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Changing dynamics of Caribbean reef carbonate budgets: emergence of reef bioeroders as critical controls on present and future reef growth potential

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Coral cover has declined rapidly on Caribbean reefs since the early 1980s, reducing carbonate production and reef growth. Using a cross-regional dataset, we show that widespread reductions in bioerosion rates—a key carbonate cycling process—have accompanied carbonate production declines. Bioerosion by parrotfish, urchins, endolithic sponges and microendoliths collectively averages 2 G (where $G = kg\ CaCO_3\ m^{-2}\ yr^{-1}$) (range 0.96–3.67 G). This rate is at least 75% lower than that reported from Caribbean reefs prior to their shift towards their present degraded state. Despite chronic overfishing, parrotfish are the dominant bioeroders, but erosion rates are reduced from averages of approximately 4 to 1.6 G. Urchin erosion rates have declined further and are functionally irrelevant to bioerosion on most reefs. These changes demonstrate a fundamental shift in Caribbean reef carbonate budget dynamics. To-date, reduced bioerosion rates have partially offset carbonate production declines, limiting the extent to which more widespread transitions to negative budget states have occurred. However, given the poor prognosis for coral recovery in the Caribbean and reported shifts to coral community states dominated by slower calcifying taxa, a continued transition from production to bioerosion-controlled budget states, which will increasingly threaten reef growth, is predicted.

1. Introduction

Caribbean coral reef ecology has changed rapidly since the early 1980s. Live coral cover has declined on all reefs, populations of key reef-building coral taxa (especially the Acroporids) have been decimated [1], reef structural complexity has diminished [2], many reefs now have high macroalgal cover [3] and reef trophic structures have been fundamentally altered [4]. These changes have been driven by hurricanes and other environmental stressors, such as temperature-induced coral bleaching and coral disease outbreaks, locally by eutrophication and by the loss of key herbivorous taxa through disease and fishing pressure. In particular, populations of the herbivorous sea urchin *Diadema antillarum* were decimated by a disease outbreak in 1983 [5], and most Caribbean reefs have suffered from chronic and sustained overfishing for at least several decades [6]. While these major drivers of Caribbean reef decline are well documented, the impacts of ecological decline on rates of reef carbonate production, on reef carbonate cycling, and upon the ability of reefs to build and maintain their physical structures is far more poorly understood. However, given the fundamental importance of the physical structure of reefs to

the provisioning of many key ecosystem goods and services [2,7], this represents a major knowledge gap.

In this context, recent studies have provided evidence that average rates of contemporary reef carbonate production are well below historical and geological averages in the Caribbean [8,9]. About a quarter of studied reefs were shown to be in net negative carbonate budget states (range: -1.7 to -0.1 G, where $G = kg\ CaCO_3\ m^{-2}\ yr^{-1}$), and a further quarter to be defined by low net positive states, but below 1 G [9]. The major implication of this is that a significant number of Caribbean reefs are now entering a period of diminished reef growth potential [9]. However, it is also apparent from these data that while many Caribbean reefs sit at the threshold of becoming net budget negative, to-date more widespread shifts towards significantly net negative budget states have not yet occurred. This contrasts to several earlier studies from the Indo-Pacific that documented marked shifts into net negative budget states and reef structural erosion following coral die-offs [10–12]. In each case, these transitions were driven by higher (relative to carbonate production) bioerosion rates. In reef settings, bioerosion is a term that describes the biological erosion of both framework and sediments by a range of reef-associated taxa through both external grazing and endolithic 'boring' life modes [13]. These include grazing species of fish (mainly parrotfish of the genera *Scarus* and *Sparisoma* in the Caribbean) and urchins (of the genera *Diadema* and *Echinometra*), and species of sponges, bivalves, worms and microorganisms as key endolithic borers. Collectively, these organisms act to denude reef substrate and are thus critically important to determining net reef carbonate production rates [14].

In the Caribbean, there is convincing evidence that parrotfish and urchins made significant contributions to high bioerosion rates prior to the period of recent ecological decline [15,16], although there was also clear variability between habitats (and especially over depth gradients) in terms of the abundance and relative importance of different bioeroding taxa [16,17]. However, Caribbean reef ecology has fundamentally changed over the past 30–40 years, and populations of bioeroding urchins (especially *D. antillarum*) and parrotfish have also declined [18]. Furthermore, the widespread loss of branching *Acropora* spp., as well as an overall decline in coral cover, have markedly reduced the structural complexity of most Caribbean reefs [2], changing habitat and substrate availability. Such habitat changes have well-documented impacts on urchin [19,20] and parrotfish [21] populations. Impacts on endolithic bioeroders are far more poorly understood. However, given that different endolithic borers appear to use and exploit different substrate types in different ways–for example, as morphology or coral skeletal density change [22]–it is reasonable to assume that as structural complexity changes, so too may boring species' abundance and diversity. Given these changes, it is pertinent to ask: (i) what are the dominant bioeroding groups (and species) now present within different reef habitats in the Caribbean? And (ii) what is the cumulative influence of these bioeroders on contemporary reef carbonate production rates across the Caribbean? We explore these questions using data from 19 coral reefs located across four geographically distinct areas of the Caribbean. We use these data to undertake a unique cross-regional census-based assessment of key Caribbean reef bioeroding taxa and associated bioerosion rates. Our study encompasses data from a range of common, shallow water, Caribbean reef habitats. Specifically, we build on previously published data describing regional net reef carbonate budget states [9] and present a novel dataset that quantifies rates of erosion by the four dominant regional bioeroders. We consider the cumulative impacts on regional carbonate budgets, and consider how these have changed in comparison to rates reported prior to the major ecological changes that have occurred since the early 1980s.

