EFFECTS OF SUBMARINE GROUNDWATER DISCHARGE ON
CORAL ACCRETION AND BIOEROSION ON TWO SHALLOW
REEF FLATS

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ABSTRACT

Porites lobata nubbins and bioerosion blocks were deployed across two groundwater gradients in Maunalua Bay to measure coral accretion and bioerosion rates at different levels of submarine groundwater discharge (SGD). Coral accretion was approximated using buoyant weights, photos and linear extension; bioerosion rates were quantified using μ CT scans. Chemical parameters, temperature and water motion were measured at each location. Coral accretion showed a modal response to SGD, and percent change in buoyant weights and nubbin surface area negatively responded to pH variation. SGD negatively affected coral survivorship indicating that at high SGD, salinity stress kills corals, but at mid-levels nutrients increase accretion. SGD positively affected bioerosion; this increase was attributed to nutrients, but bioerosion was less sensitive to salinity stress. Coral accretion rates were two orders of magnitude higher than bioerosion rates; however, low coral cover indicates that the actual amount accreted is likely lower than suggested by rates alone.

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Introduction

The biogeochemistry of a marine ecosystem has profound impacts on the biology of the organisms that inhabit it. Due to isolation from land-based processes and low biological density, open ocean water chemistry is influenced primarily by gas exchange with the atmosphere, seasonal upwelling of nutrients and temperature fluctuations (Hofmann et al. 2011; Duarte et al. 2013). Thus, the open-ocean is generally characterized by tight nutrient cycling and equilibrium with atmospheric gases, with stable chemistry on short time scales, and larger fluctuations seasonally, annually, or decadal in response to changes in atmospheric processes (Hofmann et al. 2011). In contrast, coastal systems are located at the interface of land and sea and often have high biomass relative to water column depth with water chemistry influenced by various processes occurring on land, in the open ocean, and in the atmosphere, as well as by physical and biological processes within the system itself (Edinger et al. 2000; Gagliano et al. 2010; Hofmann et al. 2011; Price et al. 2012; Duarte et al. 2013; Cyronak et al. 2014b). Thus, coastal water chemistry is complex and highly variable on short, biologically-relevant time scales (Yates et al. 2007; Gagliano et al. 2010; Hofmann et al. 2011; Price et al. 2012; Duarte et al. 2013; Guadayol et al. 2014; Drupp et al. 2011).

Land-based processes influence the biogeochemistry of coastal waters through the delivery of freshwater, nutrients, sediments, and pollutants via surface or groundwater runoff, land-use change, sedimentation, and anthropogenic impacts such as pollution (Edinger et al. 2000; Wolanski et al. 2009; Drupp et al. 2011; Cyronak et al. 2014b). Likewise, water from the open ocean, carrying its own chemical signal, can be entrained into coastal waters through internal or surface waves (McManus et al. 2012; Sevajian et al. 2012), tides, or through water mixing between coastal and oceanic systems, thus affecting the chemistry of coastal environments. These land- and ocean-based processes affect the delivery of organic and inorganic nutrients to coastal waters, and can affect carbonate parameters such as the partial pressure of carbon dioxide ($p\text{CO}_2$), total alkalinity (TA) and levels of dissolved inorganic carbon (DIC) (Drupp et al. 2011; Johnson et al. 2008; Cyronak et al. 2014; Paytan et al. 2006; Cyronak et al. 2013). Gas exchange with the atmosphere occurs in coastal environments, but due to the complexity of drivers in these systems, is not a main driver of coastal water chemistry

as it is in the open ocean, often leading to disequilibrium between gases at the air-water interface (Duarte et al. 2013).

In addition to terrigenous inputs, biological activity of coastal organisms drives patterns of short-term chemical variability in coastal systems. Many coastal systems are characterized as being “metabolically-intense” (Duarte et al. 2013) due to a large biomass of highly productive benthic organisms, such as macroalgal beds, seagrasses, coral reefs, salt marshes, or mangroves. Metabolic processes such as photosynthesis, respiration, and calcification modify seawater chemistry by using or releasing nutrients and CO₂ (Yates et al. 2007; Smith et al. 2013). The magnitude of these processes is influenced by community composition, nutrient availability, pH, pCO₂, and physical drivers affecting uptake rates, waste removal, and nutrient delivery (Edinger et al. 2000; Yates et al. 2007; Gagliano et al. 2010; Hurd et al. 2011; Price et al. 2012; Duarte et al. 2013; Smith et al. 2013). Furthermore, input of nutrients, alkalinity, or other solutes from land can modify the rates of biological processes, creating feedbacks that further drive variability in coastal water chemistry (Cyronak et al. 2014; Lee & Kim 2015). Likewise, the metabolic activity of organisms upstream can modify the chemical environment experienced by organisms downstream, thus influencing downstream metabolism (Anthony et al. 2011; Kleypas et al. 2011).

One significant source of nutrients and carbon into many coastal systems that can alter water chemistry is submarine groundwater discharge (SGD; Paytan et al. 2006; Johnson et al. 2008; Street et al. 2008; Cyronak et al. 2013; Moosdorf et al. 2014). SGD is defined as the flow of any water (meteoric, marine, or a composite of both) flowing from land through the marginal seabed and into the coastal ocean (Moosdorf et al. 2014; Lee & Kim 2015). Globally, SGD makes up 6-10% of total freshwater inputs to the coastal ocean, with one-third of the global SGD component coming from large islands, particularly in the tropics (Moosdorf et al. 2014). On volcanic islands like Hawai'i, SGD is abundant (Dimova et al. 2012; Richardson et al. 2015), can exceed river fluxes, and often makes up the largest or only source of new nutrients to the coastal ocean (Johnson et al. 2008; Street et al. 2008; Lee & Kim 2015; Moosdorf et al. 2014). Unlike riverine inputs, which are driven by peaks in precipitation (Drupp et al. 2011), SGD is driven by hydrological gradients between the subterranean estuary and the coastal ocean, and discharge is often tidally modulated, leading to diurnal or semi-diurnal inputs on a daily basis (Dimova et al. 2012; Cyronak et al. 2013; Wang et al. 2014). However, unlike

riverine inputs, the effects of SGD on coastal ecosystems, particularly coral reefs are relatively understudied and poorly understood.

SGD is often highly enriched in nutrients, particularly in nitrate, and can have N:P ratios $\gg 16$, exceeding Redfield ratios and N:P ratios of coastal waters (Moosdorf et al. 2014). Nutrient levels in SGD are sensitive to processes occurring on land, and can be elevated in areas where anthropogenic impacts are high (Moosdorf et al. 2014; Richardson et al. 2015). Additionally, SGD carries distinct carbonate signatures when compared with seawater, and can drive fluxes in TA, DIC, pH and $p\text{CO}_2$ in nearshore environments (Cyronak et al. 2013; Cyronak, et al. 2014; Wang et al. 2014). Because SGD is tidally driven, coastal systems subject to groundwater inputs often see pulses of nutrient-rich SGD on diurnal or semi-diurnal timescales, leading to high short-term variability.

In addition to chemical variability due to mixing of SGD with seawater, SGD-derived solutes can affect biological processes, creating biogeochemical feedbacks that further modify the water chemistry of the coastal zone. For instance, Cyronak et al. (2014) found that $p\text{CO}_2$ variability off of Heron Island, Australia was augmented by stimulation of the photosynthesis/respiration (P/R) cycle by SGD-derived nutrients. Despite the fact that SGD typically has lower pH than seawater, Lee and Kim (2015) found a negative relationship between salinity and pH across a groundwater gradient, indicating higher pH in areas with more SGD. They attributed this pattern to enhanced biological production driven by SGD nutrient inputs, rather than from the chemistry of the groundwater itself. However, in systems where SGD is particularly enriched in a certain solute or where groundwater fluxes are especially high, groundwater chemistry can overwhelm biological processes and drive patterns in seawater chemistry (Cyronak et al. 2014).

