al., 2014). Here, we separate and simultaneously measure secondary accretion and bioerosion along the same environmental gradient (Figure 1) and then compare the relative importance of a suite of environmental drivers to each of these processes.

In prior studies using experimental substrates, pre- and post-deployment buoyant weights have been used to calculate rates of change in density, mass, or volume (reviewed in Table 1), but this method cannot distinguish between secondary accretion and bioerosion processes. In prior studies using natural substrates, imaging methodologies in 2-dimensions and, more recently, 3-dimensions (CT and µCT) can be used to separate accretion and bioerosion on slabs or cores of reef (Table 1), but rates are difficult to estimate because the time the substrate became available to bioeroders and secondary calcifiers is unknown. Here, we describe a new analysis using µCT to separate secondary accretion and bioerosion from the same experimental substrate exposed to the same environmenital variation over the same time-scale (Figure 2). Our µCT method also allows for a 3D visualization of the experimental blocks that highlights specific areas of secondary accretion and bioerosion (See Movies S1 and S2 in Supplement). Using µCT, we calculate secondary accretion and bioerosion rates from experimental blocks deployed along a 32 m reef transect (Figure S1). Patterns in carbonate chemistry, nutrients, chlorophyll a, temperature, and depth were characterized along this same transect (Figure 1; described in Silbiger et al. (2014)), and used to compare five specific hypotheses about drivers of the accretion-erosion balance: carbonate chemistry, resource availability, temperature, depth, and hydrodynamics (distance from shore and depth). We use a model selection approach to test which of these drivers has the strongest relationship to secondary accretion and bioerosion.

Materials and Methods

(a) Experimental Design: Our study site is located in Kāne‘ohe Bay, O‘ahu on the windward (eastern) side of Moku o Lo‘e. We used the same environmental gradient as Silbiger et al. (2014), which we briefly describe here.
Twenty-one experimental blocks were deployed along a 32 m transect, stratified between reef flat and reef slope (Figure S1). Experimental blocks were cut from dead pieces of massive *Porites* sp. skeleton into 5cm x 5cm x 2cm blocks, soaked in freshwater, and then autoclaved to remove any living organisms. Collections were made under special activity permit # SAP2011-1 to the Hawai‘i Institute of Marine Biology at the University of Hawai‘i at Mānoa. The average skeletal density of each experimental block was 1.57 ±0.07(sd) g cm$^{-3}$. Blocks were deployed from March 31, 2011 to April 10, 2012. We collected both discrete water samples (pH, TA, nitrate, nitrite, ammonium, phosphate, and chlorophyll a) and data from continuous sensors (temperature and depth) along the transect. Water samples were collected directly above each block four times within 24 hours in September, December, and April in order to capture both diel and seasonal variability in the environment. Continuous sensors were stationed over each block for a minimum of two weeks to calculate high frequency (0.1 min$^{-1}$) variation in temperature and depth. These short time series were normalized 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).

(b) $\mu$CT: Secondary accretion and bioerosion rates were calculated using $\mu$CT (Figure 2). $\mu$CT 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 $\mu$CT (GE Healthcare Xradia, Inc) at the Cornell University Imaging Multiscale CT Facility (Figure 2.1-2) to scan blocks before and after deployment (voltage = 100kV, current = 50mA). A three-dimensional array of isotropic voxels at 50 $\mu$m$^3$ resolution was generated using the GE Console Software and were averaged to 100 $\mu$m$^3$ for data analysis. We used a threshold of 200 Hounsfield Units to separate coral from air (Silbiger et al., 2014) (Figure 2.3). The pre and post-deployment scans were aligned using an intensity-based registration technique (Figure 2.4), converted to binary (Figure 2.5), and subtracted from one another resulting in a matrix of 0’s, 1’s, and -1’s (Figure 2.5). All positive values were new pixels added to the post-deployment scan which indicate secondary accretion, 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 or gained per block (Figure 2.6).