2. Material and methods

(a) Study sites

Data on bioerosion rates were collected from a range of common Caribbean fore-reef habitats: nearshore hardground habitat (less than 5 m depth), relict *Acropora palmata* habitat (approx. 5 m depth), *Orbicella* (previously termed *Montastraea*) spur-and-groove habitat (approx. 10 m depth), fore-reef slope habitat (10–15 m depth) and deeper (18–20 m) shelf-edge *Orbicella* reef habitat (figure 1a). Data were collected from 19 reefs across four countries; Bahamas, Belize, Bonaire and Grand Cayman (electronic supplementary material, table S1). These countries occupy different regions of the Caribbean with respect to prevailing wave energy/hurricane frequency [23], and thus a degree of inherent variability is assumed in terms of background ecological condition and disturbance history. Although selected to provide wide geographical coverage, we recognize that the range of reefs and countries examined do not capture the full range of reef types and settings that exist across the region, nor indeed the full spectrum of disturbance histories that have affected Caribbean reefs. However, the general ecological condition of the study sites was remarkably consistent and is considered representative, based on comparisons to recent metadata analyses [2,3], of the spectrum of ecological and structural states presently observed on the region's shallow water reefs. At most sites, live coral cover was less than 25% (and was often much lower), and most shallow water sites (less than 10 m) were devoid of, or had very low cover of, living branched *Acropora* (historically a key Caribbean reef framebuilder). In addition, macroalgal cover was high (often exceeding 40%). Exceptions to the above descriptions occurred at a few sites in Bonaire, where live coral cover was higher (in places around 40%).

(b) Field data collection

We used the non-destructive census-based protocol described in the *ReefBudget* methodology [8] to measure biologically driven carbonate erosion rates, with rates described by the unit G, where $G = kg\ CaCO_3\ m^{-2}\ yr^{-1}$. Data were collected between November 2010 and March 2012. Gross and net carbonate production rates and associated census methodologies are described elsewhere [8,9]. Based on an understanding, derived from past studies, of the dominant bioeroders that occur in shallow (5–15 m depth) Caribbean fore-reef habitats, we focused specifically on determining rates of bioerosion by four main groups of bioeroders, these being: (i) bioeroding urchins of the genera *Diadema* and *Echinometra* [15,24]; (ii) parrotfish of the genera *Scarus* and *Sparisoma* [16]; (iii) endolithic sponges (mainly of the genus *Cliona*), which have been shown to dominate the endolithic macroboring community (typically more than 90% of the community) within the shallow fore-reef Caribbean habitats we consider here [25]; and (iv) micro-endolithic borers that are ubiquitous within all reef framework and sedimentary carbonate substrates in Caribbean fore-reef settings [26] and are reported to erode at rates relevant to carbonate budget assessments [27]. In this study, we did not include analysis of endolithic bivalve borers, nor of sipunculan and polychaete worms, primarily because they are not reported as key bioeroders within the habitats we examined (less than 5% of the community
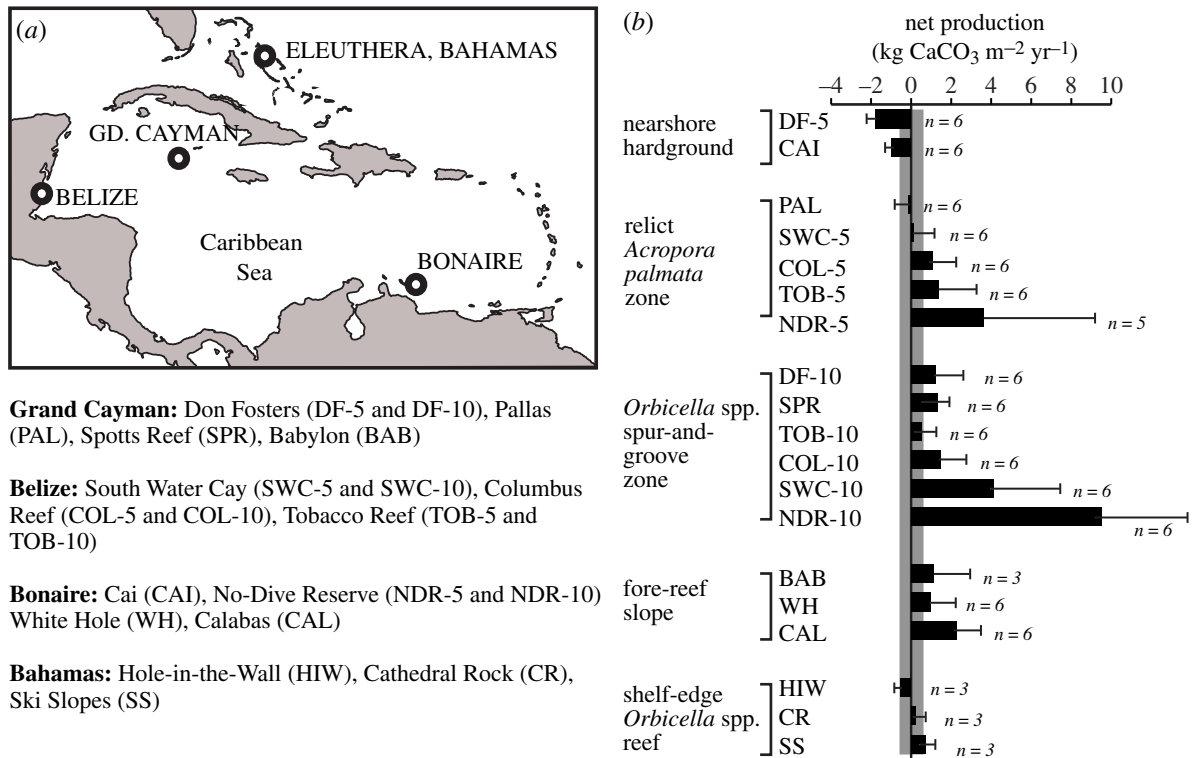
Grand Cayman: Don Fosters (DF-5 and DF-10), Pallas (PAL), Spotts Reef (SPR), Babylon (BAB)

