TITLE: The influences of diurnal variability and ocean acidification on the bioerosion rates of two reef-dwelling Caribbean sponges

RUNNING TITLE: Acidification variability affects bioerosion

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Abstract

Ocean acidification (OA) is expected to modify the structure and function of coral reef ecosystems by reducing calcification, increasing bioerosion, and altering the physiology of many marine organisms. Much of our understanding of these relationships is based upon experiments with static OA treatments, though evidence suggests that the magnitude of diurnal fluctuations in carbonate chemistry may modulate the calcification response to OA. These light-mediated swings in seawater pH are projected to become more extreme with OA, yet their impact on bioerosion remains unknown. We evaluated the influence of diurnal carbonate chemistry variability on the bioerosion rates of two Caribbean sponges: the zooxanthellate *Cliona varians* and azooxanthellate *Cliothosa delitrix*. Replicate fragments from multiple colonies of each species were exposed to four precisely-controlled pH treatments: contemporary static (8.05 ± 0.00; mean pH ± diurnal pH oscillation), contemporary variable (8.05 ± 0.10), future OA static (7.80 ± 0.00), and future OA variable (7.80 ± 0.10). Significantly enhanced bioerosion rates, determined using buoyant weight measurements, were observed under more variable conditions in both the contemporary and future OA scenarios for *C. varians*, whereas the same effect was only apparent under contemporary pH conditions for *C. delitrix*. These results indicate that variable carbonate chemistry has a stimulating influence on sponge bioerosion, and we hypothesize that bioerosion rates evolve non-linearly as a function of pCO_2 resulting in different magnitudes and directions of rate enhancement/reduction between day and night, even with an equal fluctuation around the mean. This response appeared to be intensified by photosymbionts, evident by the consistently higher percent increase in bioerosion rates for photosynthetic *C. varians* across all treatments. These findings further suggest that more variable natural ecosystems may presently experience elevated sponge bioerosion rates and that the heightened impact of OA enhanced bioerosion on reef habitat could occur sooner than prior predictions.

Introduction

Over recent decades, coral reef ecosystems have experienced global shifts to community structure and habitat altering processes in response to climate change (Gardner et al., 2003; Alvarez-Filip et al., 2009). Ocean acidification (OA), a result of rising atmospheric carbon dioxide (CO_2) concentrations (Caldeira and Wickett, 2003), is currently and will continue to impact inorganic and organic seawater chemistry (Doney et al., 2009), with important implications for the physiology and ecology of coral reef organisms (Andersson and Gledhill, 2012; Kroeker et al., 2013).

While OA trends within pelagic environments are relatively clear, patterns are more complicated within shallow marine ecosystems, such as coral reefs, where seawater carbonate chemistry varies on diurnal and seasonal cycles (Silverman et al., 2012; Bates et al., 2010). These natural fluctuations are driven by a combination of abiotic (e.g., water circulation, air-sea gas exchange, light, temperature, etc.) and biotic (e.g., photosynthesis/respiration, calcification/dissolution) factors, and are often amplified in systems with long water residence times and high community biomass (Camp et al., 2017). For most reef systems, diel pH fluctuations are predominately a light-mediated process (Shaw et al., 2012). Net photosynthesis during the day tends to elevate seawater pH and aragonite saturation state (Ω_{Ar}), with maximum values occurring around sunset (Albright et al., 2013; Delille et al., 2000). At night, net respiration has the opposite effect on seawater carbonate chemistry, leading to depressed pH and Ω_{Ar} conditions, with minimum values occurring around sunrise (Mongin and Baird, 2014). Depending on the localized reef conditions, the magnitude of these diurnal changes can be substantial, with some reef systems experiencing periodic exposure to carbonate chemistry extremes similar to that of end-of-the-century predictions (Shaw et al., 2012).

The degree to which diurnal pH variability modulates the OA response of reef organisms is poorly understood. Addressing this key knowledge gap is critical since OA is expected to reduce the buffering capacity of seawater, leading to higher amplitude carbonate chemistry oscillations in the future (Shaw et al., 2013). Since environmental variability is expected to alter the extent to which reef organisms respond to climate change (Rivest et al., 2017), it is imperative to assess the direct impact dynamic carbonate chemistry fluctuations have on their physiological and ecological functions. Prior experiments have found enhanced calcification rates for corals exposed to variable pH conditions compared to static treatment groups (Enochs et al., 2018; Chan and Eggins, 2017). These findings suggest that for coral, variable carbonate chemistry conditions have the potential to enhance daytime calcification rates due to favorable conditions associated with daytime highs in pH and Ω_{Ar}, potentially offering daily refugia from OA (Enochs et al. 2018). While these studies are in general agreement regarding the relationship between diurnal carbonate chemistry variability and calcification, the extent to which variable environmental conditions influence bioeroders (i.e., organisms responsible for the breakdown of reef framework) remains unknown.

Bioeroding sponges are important components of coral-reef ecosystems. Their diversity provides them with a large range of physiologies that allows them to fill several ecological niches within reef environments, with a distribution that spans across all reef zones and multiple latitudinal gradients (Hartman, 1957; Rutzler, 1978; Goreau and Hartman, 1963). Bioeroding sponges play an important role in shaping and modifying reef habitat (Glynn, 1997). This includes direct effects caused by their excavation of porous cavities within reef framework (MacGeachy and Stearn, 1976), which is accomplished through a combination of chemical dissolution and mechanical dislodgment of calcium carbonate ($CaCO_3$) chips/fragments (Rutzler

and Rieger, 1973; Pomponi, 1980). Sponges are responsible for some of the highest bioerosion rates measured within marine ecosystems, eroding as much as 24 kg $CaCO_3$ m^{-2} yr^{-1} of reef framework and producing up to 40% of deposited reef sediment (Acker and Risk, 1985; Neumann, 1966; Rutzler, 1975).