c) Rates: Bioerosion and secondary accretion rates were calculated using the following equations: Bioerosion Rate (kg m$^{-2}$ yr$^{-1}$) = $(Vol_i \times \rho_i)/(SA_i \times Time)$ and Secondary Accretion Rate (mm yr$^{-1}$) = $Vol_i/(SA_i \times Time)$, where $i$ represents an individual block, $Vol$ is the volume lost (bioerosion) or gained (secondary accretion) in m$^3$, $SA$ is the surface area of the pre-deployment blocks (m$^2$), $\rho$ is the skeletal density of the pre-deployment block (kg m$^{-3}$), and $Time$ is the deployment time (years). Secondary accretion rates were converted from m to mm per year to compare with literature values.

(d) Model Selection: Our goal was to compare pH with other known drivers and correlates of the accretion-erosion balance. Many of the environmental variables were collinear along the transect; thus, we removed collinearity by using the residuals of a regression of each environmental variable against log(depth) and distance from shore.
(Silbiger et al., 2014). Correlation coefficients for raw environmental data and the residual environmental data are available in Silbiger et al. (2014).

We used a model selection framework to compare models for five specific hypotheses about the accretion-erosion balance and test which of these drivers had the strongest relationship to secondary accretion and bioerosion (Table 2). In a model selection framework, Akaike Information Criterion (AIC) values are used 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 $\alpha$ levels and uninterpretable functional relationships (Johnson and 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 ($\Delta$AICc = 0) is the ‘best’ of the models considered, models with an $\Delta$AICc value of <4 have some empirical support (Anderson, 2008). We used pH to test how carbonate chemistry influenced secondary accretion and bioerosion rates. Carbonate chemistry parameters are inherently correlated, and pH had the strongest relationship of the carbonate chemistry parameters (Table S1). 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 overlaying water column and temperature covariance between the block and overlaying water column. The final model was the combination of log(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 2). Environmental data that did not meet the assumptions of normality were log-transformed, secondary accretion and bioerosion data were square-root transformed to meet assumptions of normality, and one block with a large aggregation of oysters was excluded from the analysis. Figures showing secondary accretion (Figure S2) and bioerosion (Figure S3) versus the means and variances of all environmental parameters are available in the supplement.

RESULTS AND DISCUSSION

Environmental data: The environmental gradient is detailed in Silbiger et al. (2014) and described briefly here. The 32-m experimental transect ranged from 0.1 to 4.5 m depth (Figure S1), and there were trends in the mean and variance of pH and DIN:DIP across the gradient (Figure 1). pH mean increased from 7.84 to 7.91 across the transect; over the year-long deployment, pH ranged from 7.84 to 7.94 at the deeper, least variable site and from 7.76 to 8.02 at the most variable site nearshore (Figures 1g,h and S4). Mean DIN:DIP decreased from 87.5 to 42.4 and the variance increased from 250 to 1996 (Figure 1e,f). Chl a and temperature anomalies remained relatively constant (Figure 1a-d).

Bioerosion Rates:
Bioerosion rates varied by nearly two orders of magnitude across our 32 m transect, ranging from 0.02 to 0.91 kg m\(^{-2}\) yr\(^{-1}\) (Figure S3p). These bioerosion rates are similar to rates at other Pacific reefs sites: a recent study found bioerosion rates ranging from 0 to 0.6 kg m\(^{-2}\) yr\(^{-1}\) at remote reefs across the Pacific (DeCarlo et al., 2014). Interestingly, the range of bioerosion rates on our transect was greater than the range of bioerosion rates in this Pacific wide study, highlighting the importance of small-scale, within-reef variability. Bioerosion rates were best predicted by the pH model, which explained 54% of the variance in bioerosion across the transect (Table 2a, Figure 3). The second best model, the distance and depth model, had low empirical support (\(\Delta AIC_c = -13.78\)) and explained only 9% of the variance (Table 2a) and was followed by the temperature model which explained only 7% of the variance in bioerosion rates. While the resource availability model described 21% 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 fourth in model parsimony. The full model, which included the means and variances of all parameters, described 79% of the variance in bioerosion rates indicating that the environmental data we collected adequately described patterns in bioerosion rates across the transect. Any additional environmental parameter would at most only explain 21% of the variance in bioerosion.