Belize: South Water Cay (SWC-5 and SWC-10), Columbus Reef (COL-5 and COL-10), Tobacco Reef (TOB-5 and TOB-10)

Bonaire: Cai (CAI), No-Dive Reserve (NDR-5 and NDR-10) White Hole (WH), Calabas (CAL)

Bahamas: Hole-in-the-Wall (HIW), Cathedral Rock (CR), Ski Slopes (SS)

Figure 1. (a) Location of study sites across the Caribbean; (b) mean rates (± 1 s.d.) of net carbonate production, grouped by habitat type, across the 19 reef sites examined. The grey bar indicates the zone where net carbonate production is between $+0.5$ and -0.5 kg, and within which reefs should be broadly considered to be budget neutral.

[25]) but also because analysis of these taxa is not possible without destructive sampling. Generic rates are also hard to apply for these borers due to a lack of experimental data in the Caribbean, but based on Pacific experimental rate data (and assuming such taxa may comprise up to 10% of the macroboring community) their contributions to bioerosion are unlikely to exceed 0.2 G [27]. Other bioeroders such as limpets and chitons were also excluded as these are restricted to intertidal settings [28]. Thus, while our data do not capture the entire range of reef bioeroders, it does capture that by the key fore-reef bioeroders within the region.

To determine rates of erosion by parrotfish, we conducted 10 belt transect surveys (30 m by 4 m wide) in the vicinity of each transect (electronic supplementary material, table S2). All observations were made between 11.00 and 17.00 h (the period of maximum feeding activity) [16]. We recorded abundance, life phase and fork length in the following size classes: 5–14 cm, 15–24 cm, 25–34 cm and 35–44 cm (no fish more than 45 cm were recorded in our surveys) for each of the following species of *Scarus*: *Scarus iserti*, *Scarus taeniopterus* and *Scarus vetula*, and of *Sparisoma* spp.: *Sparisoma aurofrenatum*, *Sparisoma chrysopterum*, *Sparisoma rubripinne* and *Sparisoma viride*. Bioerosion rates for each species/size class were calculated using a model based on fork length as a predictor of bite rate (bites/hour) derived from two species (*Sparisoma viride* and *Scarus vetula*) at different life phase stages [29–31]. We made the assumption that relationships between fork length and bite rate, and fork length and bite size, can be extrapolated within genera [32]. Estimates of overall parrotfish erosion rates at each site were based on these calculations. The main echinoid bioeroders in the Caribbean belong to the genera *Diadema* (*Diadema antillarum*) and *Echinometra* (*Echinometra viridis* and *E. lucunter*), and erosion rates have been shown to vary as a function of species and test size [10,15]. To determine urchin erosion rates, we thus counted the number and size class of urchins (to species) within an area 1 m either side of each transect (total 20 m^2), with the number of individuals in the following test size classes recorded: 0–20 mm, 21–40 mm, 41–60 mm, 61–80 mm, etc. (electronic supplementary material, table S3). Erosion rates were determined using published data on test size and erosion

rate relationships: for *D. antillarum* using the relationship between urchin bioerosion rate y (g/urchin/day) and test size, where $y = 0.0029x^{1.6624}$ [33], and for *Echinometra* spp., where $y = 0.0007x^{1.7309}$ [24].

For reasons outlined above, estimates of endolithic bioerosion were made for two bioeroding groups, the endolithic sponges and the microboring endoliths. To estimate rates of endolithic sponge bioerosion, we used an adapted version of the non-destructive census methodology of Ward-Paige *et al.* [34] to determine the % surface area covered by the following species of endolithic sponges: *Cliona aprica*, *Cliona caribbaea*, *Cliona delitrix*, *Cliona tenuis*, *Cliona varians* and *Siphonodictyon coralliphagum*. Using a transparent grid, we measured the surface area (cm^2) colonized by the above species within an area 0.5 m either side of each transect (total 100 000 cm^2). Sponge area was measured based on the occurrence of visible papillae, or the area covered by surficial tissue, depending on species. To estimate erosion rates by sponges, we then used published datasets to derive a relationship between sponge tissue cover and bioerosion rate, as reported by Perry *et al.* [8]. This was based on published data on the relationship between % surface area of sponge tissue or papillae cover and the % volume of substrate removed [35], and between % volume of substrate removed and bioerosion rate (kg $CaCO_3\,m^{-2}\,yr^{-1}$) [27,33,36]. These data were then used to derive a relationship between % surface area of sponge papillae (in relation to volume of substrate removed) and bioerosion rate, whereby bioerosion rate = % surface area of sponge tissue/papillae × 0.0231 (electronic supplementary material, table S4). At present, it is not possible to differentiate erosion rates by different bioeroding sponges and so until species-specific rate data are available our calculations assume that rates do not differ between species.