Boring sponges could gain a competitive advantage over corals as a result of global climate change as they appear to benefit from environmental conditions that are otherwise stressful to reef calcifiers (Bell et al., 2018). Elevated seawater temperatures (Stubler et al., 2015; Fang et al., 2014) and eutrophic conditions (Ward-Paige et al., 2005; Holmes et al., 2009; Webb et al., 2017) are reported to have positive effects on sponge bioerosion rates. This implies that sponges are capable of thriving in poor water quality environments that are often unfavorable for more oligotrophic calcifying reef organisms (Chaves-Fonnegra et al., 2007) and suggests that their relative importance within coral reef ecosystems could grow under future climate scenarios.

Numerous lab studies have also found elevated sponge bioerosion rates in response to OA conditions (Wisshak et al., 2013; Wisshak et al., 2014; Duckworth and Peterson, 2013; Enochs et al., 2015; Fang et al., 2013). While OA-stimulated bioerosion has been measured for both zooxanthellate and azooxanthellate species, the response is thought to be more pronounced among photosynthetic sponges due to an increase in the photosynthetic efficiency of sponge symbionts associated with OA (Achlatis et al., 2017). Models from these studies predict that sponge bioerosion rates could increase by as much as 100% under end-of-the-century pH conditions, which could have substantial ramifications for reef habitat persistence (Enochs et al., 2015; Wisshak et al., 2014).

While the relationship between OA and sponge bioerosion appears relatively clear, the impacts of OA-intensified diurnal carbonate chemistry variability are unknown. Since sponge

bioerosion is an extracellular mechanism sensitive to ambient seawater conditions, OA is thought to reduce the metabolic cost, resulting in enhanced bioerosion efficiency (Schönberg, 2008). The sensitivity of this process to local seawater conditions indicates that environments with high diurnal carbonate chemistry variability may experience altered sponge bioerosion capabilities. For example, daytime highs in pH and Ω_{Ar} could increase the pH gradient between ambient seawater and the sponge/substrate interface, resulting in a higher metabolic cost for daytime sponge bioerosion and reduced overall rates. Conversely, the nighttime lows in pH and Ω_{Ar} could instead be advantageous to the process and lead to accelerated nighttime bioerosion rates. This could also be modulated by the harboring of autotrophic endosymbionts, as prior studies have found that sponge bioerosion is stimulated by photosynthates and other by-products of photosynthesis (e.g., oxygen) (Achlatis et al., 2019). However, this symbiont-driven response could be lost under future OA conditions as light-enhanced bioerosion appears to become negligible at high seawater pCO_2 concentrations (>1000 μatm) (Webb et al., 2017).

In order to investigate the impact of diurnal variability on the physiology and bioerosion rates of reef-excavating sponges, we subjected zooxanthellate (*Cliona varians*) and azooxanthellate (*Cliothosa delitrix*) Caribbean species to static and dynamic carbonate chemistry fluctuations under contemporary and OA conditions. This is the first study to consider the influence of carbonate chemistry variability on coral reef bioerosion, a process that has strong implications for the structure and persistence of coral reef habitats and for their function under future climate scenarios.

Materials and Methods

Experimental design

Dead coral colonies (*Siderastrea siderea*) were collected from an inshore reef in the upper Florida Keys (24.8977 N, 80.6170 W). Care was taken to ensure that the coral skeletons were clean with no visible signs of prior bioerosion. Colonies were transported to National Oceanic and Atmospheric Administration's (NOAA) Atlantic Oceanographic and Meteorological Laboratory (AOML), trimmed into slabs of consistent height (1 cm) using a tile saw (MK Diamond 101), and cut into circular "pucks" using a 5 cm diameter hole saw bit attached to a drill press. The unbored skeleton pucks were treated with 12.5% sodium hypochlorite for 48 hrs to remove microscopic organic matter (Fang et al., 2013), rinsed with deionized water, dried for 24 hrs at 60°C, and weighed using a calibrated analytical balance (0.0001 g precision, Ohaus).

Fragments of reef rock colonized by *Cliothosa delitrix* (*forma incrustans*) and *Cliona varians* (*forma incrustans*) were collected from the Florida Keys (Cheeca Rocks, 24.8966 N, 80.6169 W) and Miami-Dade state waters (Emerald Reef, 25.6742 N, 80.0987 W) using a pneumatic drill. A total of 81 fragments of *C. delitrix* were collected from five different colonies and 80 fragments of *C. varians* were obtained from six colonies. Each fragment contained a minimum of one protruding oscula to maintain filter-feeding capacity. Sponge samples were brought to shore where the cores were cut to consistent height (1 cm) using a diamond band-saw (Gryphon AquaSaw XL) and attached to the unbored skeleton pucks using monofilament (0.8 mm diameter) and stainless-steel crimps. Fragments were then returned to their collection site and left in flow-through baskets attached to cinder blocks to ensure that they were elevated off the sediment floor. Sponges were left in the baskets for three weeks to recover scarred tissue, develop an ectosome, and encourage attachment to the skeleton pucks.

Following the recovery period, the samples were transported to the University of Miami Cooperative Institute for Marine and Atmospheric Studies (CIMAS) and NOAA AOML's Experimental Reef Lab (ERL) where they were randomly distributed across eight independent aquarium systems (Enochs et al., 2018). Each system consisted of a 75 L glass tank circulating with a 75 L temperature and CO_2 controlled sump tank. Incoming seawater was pumped from Biscayne Bay, filtered to 1 μm, and introduced into each tank system at a rate of 250 mL min^{-1} to achieve a complete system turnover every 15 hrs. Each tank contained a circulation pump (Tunze Turbelle Nanostream 6040) to ensure continuous water motion. Light was supplied by 135 W LED arrays (Aqua Illumination Hydra 52 HD) set to a peak photosynthetically active radiation (PAR) of 250 mmol m^{-2} s^{-1}. Lights were programmed to incorporate dawn and dusk conditions, with a gradual morning intensification (06:00-09:00 hr), static mid-day peak values (09:00-15:00 hr), and a gradual late-afternoon abatement (15:00-18:00 hr).