In this way, nutrients derived from SGD can alter and enhance the chemical variability in nearshore systems. pH variability, for example, is driven by the P/R cycle in nearshore environments, and the enhancement of these processes from the addition of new nutrients may lead to extreme fluctuations in pH over diel cycles. pH of seawater is related to the $p\text{CO}_2$ of the system via the following equation:

(Drupp et al. 2011). Photosynthesis consumes CO_2 , thus raising the pH by removing protons, while respiration releases CO_2 into the water column, releasing protons and

acidifying the surrounding water (Drupp et al. 2011; Smith et al. 2013). Therefore, the high levels of metabolic activity characteristic of coastal systems drive high variability in pH (and pCO₂) over the course of the P/R cycle (Yates et al. 2007; Drupp et al. 2011; Hofmann et al. 2011; Wisshak et al. 2012; Smith et al. 2013). Duarte et al. 2013 report a mean diel pH range of 0.3 units for coastal systems, with range of up to 1.0 unit observed in the most productive systems. Likewise, Price et al. (2012) report high diel pH variation on coastal coral reefs, with the largest fluctuations in shallow areas. These fluctuations occur at much higher scales than the predicted change in oceanic pH due to ocean acidification (Hofmann et al. 2011; Crook et al. 2013). The availability of organic and inorganic nutrients to benthic organisms is a major driver of productivity rates (Drupp et al. 2011); thus, the delivery of nutrients into coastal systems via SGD will have an indirect effect on the magnitude of pH variation (Drupp et al. 2011; Duarte et al. 2013).

Although many coastal coral reefs, particularly those around volcanic islands, are affected by SGD, few studies exist on the effects of SGD on coastal water chemistry around reefs, and even fewer investigate the effect of SGD on the metabolism of the organisms that inhabit reefs. For example, SGD is the major source of freshwater to the Kona coast of the Big Island of Hawai'i (Street et al. 2008; Johnson et al. 2008), an area which hosts some of the highest coral cover in the main Hawai'ian Islands (Franklin et al. 2013). However, studies of SGD in this area are restricted to characterization of seawater chemistry across groundwater gradients, and effects on biology are only inferred. Likewise, in studies of SGD onto reefs in Rarotonga, Cook Islands and Heron Island, Australia, Cyronak et al. (2013,2014) infer biological responses to SGD, but do not directly measure changes in metabolism driven by groundwater. An exception is a study of calcification and bioerosion rates of corals near low-pH groundwater seeps in Mexico by Crook et al. (2013).

Scleractinian corals, the primary reef builders of tropical coral reefs, secrete calcified skeletons of calcium carbonate (CaCO₃) that make up the structure of reefs. Calcification is a metabolic process by which corals and other calcifying organisms utilize Ca²⁺ and HCO₃⁻ ions available in seawater to create CaCO₃ skeletons via the following equations:

(Drupp et al. 2011; Jokiel et al. 2014). This process is sensitive to various physical and chemical factors, such as nutrient availability, carbonate chemistry, temperature, and water motion (Andersson et al. 2005; Fabricius 2005; Cooper et al. 2008; Andersson et al. 2009; Ries et al. 2009; Castillo et al. 2014) which can vary over time and space. However, it is in some cases unclear as to how each of these factors affect accretion, and in many cases, responses vary between taxa (Andersson et al. 2009; Ries et al. 2009).

The calcification rates of corals vary with changes in seawater nutrients, carbonate chemistry, and temperature, all of which can be affected by SGD. Many studies have shown decreases in coral calcification with increased nutrients (reviewed in Fabricius 2005); however the nutrient loads used in many of these experiments are unrealistically high and might only be found on the most eutrophic reefs. In contrast some studies have found little to no difference between accretion rates on reefs with different nutrient loads (Edinger et al. 2000; Cooper et al. 2008). However, because photosynthesis and calcification are highly coupled in organisms hosting symbiotic zooxanthellae (Andersson et al. 2005; Sawall et al. 2011) moderate increases in inorganic and organic nutrients have been shown to increase calcification in some cases (Tanaka et al. 2007; Sawall et al. 2011). Importantly, nutrient enrichment has also been found to counteract decreases in calcification due to ocean acidification, indicating that release from nutrient limitation can increase photosynthesis, and therefore, calcification rates (Holcomb et al. 2010).

With the increased interest in the effects of ocean acidification on the fate of coral reefs in the past decade, many studies have attempted to understand changing carbonate chemistry on accretion, with mixed conclusions. In general, coral calcification tends to decrease with decreasing pH (increasing $p\text{CO}_2$; Andersson et al. 2005; Andersson et al. 2009; Price et al. 2012), however studies have also found parabolic relationships (Castillo et al. 2014) or no relationship (Barkley et al. 2015) of accretion in response to changes in acidification. Importantly, however, most laboratory studies are conducted in mesocosms with fixed $p\text{CO}_2$ values corresponding to IPCC projected values by the end of the century, which ignore the chemical variability inherent on reefs and are likely not representative of the conditions on coral reefs (Price et al. 2012; Duarte et al. 2013). Similarly, studies have shown varied responses of coral calcification to increasing sea surface temperature (Cooper et al. 2008; Castillo et al. 2014), but as with

carbonate chemistry, treatments in laboratory experiments are often held steady throughout the study.

In contrast to accretional reef processes, bioerosion is the process by which organisms break down carbonate structures, either by mechanical or chemical means (Glynn 1997). Bioeroders belong to various diverse taxa, and include boring sponges, endolithic algae, sipunculid worms, parrotfishes, sea urchins and mollusks, among others (Glynn 1997; Le Grand & Fabricius 2011; Wisshak et al. 2012; Reyes-Nivia et al. 2013; Andersson et al. 2014). Bioerosion contributes to a major portion of total reef erosion, with rates of bioerosion estimated to be significantly higher than rates of community and sediment CaCO_3 dissolution (Andersson et al. 2014). For example, a single species of boring sponges on the Great Barrier Reef have been noted to remove between $10\text{-}20 \text{ kg m}^{-2} \text{ yr}^{-1}$, often surpassing rates of accretion at certain sites (Wisshak et al. 2012).

Unlike accretion, bioerosion rates have been found to increase predictably with increasing nutrients and decreasing pH. Many bioeroders are filter feeders (Glynn 1997; Le Grand & Fabricius 2011), and various studies have found increases in rates of internal bioerosion across eutrophication gradients on reefs around the world (Edinger et al. 2000; Holmes 2000; Osorno et al. 2005; Fabricius 2005; Le Grand & Fabricius 2011). Likewise, many studies have found increases in bioerosion rates with increases in pCO_2 (Wisshak et al. 2012; Fang et al. 2013; Reyes-Nivia et al. 2013) or decreases in pH (Silbiger et al. 2014; Barkley et al. 2015; Silbiger et al. 2016). Many bioeroders dissolve coral skeletons chemically by decreasing pH at the site of erosion, so more acidic conditions may aid in the efficiency of biochemical dissolution (Fang et al. 2013; Barkley et al. 2015; Silbiger et al. 2016). Conversely, it is possible that lowered pH leads to decreased skeletal density in corals, thereby making it easier for bioeroders to penetrate (Barkley et al. 2015; Silbiger et al. 2014). Unlike patterns of accretion under eutrophication or acidification, bioerosion responses to these factors are well documented and generally predictable.

On coral reefs, the ratio of the rate of accretion to the rate of erosion/dissolution determines whether the reef is growing, dissolving, or in a state of stasis. When accretion outweighs erosion, the reef is in a state of net growth, and when the ratio drops below 1, the reef is in a state of net dissolution (Bates et al. 2010; Andersson et al. 2014). Therefore, for a reef to maintain its structure, conditions must favor an

accretion/erosion ratio of at least 1. In order to obtain a full picture of reef health, it is imperative to measure both calcification and erosion rates (Wisshak et al. 2012), as measurements of only one metric may be misleading. For example, neither nutrients (Edinger et al. 2000) nor acidic conditions (Crook et al. 2013) were shown to significantly affect coral growth rates compared to control reefs, but both increased bioerosion rates, sometimes leading to net dissolution on affected reefs.

This study aims to understand the effects of SGD-driven chemical variability on the accretion-erosion dynamics of two nearshore reef flats in Maunalua Bay, O'ahu. We characterized short-term (diel- and tidal-scale) variability of various chemical parameters across natural groundwater gradients at Black Point and Wailupe Beach Park, two sites identified as having high levels of nutrient-rich SGD (Dimova et al. 2012; Nelson et al. 2015; Richardson et al. 2015). We measured coral accretion and growth rates across the groundwater gradient by deploying nubbins of the lobe coral *Porites lobata* across each site for six months, and comparing before and after buoyant weights and photographs, and measuring the linear extension of each nubbin. In addition, we placed blocks of dead *Porites* skeleton, which act as a settling substrate for bioeroders, across the SGD gradient and measured rates of bioerosion after one year by comparing pre- and post-deployment μ -CT scans. In this way, we are able to synthesize a comprehensive understanding of the effects of SGD on the carbonate cycling of these reefs.