Carbonate substrate degradation by endolithic microorganisms is more problematic to measure directly using non-destructive census approaches but, as outlined above, because published microendolithic erosion rates are often within the ranges calculated for macroborers [27], it is a process that carbonate budget assessments should not ignore. As a result, we take the approach of applying known rates of microendolithic bioerosion to all available dead reef
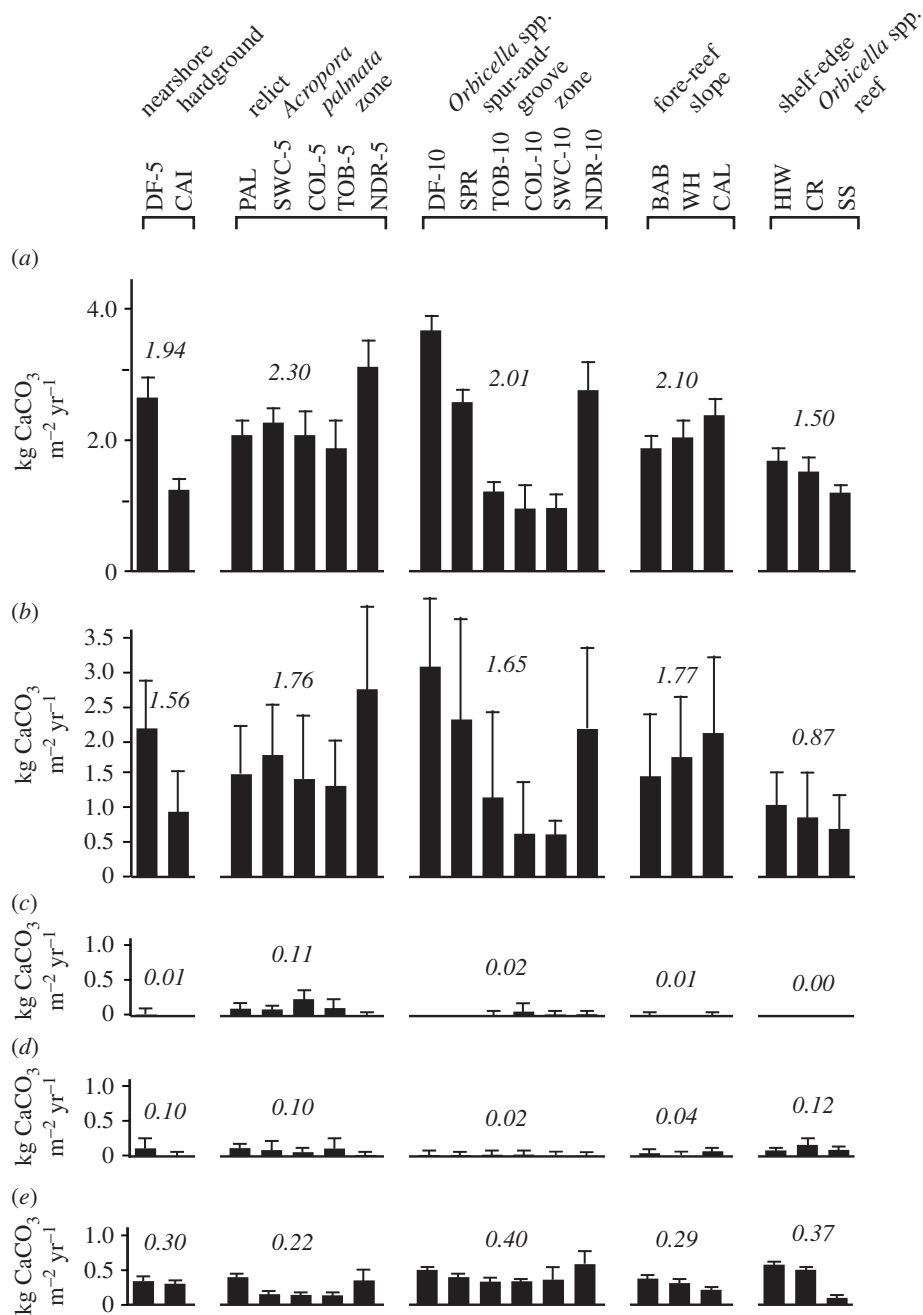
Figure 2. Average reef bioerosion rates (kg CaCO$_3$ m^{-2} yr^{-1}) grouped by habitat for sites across the Caribbean. (a) Total bioerosion rate, (b) parrotfish bioerosion, (c) urchin bioerosion, (d) endolithic sponge bioerosion and (e) microendolith bioerosion. Figures are habitat averages. Error bars are 1 s.d.. See figure 1 for site codes.

framework within each study transect. To the best of our knowledge, only one previous experimental study has reported microendolithic erosion rates in the Caribbean across a range of depth intervals [26]. Erosion rates declined significantly with depth, but rates of 0.27 G are reported for sites between 0 and 10 m depth. Here we use this rate, which is also within the range of rates reported from Indo-Pacific sites [27], and apply this to all areas of dead, exposed reef substrate within each reef zone. Means, medians and standard errors were calculated across the samples. To test for differences in gross and taxa-specific erosion rates between habitats, ANOVA tests were run using SPSS and, where appropriate, a Tukey post-hoc test. Data were tested for normality and equality of variances.

