ICES Journal of Marine Science

Comment

Comment on "Bioerosion: the other ocean acidification problem": on field studies and mechanisms

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In a recent review, "Bioerosion: the other ocean acidification problem," Schönberg et al. claim that studies of bioerosion across natural chemical gradients are "flawed" or "compromised" by co-variation among environmental factors. Their discussion falls largely on two publications, Silbiger et al. and DeCarlo et al. Here, we demonstrate that critical errors in plotting, statistical analysis, and data selection in Schönberg et al.'s reanalysis, result in a gross misrepresentation of these studies. Further, we argue three key points regarding field-based studies that require broader discussion within the bioerosion community and marine scientists in general: (1) that natural variability in field studies is not a flaw, (2) interpretations must be supported by mechanistic understanding, and (3) field-based studies play an essential role in elucidating interactions between OA and natural variability that is not captured by laboratory CO_2-manipulation experiments. Our goal with this comment is to encourage open discussion of the advantages and caveats of field-based studies in general, and ultimately, advance our understanding of bioerosion patterns observed in nature.

Keywords: bioerosion, field studies, natural gradients, ocean acidification.

In a recent review paper, Schönberg et al. (2017) (hereafter "S17") synthesize the literature on the sensitivity of coral reef bioerosion to ocean acidification (OA). Their review brings a broad range of studies and results into a cohesive whole that will no doubt be a valuable resource for the bioerosion research community. However, S17 go on to claim that previous investigations of bioerosion sensitivities across natural pH gradients are "compromised" by co-variations within the natural environment. Their critiques primarily fell on our publications (Silbiger et al., 2014; DeCarlo et al., 2015), declaring that our studies are "flawed" because S17 found statistically significant correlations between subsets of our data and other factors beyond the patterns we originally reported. Unfortunately, S17's assessments are plagued by critical errors in plotting and statistical analysis, and

ultimately their claims are not supported by our published data. Besides these regrettable mistakes, we feel that larger issues are at stake here. S17 used high-order polynomials to re-fit our data but provided no mechanistic bases for why such relationships should exist. This is a recipe for finding artificial correlations. After describing the specific problems with how S17 misrepresented our data, we argue three key points regarding field studies that, in light of S17's assertions, we believe deserve a broader discussion within the bioerosion community. First, field studies are naturally characterized by co-variability, but this does not make them "flawed". Second, a key requirement of reporting an observed pattern is to support it with a mechanistic foundation. Finally, when field studies are properly designed and interpreted, they serve an essential role not only in validating laboratory results,

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but also in elucidating interaction between OA and natural variability that is difficult to simulate in a laboratory setting. Our goal with this comment is to promote an open discussion on how we as a community can design studies that advance our understanding of coral reef bioerosion in a high-CO_2 world.

Specific response to S17's assessments of Silbiger *et al.* (2014) and DeCarlo *et al.* (2015)