Temperature was measured using RTD sensors (ProSense TTD25C) with heating (300 W aquarium heater, Finnex TH-300) and cooling (titanium chiller coil, Hotspot Energy) applied to the sump tank water. Seawater pH (total scale) was measured every 5 sec using low-drift Durafet pH electrodes (Honeywell). Probes were calibrated twice a week using water samples analyzed for pH (8454 UV-Vis Spectrophotometer, Agilent Cary), total alkalinity (TA; 855 Robotic Titrosampler, Metrohm), and dissolved inorganic carbon (DIC; AS-C3, Apollo SciTech). These three parameters were used with CO2SYS (van Heuven et al., 2011) to calculate the partial pressure of CO_2 (pCO_2) and Ω_{Ar}. Tank conditions were controlled and monitored using custom software programmed in LabView (National Instruments) and data acquisition systems (CompactDAQ, National Instruments), with mass flow controllers (Aalborg GFC series) set to regulate concentrations of air and CO_2 injections within the sump tanks for precise control of pH

conditions. Attached to each tank was a custom-built automatic feeder set to distribute an aqueous protein-rich macroalgal mix (N-rich High Pro, Reed Mariculture) into each tank at four increments throughout the night (6 pm, 9 pm, 12 pm, 3 pm), achieving a cumulative daily concentration of 25 μL L^{-1} (Achlatis et al., 2017).

Within their allocated tanks, sponges were acclimated to the indoor laboratory setting for one week using conditions similar to those at their collection sites (27.1°C and 8.05 ± 0.02 pH; mean pH ± diurnal pH oscillation). Two replicate tanks were used per treatment, with each tank containing 10 sponge samples of each species. Two control skeleton pucks without a sponge attached to them were added to each tank to measure any abiotic dissolution of $CaCO_3$ resulting from treatment conditions. The lab acclimation period was followed by a gradual one-week ramping period to target treatment conditions. Treatments consisted of contemporary (CT) and future OA mean pH conditions and two variability regimes for a total of four treatments: CT static (8.05 ± 0.00), CT variable (8.05 ± 0.10), OA static (7.80 ± 0.00), OA variable (7.80 ± 0.10). The variable treatment groups followed 24 hr sinusoidal oscillations that mimic natural reef environments (Albright et al., 2013), with minimum pH conditions occurring at 06:00 hr and maximum pH conditions at 18:00 hr. Sponges were exposed to treatment conditions for a total of 38 days.

Sponge bioerosion

Bioerosion rates were determined using the buoyant weight technique (Dodge et al., 1984) within a temperature-controlled seawater tank. This method was selected since the derived skeletal weights are insensitive to neutrally buoyant tissue, mucus, and water found within the internal substrate voids of bioeroding sponges. This technique also ensured that sponges

remained submerged in water throughout the measurements to prevent pores from filling with air and causing necrosis. Samples were suspended on a stainless-steel platform attached to the analytical balance with hydrophobic tungsten wire (0.05 mm). Mass was measured using a calibrated analytical balance (0.0001 g precision, Ohaus). Prior to each measurement, temperature was recorded by a high-accuracy temperature probe (Digi-Sense). Seawater samples were collected from the buoyant weight tank at the start and end of each session to measure average salinity using a densitometer (DMA 5000M densitometer, Anton Paar). Temperature and salinity were used to calculate seawater density to convert buoyant weight to total skeletal mass. The control skeletal pucks were included in the buoyant weight measurements, with their change in skeletal mass used as an offset in the bioerosion calculations to ensure that the change in skeletal mass of the samples was exclusively sponge related. A caliper was used to measure the diameter and height of each sponge sample to calculate the surface area of sponge tissue (cm^2). Surface area was used to standardize the change in mass for each sponge sample. Measurements were taken at day 2 and day 38 of treatment conditions, with change in mass interpreted as being due to sponge bioerosion (mg cm^{-2} d^{-1}).

Sponge photochemical efficiency

In order to evaluate whether treatment conditions impacted the photosymbionts of zooxanthellate *C. varians*, the photochemical efficiency of Photosystem II (PSII) was quantified from chlorophyll *a* maximal fluorescence (F_v/F_m) using an Imaging Pulse Amplitude Modulated (I-PAM) fluorometer (Walz GmbH, Effeltrich, Germany). The settings used within the imaging software (ImagingWin v2.56p) remained constant throughout the experiment (saturation pulse = 0.8, saturation intensity = 12, gain = 12, damping = 2). All sponges were dark-acclimated for 45

min prior to the start of each I-PAM session. Sponges were randomly grouped into sets of five within a clear plastic bin and placed directly below the LED-Array-Illumination unit. An area of interest was placed on each sponge sample and a saturation pulse was provided to measure photosynthetic efficiency of PSII based on images of near-infrared and red-light remission. Measurements were taken at day 1 and day 36 of treatment conditions.

Statistical analysis

Sponge bioerosion rates were analyzed for treatment effects and species differences using a two-way crossed ANOVA. The interaction between treatment and sponge colony were used as fixed effects and tank was used as a random effect. The assumptions of normality were confirmed using Q-Q plots where it was determined that data transformations were not needed. Post hoc Tukey's test was used to evaluate differences due to treatment and sample colony. Statistical analyses were performed using R (R Core Team, 2020) with the R Studio extension (RStudio Team, 2015) and plots were created using ggplot2 package (Wichkham, 2016).