3. Results

Bioerosion rates across the range of reefs and habitats examined average 2.0 G, ranging from 2.3 G in relict *A. palmata* habitat, to

1.5 G in shelf-edge *Orbicella* habitat (figure 2a), but differences between habitats are not significant ($F = 0.522$, $p = 0.721$). However, it is clear that different bioeroding taxa make markedly different contributions to overall bioerosion rates. Highest rates overall are attributed to parrotfish, with erosion averaging 1.6 G across all habitats, but are highest in sites shallower than 10 m depth (range: 1.5–1.7 G; figure 2b), although these differences are also not significant between habitats ($F = 0.854$, $p = 0.511$). Highest rates at the individual reef scale occur within the marine reserves in Bonaire and Grand Cayman, reaching 3.1 G (figure 2b) and are lowest within shelf-edge *Orbicella* habitat (figure 2b). Urchin erosion rates are very low across all habitats, averaging less than 0.1 G (range 0–0.1 G; figure 2c) and reflect both the very low abundances and small test sizes of *Diadema* spp. and *Echinometra* spp. at most sites. No urchins were observed on the deeper shelf-edge *Orbicella* reefs. Sponge bioerosion rate estimates are also low,
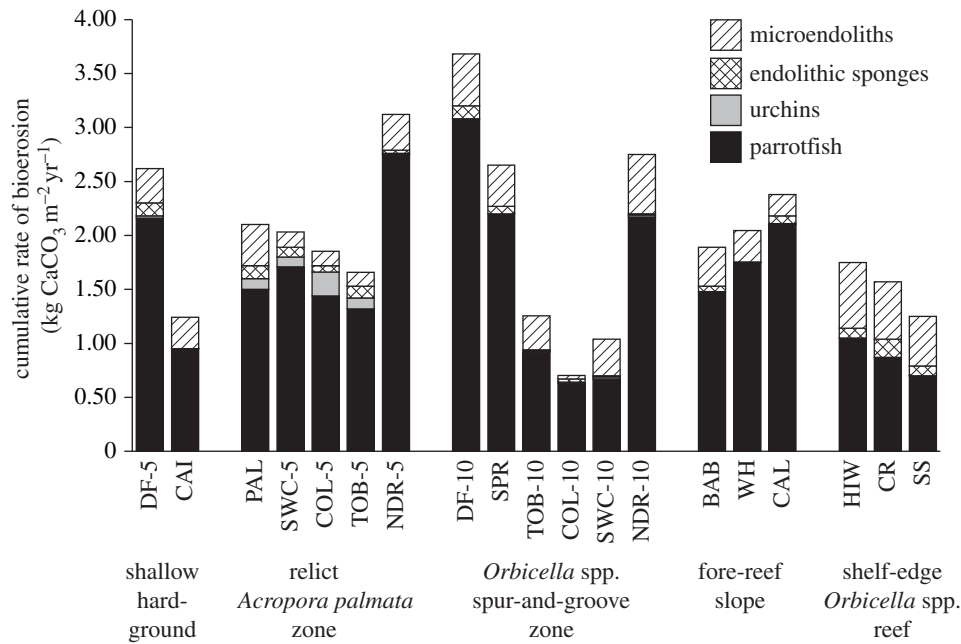
Figure 3. Cumulative rates of bioerosion for each group of bioeroder. Data are grouped by habitat for sites across the Caribbean. See figure 1 for sites names and codes.

averaging 0.1 G (range 0.1–0.02 G; figure 2*d*) and reflect the low percentage cover of bioeroding sponges measured at most sites. Rates of microendolithic erosion average 0.3 G across all habitats (range 0.2–0.4 G; figure 2*e*).

Gross erosion rate data at the taxa level thus indicate that parrotfish are the dominant bioeroders on contemporary Caribbean reefs and are responsible for an average 76% of bioerosion across all sites (figure 3). Across the shallower sites (less than 10 m depth) the range is 78.8–84.4%. Parrotfish bioerosion rates are only significantly lower ($F = 7.644$, $p = 0.002$) in the shelf-edge *Orbicella* reef habitat (57.4%), where overall erosion rates are also reduced (figures 2*a* and 3). This trend is consistent with general patterns of declining parrotfish bioerosion with increasing depth, as reported even from low fishing pressure reefs [16], but we emphasize that the overall magnitude of erosion is also reduced. We also note that there is no clear partitioning across the shallow water habitats in terms of the key taxa driving bioerosion, nor in terms of their relative contributions to bioerosion. The relative contribution of urchins to overall bioerosion, which was previously a key shallow water bioeroder [15], is now limited across all habitats (figure 3). Indeed, as a function of their low abundances and small test sizes, urchins are at present functionally irrelevant to reef bioerosion at our study sites. We also observe that sponges and microendolithic taxa only make a meaningful relative contribution (7.7% and 35%, respectively) to bioerosion within the deeper shelf-edge *Orbicella* habitat. However, we emphasize that actual erosion rates are also lower in these deeper habitats, averaging 1.5 G (figure 2*a*). While some uncertainty remains about the relationship between sponge tissue cover and erosion rates [8], we note that the measured % of substrate infested by sponges is low across all sites (maximum site average is 5.2% cover). This is, however, in line with estimates from high nutrient enriched sites in the Florida Keys [34], suggesting our methods do not underestimate endolithic sponge cover. Competition with fleshy macroalgae may be one reason for the relatively low cover of sponges observed [37]. We also note that microendolithic bioerosion, in the absence of more extensive erosion by fish and urchins, is