S17 claim that Silbiger *et al.* (2014) have "compromised conclusions" based on a re-analysis of the raw data. We believe that the conclusions reported in the S17 re-analysis are unsubstantiated due to (1) misclassification of reef flat and reef slope data, (2) incorrect plotting of the data and removing outliers without justification, and (3) not accounting for high collinearity among environmental parameters. First, S17 state that there were 14 samples on the reef flat and 7 samples on the reef slope when, in fact, there were 10 samples at each location in our published analysis (Figure 1a and b), and we believe this led to false conclusions. For example, S17 stated, *pH remained stable on the reef flat (14 samples) and only changes along the reef slope (7 samples).* Yet the actual pH ranges are nearly identical (flat: 0.0396 vs. slope: 0.0355). Further, even when we recalculated the ranges using the S17 reef flat/slope classifications (we assumed 13 vs. 7 data points as only 20 data points were used in the final analysis and available in the online repository), this statement is still false: the pH range on the reef flat (0.0418) was nearly three times higher than the reef slope (0.0152). Indeed, when S17 excluded the reef flat data from their re-analysis the *relationships with the carbonate system became worse.* Second, after careful examination of the re-replotted data in S17 (S17 Figure 8b and c), we noticed several discrepancies with the raw data. An "outlier" was removed without explanation (point with X overlaid in Figure 1e), and most alarmingly, two plotted data points were inconsistent with the original dataset (open circles in Figure 1e). Thus, of the seven points that S17 classified as being on the reef slope, three were apparently misrepresented, which led to the erroneous conclusion that there was a parabolic relationship between depth and net accretion–erosion on the reef slope. Third, the environmental data collected in Silbiger *et al.* (2014) are highly co-linear [Figure S2 here and Figure S5 in Silbiger *et al.* (2014)], as is common in field data, and it is risky to make inference from raw environmental data without accounting for this (Figure 1c and as done in S17 Figure 8b). Silbiger *et al.* (2014) removed the collinearity in the data by using a residuals regression, which is a common technique used to disentangle covarying parameters (Graham 2003). After regressing each environmental parameter with depth and distance from shore, the residuals were used in the bioerosion analysis. These residuals are the effects of each parameter on net accretion–erosion rates above and beyond the effect of any parameter that correlates with depth and distance from shore. Following this, pH showed the strongest fit to net accretion–erosion rates, explaining 64% of the variance (Figure 1d). Further, when ranking hypothesized drivers of accretion–erosion rates (pH, resource availability, temperature, depth, and distance from shore) using a model selection approach, pH was the best of the candidate models (see Silbiger *et al.* 2014 for details). Even with a sample size of 20, we found it striking to find such high explanatory power between net accretion–erosion and pH and on a small spatial scale (34 m), highlighting the importance of small-scale variability in driving accretion–erosion patterns.
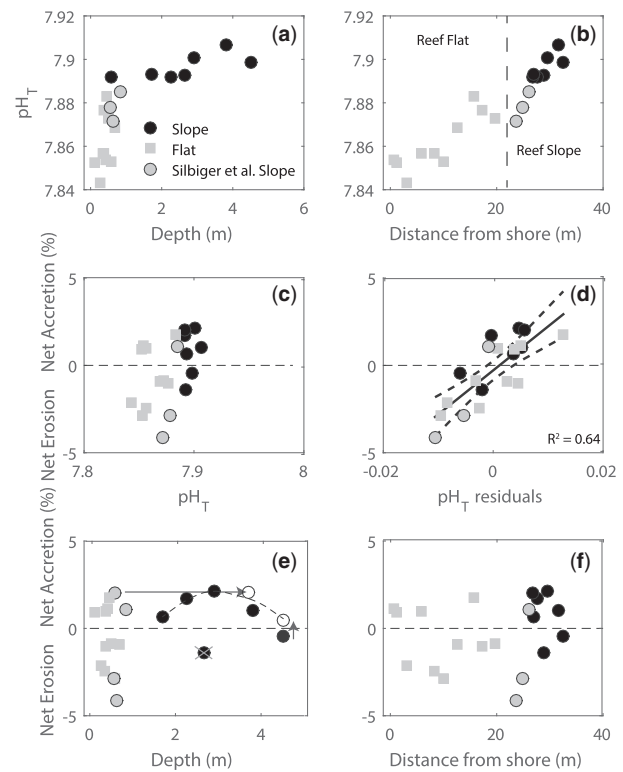

Figure 1. Data published in Silbiger *et al.* (2014) with reef flat and reef slope locations in grey squares and black circles, respectively, as described by S17. Grey circles are the data points that S17 classified as reef flat, but were classified as reef slope by Silbiger *et al.* 2014. Panel (a) and (b) are pH on the total scale versus depth (m) and distance from shore (m), respectively. Panel (c) is net accretion–erosion rates versus pH_T. This figure was recreated in S17 (Figure 8b), but they only plotted 5 points on the reef slope and 13 on the reef flat. Two data points from the original publication were missing in S17's plot (Figure 8b). Net accretion and erosion data are the percent change in volume of $CaCO_3$ blocks after 1-year exposure on a reef in Kaneohe Bay, Hawaii. Net accretion–erosion rates are square-root transformed here, and in Silbiger *et al.* (2014), to meet assumptions of normality (see, Supplementary Figure S1 for plots with untransformed data). R^2 value, solid line (best fit line), and dashed lines (95% confidence interval) in (d) are from a simple linear regression between net accretion–erosion rates and mean pH residuals (Figure 3a in Silbiger *et al.*, 2014). Panel (e) visualizes net accretion–erosion versus depth (data used to create Figure 8c in S17). The point with an X overlaid is the outlier removed in S17, and the open circles are the misrepresented data points; the closed circles are the original data, and the open circles are what was plotted in S17. The dashed line in panel (e) shows the parabolic trendline plotted in S17. Here, we show just the net accretion–erosion response; however, see Silbiger et al. 2016 for a similar analysis with accretion separated from erosion.