While all the parameters in these models interact to drive patterns in bioerosion, a of ranking individual of parameters indicates that pH was the dominant driver. It is becoming clear that ocean acidity facilitates erosion (Tribollet et al., 2009; Wisshak et al., 2012; Reyes-Nivia et al., 2013; Fang et al., 2013; Silbiger and Donahue, 2015; Silbiger et al., 2014), but the mechanisms that control this relationship are still not well known. Several studies suggest that ocean acidification could enhance chemical erosion (e.g., Wisshak et al., 2012; Silbiger and Donahue, 2015; Reyes-Nivia et al., 2013) because many bioeroders erode the coral skeleton by secreting acidic compounds. Lower pH in the overlaying water-column might make it metabolically easier for the bioeroders to reduce pH at the site of erosion and therefore promote erosion.

**Secondary Accretion Rates:**

Secondary accretion rates ranged from 0.01 to 0.4 mm yr\(^{-1}\) across the transect (Figure S2p). These rates are slightly lower than secondary accretion rates from a Kâne‘ohe Bay study that saw 2 mm crusts of CCA after a 6 mo. exposure, perhaps due to differences in grazing between study sites or the size of the experimental blocks (Tribollet et al., 2006). For secondary accretion, pH was not the best predictor for patterns in accretion across the transect (\(R^2 = 0.13\); Table 2b). Rather, the distance from shore and depth model ranked highest explaining 23% of the variance in the data (Figure 4). Differences in light and hydrodynamics along the transect could be mediating the relationship between secondary accretion and distance from shore and depth. Notably, our accretion rates were limited to secondary calcifiers such as CCA and encrusting invertebrates (e.g., oysters and barnacles), and excluded corals. We did not measure light or photosynthetically active radiation across our transect, but our deepest site was only 4.5m deep, and, therefore, it is unlikely that light limited CCA growth across the transect. Further, distance from shore explained more of the variation in secondary accretion than depth (23% vs 13%;
Figure 4), and there is a tight correlation between distance from shore and turbulent kinetic energy dissipation rate ($R^2 = 0.88$, Figure S5), suggesting that hydrodynamics, rather than light, may be driving the patterns in accretion. Hydrodynamic energy (e.g., turbulence, wave action, tidal mixing) could impact secondary accretion in several ways: 1) both the delivery of dissolved compounds and particulates are positively correlated with hydrodynamic parameters increasing nutrient availability for benthic organisms (Nowell and Jumars, 1984; Butman and Geyer, 1989), 2) increased flow could promote accretion by facilitating settlement of benthic invertebrate larval recruits, such as oysters and barnacles (Abelson and Denny, 1997), and 3) different exchange, or mixing, rates with offshore waters could impact accretion by replenishing food supplies and removing waste (Smith, 1984). On our reef transect, the furthest offshore sites on the reef slope were constantly mixed with offshore deep water masses, whereas the water inside the reef flat was sometimes isolated. Therefore, large-scale mixing is a likely mechanism driving the patterns between accretion and distance from shore. Lastly, the full model explained 90% of the variance in secondary accretion. Again, this indicates that the measured parameters adequately described patterns in secondary accretion. Any additional parameter would only add at most 10% explanatory power to the over-all model.