probably now making a more significant contribution to bioerosion than is often appreciated [27]. Our data suggest that microborers are removing (eroding) an estimated 0.2–0.4 kg (as habitat averages) of carbonate, which is equivalent to between 10 and 20% of total estimated bioerosion, depending on habitat. This rate may seem high, but we note that both the rates and the proportions of microendolithic bioerosion we report are very comparable to those calculated from experimental substrates deployed in various reef settings on the Great Barrier Reef [27], suggesting that such high relative contributions are realistic.

4. Discussion

These data provide a novel insight into contemporary rates and patterns of bioerosion across multiple reef sites and habitats in the Caribbean. In contrast to several localities in the Indo-Pacific where loss of coral cover has been accompanied by a rapid increase (or relative increase) in bioerosion rates, leading to negative carbonate budgets and reef framework erosion, this state is not currently widely observed in the Caribbean. Indeed, despite low gross carbonate production rates on Caribbean reefs (average 3.5 G) [9], about two-thirds of the 19 reefs examined retain low net positive carbonate budgets (rates below 2 G), as reported in [9], with about a quarter having thus far shifted to net erosional states. In other words, most reefs are not adding much net carbonate to their structures, and while surficial complexity has been denuded by coral skeletal breakdown, widespread erosion of the underlying reef framework has not to-date ensued. Census data reported here suggest that this is in part a function of a reduction in rates of bioerosion, and point to some fundamental changes in the recent dynamics of Caribbean reef carbonate production and erosion.

Our estimates of bioerosion are based on rates associated with the major bioeroding taxa that operate in shallow fore-reef habitats in the Caribbean. These data clearly show that parrotfish are now the major reef bioeroders in the region.
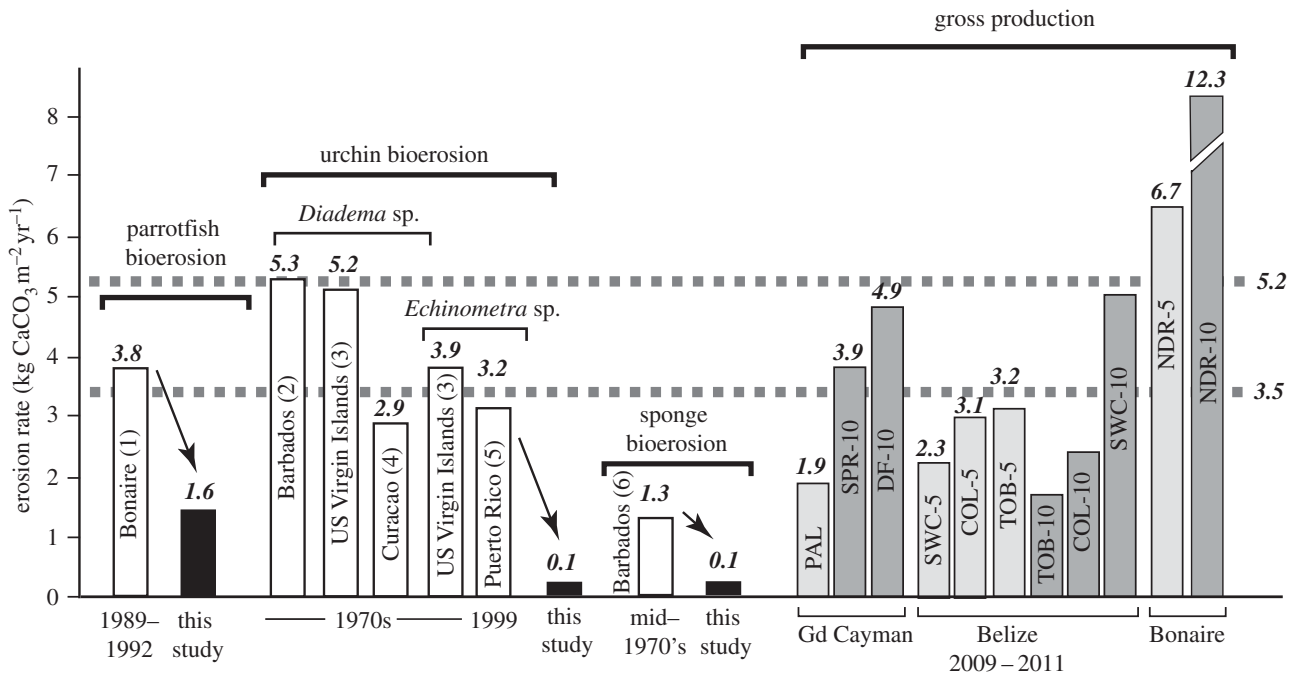
Figure 4. Comparison of past (white bars) and present (black bars) rates of bioerosion in shallow water (less than 10 m depth) Caribbean reef habitats against measured contemporary rates of gross carbonate production (light grey bars are relict *Acropora palmata* habitat, dark grey bars are *Orbicella* spur-and-groove habitat). Dotted horizontal lines show regional average net carbonate production rates for relict *Acropora palmata* habitat (lower line) and *Orbicella* spur-and-groove habitat (upper line) (data from Perry *et al.* [9]). Historical erosion rate data are from (1) Bruggemann *et al.* [16], (2) Scoffin *et al.* [33], (3) Ogden [39], (4) Bak *et al.* [40], (5) Griffin *et al.* [24] and (6) Scoffin *et al.* [33]. See figure 1 for site codes.