Likewise, S17 purport to show several "compromising" factors in their re-analysis of DeCarlo *et al.* (2015). We believe that all the differences they report between their re-analysis and the original publication arise due to their inconsistent selection of nitrate data across the reef sites. In the original study, *in situ* seawater chemistry measurements were reported for all sites (except for Wake Atoll where no *in situ* data were available, but data from this site did not impact the conclusions). The *in situ* data were critical because for many coral reefs, local water chemistry differs

substantially from open-ocean "climatological" values. At the Panama sites, local nitrate concentrations exhibit strong seasonality, from ~0.3 to ~14 µM in the non-upwelling and upwelling seasons, respectively (D'Croz and O'Dea, 2007). The World Ocean Atlas (WOA) climatology, which does not resolve this local upwelling in space or time, implies an average nitrate concentration of 1.2 µM for the surrounding 1° gridbox, not representative of the actual reef environment. S17 chose to use the *in situ* data for all of the sites in DeCarlo *et al.* (2015), except for Panama where they chose to use the WOA data. Because the two Panama reef locations had the highest bioerosion rates, selecting the unrepresentative WOA nitrate data had a large effect on the overall statistics. This led to S17's claims that (1) there is a parabolic effect of nitrate on bioerosion, including negative bioerosion over a certain nitrate range, and (2) after accounting for the effect of aragonite saturation state (Ω_{Arag}), there is no significant effect of nitrate on bioerosion. We acknowledge the uncertainty in defining the biologically relevant nitrate concentrations in Panama, and this is partly why the original paper treated nutrients categorically to distinguish between eutrophic (> 1 µM nitrate) and oligotrophic (≤ 1 µM) sites. Nevertheless, we repeated S17's analysis using the mean nitrate of non-upwelling and upwelling seasons for Panama, excluding Wake Atoll since *in situ* data were not available. Neither of S17's claims (1–2) listed above hold true. Rather, there is a significant correlation between nitrate concentration and bioerosion rate (Figure 2a); significant correlations between Ω_{Arag} and bioerosion rate for oligotrophic and eutrophic sites, respectively (Figure 2b); and a significant correlation between nitrate and the residuals of a Ω_{Arag}-bioerosion regression (Figure 2c), and no relationship between depth and nitrate (Figure 2d). These are essentially the same conclusions reached in the original paper, in which statistical tests were performed on the 103 individual cores rather than site averages.

Broader discussion on purported flaws in bioerosion literature

S17 argue that it can be difficult to disentangle many covarying parameters in field studies or along natural gradients. We agree with this sentiment, but not S17's assertion that this natural co-variability makes most field studies "flawed". In fact, field studies are essential for validating relationships and establishing the ecological relevance of mechanisms identified in controlled laboratory experiments. Specifically, it is difficult to predict how biological processes may shift in response to ocean acidification based on laboratory studies alone because mesocosms do not possess the full suite of natural variability. Climate change is happening in a natural environment, not in a controlled lab. Both types of experimental designs are complementary to each other, and both have limitations that need to be considered when interpreting results. For example, laboratory studies are critical for determining mechanisms and testing how individual or multiple parameters influence a biological response, but they cannot easily cope with mechanisms that involve interactions between several independent variables, long-term effects, and temporal variability. Further, controlled laboratory studies remove organisms from their natural environment and often assess changes in the mean rather than variance of a parameter (but see e.g. Putnam and Edmunds, 2011; Oliver and Palumbi, 2011), challenging our ability make predictions in the context of a naturally varying environment. As stated by S17, field studies often have many covarying