Methods

Site Selection

Two sites with previously identified SGD (Richardson et al. 2015) were selected in Maunalua Bay, on the southern shore of O'ahu. The sites, Black Point and Wailupe (Figure 1), are shallow reef flats located 3 km apart, each with a discrete, nearshore SGD seep. The offshore bounds of each site were defined as the area from the shore to the reef crest (500m at Wailupe, 250m at Black Point), with the alongshore bounds chosen to capture the SGD gradient at each site (350m at Wailupe, 250m at Black Point). Both sites are very shallow (<1m deep at MLLW), and are characterized by patches of hard bottom surrounded by sand. The hard bottom at Wailupe is made up of carbonate platforms in a spur and groove pattern, whereas Black Point hosts a mix of continuous

carbonate shelves and isolated boulders. Maunalua Bay is flanked by highly urbanized watersheds (Wolanski et al. 2009), and the use of cesspools in some areas has been linked to elevated nutrients in SGD (Richardson et al. 2015). For detailed descriptions of the sites, see Nelson et al. 2015 and Richardson et al. 2015.

At each site, 20 experimental locations were established across the SGD gradient as identified in Nelson et al. 2015 (Figure 1). Experimental locations were organized in an approximate grid, with shore-parallel rows organized in a logarithmic design in order to effectively capture the gradient nearshore. All locations were established on hard carbonate substrate, except when carbonate substrate was absent and sites were established on basalt boulders (n=2 at Black Point).

Three offshore locations were established outside of the reef crest at each site, for a total of six offshore locations. Offshore locations were located in ~20-25 ft of water at a distance of 200-350 m offshore of the reef crest. Each offshore location was positioned ~10m from others.

Coral Accretion Study

To assess the effect of SGD on coral growth and accretion rates, we collected nubbins of the lobe coral *Porites lobata* from coral colonies at the offshore sites, processed them in flow through water tables, and then deployed them at each of the experimental locations at both sites for a period of 6 months, from February 2015-August 2015 (Table 1, Appendix). *P. lobata* was chosen because it is present at both sites and is abundant in Maunalua Bay. Fragments were collected from three large colonies near the offshore experimental locations at Wailupe, at a depth of about 25 ft. Offshore donor colonies were chosen to avoid any acclimation of corals to SGD. Nubbins were attached to PVC plates, which acted as the experimental units in the study. At each experimental location, three PVC plates (6 cm x 13 cm), one from each donor colony, with three coral nubbins each, were attached to three upward-facing bolts using stainless steel nuts, for a total of nine nubbins (3/donor colony) at each location. Sustained high water temperatures during late summer 2015 forced the removal of coral plates after 174 days in order to avoid bleaching-related mortality. Nubbins were processed before and after deployment at the Anuenue Fisheries Research Center in Honolulu, Hawai'i.

To establish the experiment, fragments collected from each donor colony were kept separate and immediately placed in a 10 mg/L Alizarin red solution to dye the coral skeleton at the edge of the tissue for linear extension analysis. Fragments were removed from the dye solution after 24 hours and placed in flow-through water tables. Small nubbins (area of live tissue $\sim 2 \text{ cm}^2$) were cut from the fragments using tin snips (Forsman et al. 2006) and three nubbins from the same donor colony were mounted on PVC plates using All-Fix epoxy.

Each plate was buoyant weighed in seawater using an Ohaus Adventurer Pro precision balance to the nearest 0.01g before and after deployment in the field (following Jokiel et al. 1978) Temperature and salinity of the water were recorded with each weight in order to calculate water density, while the density of aragonite (i.e., the mineral crystal form of CaCO_3) was used to estimate coral density. The buoyant weight of the PVC plate itself was subtracted from the total weight in order to calculate the weight of the nubbins, and plates were thoroughly cleaned of all sediment, algae and other organisms before post-deployment weighing. Accretion was reported as percent change in buoyant weight during the deployment.

Standardized photos of each plate were taken before and after deployment using a camera mounted on a PVC stand to ensure that each photo was taken from the same distance and angle. Each plate was photographed from above, with a size and color standard in each photo. Surface area of the total area of each nubbin (including areas of partial or full mortality where tissue had grown and died away) was calculated in Adobe Photoshop. Coral growth was reported as the percent change in surface area. Coral survivorship was recorded as a percentage of live tissue: 100% live tissue, X% partial mortality, or 0% live tissue (i.e., complete mortality).

Survivorship was determined using the post-deployment standardized photos. In order to understand which locations were optimal for coral survival versus those leading to a degraded or completely dead state, nubbins were identified as either 100% alive, or by having experienced any partial or total mortality.

After the post-deployment buoyant weights and photos were collected, nubbins were broken off of the plates with a chisel and a slice was extracted from the middle of each nubbin using a diamond blade saw. Coral slices were photographed under a dissecting scope for linear extension analysis. In Adobe Photoshop, a grid with five evenly spaced vertical lines was placed on each photo, and the perpendicular distance

from the Alizarin red band to the edge of the coral was recorded at the first, third, and fifth vertical line in order to compute a mean value that captures variation in growth across the coral nubbin. Extension measurements were calibrated to a size standard photographed under the same magnification. In the case that the Alizarin band did not intersect one of the pre-selected grid lines or the nubbin was too small, the third measurement was taken at the second or fourth grid line instead of the first or fifth, respectively.

Bioerosion Study

Experimental blocks were cut from dead *P. lobata* rubble collected from above the high tide mark. Coral skeletons were cut into blocks measuring 6 cm x 5 cm x 1.5 cm using a diamond blade rock saw and were attached to a PVC mount (2 cm x 5 cm x 1.5 cm) at one end using JB Weld Steel Reinforced two part epoxy. A small hole was drilled in each block 2 cm from the PVC mount in order to cable tie the block to the mount in the case the attachment failed. Only blocks without visible calices or bore holes were used. Skeletal density of the blocks was estimated using the methods detailed in Silbiger et al. (2016), yielding an average skeletal density of 1.42 g cm⁻³.

Blocks were scanned before and after deployment using micro computed tomography (μ CT) at the Multiscale CT Facility at Cornell University using an eXplore CT120 μ CT (GE Healthcare Xradia, Inc) in order to construct a 3D image of object densities in the interior and exterior of each block (Silbiger et al. 2014; Silbiger et al. 2016). μ CT analysis followed methods outlined in Silbiger et al. 2016. Pre- and post-deployment scans were registered using an intensity-based image registration algorithm from the MATLAB Image Processing Toolbox, each pixel converted to binary (1=a pixel with CaCO₃, 0=Air), and scans were subtracted from each other in order to identify areas of secondary accretion and bioerosion. Pixels with a subtracted value of +1 represented areas of CaCO₃ accretion, pixels with a subtracted value of -1 represented areas of bioerosion, and pixels with subtracted values of 0 represented areas of no change. However, due to high sedimentation on many of the blocks, secondary accretion rates were anomalously high and were excluded from the analysis.

Volumes of bioerosion were calculated by summing all negative subtracted values, and multiplying by the voxel size ($100 \mu\text{m}^3$) to give the total volume of the CaCO_3 lost. Bioerosion rates were calculated using the following equation

$$\text{Bioerosion rate}(\text{kg m}^{-2} \text{ yr}^{-1}) = \frac{\text{Vol}_i \times \rho_i}{\text{SA}_i \times \text{Time}}$$

where i represents each block, Vol is the volume of CaCO_3 lost through erosion in m^3 , ρ is the skeletal density of the blocks, SA is the surface area of the block in m^2 , and Time is the time the block was deployed on the reef in years. Surface area of each block was measured by hand using calipers and excluded the surface of the block adhered to the PVC mount, as this surface was not available to bioeroders.

One bioerosion block was deployed at each of the 46 experimental locations described above (40 on the reef flats, and 6 in ~ 25 ft at the offshore locations). Blocks were threaded onto upward-facing bolts through a hole in the PVC mount and secured with two stainless steel nuts. Blocks were deployed between October 29 and November 14, 2015, with lost blocks replaced with new ones until December 2015, and recovered between November 16 and 18, 2015 on the reef flats, and on December 4, 2015 at offshore sites (Table 1, Appendix). After recovery, blocks were dried in a drying oven at 60°C for 24 hours and sent to Cornell University for post-deployment scanning.