This is most significant given the general declines in fish (including parrotfish) biomass that have occurred across the Caribbean [4,6]. By contrast, urchins now make a negligible contribution at our sites, although we note that increases in numbers of *Diadema* have been reported from select localities in the Caribbean [38]. Comprehensive comparative bioerosion datasets (that include data from all bioeroding taxa) from the period pre-dating the recent collapse of Caribbean reefs (i.e. prior to the late 1970s) do not exist, but there are a number of erosion rate studies that can be considered typical of relatively 'healthier' (or less impacted) Caribbean reefs, and that thus provide a benchmark against which current rates can be compared. These clearly indicate that the relative importance of bioerosion processes has changed. Historically, parrotfish and *Diadema* were probably both important bioeroders [6]. However, studies conducted on Caribbean reef bioerosion in the 1970s and early 1980s show that the urchin *D. antillarum* had become the dominant bioeroder on the region's shallow water reefs, as parrotfish bioerosion was suppressed by fishing pressure. *Diadema* bioerosion rates for this period are reported to have been in the range 3–5 G [24] and responsible for approximately 80–90% of total reef bioerosion [15]. However, since the regional *Diadema* die-off in 1983, that balance has clearly changed again, and while parrotfish populations remain low on many reefs, their relative role as substrate bioeroders has increased significantly and they are now responsible for an average of approximately 75% of total bioerosion. Quantitative data on past rates of bioerosion by sponges are sparse, but data from shallow reefs in Barbados [33] report rates of 1.3 G.

A key observation that can be made based on the above historical rate estimates, which can be conservatively estimated at approximately 8 G (see data in figure 4), is that such rates exceed measures of contemporary reef carbonate production (data reported in [9]) at nearly all shallow water Caribbean reef sites in our study (figure 4). Thus, if these historical erosion rates were applied to most contemporary Caribbean reefs, the net effect would be a rapid transition to net negative carbonate budget states and consequent widespread reef erosion. This has not yet, at most sites, been the outcome. Although carbonate production rates by corals have declined in most Caribbean fore-reef habitats, largely because of the loss of branched *Acropora* species, there has also been a reduction in rates of total bioerosion. We do not suggest that this decline has necessarily been linear, but rather that the balance between production and erosion, and the impact on current net budget states, has been temporally variable. Indeed, it is reasonable to assume that bioerosion rates may initially have been much higher immediately following past coral mortality events and where the structural complexity of the reefs remained intact, e.g. following coral disease outbreaks, and that rates then declined over time as habitat complexity was slowly lost. However, it is unlikely that any simple linear relationships exist between changes in live coral cover, the associated structural complexity provided by coral skeletons and overall reef carbonate budget states as a function of changing production and erosion regimes. The dynamics of bioerosion de-couple this relationship and may do so in temporally variable ways as both intrinsic (e.g. reef structural changes) and extrinsic (e.g. fishing pressure, nutrification, etc.) factors change the abundance and composition of bioeroder communities and the habitats on which they depend.

A critical issue for the future maintenance of reef framework structures is how might rates of bioerosion, and the balance between production and erosion, change in the near-future. Uncertainty in feedbacks between reef structural change and habitat complexity change, which would especially impact upon fish and urchin grazing taxa [19–21], and uncertain species responses to environmental change, make such
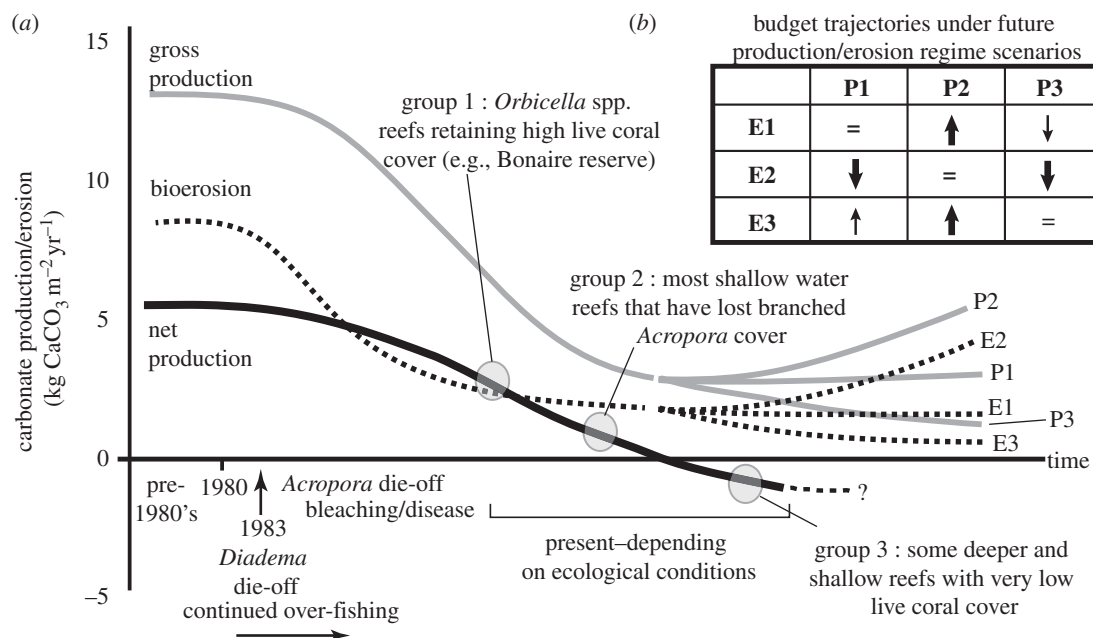
Figure 5. (a) Conceptual diagram showing temporal historical trends in rates of reef carbonate production and erosion, and resultant net production rates (kg CaCO$_3$ m^{-2} yr^{-1}) based on published data for the Caribbean, and a range of future production (P) and erosion (E) rate scenarios. The range of net production states in which contemporary Caribbean reefs exist are shown as groups 1–3 based on the data of Perry et al. [9]. Note that these groups are indicative of present states and do not suggest a linked temporal continuum. (b) Inset, different future budget trajectories depending upon the interactions between different future production and erosion scenarios.