**Advancing methods for examining secondary accretion and bioerosion**

Our new µCT method allowed the separation of secondary accretion and bioerosion processes and demonstrated that these processes are driven by different environmental parameters. Indeed, accretion and erosion rates on coral reefs are controlled by different organisms, so it is not surprising that they respond to different environmental parameters. Yet, this is the first study to simultaneously measure secondary accretion and bioerosion on the same time-scale and correlate them with multiple drivers of the accretion-erosion balance. In a prior study, we used before and after µCT scans to calculate the net change in volume (Silbiger et al., 2014). In the present study, we advance this method by aligning and differencing before and after scans to separate changes due to secondary accretion and bioerosion. With µCT we can calculate how much volume is added or removed from an experimental block to accuracy determined by the resolution of the scan (here, 100 µm). We also compared the volume of the pre-deployment blocks calculated with µCT to the volume calculated using buoyant weight and the data are in close agreement: the volumes calculated from µCT are nearly identical to standard buoyant weight methods (Figure S6; $F_{19} = 859$, $p<0.001$, $R^2 = 0.98$, $y = 0.96x + 1.9$) and provides a more complete analysis of secondary accretion and bioerosion processes.

**Secondary accretion versus bioerosion in a high CO₂ world**

Our data indicate that bioerosion is more sensitive to ocean acidity than secondary accretion. Both the effect size (Figure 5) and the proportion of variance explained ($R^2$ in Table 2: 0.54 vs 0.13) of the pH model was higher for bioerosion than for accretion. For a 0.1 increase in pH, we saw a 2.35 kg m$^{-2}$ yr$^{-1}$ increase in bioerosion compared to a 0.77 mm yr$^{-1}$ decrease in secondary accretion, indicating that bioerosion responded more strongly to pH than secondary accretion. Bioerosion also responded to pH mean 1.7× more strongly than pH variance. In a
prior study, we saw a shift from net accretion to net erosion with increasing ocean acidity (Silbiger et al., 2014), but we were unable to uncover the underlying mechanisms driving this shift. Here, our data indicate that reef erosion (and dissolution), rather than reef accretion, may be driving the negative relationship between ocean acidification and net calcification of coral reefs. Recent studies support this hypothesis (Silbiger and Donahue, 2015; Rodolfo-Metalpa et al., 2011; Erez et al., 2011): in a laboratory experiment, chemical dissolution from bioeroders was more strongly correlated with ocean acidity than was secondary calcification (Silbiger and Donahue, 2015), and in a field study, live coral and mollusc calcification was unaffected by natural acidification at CO$_2$ vents in the Mediterranean at normal temperatures, but dissolution of dead skeletons increased with decreasing pH (Rodolfo-Metalpa et al., 2011). Here, we demonstrate that bioerosion is more sensitive to ocean acidity than secondary accretion along a natural environmental gradient. Our results and those from previous studies (Silbiger et al., 2014; Silbiger and Donahue, 2015; Wisshak et al., 2012; Fang et al., 2013; Tribollet et al., 2009; DeCarlo et al., 2014) provide compelling evidence that erosion rates will increase under future ocean conditions. The sensitivity of erosion to ocean acidification could tip the balance of coral reefs in favor of net reef erosion in a more acidic ocean.