Characterization of the SGD gradient

In order to characterize the water chemistry across the SGD gradient, as well as the variation in water chemistry driven by tidal and daily cycles, water was collected at each experimental location at each high and low tide over two 24 hour cycles at each site and analyzed for a suite of chemical parameters. Sampling dates were chosen to coincide with maximum spring tides during the Spring and the Fall of 2015, in order to capture the most extreme extent of the groundwater gradient and to account for seasonal variability. Sampling dates were April 18, 2015 and September 28, 2015 at Wailupe and May 2, 2015 and October 26, 2015 at Black Point.

Samples for pH, total alkalinity (TA), inorganic nutrients (SiO_4^{2-} , $\text{NO}_3^- + \text{NO}_2^-$, and PO_4^{3-}), and Chlorophyll a were hand-collected on snorkel from each experimental

location within +/-30 minutes of low and high tides during each sampling day, yielding 4 samples of each parameter per day. Each water sample was collected directly above the experiment in order capture the chemistry of the water delivered to each experimental unit. Samples were collected into acid-washed and triple-rinsed polypropylene sample bottles; sample bottles were rinsed three times with sample water and then filled completely so that no head space remained. Samples were processed or appropriately stored for processing immediately following collection.

pH and Total Alkalinity

pH on the total scale (pH_{Tot}) was measured using an Orion Star Portable meter calibrated against a Tris buffer of known pH from Andrew Dickson's laboratory at the Scripps Institution of Oceanography. Calculated pH values were corrected for in situ temperature recorded by the temperature loggers at each experimental location using CO₂SYS (Lewis & Wallace 1998) using pH, TA, temperature, and salinity. HSO_4^- dissociation constants were taken from Uppström 1974 and Dickson 1990, while K₁K₂ dissociation constants were taken from Mehrbach 1973 and refit by Dickson & Millero 1987.

Total alkalinity samples were fixed immediately following collection with 200 μL HgCl_2 /250 ml water and technical duplicates were analyzed using open cell potentiometric titrations on a Mettler Toledo T-50 autotitrator. Titrations were calibrated against Certified Reference Materials (CRM) from Andrew Dickson's lab following Dickson et al. 2007 protocols. All samples were measured within 1% accuracy of the CRM value, and measured values were corrected for this error.

Inorganic Nutrients

Nutrient samples were collected in acid washed 140 cc Monoject luer lock syringes and filtered through combusted 25 mm glass fiber filters (GF/F 0.7 μm) immediately after collection. Volume of the filtrate was recorded and filters were retained for chlorophyll a analysis. Filtered samples were stored in acid-washed polypropylene bottles and refrigerated until analysis. Nutrient analysis for SiO_4^{2-} , $\text{NO}_3^- + \text{NO}_2^-$, and PO_4^{3-} was performed in the SOEST Laboratory for Analytical

Biogeochemistry (S-LAB) at the University of Hawai'i at Mānoa using a Seal Analytical AA3 Nutrient Autoanalyzer.

*Chlorophyll *a**

Used GF/F filters from nutrient sample filtration were folded in half, wrapped in foil, and immediately frozen for chlorophyll *a* analysis. Frozen filters were crushed in 8 ml of 90% acetone and stored in a freezer for 24 hours for extraction of chlorophyll. Extractions were performed in the dark, and all sample containers were covered with aluminum foil to minimize exposure to light. After 24 hours, samples were centrifuged to separate out any solids, transferred to clean test tubes, and analyzed for fluorescence on a Turner 10-AU Fluorometer.

Salinity

Salinity values were calculated using known relationships between silicate and salinity at these sites reported by Richardson et al. 2015. Silicate has been used successfully as an SGD tracer in Hawai'i (Street et al. 2008), and silicate uptake is at most 10% of the total inventory at these sites (Richardson et al. 2015). Silicate and salinity were found to mix conservatively at levels of silicate below ~300 $\mu\text{M/L}$, and the highest recorded silicate value in our study was 198.43 $\mu\text{M/L}$. Because salinity values were calculated from silicate and not measured in the field, silicate is used as the SGD tracer in this study, and calculated salinity values were used to calculate carbonate parameters.

Physical Characterization of Experimental Locations

Depth

Depth at each experimental location was measured by dropping a weighted transect tape at each location and measuring distance to the surface. The time of each depth measurement was recorded in order to identify location in the tidal cycle, and

measurements were normalized to tidal height at Mean Lower Low Water (MLLW). Tide predictions were obtained from NOAA at the Honolulu station (Station ID 1612340), and offsets in the timing of tidal predictions were calculated using data from a stationary depth sensor placed nearshore at Black Point for four days in August 2015.

Bulk Dissolution

Relative water motion was measured by bulk dissolution using the clod card method (Doty 1971). Clod cards were made from plaster of Paris using ratios of water and plaster adapted from Jokiel & Morrissey (1993). The plaster mixture was poured into ice cube trays, gently tapped to remove any bubbles, and left to dry. Once solid, the clods were transferred into a drying oven heated to 60°C for 24 hours to remove any excess moisture. Dry clods were weighed and sanded to a standard mass of 25 g (± 0.1 g), and then glued to a small square of flexible plastic. Once the glue had dried, the clod cards were reweighed to determine total pre-deployment weights.

Three replicate clod cards were attached to a brick with cable ties, and one brick was placed at each experimental location for two hours before and after high and low tide, for a total of two 4-hour long deployments at each location. Deployment dates were chosen to coincide with spring tides at each location, with deployments at Black Point on August 1, 2015 and at Wailupe on September 12, 2015. After recovery, clod cards were dried in a drying oven at 60°C for 24 hours and reweighed to calculate change in mass during the deployment.

Field measurements were normalized for the rate of clod dissolution in standing water by placing control clod cards in aquaria for 4 hours to match the length of deployment in the field. Six control aquaria were prepared, each with one clod card. In order to account for differences in clod dissolution due to salinity (Jokiel & Morrissey 1993), control aquaria were separated into high and low salinity treatments of 35 psu and 27 psu, respectively, in order to cover the range of salinities recorded across the SGD gradients at both sites. Experimental locations were separated into high and low salinity categories based on measured salinity values at low and high tide, and values from the corresponding control treatment were used in calculations.

The dissolution factor (DF), a dimensionless index of clod dissolution (Doty 1971) of each clod card was calculated using the following equation:

$$DF = \frac{M_f}{t_f} / \frac{M_c}{t_c}$$

where M_f and M_c are the change in mass of clods in the field and control, respectively, and t_f and t_c are the length of field and control deployments in minutes. High and low tide values were averaged to calculate the mean DF for each experimental location.

Temperature

Temperature was recorded at each experimental location, including offshore locations, throughout the experiment by Hobo Tidbit loggers (accuracy: +/- 0.2 °C, resolution: 0.02°C at 25°C) attached to each bioerosion block. Loggers were set to record temperature every 15 minutes. Each logger was coated in Plasti-Dip Multipurpose Rubber Coating to prevent deviations in temperature measurements due to light, and cable tied to the PVC mount on each bioerosion block. Following deployment, loggers were placed in a common garden and calibrated to a reference thermometer, and time series were adjusted for this calibration.

Time series were truncated to correspond with the dates of deployment for coral nubbins and bioerosion blocks. Due to an initial loss of loggers at the beginning of the deployment, time series for the bioerosion blocks only cover the period of February-November 2015. Various temperature metrics were calculated in comparison to temperatures recorded at the site of coral collection (Wailupe Offshore) in order to understand deviations in temperature experienced by nubbins compared to the donor colonies. The difference in mean temperature between the collection site and the experimental location (Δ mean T) was calculated as

$$\Delta \text{ mean T} = T_{\text{experimental location}} - T_{\text{collection site}}$$

and was therefore positive if nubbins experienced hotter than average temperatures, and negative if temperatures were below average. In addition, the number of hot and cold anomalies, defined as any temperature recording greater or less than 2 standard deviations from the mean of the collection site, respectively, were calculated for each experimental location.