predictions difficult. However, recent budget modelling approaches, integrating a range of climate change projections, indicate that bioerosion is likely to become especially important to future carbonate budget dynamics [41]. In addition, there is emerging experimental evidence to suggest that future changes in ocean chemistry may increase endolithic bioerosion rates [42–44], and good evidence that endolithic bioerosion rates increase under higher nutrient loading regimes [34,35,45], such as can occur under increased agricultural run-off, or associated with tourist development [46].

Future trajectories for grazer-driven bioerosion are more uncertain. Management interventions may increase parrotfish numbers, both increasing bioerosion, but also having wider benefits for coral recruitment [47], although the integrity of reef structural complexity and others drivers of environmental stress, will be an influence on this. For example, a recent model of carbonate budget dynamics under physical and ecological stress [41] found that chronic nutrification could reduce carbonate budgets even in the presence of healthy parrotfish populations. Nutrification can benefit the growth of microendoliths [48] and filter-feeding macrobioeroders, such as molluscs and sponges [35], while also reducing coral calcification and extension rates [49,50]. Thus, while maintaining healthy fish stocks, for example, in marine protected areas (MPAs), tends to have a net positive effect on carbonate budgets by increasing the turnover and recovery of corals [41,47], activities outside MPAs may still have a profound (and in some cases over-riding) impact on carbonate budgets. While much has been written about the importance of managing entire watersheds [51], a further consideration is thus their impact on reef carbonate budgets.

A range of future budget trajectories can thus be envisaged that have differing budgetary outcomes depending on future trajectories of both production and erosion (figure 5). Scenarios P1 and E1 envisage rates of production and erosion essentially continuing as at present, the net effect being limited change in net carbonate production. Persistence of shallow reef habitats dominated by Porites and Agaricia spp. [52] would be a scenario in which steady-state carbonate production rates might occur. Scenario P2 envisages a slow steady recovery of live coral cover and thus of carbonate production rates, such as might accompany the repopulation of shallow sites by branched Acropora spp. or other coral taxa. Depending on the associated trajectories for reef bioeroder populations, net production rates may either increase or remain static. Scenario E2 would see bioerosion rates increasing as parrotfish or Diadema populations increase as habitat structure slowly returns, or as changing marine environmental conditions elevate rates of endolithic bioerosion [42–44], while scenario E3 envisages a continued slow steady decline of erosion rates, perhaps through a lack of Diadema recovery, as a result of sustained fishing pressure, or as a function of slow, on-going habitat structural loss. Scenario P3 envisages a further decline in carbonate production rates, as further environmental pressures (bleaching, disease, ocean acidification) further denude coral assemblages. Under P3 scenarios further net reductions in carbonate production are most likely, shifting reefs into net negative budget states, unless further declines in bioeroder populations occur as habitat and structure are further denuded.

Ultimately, coral reef growth is the net result of the interactions between a range of constructive (carbonate-producing) and destructive (bioerosion and physical/chemical erosion) processes, and it is the balance between these processes that will determine future reef growth performance and trajectories. Across the Caribbean, reef carbonate budget states are presently in a period of major transition. Production rates have been radically diminished due to widespread coral cover loss and have been especially impacted by the loss of high carbonate-producing branched Acropora species [9]. Carbonate production rates in shallow fore-reef habitats have thus declined from rates in the range 10–17 G [53], to an average of approximately 3.5 G [9]. However, rates of bioerosion have also been

diminished from (conservative) estimates of approximately 7–8 G, to an average of approximately 2 G. Thus while net carbonate production rates have undergone a significant decline, associated declines in rates of bioerosion have, to-date at least, partially offset this, such that many reefs exist in low net (but slightly positive) production states. However, given the low net rates of production now evident on most reefs, and the poor prognosis for coral recovery in the region, it is the future trajectories of bioerosion that will be especially critical to determining whether reefs persist in states of very low net production (accretionary 'stasis'; [14]) or, as seems likely, may start to progressively shift towards more net negative (erosional) budget states. The latter will have significant implications for a very wide range of ecosystem goods and services that are inherently dependent upon the maintenance and continued growth of reef framework structures.

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