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References


<table>
<thead>
<tr>
<th>Method</th>
<th>Method Description</th>
<th>Benefits</th>
<th>Constraints</th>
<th>Publications</th>
</tr>
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<tbody>
<tr>
<td>Change in weight, height, volume, or</td>
<td>Deploy blocks of $\text{CaCO}_3$ on a reef for a set time and measure the difference in weight, height, volume, or density between the pre- and post-deployment blocks.</td>
<td>• Calculates an accurate rate because the block deployment time is known. • Erosion rate is inclusive of both internal and external eroders.</td>
<td>• Measures a net change in the block and confounds accretion and erosion processes. • Blocks need to be deployed for approx. 5 years to include late successional stage eroders.</td>
<td>Dumont et al. (2013); Londoño-Cruz et al. (2003); Márquez and Zea (2012); Reaka-Kudla et al. (1996); Reyes-Nivia et al. (2013); Rützler (1975); Wisshak et al. (2012)</td>
</tr>
<tr>
<td>density of experimental block</td>
<td></td>
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<tr>
<td>Casts or Molds</td>
<td>Impregnate samples with epoxy resin and dissolve sample with dilute HCl. Results in 3D cast of bioerosion scars.</td>
<td>• Separates accretion and erosion. • Visualize boring scars in 3D</td>
<td>• Poor estimate of bioerosion rate because the actual time when $\text{CaCO}_3$ becomes available is unknown.</td>
<td>Carreiro-Silva et al. (2009, 2005); Golubic et al. (1970)</td>
</tr>
<tr>
<td>X-ray and other 2-dimensional image analyses</td>
<td>Collect live coral cores or dead coral rubble, cut the sample into slabs, and take a picture, X-ray, or trace erosion scars onto a piece of paper.</td>
<td>• Separates accretion and erosion. • Using reef samples, as opposed to experimental blocks, likely includes an advanced successional stage of eroders and calcifiers.</td>
<td>• Poor estimate of bioerosion rate because the actual time when $\text{CaCO}_3$ becomes available is unknown. • Results may under- or over-estimate erosion rates depending on where the slab was cut.</td>
<td>Chazottes et al. (1995, 2002); Eadinger et al. (2000); Harney and Fletcher (2003); Hernández-Ballesteros et al. (2013); Highsmith (1981a); Holmes et al. (2000); Manzello et al. (2008); Moran and Reaka (1988); Perry (1998); Reaka-Kudla et al. (1996); Rose and Risk (1985); Scott and Risk (1988); Tribollet et al. (2002); Tribollet and Golubic (2005); Hein and Risk (1975); Highsmith (1981b); Hutchings et al. (2005); Nava and Carballo (2008); Pari et al. (2002); Risk et al. (1995a); Sammarco et al. (1990); MacGachy (1977); Sammarco et al. (1987); Peyrot-Clausade et al. (1999)</td>
</tr>
<tr>
<td>Count grazing scars by eroding fish</td>
<td>Track parrotfish, note when they remove $\text{CaCO}_3$ from the reef, and measure volume of grazing scar.</td>
<td>• Able to calculate grazing rates based on size or species of fish.</td>
<td>• Only accounts for parrotfish erosion.</td>
<td>Alwany et al. (2009); Bellwood (1995); Ong and Holland (2010)</td>
</tr>
</tbody>
</table>
Count bore holes along a reef transect

- Only accounts for macroborers large enough to make a hole that is visible without magnification.
- Poor estimate of bioerosion rate because the actual time when CaCO_3 becomes available to borers is unknown.

- Inexpensive and quick.
- Includes counts of different types of macroborers.

Le Grand and Fabricius (2011);
Koen and Hughes (1994);
Edinger and Risk (1996)

Count bore holes from biocoroding animals on the surface of live or dead coral in situ

- Only uses a very small sample for this analysis.
- Only accounts for macroerosion.
- Results are highly dependent on where cuts are made.

- Very high resolution images of microborers.
- Only uses a very small sample for this analysis.
- Only accounts for microerosion.
- Results are highly dependent on where cuts are made.

Carreiro-Silva et al. (2005); Chazottes et al. (1995); Tribollet et al. (2008); Golubic et al. (1970); Godinot et al. (2012);
Le Campion-Alsumard et al. (1995); Zobia and Peyrot-Chlaude (2001)

Scanning Electron Microscopy (SEM)

Millimeter sections of a sample are cut with a diamond blade saw, embedded with resin, etched with dilute HCl, and sometimes coated in platinum. Surface area bioeroded from each sample is quantified with 2D image analysis.

- Separates accretion from erosion.
- Visualizes erosion scars in 3D.
- Calculates accretion rates.

- Blocks need to be deployed for a long period of time to quantify late succesional stage bioeroders.
- Can be costly depending on resolution of scan.