Results

Carbonate chemistry treatments

Ramping and the four carbonate chemistry treatments were successfully achieved in this experiment (Fig. 1). Temperature and salinity were consistent across treatment conditions and replicate tanks (Table 1). Deviations (mean ± stdev) from programmed pH values at four time points within the diurnal cycle (i.e., 00:55 hr, 6:55 hr, 12:55 hr, 18:55 hr) indicate that the target pH values were attained (Table 1). Durafet probe error, calculated as the difference between measured pH (Durafet) and pH determined from water sample DIC and TA, show that the pH

277 probes were stable and accurate throughout experimental conditions (Table 1). Variability in
278 carbonate chemistry parameters (i.e., TA, DIC, pCO_2, Ω_{Ar}) measured from water samples at the
279 maximum and minimum point within a diurnal cycle (i.e., 6 am and 6 pm) were reported for each
280 treatment group (Table 2).
281
282 *Influence of carbonate chemistry variability on bioerosion*
283 OA and variability treatments significantly influenced sponge bioerosion rates in *C.*
284 *varians* ($p < 0.0001$) and *C. delitrix* ($p < 0.001$). Post hoc analysis revealed that for *C. varians*
285 (Fig. 2a), bioerosion rates were significantly higher under CT variable and OA variable
286 conditions compared to those from the static treatments of the same mean pH ($p < 0.001$ for CT
287 variable; $p = 0.023$ for OA variable). A 62% increase in bioerosion was measured from CT static
288 (0.47 ± 0.04 mg $CaCO_3$ cm^{-2} d^{-1}; mean ± SE) to CT variable (0.76 ± 0.07 mg $CaCO_3$ cm^{-2} d^{-1})
289 conditions (Fig. 3). The relative increase in bioerosion for the OA treatment groups was
290 significant but less pronounced, comprising a 21% increase from OA static (0.70 ± 0.03 mg
291 $CaCO_3$ cm^{-2} d^{-1}) to OA variable (0.85 ± 0.03 mg $CaCO_3$ cm^{-2} d^{-1}) conditions. Additionally, a
292 significant increase in bioerosion rates was found from CT static to OA static (49%, $p < 0.001$)
293 and OA variable (81%, $p < 0.001$) conditions. No significant difference was detected between
294 the CT variable and OA static treatment groups ($p = 0.69$).
295 *C. delitrix* (Fig. 2b) CT static bioerosion rates were significantly lower than those from
296 the CT variable ($p = 0.012$), OA static ($p = 0.025$), and OA variable ($p < 0.001$) treatments.
297 While the relative increase in bioerosion rates measured from CT static (0.67 ± 0.05 mg $CaCO_3$
298 cm^{-2} d^{-1}) to the other three treatments were consistently lower than that of *C. varians* (Fig. 3), an
299 increase was still evident from CT static to CT variable (39%, 0.93 ± 0.07 mg $CaCO_3$ cm^{-2} d^{-1}),

OA static (36%, 0.91 ± 0.05 mg $CaCO_3$ cm^{-2} d^{-1}), and OA variable (52%, 1.02 ± 0.06 mg $CaCO_3$ cm^{-2} d^{-1}). Bioerosion rates were not significantly different between the OA static and OA variable treatments ($p = 0.51$).

An across-species comparison confirmed that *C. delitrix* and *C. varians* bioerosion rates were significantly different ($p < 0.001$), but no interaction was found between species and treatment ($p = 0.97$). *C. delitrix* bioerosion pooled across all treatments was on average 21% higher than that of *C. varians*.

There was no statistical difference between bioerosion and colony ($p = 0.619$, Fig. S1) for *C. varians*. Colony-specific rates were statistically different for *C. delitrix* ($p = 0.026$, Fig. S2), primarily driven by significantly higher bioerosion (58%) in colony E (1.02 ± 0.09 mg $CaCO_3$ cm^{-2} d^{-1}) than colony C (0.75 ± 0.05 mg $CaCO_3$ cm^{-2} d^{-1}, $p = 0.028$), whereas no significant difference was found between the other colonies.

Influence of carbonate chemistry variability on photochemical efficiency

There was a significant difference detected between treatment and photochemical efficiency of PSII ($p < 0.001$, Fig. S3) for *C. varians*. Post hoc analysis revealed that photochemical efficiency was significantly lower under CT variable conditions compared to OA static ($p = 0.011$) and OA variable ($p = 0.001$), but no significant difference was found between CT static ($p = 0.491$).

There was a significant colony difference in photochemical efficiency ($p < 0.001$; Fig. S4). Post hoc analysis indicated that photochemical efficiency for colonies A and C was significantly lower than colonies D ($p = 0.009$ and $p < 0.001$ respectively) and F ($p = 0.005$ and p

322 < 0.001 respectively). No significant differences in photochemical efficiency were measured for
323 the remaining colonies.
324
325 **Discussion**
326 *Ocean acidification, carbonate chemistry variability, and bioerosion*
327 These data indicate that sponge bioerosion is stimulated by the combined effects of OA
328 and increased carbonate chemistry variability. The response may be parabolic rather than linear,
329 with the positive effect of dynamic carbonate chemistry becoming relatively less pronounced
330 under future high pCO_2 scenarios. For both species, bioerosion rates were considerably higher
331 for the two OA treatment groups when compared to CT static conditions (Fig. 2a,b). This
332 response supports prior sponge studies investigating the influence of OA on sponge bioerosion
333 under static conditions (Wisshak et al., 2013; Wisshak et al., 2014; Enochs et al., 2015), further
334 underlining the positive impact of OA on sponge bioeroding capacity. The majority of these
335 studies, however, measured biologically-mediated chemical dissolution rather than buoyant
336 weight derived bioerosion, and direct comparisons should be cautiously applied.
337 Our measured bioerosion rates are similar to those recorded in a study using a Pacific
338 zooxanthellate sponge (*C. orientalis*: Wisshak et al., 2012), although the rates they measured
339 may be more representative of those from our static treatments since diurnal carbonate chemistry
340 was kept constant within their experimental conditions. In our study, *C. varians* bioerosion rates
341 were notably lower than *C. orientalis* for the two static treatments and higher for the two variable
342 treatments, whereas *C. delitrix* rates were consistently higher across all treatments. This result
343 was not surprising, since *C. delitrix* is known to be one of the more aggressive reef-excavating
344 sponge species (Chaves-Fonnegra and Zea, 2007; Chaves-Fonnegra and Zea, 2010).