Statistical Analysis

Due to the approximately conservative mixing of SGD-derived solutes with seawater at these sites, nutrients ($\text{NO}_3^- + \text{NO}_2^-$, PO_4^{3-}) and TA were highly correlated with silicate at each site ($0.97 < |\rho| < 0.99$ for nutrients, $0.68 < |\rho| < 0.82$ for TA; Figures 1 and 2, Appendix). Therefore, nutrients and TA were assumed to vary with silicate in all analyses and were not included in the models. Because the groundwater endmembers at each site contain different ratios of silicate to nutrients (Richardson et al. 2015), a standardized measurement of groundwater was calculated as

$$\% \text{ SGD} = \frac{\text{Mean silicate}}{\text{Silicate}_{\text{GW}} - \text{Silicate}_{\text{SW}}}$$

where Mean silicate is the mean value at each experimental location, $\text{Silicate}_{\text{GW}}$ is the value of the groundwater endmember, and $\text{Silicate}_{\text{SW}}$ is the value of the seawater endmember for each site. Endmember values were taken from Richardson et al. 2015. pH was not correlated with groundwater, and principal components analyses at each site showed pH separating into a different PC axis than groundwater derived solutes (Figures 2 and 3), so mean pH and pH variation at each experimental location were included in the models. pH variation was calculated as

$$\text{pH variation} = \frac{\text{Variance}_{\text{pH}}}{\text{Mean}_{\text{pH}}^2}$$

in order to obtain a measure of dispersion independent of the mean. Chlorophyll *a* measurements were highly variable due to the amount of suspended sediment in the water at these sites, so these measurements were excluded from the analysis.

Bulk dissolution was included in the models as mean DF at each experimental location. Depth was included in the initial analysis, but was dropped from the final analysis for the following reasons: 1) the range in depths was small between locations (0.85 m) and was therefore not hypothesized to affect any of the responses, and 2) initial analyses with depth included indicated that depth did not have an effect on the

models. Similarly, the number of hot and cold anomalies at each site did not affect the models and were correlated with each other, so only Δ mean T was included in the analysis.

Offshore sites were not included in the analyses because weather and gear restrictions did not allow for the collection of chemical and physical data from these sites. However, response values from offshore experiments are included in Figure 4 to indicate how offshore experiments compared to inshore units.

In order to account for the hierarchical structure of the coral experiment and the use of nubbins from different donor colonies, % change in buoyant weight, % change in surface area, and linear extension were analyzed using linear mixed effects models, and survivorship was analyzed using a mixed effects logistic regression. Because the bioerosion experiment was not hierarchically structured, these data were analyzed using a linear regression. % SGD² was included in all coral accretion models, while $\sqrt{\%SGD}$ was included in the bioerosion model, in order to account for apparent non-linearity in the data. The equations for the models for % change in buoyant weight (% ΔBW ; equation 1), % change in surface area (% ΔSA ; equation 2), linear extension (LE ; equation 3), survivorship (equation 4) and bioerosion rate (equation 5) are shown below.

$$(1) \% \Delta BW \sim \%SGD + \%SGD^2 + pH + pH\ Variation + \Delta mean\ T + DF + (1|Location) + (1|Donor\ Colony)$$

$$(2) \% \Delta SA \sim \%SGD + \%SGD^2 + pH + pH\ Variation + \Delta mean\ T + DF + (1|Plate/Location) + (1|Donor\ Colony)$$

$$(3) LE \sim \%SGD + \%SGD^2 + pH + pH\ Variation + \Delta mean\ T + DF + (1|Plate/Location) + (1|Donor\ Colony)$$

$$(4) Survival \sim \%SGD + pH + pH\ Variation + \Delta mean\ T + DF + (1|Plate/Location) + (1|Donor\ Colony), family = binomial$$

$$(5) Bioerosion\ rate \sim \sqrt{\%SGD} + pH + pH\ Variation + \Delta mean\ T + DF$$

The estimated mean accretion rates at each experimental location were calculated using the following formula:

$$Accretion\ rate = \frac{\Delta BW_{plate}}{SA_{init_{plate}} \times time}$$

where ΔBW_{plate} is the change in buoyant weight for a single coral plate in kg, $SA_{init_{plate}}$ is the initial surface area of all three nubbins on the plate in m², and time is the time of deployment in years.

Results

Site Characterization

Summary statistics for chemical and physical parameters can be found in Table 1. Wailupe saw a wider range of % SGD values, with mean %SGD values ranging from 0.20%-8.88%, whereas mean values at Black Point ranged from 0.23%-4.50%. However, because of higher levels of nutrients in the groundwater endmember at Black Point (Richardson et al. 2015), the range of nutrients delivered to the experimental units was similar at both sites. Interestingly, although TA correlated highly with SGD, the TA gradient was opposite between the sites, with TA in SGD at Black Point higher than the marine endmember, and lower than the marine endmember at Wailupe (Figure 3, Appendix). TA values converge at the lowest values of %SGD, indicating that we captured the marine endmember at both sites. pH varied between 7.86-8.33 at Black Point and 7.85-8.20 at Wailupe, while mean pH was similar between sites (BP=8.06, W=8.02).

DF was similar at both sites, with a slightly wider range and higher mean at Wailupe, likely due to the greater size of the site allowing for more heterogeneity in water motion. All experimental locations were less than 0.9 m deep at MLLW, with Black Point slightly deeper on average. The shallowest location at Wailupe was 0.003 m at MLLW, indicating that this site was likely exposed during spring low tides. Spatial patterns for the SGD gradient, pH variability, and DF at each site are shown in Figures 2 and 3, panels b, d, and f.

Accretion, Survivorship, and Bioerosion

Summary statistics for all response variables are summarized in Table 2, and significant model results for all response variables are summarized in Table 3. All three accretion metrics showed a significant negative effect of %SGD², indicating a unimodal response of accretion to %SGD (Table 3, Figure 4). In addition, %SGD showed a significant positive effect on % change in surface area, and a near-significant positive effect ($t=1.813$, $p=0.07$) on % change in buoyant weight. pH variation had a significant negative effect on % change in buoyant weight and % change in surface area, while DF only showed a significant negative effect in the buoyant weight model. % SGD was found to significantly decrease survivorship (Figure 4, Appendix), while no other fixed effects were significant for this response. Spatial patterns of all accretion metrics and significant drivers can be found in Figures 2 and 3.

Patterns in the random effects were not consistent between models (Table 3). Donor colony accounted for 31.8% of the variance in the buoyant weight model, but only 0.53% in the surface area model, and 0% of the variance in the linear extension model, from which it was dropped. Coefficients for donor colonies A, B, and C were -6.91, 12.52, and -5.61, respectively, in the buoyant weight model, and -2.628, 2.4216, and 0.2065 in the surface area model, indicating higher accretion rates in colony B. However, in the survivorship model, where donor colony accounted for 36% of the variance, colony A had the highest rate of survivorship, with coefficients for colonies A, B, and C estimated at 0.5986, -0.0479, and -0.9752, respectively. Plate and experimental location accounted for 7.52% and 8.22% of the variance in the surface area model, 0.57% and 13.95% in the linear extension model, and 37% and 27% in the survivorship model, respectively. Experimental location accounted for 0% of the variance in the buoyant weight model, and was dropped from the final analysis.

$\sqrt{\text{ }}$ %SGD had a significant positive effect on bioerosion, indicating that bioerosion increases non-linearly with %SGD. None of the other terms in the model showed a significant response. The overall model was significant and explained 35% of the variance ($p=0.03$, $R^2= 0.351$).

Accretion rates were two orders of magnitude higher than bioerosion rates (Figure 5), and ranged between 2.91 and 19.48 kg m⁻² of live coral yr⁻¹, with a mean of 11.06 kg m⁻² of live coral yr⁻¹ and a standard deviation of 4.01. Bioerosion rates ranged

between 0.003-0.174 kg m⁻² yr⁻¹, with a mean of 0.040 kg m⁻² yr⁻¹ and a standard deviation of 0.032.

Discussion

All three coral accretion metrics showed a unimodal response to %SGD, with lower growth rates at high and low %SGD, and the highest rates at mid-range %SGD values. The strength of this relationship relative to other significant effects, and the fact that this was the only consistent pattern across all three accretion metrics suggests that %SGD is the main driver of differences in accretion across these reef flats. Because of the near-conservative nature of SGD-derived solutes at the locations included in this study (Richardson et al. 2015), delivery of these solutes to each experimental location was likely driven by physical mixing of the groundwater with seawater, rather than by biological processing.