parameters that complicate our ability to parse out the direct effects of individual parameters on a biological response, although there are several statistical tools available to help disentangle collinearity among variables (Graham 2003). Thus, it is equally important to conduct experiments in both the lab and along natural gradients to test how bioerosion responds to changes in pH or other factors. The fact that studies have shown that rising ocean acidity increases bioerosion in both a controlled laboratory (e.g. Tribollet *et al.*, 2009; Wisshak *et al.*, 2012; Silbiger and Donahue, 2015; Enochs *et al.*, 2015) and naturally varying field experiments (e.g. Fabricius *et al.*, 2011; Crook *et al.*, 2013; Silbiger *et al.*, 2014; DeCarlo *et al.*, 2015; Barkley *et al.*, 2015; Enochs *et al.*, 2016a,b; Silbiger *et al.*, 2016) strengthens our collective conclusion that ocean acidification could be a serious problem for net reef growth.

One essential approach to disentangling the co-variations that naturally exist in most, if not all, field studies is to consider mechanisms. The adage "correlation does not imply causation" is especially apt in the field. Once a correlation is found, evaluating whether there is a plausible underlying mechanism can help, but by no means guarantee, to determine whether there is causation. Indeed, nutrients may be beneficial to filter-feeding and photosynthetic bioeroders, and decreasing pH potentially "softens" $CaCO_3$ substrate or lowers the energetic cost of driving dissolution (we refer the reader to the thorough discussions of these topics in S17). These mechanistic foundations not only guided the design of our studies, but also provided us a basis upon which to reach our conclusions that OA and nutrients drove increases in bioerosion. Yet as S17 demonstrate in their re-analyses of our data, it is certainly possible to find other statistically significant correlations by sub-setting the data, picking and choosing among data sources, and especially by using high-order polynomials (Figures 1 and 2). But do any of these correlations imply causation? To the best of our knowledge, there is no published explanation of why depth (a change in pressure) would drive bioerosion directly, and S17 did not provide one. Rather variables that correlate with depth such as pH, temperature, hydrodynamic energy, grazing intensity, substrate type/availability, and many others (e.g. Guadayol *et al.*, 2014; Weinstein *et al.*, 2014) are likely to be the direct drivers. Further, while nutrients do influence bioerosion, we can think of no mechanism to explain why the relationship would be parabolic (as implied in S17 Figure 8d), and again none is provided by S17. Although we cannot exclude S17's parabolas entirely, we do not think that fitting the data in such ways is justified, and we certainly do not think the existence of these parabolic correlations in subsets of our data warrants S17's claims that our original conclusions are "compromised."

Of course, there are limits to the conclusions that can be drawn from any single field study because the agents of bioerosion, and the substrates they erode, are diverse (see S17's review). Measuring all components of coral reef bioerosion simultaneously would be a momentous task, and no single study has yet achieved this feat or should attempt to. Indeed, our studies describe net erosion/accretion in blocks of dead *Porites* skeleton (Silbiger *et al.*, 2014), and macrobioerosion (> 1 mm diameter) of living *Porites* colonies (DeCarlo *et al.*, 2015), respectively. Like all field studies, trade-offs exist in our experimental designs. Experimental blocks track early successional bioeroder communities, and the rates of erosion depend on the length of deployment (Tribollet and Golubic, 2005). Investigating early successional communities is an aspect of the study, but it is certainly not a
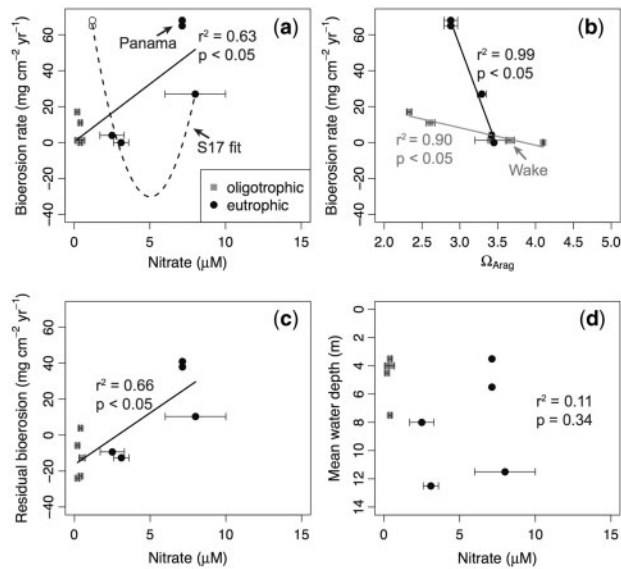
Figure 2. Data published in DeCarlo *et al.* (2015) with oligotrophic sites in grey and eutrophic sites in black. Horizontal error bars show uncertainty (1 standard error of sampling over multiple years) of water chemical properties. For Panama, the points represent the mean nitrate between non-upwelling and upwelling seasons (see D'Croz and O'Dea, 2007). The plotted bioerosion rates represent the mean macrobioerosion (>1 mm diameter borings) rate measured in multiple *Porites* skeletal cores at each site. Panel (a) is the bioerosion rate plotted with *in situ* nitrate concentration, as shown in Figure 8d of S17. However, S17 plotted the *in situ* nitrate data for all but two sites in Panama, for which they used the World Ocean Atlas data that does not capture local upwelling (open circles). S17's parabolic fit is shown as the dashed line. Considering the *in situ* data, bioerosion increases significantly with increasing nitrate, contrary to the claim made by S17. Panel (b) is bioerosion plotted with Ω_{Arag} (same as shown in DeCarlo *et al.*, 2015, Figure 3). Bioerosion significantly increases with decreasing Ω_{Arag} for both oligotrophic and eutrophic reefs. Panel (c) is the residual bioerosion rate after removing the Ω_{Arag} effect plotted again with nitrate concentration. Even after accounting for Ω_{Arag}, bioerosion significantly increases with increasing nitrate. Panel (d) shows there is no significant correlation between nitrate and mean depth of coral samples, contrary to S17's assertion.