Carreiro-Silva et al. (2009, 2005); Chazottes et al. (1995); Tribollet et al. (2008); Golubic et al. (1970); Godinot et al. (2012); Le Campion-Alsumard et al. (1995); Zobia and Peyrot-Chlaude (2001)

Single CT or µCT scan

Scan live or dead coral cores using a CT or µCT scanner.

- Separates accretion from erosion.
- Visualizes erosion scars in 3D.
- Calculates accretion rates.

- High resolution 3D measure of both accretion and erosion.
- Visualizes boring scars in 3D.
- Using before and after scans allows for the removal of any pre-existing boring scars.
- Calculates an accurate rate since deployment time is known.

- Blocks need to be deployed for a long period of time to quantify late succesional stage bioeroders.
- Can be costly depending on resolution of scan.

Beuck et al. (2007); Schönberg and Shields (2008)

Before and after µCT scan

See methods section.

- High resolution 3D measure of both accretion and erosion.
- Visualizes boring scars in 3D.
- Using before and after scans allows for the removal of any pre-existing boring scars.
- Calculates an accurate rate since deployment time is known.

Silbiger et al. (2014), Present Study
Table 2: Model Selection: Each model is a linear regression of bioerosion or secondary accretion versus the means ($\bar{X}$) and variances ($\text{Var}(X)$) or covariance ($\text{Cov}(X)$) of each parameter. The Resource Availability Model includes DIN:DIP and chlorophyll a concentration and the Full Model includes means and variances (or, for temperature anomaly, covariance) for all environmental parameters. Environmental data are the residuals from a regression between each parameter versus log(depth) and distance from shore. Secondary accretion and bioerosion rates were square-root transformed to meet model assumptions. The upper table is the model selection for bioerosion and the lower table is the model selection for secondary accretion.