The observed patterns are likely due to a combination of low salinity stress at high levels of %SGD, and increases in accretion due to moderate nutrient input at mid-levels of %SGD. At the highest levels of %SGD, accretion and survivorship were lowest. High levels of %SGD were only observed at Wailupe as low water motion and shallow depth nearshore allowed for less mixing and higher delivery of SGD to nearshore experimental locations (Figure 2b), leading to high mortality and little accretion close to shore; although examination of the data at each site indicate the same pattern may exist at Black Point at similar levels of %SGD. Indeed, when analyzed together, %SGD was the only significant predictor of survivorship and the best predictor of accretion across sites. The decrease in survivorship and accretion at high %SGD is likely due to salinity stress; although we did not measure salinity directly in this study, predicted means of salinity based off of silicate measurements at the highest %SGD sites are approximately 31.6 psu, with minimum values at low tide as low as 25.9 psu. Initial surface area of nubbins had no significant effect on survivorship, which is consistent with previous studies on the survivorship of small *P. lobata* nubbins (Forsman et al. 2006), and indicates that differences were due to environmental factors.

Elevated nutrients are generally found to be detrimental to coral health and calcification (reviewed in Fabricius 2005), and nutrients from SGD have been implicated

in reef degradation, leading to increases in macroalgae and decreases in coral cover (Naim 1993). However, some studies have found either no effect of increased nutrients on coral growth (Edinger et al. 2000), or have seen moderate (Tanaka et al. 2007; Sawall et al. 2011) or even large increases in coral accretion in response to elevated nutrients (Bongiorni et al. 2003). Indeed, Chauvin et al. (2011) found that corals collected from areas affected by high-nutrient SGD had higher chlorophyll *a*, protein and zooxanthellae densities, and showed higher rates of photosynthesis and calcification per unit surface area than corals collected from SGD-free locations. Importantly, studies that have found increased accretion rates under elevated nutrient conditions isolated corals from secondary effects of nutrient enrichment, such as competition with macroalgae (Bongiorni et al. 2003). Similarly, our coral plates were elevated above the substrate and therefore released from competition stress, allowing the effect of nutrients on accretion to be isolated from confounding processes.

Because of the conservative nature of groundwater mixing at these sites, it was impossible to disentangle SGD-derived solutes (nutrients, TA) from silicate, making it difficult to quantitatively determine which parameters are driving the observed growth and accretion patterns. However, examination of the TA data from both sites reveals opposite patterns in the alkalinity of SGD (Figure 3, Appendix), with groundwater at Black Point and Wailupe having higher and lower TA than the surrounding seawater, respectively, and converging to the same marine endmember value. This pattern is consistent with findings by Nelson et al. 2015, and is likely due to the fact that SGD at these sites is derived from two isolated aquifers, each with a distinct water chemistry (Richardson et al. 2015). Although it has been hypothesized that increases of TA from SGD may affect reef health by buffering against the negative effects of ocean acidification (Cyronak et al. 2013; Cyronak et al. 2014), it is unlikely that the opposite patterns of TA at these sites led to the consistent pattern in coral growth observed across both sites.

Bioerosion showed a non-linear, increasing response to %SGD. However, unlike accretion, bioerosion rates did not decrease dramatically at high levels of %SGD, and instead leveled off at a maximum around 3% SGD. This indicates that SGD-derived nutrients likely increase bioerosion rates until nutrients become saturating, at which point they plateau. This is consistent with previous studies that have noted increased bioerosion with increasing nutrients (Edinger et al. 2000; Holmes 2000; Le Grand &

Fabricius 2011). In addition, these results suggest that bioerosion is less sensitive to low salinities than accretion by corals.

SGD-derived nutrients can increase bioerosion rates by providing an ample food source for boring organisms, many of which are filter feeders (Glynn 1997). Indeed, this relationship has been documented across eutrophication gradients on reefs around the world, including in Australia (Le Grand & Fabricius 2011), Indonesia (Edinger et al. 2000) and Barbados (Holmes 2000; also see Fabricius 2005 and Le Grand & Fabricius 2011 for reviews on this topic). Higher rates of microbioerosion were found in areas of mid- and high levels of nutrient-rich SGD on Reunion Island (Chazottes et al. 2002). This trend holds true on larger scales as well, with bioerosion increasing along a nutrient gradient spanning the entire Pacific basin (DeCarlo et al. 2015). Nutrients and terrestrial inputs can also drive community composition to include more bioeroding organisms that benefit from nutrient input. For example, inshore reefs in Australia affected by freshwater runoff and sedimentation had lower levels of external bioeroders, such as grazing fishes, and higher levels of internal bioeroders, including boring sponges and polychaetes (Osorno et al. 2005).

Interestingly, mean pH had no significant effect on any of the response variables measured in this study, but pH variation had a significant negative effect on the percent change in buoyant weight and surface area. Therefore, experimental locations that experienced larger fluctuations in pH had lower rates of accretion. pH varied widely at both sites, with maximum ranges between 7.86-8.33 at Black Point and 7.85-8.20 at Wailupe, while the range in mean pH values was much smaller (7.99-8.08 across both sites). This pattern of variability is comparable to that recorded in other coastal systems (Hofmann et al. 2011; Price et al. 2012; Shaw et al. 2012; Duarte et al. 2013), and highlights the importance of including pH variability, rather than just mean pH, when examining the effects of ocean acidification on coastal organisms.

These findings are consistent with studies of corals near persistent low-pH, low- Ω_{arag} groundwater seeps in Mexico, which found decreases in calcification and skeletal density, but not linear extension, in corals exposed to SGD (Crook et al. 2013). Although the Mexico study measured mean Ω_{arag} rather than pH variability, other research has shown that pH at this site exhibits extremely high short-term variability (range=0.905 pH units over a 30 day period) due to the discharge of SGD (Hofmann et al. 2011). However, when interpreted in the context of nutrient-enriched groundwater, the

relationship is more complex, as coral nubbins collected from sites impacted by SGD were found to have higher calcification rates per unit surface area across Ω_{arag} treatments than those collected from non-SGD sites (Chauvin et al. 2011). This indicates that although changes in carbonate chemistry may lead to decreases in calcification, these effects may be mediated by the positive effects of SGD-derived nutrients. This relationship is consistent with other studies that have found a mediating effect of nutrients on calcification rates in high $p\text{CO}_2$ conditions (Atkinson et al. 1995; Holcomb et al. 2010).

Most laboratory and field studies use fixed $p\text{CO}_2$ conditions or mean pH as predictors of calcification, which ignores natural variability and makes it difficult to apply conclusions to reef systems (Price et al. 2012; Duarte et al. 2013). Shaw et al. 2012 note that corals in most mesocosm studies of ocean acidification spend more time exposed to high $p\text{CO}_2$ conditions than those on shallow reef flats, which only experience extreme conditions for a couple hours a day. Indeed, the amount of time spent exposed to acidified conditions seems to be important in driving rates of calcification in the field. Price et al. 2012 identified duration and magnitude of daily pH maxima as predictors of calcification on reefs in the central Pacific, noting that more time spent at higher pH lead to higher rates of calcification. This is likely the case in Maunalua Bay as well; although mean pH did not vary greatly across space, experimental locations that experienced higher variation in pH spent more time at low pH than those with more stable water chemistry, perhaps leading to decreased calcification in the more variable locations.

Interestingly, neither mean pH nor pH variation had a significant effect on bioerosion rates. Numerous studies have found increases in bioerosion rates under acidified conditions (Tribollet et al. 2009; Wisshak et al. 2012; Crook et al. 2013; Reyes-Nivia et al. 2013; Silbiger et al. 2014; Barkley et al. 2015; DeCarlo et al. 2015; Silbiger et al. 2016). However, most of these studies have seen a bioerosion response due to differences in mean pH or across a range of fixed $p\text{CO}_2$ treatments, rather than with variation in pH. For example, Crook et al. 2013 found higher rates of bioerosion near persistent low-pH groundwater seeps, and attributed this increase to decreased skeletal density of corals exposed to SGD. It is possible that the range in mean pH at our sites was not wide enough to detect a response in bioerosion rate, or that the use of bioerosion blocks did not allow for natural variation in skeletal density due to changes in pH. In addition, nutrients have been found to exacerbate the effect of acidification on

bioerosion by ten fold (DeCarlo et al. 2015), suggesting that perhaps across our narrow gradient in mean pH, the effect of nutrients may be more pronounced than the effect of pH.