Our evaluation of the relationship between variable carbonate chemistry conditions and sponge bioerosion showed a clear trend towards variability-enhanced bioerosion (Fig. 2a,b). For both species, bioerosion rates measured from the variable treatment groups were markedly higher than that of their respective static treatment conditions. Carbonate chemistry variability had a greater influence on bioerosion under CT pH conditions compared to future OA, suggesting that the most substantial relative increase in sponge bioerosion may already be occurring at present in highly variable reef ecosystems. While these data point to variability-stimulated bioerosion being a generalized sponge response, the effect may be more pronounced for photosynthetic species, evident by the consistently higher percent increase in bioerosion seen for *C. varians* under variable conditions (Fig. 3). However, while the relative change was greater for *C. varians*, the overall impact of accelerated bioerosion will be larger for *C. delitrix* due to the higher bioerosion rates consistently measured across all treatments.

Although the present study is the first to assess the relationship between carbonate chemistry variability and sponge bioerosion, we can compare our results to prior experiments investigating the response of calcification (arguably the antithesis of bioerosion) to OA and variability. As with our bioerosion results, Chan and Eggins (2017) measured higher calcification rates for *Acropora formosa* when exposed to variable pH conditions compared to that of three static treatments. Enochs et al. (2018) found the most significant increase in *Acropora cervicornis* calcification rates under CT variable conditions. This variability-enhancement was also evident for the OA variable treatment group within their study, although the difference between the OA static treatment was not significant. However, their incorporation of a highly variable OA treatment group (7.80 ± 0.20 pH) resulted in comparably lower calcification rates than that of the other two OA treatments, indicating that the stimulated calcification rates

368 measured in the moderately variable OA treatment was lost under intense variability. This could
369 indicate coral physiological impairment in the highly variable treatment due to daily exposure to
370 acutely low pH conditions. If we had included a highly variable OA treatment in our study, we
371 may have found a similar impairment for sponge bioerosion.

372 Despite the differences in OA static and CT variable experimental seawater chemistry
373 parameters (Table 2), bioerosion rates were nearly identical between the two treatments, a trend
374 that was consistent for zooxanthellate and azooxanthellate species (Fig. 2a,b). This result was
375 surprising since sponges in the CT variable treatment were exposed to consistently higher pH
376 conditions, with the minimum pH within the diurnal cycle being 0.15 units higher than that of
377 OA static. Moreso, the CT variable treatment reached the most acidified conditions for a
378 comparably shorter period of time each day (<8.0 pH for 6 hrs, CT variable; 7.80 pH for 24 hrs,
379 OA static). Based on these discrepancies, results from prior literature would lead us to expect
380 higher bioerosion rates for sponges exposed to the static OA treatment due to the stimulating
381 effect of reduced pH conditions (Wisshak et al., 2013; Wisshak et al., 2014; Enochs et al., 2015).
382 In our present study, however, the similar rates between the two treatments suggest that diel pH
383 variability may modulate the sponge OA response in a way that requires an updated
384 interpretation of the previously described relationship.

385 While this characterization requires further testing and validation, these results can be
386 interpreted from two general perspectives. First, fluctuating carbonate chemistry conditions in
387 the variable CT treatment may accelerate sponge bioerosion to an equal extent as that of the
388 notably lower pH conditions present in the static OA treatment. On the contrary, the similar rates
389 found across the two treatments could instead be a function of sponge physiological impairment
390 in the static OA treatment (Emson 1966; Bates and Bell 2017). If the sponges in this treatment

group were adversely affected by continuous exposure to low pH conditions, this could have depressed their bioeroding activity. This could also imply that sponges exposed to variable conditions may experience daytime respite from the more extreme OA conditions, which could benefit sponges in the variable OA treatment, where the minimum pH (7.70 pH) was lower than that of the static OA treatment.

Conceptual model behind the bioerosion response

Although the design of this present study does not enable us to directly address the mechanistic hypotheses that underpin the impact of diurnal carbonate chemistry fluctuations on chemical bioerosion rates, we can use these data to infer some possible explanatory mechanisms and build a working model for sponge bioerosion in variable environments. We hypothesize that a non-linear relationship between pH and sponge bioerosion causes the enhanced rates under the variable treatments in both zooxanthellate and azooxanthellate sponges. The presence of photosymbionts further amplifies this effect.

More specifically, if the relationship between pH and sponge bioerosion was linear, then static pH conditions equivalent to nighttime lows in the CT variable treatment would result in higher bioerosion rates than for CT variable pH conditions. Here, the static OA treatment had a substantially lower average pH than the minimum values from the CT variable treatment. However, for both species, no significant difference in bioerosion was found between these two treatments, with nearly identical rates being measured under these conditions (Fig. 2a,b). This implies that the OA static treatment might be impeding sponge bioerosion. Enochs et al. (2015) observed a parabolic response for the chemical dissolution rates of *P. lampa* as a function of pCO_2, with relatively depressed bioerosion rates at 986 μatm. Webb et al. (2017) also described

depressed day-time bioerosion rates under low pH conditions, suggesting that the symbiont-driven bioerosion enhancement becomes negligible due to OA. In the present study, the pCO_2 concentration for the OA static treatment was around 960 μatm, which may have resulted in relatively lower bioerosion rates for sponges exposed to these conditions.