<table>
<thead>
<tr>
<th>Model Parameters</th>
<th>k</th>
<th>$-\log(\mathcal{L})$</th>
<th>AICc</th>
<th>$\Delta$AIC</th>
<th>$R^2$</th>
<th>Rank</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a) Model selection for bioerosion vs environmental parameters</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td><strong>pH</strong></td>
<td>4</td>
<td>-13.34</td>
<td>-18.97</td>
<td>0</td>
<td>0.54</td>
<td>1</td>
</tr>
<tr>
<td>$Y \sim p\bar{H} + \text{Var}(pH)$</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Depth &amp; Distance</strong></td>
<td>4</td>
<td>-6.34</td>
<td>-5.19</td>
<td>13.78</td>
<td>0.09</td>
<td>2</td>
</tr>
<tr>
<td>$Y \sim \text{Depth} + \text{Distance}$</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Temperature</strong></td>
<td>4</td>
<td>-6.11</td>
<td>-5.19</td>
<td>14.26</td>
<td>0.07</td>
<td>3</td>
</tr>
<tr>
<td>$Y \sim \overline{\text{Temp}} + \text{Covar}(\text{Temp})$</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Resource Availability</strong></td>
<td>6</td>
<td>-7.44</td>
<td>-0.60</td>
<td>18.38</td>
<td>0.21</td>
<td>4</td>
</tr>
<tr>
<td>$Y \sim \overline{\text{Chl}} + \text{Var}(\text{Chl}) + \overline{\text{DIN:DIP}} + \text{Var}(\text{DIN:DIP})$</td>
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<td></td>
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<tr>
<td><strong>Full</strong></td>
<td>12</td>
<td>-18.61</td>
<td>17.79</td>
<td>36.76</td>
<td>0.79</td>
<td>5</td>
</tr>
<tr>
<td>$Y \sim \overline{p\bar{H}} + \text{Var}(pH) + \overline{\text{Temp}} + \text{Covar}(\text{Temp}) + \overline{\text{Chl}} + \text{Var}(\text{Chl}) + \overline{\text{DIN:DIP}} + \text{Var}(\text{DIN:DIP}) + \text{Depth} + \text{Distance}$</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(b) Model selection for secondary accretion vs environmental parameters</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td><strong>Depth &amp; Distance</strong></td>
<td>4</td>
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<td>-24.89</td>
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<td>0.23</td>
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<tr>
<td><strong>pH</strong></td>
<td>4</td>
<td>-15.00</td>
<td>-22.51</td>
<td>2.38</td>
<td>0.13</td>
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<td><strong>Temperature</strong></td>
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<td>-21.15</td>
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<tr>
<td><strong>Resource Availability</strong></td>
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<td>-13.97</td>
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<td>0.08</td>
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<tr>
<td><strong>Full</strong></td>
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<td>-33.81</td>
<td>-12.62</td>
<td>12.26</td>
<td>0.90</td>
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Figure 1: **Environmental data.** Means and variances for temperature anomalies (a-b), chlorophyll $a$ (c-d), DIN:DIP (e-f), and pH$_t$ (g-h) along the transect (N=21).
Figure 2: **Schematic illustrating the \(\mu\text{CT}\) methods.** (1) Experimental blocks were cut from dead *Porites lobata* skeleton and sent to the Cornell University Multiscale CT facility for Imaging and Preclinical Research for pre-deployment scans. Blocks were scanned at a resolution of 50 \(\mu\text{m}^3\) and then averaged to 100 \(\mu\text{m}^3\) for data analysis. (2) Pre-scanned blocks were deployed along the reef transect for one year, retrieved, and scanned a second time. (3) During data analysis a threshold of 200 Hounsfield Units (shown by the grey line) was set to remove edge effects and separate \(\text{CaCO}_3\) fom air. Figure shows histograms for a pre-deployment block (green) and a post-deployment block (magenta). The inset shows the histograms of the blocks after thresholding. (4) Pre and post-deployment scans were aligned using image registration tools in MATLAB’s Image Processing Toolbox. Images are pre and post-deployment scans overlayed on top of each other before (left) and after (right) image registration. (5) Images were converted to binary (white is a value of 1 and black is a value of 0) and subtracted from each other. All positive values (red) were new pixels and were counted as secondary accretion and all negative values (blue) were lost pixels and counted as bioerosion. Values of zero (green) correspond to areas where there were no changes between pre and post-deployment scans. (6) We calculated secondary accretion by summing all positive values and bioerosion by summing all negative values in the subtracted image. Images are 3D representations highlighting only secondary accretion (left) and bioerosion (right). See supplement for 3D movies of secondary accretion (Movie S1) and bioerosion (Movie S2). Image credits: N. Silbiger and M. Riccio.
Figure 3: **pH versus bioerosion.** Best fit model and 95% confidence intervals for bioerosion (kg CaCO$_3$ m$^{-2}$ yr$^{-1}$) of experimental blocks (N=20) versus mean pH residuals ($y = -22.45x + 0.55$, $R^2 = 0.54$). pH mean was regressed against log(depth) and distance from shore, and the residuals were used in the analysis and this figure. Bioerosion rate for each block was square-root transformed to meet model assumptions. Color represents depth (m) along the transect with blue representing blocks closest to shore and red representing blocks the farthest.
Figure 4: **Depth and distance from shore versus secondary accretion.** Best fit model and 95% confidence intervals for secondary accretion (mm CaCO$_3$ yr$^{-1}$) of experimental blocks (N=20) versus a) distance from shore (m) ($y = 0.0055x + 0.29$, $R^2 = 0.23$) and b) log(depth) (m) ($y = 0.048x + 0.41$, $R^2 = 0.14$). Accretion rate for each block was square-root transformed to meet model assumptions.
Figure 5: **Mean pH effect size for secondary accretion and bioerosion.** The effect size was calculated as the absolute value of the partial slope for mean pH in each model.