Although the offshore sites were not included in the formal analysis, Figure 4 shows that for all accretion metrics, mean values from these sites agreed well with data from the low %SGD experimental locations. However, bioerosion was much higher than expected by the model at both outer sites, particularly Wailupe. This is likely due to higher rates of grazing on the forereef. Chazottes et al. 2002 found higher rates of grazing, and therefore overall bioerosion rates, by urchins on reefs without SGD input than on those with high or mid-levels of SGD. Rates of external bioerosion have been found to be higher at offshore locations on the Great Barrier Reef (Osorno et al. 2005). It is therefore likely that larger populations of macro-eroders such as parrotfish and urchins on the forereef may have contributed to higher bioerosion rates at outer sites.

Surprisingly, the results of this study show a negative relationship between DF and percent change in buoyant weight, indicating a negative effect on accretion. This relationship is in contrast with myriad studies that indicate that increased water motion increases coral metabolism by decreasing boundary layer thickness, increasing rates of mass transfer, and facilitating the delivery of important solutes and removal of wastes. However, we hypothesize that in this experiment, the positive effects of increased water motion were overshadowed by the negative effects of scouring and physical damage in high flow environments.

Both sites were characterized by high levels of suspended sediment, which may have scoured nubbins in high flow locations, stressing the corals and perhaps removing accreted material. Indeed, some clod cards that were deployed in higher flow environments were recovered with grains of sand imbedded in them, indicating high scour at these locations (In addition, scouring at these experimental locations likely increased DF measurements at these locations, leading to overestimation of water motion where scouring occurred). Likewise, although coral plates were tightly anchored to the bolts, the nuts holding the plates in place sometimes became loose, or plates were completely dislodged from the reef, potentially causing damage to the nubbins as plates rotated around the bolts or were tossed about. Dislodged units were quickly reattached to the reef and nuts were tightened regularly, but nubbins may have suffered damage

before repairs could be made. This may explain why DF only affected buoyant weight, as this metric is the most sensitive to the removal of small amounts of CaCO_3 .

Accretion rates were 2 orders of magnitude higher than bioerosion rates across both sites (Figure 5). Simply based on rates alone, this indicates that nearshore reefs in Maunalua should be in a state of net accretion. However, these rates may be misleading for several reasons. It is important to note that units of accretion are in kg per m^2 of *live coral tissue* per year, while bioerosion rates are in kg per m^2 of *substrate* per year. Urbanization and land use change have lead to marked decreases in coral cover in Maunalua Bay over the past century, and coral cover remains very low, especially on the reef flats (Wolanski et al. 2009). Therefore, there is much more substrate available to bioeroders than is occupied by coral at these sites, and the amount of CaCO_3 removed by bioeroders at these sites may in fact be higher than the amount accreted by corals. In addition, our bioerosion blocks were only deployed for one year, and therefore only captured the early successional stages of the bioeroder community (Silbiger et al. 2014). Bioerosion rates in similar experimental blocks was found to increase significantly between 2- and 4-year deployments on the Great Barrier Reef (Osorno et al. 2005), indicating that measured bioerosion rates at our sites would likely be higher given a longer deployment time.

Moving forward, future studies should include measurements of benthic cover in Maunalua Bay in order to normalize the rates reported in this study to the cover of coral and available substrate for bioerosion, and determine whether these reef flats are in a state of net accretion or erosion. In addition, this study only investigated the physiological effects of SGD on coral accretion, so further work on the interactions between SGD and other factors, such as macroalgae, on coral accretion would help shed light on the complexities of the accretion-erosion balance at these sites. Finally, as there were noticeable differences in accretion rates for nubbins from different donor colonies in the buoyant weight and surface area models, it would be interesting to study the donor colonies themselves in order to understand what is driving this variability.

The results of this study indicate that SGD is an important source of new nutrients to nearshore reef flats in Maunalua Bay. SGD-derived nutrients increase rates of accretion and bioerosion, although at the highest %SGD locations low salinity stress induces mortality and decreases coral growth. The tidally modulated discharge of SGD to these sites delivers semi-diurnal pulses of low-sediment, nutrient-rich water onto the

reef flat, which contrasts with the periodic inundations of nutrients and sediment by surface waters driven by precipitation. Whereas corals on reefs impacted by surface water may be nutrient-limited between pulses, the daily, moderate enrichment by SGD may relieve corals of nutrient limitation, allowing for higher accretion rates.

Short-term pH variability negatively affects calcification rates, even though mean pH had no effect. This supports the hypothesis that the duration of exposure to low pH may drive accretion rates on reefs (Price et al. 2012), particularly those with high levels of variability. This finding stresses the need to include metrics of variation when conducting ocean acidification studies on nearshore reefs, and cautions against applying findings from the open ocean to variable coastal environments (Duarte et al. 2013). In contrast, neither mean pH nor pH variation had an effect on bioerosion, despite a large body of literature suggesting that bioerosion increases with decreasing pH. This indicates that bioerosion responses may be site specific and depend on interactions between local and global stressors, and care should be taken when generalizing results.

In this study, calcification rates far exceeded rates of bioerosion. However, the extremely low coral cover in Maunalua Bay compared with dead substrate suggests that net calcification likely does not exceed bioerosion at these sites. However, on SGD-impacted reefs with high coral cover, SGD-derived nutrients may promote a state of net accretion. Future studies should measure bioerosion over longer periods of time in order to capture the full successional community and measure maximum erosion rates in order to fully understand the effect of SGD on bioerosion. In addition, this study isolated coral nubbins from indirect stressors such as competition with macroalgae. However, both sites have very high macroalgal cover, and competition is likely to decrease growth rates of corals in the field. However, the results of this study indicate that in isolation from other processes, SGD-derived nutrients increase coral growth and calcification, and to a lesser extent, bioerosion, on nearshore reefs.

TABLES

Table 1: Summary statistics of chemical and physical drivers. Measurements for Silicate, N+N, Phosphate, pH, Total Alkalinity (TA), and Temperature are from discrete water samples in the Spring and Fall.

Site	Parameter	Mean	Maximum	Minimum	Standard Deviation
Wailupe					
	Silicate ($\mu\text{mol/L}$)	15.60	198.43	1.03	33.74
	Salinity (psu)	33.99	34.64	25.96	1.48
	N+N ($\mu\text{mol/L}$)	0.73	11.69	0.04	1.69
	Phosphate ($\mu\text{mol/L}$)	0.13	0.62	0.04	0.10
	pH _{Tot}	8.015	8.199	7.845	0.084
	TA ($\mu\text{Eq/L}$)	2252.11	2336.32	2129.37	34.34
	Temperature ($^{\circ}\text{C}$)	25.30	28.50	22.64	1.29
	Clod DF	4.43	6.26	3.14	0.93
	Depth (m at MLLW)	0.323	0.813	0.003	0.225
Black Point					
	Silicate ($\mu\text{mol/L}$)	16.27	136.95	1.09	22.70
	Salinity (psu)	34.04	34.67	29.00	0.95
	N+N ($\mu\text{mol/L}$)	2.79	32.39	0.02	4.95
	Phosphate ($\mu\text{mol/L}$)	0.20	0.89	0.09	0.13
	pH _{Tot}	8.058	8.325	7.86	0.107
	TA ($\mu\text{Eq/L}$)	2271.54	2413.56	2005.77	45.04
	Temperature ($^{\circ}\text{C}$)	25.75	28.80	23.45	1.36
	Clod DF	4.39	5.99	3.44	0.628
	Depth (m at MLLW)	0.580	0.863	0.312	0.156

Table 2: Summary statistics of response variables. Values are aggregated across sites. Negative values likely reflect physical damage to nubbins during the deployment.