Assuming the non-linear relationship between pCO_2 and chemical bioerosion rates of *P. lampa* described in Enochs et al. (2015) holds true for *C. varians* and *C. delitrix*, and across day and night scenarios, then the enhancement/reduction in rates during the day and night would differ in magnitude and direction, even with an equal fluctuation around the mean (Fig. 4). For instance, a large increase in pH during the day for the CT variable treatment group may decrease bioerosion rates only slightly if the response region is near the asymptote, while an opposite but equal nighttime decline in pH could strongly increase bioerosion if the response region is along the steepest part of the relationship curve. Comparable, but antagonistic effects, were described for *Acropora cervicornis* calcification rates measured across different diel carbonate chemistry variability regimes (Enochs et al., 2018).

If static OA rates are indeed depressed, then the direction of dark enhanced and light reduced bioerosion that we propose for the CT treatments would be reversed under OA conditions. Benefiting at a physiological level from an increase in daytime pH, bioerosion rates within the variable OA treatment would instead increase during the day, whereas an opposite, but equal nighttime decline in pH would cause dark rates to decrease only slightly (see Fig. 4). This suggests that the ratio between the magnitude of the decrease/increase in bioerosion rates under daytime/nighttime conditions will ultimately determine the difference in rates between static and variable treatments.

The presence of symbionts in *C. varians* may reduce the impact of elevated daytime pH for the CT variable treatment group. This would result in a smaller decrease in bioerosion rates when the pH oscillates to the higher values within a diel cycle (Fig. 4). This could explain the larger difference in rates found between static and variable treatments for *C. varians* relative to azooxanthellate *C. delitrix* (Fig. 3). Likewise, symbionts would enhance the impact of increased bioerosion rates under daytime OA variable conditions (Fig. 4), resulting in a bigger gap between the daytime increase and the nighttime decline.

To test this mechanistic model, we propose that future studies incorporate day and night measurements of chemical and mechanical bioerosion within their experimental design in order to evaluate whether the ratio between day/night rates is modified by different pCO_2 and diel variability treatment conditions.

Implications for reef persistence

These data suggest that the combination of variable carbonate chemistry and reduced seawater pH will accelerate sponge bioerosion rates in the future, which could have ramifications for reef ecosystem function and habitat persistence. However, the impact of these enhanced bioerosion rates will likely be contingent on site-specific differences in localized environmental conditions and the degree to which other reef-shaping organisms (i.e., calcifiers and bioeroders) respond or adapt to the same environmental stimuli (Cyronak et al., 2019; Rivest et al., 2017). For example, while we measured the highest sponge bioerosion rates under variable OA conditions, other studies looking at the response for corals found that variable conditions could mitigate some of the adverse effects of OA (Enochs et al., 2018). While this interpretation does not consider the effects of coral bleaching and other climate associated stressors, this could

459 indicate that increased sponge bioerosion may be less impactful or even offset by coral
460 calcification under future carbonate chemistry variability. The highly dynamic nature of
461 carbonate chemistry in reef ecosystems could be an additional regulatory factor that controls the
462 overall effect of variability-enhanced bioerosion rates, where any change to the physical (e.g.,
463 water depth, tidal flushing), chemical (e.g., pCO_2), and/or biological (e.g.,
464 photosynthesis/respiration and calcification/dissolution) processes involved in carbonate
465 chemistry variability could create a downstream feedback loop that enhances or diminishes the
466 sponge response.
467 Extreme diurnal carbonate chemistry variability has been previously reported across
468 several reef sites, some of which experience diel pH fluctuations that range from pre-industrial to
469 end of the century levels (Shaw et al., 2012). Reefs located around Lady Elliot Island (Great
470 Barrier Reef) are exposed to intense carbonate chemistry oscillations, with diurnal pH conditions
471 ranging from 7.6 to 8.6 (Shaw et al., 2012). Similar diurnal variability regimes have been
472 measured for other Australian reefs, such as those located near One Tree Island (7.4 to 8.1 pH,
473 see Silverman et al., 2012) and Heron Island (7.9 to 8.2 pH, see Kline et al., 2012), in addition to
474 reefs in Japan (7.7 to 8.4 pH, see Ohde and Van Woesik, 1999) and Palmyra Atoll (7.8 to 8.1 pH,
475 see Hoffmann et al., 2011). In the theoretical absence of other environmental stressors (e.g.,
476 ocean warming, eutrophication), our study implies that sponge bioerosion in these variable
477 ecosystems could already be accelerated to rates that were not expected to occur until the end of
478 the century (Enochs et al., 2015). However, since the magnitude of the pH oscillations from
479 many of these sites is greater than those of our variable treatment groups, this should be tested
480 further using highly variable pH treatment conditions. This could help decipher whether there is

a variability threshold that results in impaired sponge bioerosion similar to that found for coral calcification (Enochs et al., 2018).