flaw, in much the same way that looking at differential responses of juveniles and adults or individuals versus mixed community members is not a flaw. Rather, it is necessary to test responses of individual species and interactions between community members, and to do so at different successional stages, to gain a more complete understanding of anthropogenic impacts on accretion–erosion rates. Sampling live *Porites* colonies also addresses a specific question as it captures only part of the bioeroder community, represents a certain substrate, and presents challenges in terms of the replication possible, as logistical and permitting constraints often limit the number of corals that can be drilled. We acknowledge these aspects of our studies, but we believe the key is to look for patterns that emerge across multiple field and laboratory investigations. S17 describe how low-pH and eutrophication are consistently reported to drive increases in bioerosion, consistent with our original findings. In fact, our studies were among the first to investigate bioerosion changes across natural pH gradients, and together the results suggest that bioerosion is sensitive

to seawater pH on scales from within a reef (Silbiger *et al.*, 2014, 2016) to across an ocean (DeCarlo *et al.*, 2015). S17 go on to conclude that "nutrients are expected to aggravate OA-effects," a conclusion apparently drawn entirely based on DeCarlo *et al.* (2015), as this is the only study listed in S17's Table 3 and Supplementary data 4 under "Higher levels of nutrients and higher $p\text{CO}_2$." Strangely, S17's claim that the nutrient effect in DeCarlo *et al.* (2015) was "compromised," thus contradicts the overall conclusions of their paper.

We appreciate the very thorough review by S17 and, overall, agree with their conclusions about the response of bioeroders and bioerosion rates to shifting environmental conditions. However, we are very concerned with their misrepresentation and misinterpretation of our data (Silbiger *et al.*, 2014; DeCarlo *et al.*, 2015), as well as their assertion that most field studies are "flawed" or "compromised." We have clarified some major issues in S17's re-analyses of our data and discussed both the benefits and limitations of field studies in bioerosion research. We hope this will advance thinking on interpretation of field data in general. Understanding how bioerosion will change in response to climate change or other human-related stressors is increasingly being recognized as a topic of concern. This is evident by the fact that publications on this topic have increased substantially over the past decade (S17), and that federal agencies are beginning to include bioerosion rates as part of their monitoring protocols (https://www.pifsc.noaa.gov/cred/ocean_acidification.php). However, there is still important work to be done, as the predicted increases in bioerosion rates under OA threaten the calcium carbonate balance of coral reefs. Advancing our knowledge on this timely and complex problem requires a diversity of experimental approaches, ideas, and expertise.

Acknowledgements

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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Handling editor: Joanna Norkko