Response Variable	Mean	Maximum	Minimum	Standard Deviation
% Change in Buoyant Weight	40.99	114.41	-9.17	21.22
% Change in Surface Area	89.29	627.76	-74.66	66.18
Linear Extension (mm)	1.85	6.18	0.32	0.94
Coral Accretion Rate (kg m^{-2} of live coral yr^{-1})	11.06	19.48	2.91	4.01
Bioerosion Rate ($\text{kg m}^{-2} \text{yr}^{-1}$)	0.040	0.174	0.003	0.032

Table 3: Summary of significant model results and random effects. Empty cells signify non-significant terms, NA indicates that a term was not included in the final model. Values for fixed effects indicate the coefficient of each term (β), t values and p-values. Values for random effects are the percentage of variance explained by each term

	Fixed Effects							Random Effects		
	% SGD	% SGD ²	$\sqrt{\% \text{SGD}}$	pH	pH Variation	Δ mean T	DF	Plate	Experimental Location	
Response										
% change in Buoyant Weight		$\beta=-7.54$, $t=-3.550$, $p<0.001$	NA		$\beta=-6.92$, $t=-2.668$, $p=0.009$		$\beta=-6.46$, $t=-3.264$, $p=0.002$	NA	NA	31.8%
% change in Surface Area	$\beta=50.02$, $t=4.779$, $p<0.001$	$\beta=-30.57$, $t=-5.546$, $p<0.001$	NA		$\beta=-19.28$, $t=-2.809$, $p=0.008$			7.52%	8.22%	0.53%
Linear Extension		$\beta=-0.22$, $t=-2.206$, $p=0.03$	NA					0.57%	13.95%	NA
Survivorship	$\beta=-0.97$, $p<0.001$	NA	NA					37%	27%	36%
Bioerosion	NA	NA	$\beta=0.009$ $p=.003$					NA	NA	NA

FIGURES

Figure1: a) Map of the Hawaiian Islands and the island of O'ahu. Maunaulua Bay is enclosed in the black box. b) Map of Maunaulua Bay, with study sites enclosed in black boxes. Experimental locations, including offshore locations, are identified as red dots at c) Black Point and d) Wailupe. Yellow dots represent the location of the groundwater seeps at each site.

Figure 2: Contour plots of response variables (a, c, e) and significant drivers (b, d, f) of coral accretion at Wailupe. Black dots indicate experimental locations, and the star indicates the location of the groundwater seep.

Figure 3: Contour plots of response variables (a, c, e) and significant drivers (b, d, f) of coral accretion at Black Point. Black dots indicate experimental locations, and the star indicates the location of the groundwater seep. Note that experiments from two locations got lost, resulting in only 18 data points for this site.

Figure 4: Plots of % SGD versus a) % change in buoyant weight, b) % change in surface area, c) linear extension and d) bioerosion rate. Dark blue dots indicate data from Wailupe, light blue dots indicate data from Black Point. The dark and light blue triangles are the mean values of each response at the offshore Wailupe and Black Point sites, respectively, and have been plotted at 0% SGD in lieu of chemical data. The thick black line represents the best fit between the data and %SGD ($y \sim \%SGD + \%SGD^2$ for Accretion Rate, $y \sim \sqrt{\%SGD}$ for Bioerosion Rate). In panels a and b, the colored lines represent each donor colony, with purple=colony A, yellow=colony B, and green=colony C.

Figure 5: Plot of %SGD versus accretion rate, in purple, and bioerosion rate, in blue. Values of accretion rate are on the left-hand y-axis, while values of bioerosion rate are on the right-hand y-axis. Curves are the best fit for each response and %SGD ($y \sim \%SGD + \%SGD^2$ for Accretion Rate, $y \sim \sqrt{\%SGD}$ for Bioerosion Rate).

APPENDIX

Figure 1, Appendix: (a) PCA and (b) correlation plot of chemical groundwater parameters at Wailupe. Numbers plotted in panel (a) refer to experimental location ID's. Numbers below the diagonal in panel (b) correspond to the correlation coefficient ρ , and the circles above the diagonal represent these values graphically, with larger circles representing values of $|\rho|$ closer to 1, while colors correspond to the values indicated in the legend to the right.

Figure 2, Appendix: (a) PCA and (b) correlation plot of chemical groundwater parameters at Black Point. Numbers plotted in panel (a) refer to experimental location ID's. Numbers below the diagonal in panel (b) correspond to the correlation coefficient ρ , and the circles above the diagonal represent these values graphically, with larger circles representing values of $|\rho|$ closer to 1, while colors correspond to the values indicated in the legend to the right.

Figure 3, Appendix: Plot of measured silicate values versus TA from all water samples for Wailupe (blue) and Black Point (purple). Lines show the best fit for each site.

Figure 4, Appendix: Fit of logistic regression of survivorship against %SGD. %SGD was the only significant driver of survivorship in this study ($p < 0.001$).

Table 1, Appendix: Coordinates of experimental locations and deployment/ recovery dates of bioerosion blocks and coral plates. “Lost” indicates that units were lost during the course of the experiment or could not be found.

Site	Location Number	Latitude	Longitude	Blocks-Date in	Blocks-Date out	Corals-Date in	Corals-Date out
Wailupe	1	21.27531	-157.76181	10/29/14	11/18/15	3/1/15	8/22/15
	2	21.27523	-157.76265	10/29/14	11/18/15	3/1/15	8/22/15
	3	21.27504	-157.76328	10/30/14	11/18/15	3/1/15	8/22/15
	4	21.27449	-157.76402	10/29/14	11/18/15	3/1/15	8/22/15
	5	21.27503	-157.7617	10/30/14	11/18/15	3/1/15	8/22/15
	6	21.27485	-157.76234	10/30/14	11/18/15	3/1/15	8/22/15
	7	21.27463	-157.76318	10/31/14	11/18/15	3/1/15	8/22/15
	8	21.27436	-157.76364	10/29/14	11/18/15	3/1/15	8/22/15
	9	21.27456	-157.76126	10/29/14	11/18/15	3/1/15	8/22/15
	10	21.27427	-157.76208	10/30/14	11/18/15	3/1/15	8/22/15
	11	21.27399	-157.76295	10/31/14	11/18/15	3/1/15	8/22/15
	12	21.27377	-157.76344	10/29/14	11/18/15	3/1/15	8/22/15
	13	21.27353	-157.76089	10/30/14	11/18/15	3/1/15	8/22/15
	14	21.27328	-157.76164	10/30/14	11/18/15	3/1/15	8/22/15
	15	21.27309	-157.76244	10/29/14	11/18/15	3/1/15	8/22/15
	16	21.27288	-157.76306	12/5/14	11/18/15	3/1/15	8/22/15
	17	21.27254	-157.76073	10/30/14	11/18/15	3/1/15	8/22/15
	18	21.27214	-157.76118	10/31/14	11/18/15	3/1/15	8/22/15
	19	21.27206	-157.76196	10/30/14	11/18/15	3/1/15	8/22/15
	20	21.27185	-157.76279	10/31/14	11/18/15	3/1/15	8/22/15
Black Point	21	21.2598	-157.78912	10/31/14	11/16/15	2/28/15	8/20/15
	22	21.25931	-157.78983	11/3/14	11/16/15	2/28/15	8/20/15
	23	21.259	-157.79021	11/3/14	11/16/15	2/28/15	8/20/15
	24	21.25873	-157.79053	11/14/14	11/17/15	2/28/15	8/20/15
	25	21.25954	-157.78909	10/31/14	Lost	2/28/15	8/20/15
	26	21.25891	-157.78981	11/3/14	11/16/15	2/28/15	8/20/15
	27	21.25889	-157.79007	10/31/14	11/17/15	2/28/15	8/20/15
	28	21.25846	-157.79051	11/3/14	11/17/15	2/28/15	8/20/15
	29	21.25939	-157.78873	12/16/14	Lost	2/28/15	Lost
	30	21.25857	-157.78987	11/3/14	Lost	2/28/15	8/20/15
	31	21.25853	-157.79005	11/4/14	11/17/15	2/28/15	8/20/15
	32	21.25817	-157.79045	12/6/14	11/17/15	2/28/15	8/20/15
	33	21.25885	-157.78902	11/3/14	Lost	2/28/15	Lost
	34	21.25832	-157.78957	11/4/14	Lost	2/28/15	8/20/15
	35	21.25809	-157.78984	11/4/14	11/17/15	2/28/15	8/20/15
	36	21.25784	-157.79033	11/4/14	11/17/15	2/28/15	8/20/15
	37	21.25962	-157.7888	12/16/14	11/16/15	2/28/15	8/20/15
	38	21.25893	-157.78972	11/14/14	11/16/15	2/28/15	8/20/15
	39	21.25864	-157.79005	11/14/14	11/16/15	2/28/15	8/20/15
	40	21.25834	-157.79048	11/14/14	11/17/15	2/28/15	8/20/15
Wailupe	Offshore	21.26658	-157.76303	1/23/15	12/4/15	2/21/15	9/8/15
Black Point	Offshore	21.25600	-157.78843	12/6/14	12/4/15	2/21/15	10/5/15

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