While the primary purpose of this study was to evaluate the influence of diel carbonate chemistry on sponge bioerosion rates, our results can be applied to the interpretation of seasonal and spatial (i.e., inshore vs offshore) differences in sponge bioerosion rates as they relate to carbonate chemistry variability. At a seasonal scale, the magnitude of carbonate chemistry has been shown to fluctuate in response to regular changes in temperature, light availability, and rainfall (Bates et al., 2010; Enochs et al., 2019). These changes have been described by Roik et al. (2018), where larger diurnal pH fluctuations were measured in the summer months (0.6 pH units) than in the winter months (0.3 pH units) for reef sites in the Red Sea. Our results could therefore indicate the potential for reef ecosystems to experience seasonally enhanced sponge bioerosion rates during the summer and seasonally depressed bioerosion rates during the winter, corresponding to differences in pH variability. Similarly, inshore reefs tend to be more dynamic environments than offshore reef systems and are often exposed to more extreme carbonate chemistry oscillations (Manzello et al., 2012; Gagliano et al., 2010). It is therefore possible that sponge bioerosion is relatively greater at inshore reefs owing to the more variable nature of carbonate chemistry characteristic of these inshore ecosystems.

Despite the stimulating effects of OA and variable carbonate chemistry conditions that we measured for sponge bioerosion, it is important to consider that future reef ecosystems are expected to be concurrently impacted by several environmental stressors that could potentially modify the response. Considering that an increase in the concentration of atmospheric CO_2 is simultaneously driving OA and ocean warming (Meehl et al., 2007), predictions should recognize the interconnectivity of the two, as prior studies have described a modified sponge OA

response when temperature treatments were included (Achlatis et al., 2017; Fang et al., 2013). Long-term exposure to both OA and elevated temperatures has been shown to cause tissue bleaching, necrosis, and an unsustainable energy budget (Wisshak et al., 2013; Fang et al., 2014; Stubler et al., 2015), indicating that if sponges become physiologically impaired under future environmental scenarios, in particular from temperature stress and thermally-induced bleaching (Hill et al., 2016), then any bioerosion enhancement caused by OA and carbonate chemistry variability could be lost.

Nutrient enhancement in reef ecosystems could alter the sponge response in the opposite manner. Elevated nutrient loads have been shown to positively influence sponge energy budgets and bioeroding activity (Webb et al., 2017), suggesting that the stimulating effect they provide sponges could be enhanced when combined with OA and variable carbonate chemistry conditions. Additionally, eutrophication could potentially ameliorate the adverse physiological effects of temperature stress, helping sponges persist under future environmental scenarios. However, when evaluating any interactive properties caused by nutrients, it is important to consider that zooxanthellate and azooxanthellate species could experience unique responses to eutrophication due to inherent differences in their metabolic requirements.

Conclusions

This study represents the first evaluation of the combined impact of OA and diurnal carbonate chemistry variability on sponge bioerosion. The results demonstrate that sponge bioerosion rates are accelerated by OA and pH variability, a trend that was consistent for both zooxanthellate (*C. varians*) and azooxanthellate (*C. delitrix*) species. The stimulating effect of diurnal variability was more pronounced for the CT treatments compared to that of OA, which

suggests a threshold response for sponges exposed to the lowest pH conditions, possibly causing physiological impairment. While rates were consistently greater for *C. delitrix* across all treatment groups, the relative increase in bioerosion from static to variable and CT to OA treatments was consistently higher for *C. varians*. This implies that autotrophic symbionts may influence the ratio between the magnitude of the decrease/increase in bioerosion rates under daytime/nighttime conditions, resulting in an enhanced sponge response. These data indicate that contemporary reef ecosystems exposed to variable diel carbonate chemistry fluctuations could already be experiencing sponge bioerosion rates that had previously been predicted under end-of-the-century OA scenarios. From a reef persistence perspective, this could result in a consequential shift towards net habitat loss and reduced ecosystem services.

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Data Availability

The datasets generated during and/or used for the analysis of the current study will be made publicly available through NCEI.

Additional Information

Competing Interests: The authors declare no competing interests.

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Tables

Table 1 | Mean temperature (°C), salinity (PSU), pH deviation from set point at four time points (00:55 hr, 6:55 hr, 12:55 hr, 18:55 hr), and pH probe error across treatment conditions and replicate tanks. Treatment reflects the mean pH ± diel pH fluctuations with all pH values being in total scale. pH set point deviation represents the difference between measured pH (Durafet) and the coded pH set point for the tank. pH probe error is calculated as the difference between measured pH (Durafet) and the pH calculated using DIC and TA. Standard deviation is represented in parentheses.

pH Treatment	**Temperature**	**Salinity**	**pH Set Point Deviation**				**pH Probe Error**
Tank	[n = 6328]	[n = 6]	[n = 37]				[n = 7]
			0:55	6:55	12:55	18:55	
8.05 ± 0.00	27.02 (0.03)	35.33 (0.51)	0.016 (0.01)	0.016 (0.01)	0.006 (0.03)	0.010 (0.01)	0.006 (0.01)
Tank 1	27.02 (0.03)	35.54 (0.84)	0.026 (0.01)	0.027 (0.01)	0.006 (0.03)	0.017 (0.01)	0.010 (0.01)
Tank 2	27.03 (0.03)	35.12 (0.67)	0.005 (0.00)	0.004 (0.00)	0.006 (0.03)	0.004 (0.00)	0.002 (0.01)
8.05 ± 0.10	27.02 (0.03)	35.58 (0.55)	0.006 (0.00)	-0.001 (0.00)	0.011 (0.04)	0.050 (0.02)	0.003 (0.01)
Tank 3	27.03 (0.03)	35.58 (0.80)	0.005 (0.00)	-0.001 (0.00)	0.009 (0.04)	0.043 (0.02)	0.007 (0.01)
Tank 4	27.02 (0.01)	35.59 (0.83)	0.006 (0.00)	-0.001 (0.00)	0.013 (0.03)	0.057 (0.02)	-0.002 (0.01)
7.80 ± 0.00	27.03 (0.03)	35.51 (0.53)	0.001 (0.00)	0.000 (0.00)	0.002 (0.02)	0.000 (0.00)	-0.004 (0.02)
Tank 5	27.04 (0.04)	35.44 (0.78)	-0.002 (0.00)	-0.002 (0.00)	0.001 (0.03)	-0.002 (0.00)	-0.005 (0.01)
Tank 6	27.02 (0.03)	35.59 (0.80)	0.003 (0.00)	0.002 (0.00)	0.003 (0.02)	0.002 (0.00)	-0.002 (0.02)
7.80 ± 0.10	27.03 (0.03)	35.59 (0.55)	-0.028 (0.00)	-0.002 (0.00)	0.021 (0.00)	-0.012 (0.00)	-0.013 (0.03)
Tank 7	27.03 (0.03)	35.54 (0.82)	-0.028 (0.00)	0.000 (0.00)	0.023 (0.00)	-0.011 (0.00)	0.001 (0.02)
Tank 8	27.03 (0.03)	35.64 (0.81)	-0.029 (0.01)	-0.003 (0.00)	0.020 (0.02)	-0.012 (0.00)	-0.027 (0.03)

720 **Table 2 |** Mean TA (µmol/kg), DIC (µmol/kg), pCO_2 (µatm), and Ω_{Ar} across treatment
721 conditions at the maximum and minimum time points within a diurnal cycle (6am and 6pm).
722 Treatment reflects the mean pH ± diel pH fluctuations with all pH values being in total scale. pH,
723 TA, and DIC were directly measured, whereas pCO_2 and Ω_{Ar} were calculated from these
724 parameters using CO2SYS. Standard deviation is represented in parentheses.

pH Treatment Time	**TA (µmol/kg)**	**DIC (µmol/kg)**	***p*CO2 (µatm)**	**Ω_{Ar}**
8.05 ± 0.00	2287.2 (8.2)	2020.4 (9.7)	502.6 (13.8)	3.1 (0.1)
6am	2290.0 (9.6)	2028.6 (17.5)	506.2 (24.0)	3.1 (0.1)
6pm	2278.2 (16.5)	2031.0 (17.0)	552.2 (50.0)	2.9 (0.2)
8.05 ± 0.10	2293.2 (7.2)	2054.7 (12.4)	611.5 (42.6)	2.8 (0.1)
6am	2298.5 (13.4)	2102.5 (11.5)	720.1 (22.0)	2.4 (0.1)
6pm	2299.0 (12.9)	1999.7 (10.1)	422.3 (12.4)	3.5 (0.1)
7.80 ± 0.00	2293.2 (8.4)	2136.7 (9.3)	954.7 (15.5)	2.0 (0.0)
6am	2265.4 (4.9)	2103.8 (5.3)	920.2 (18.8)	2.0 (0.0)
6pm	2271.1 (6.2)	2114.0 (1.8)	952.5 (25.2)	2.0 (0.1)
7.80 ± 0.10	2280.1 (7.6)	2119.8 (12.9)	982.9 (55.8)	2.0 (0.1)
6am	2259.6 (9.2)	2120.6 (20.6)	1108.5 (98.8)	1.8 (0.2)
6pm	2268.1 (11.7)	2049.4 (14.9)	674.9 (34.5)	2.5 (0.1)

725

726 ***Figure legends***

727 **Fig. 1 |** pH (total scale) measured for each hour within the diurnal cycle averaged across the 38
728 days of treatment conditions. The four treatment groups are characterized by mean pH ±
729 amplitude of diel pH oscillations: 8.05 ± 0.00 (dark blue), 8.05 ± 0.10 (light blue), 7.80 ± 0.00
730 (dark red), 7.80 ± 0.10 (light red). For each treatment, data from the two replicate tanks were
731 pooled together and used to calculate the mean pH for each hour point (n = 76). Errors bars
732 around each point describe standard deviation. Yellow shaded area represents daytime conditions
733 and dark shaded areas represent nighttime conditions.

734

735 **Fig. 2 |** Bioerosion rates (mg cm^{-2} day^{-1}) of zooxanthellate sponge *C. varians* (a) and
736 azooxanthellate sponge *C. delitrix* (b) subjected to four treatment conditions (left to right): CT
737 static (8.05 ± 0.00); CT variable (8.05 ± 0.10); OA static (7.80 ± 0.00); OA variable (7.80 ±
738 0.10). Values that share a Greek letter are not significantly different. P values for significant
739 differences across treatments are indicated.

740

741 **Fig. 3** | Percent increase in sponge bioerosion rates (mg cm^{-2} day^{-1}) from CT static (8.05 ± 0.00,
742 top-left) conditions to CT variable (8.05 ± 0.10, bottom-left), OA static (7.80 ± 0.00, top-right),
743 and OA variable (7.80 ± 0.10, bottom-right). Percent increase in bioerosion rates are represented
744 alongside each arrow, with *C. varians* (green) and *C. delitrix* (orange). Significant differences
745 across treatment conditions are denoted by *.

746

747 **Fig. 4** | Theoretical effects of diel carbonate chemistry fluctuations (pH) on sponge bioerosion
748 rates. The figure depicts the influence of a non-linear chemical bioerosion/pH relationship on

bioeroding sponges' sensitivity to diel variability and the shift from night bioerosion enhancement to day bioerosion enhancement in the pH oscillating treatments. The positive and/or negative influence of variable conditions, under day and night scenarios, is detailed by the arrows, with the length of the arrow representing the magnitude of change. In CT variable pH conditions (blue shaded area), the positive effects of nighttime conditions are greater than the negative effects of daytime conditions as the daytime response region is located near the lower asymptote. In OA conditions (red shaded area), the positive effects of daytime conditions are larger than the negative effects of nighttime conditions, but the magnitude of the impact is depressed as the response region is near the asymptote. The influence of symbionts on the sponge bioerosion response is depicted by the green lines.