

Estimating rates of biologically driven coral reef framework production and erosion: a new census-based carbonate budget methodology and applications to the reefs of Bonaire

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Received: 6 December 2011 / Accepted: 22 March 2012
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Abstract Census-based approaches can provide important measures of the ecological processes controlling reef carbonate production states. Here, we describe a rapid, non-destructive approach to carbonate budget assessments, termed *ReefBudget* that is census-based and which focuses on quantifying the relative contributions made by different biological carbonate producer/eroder groups to net reef framework carbonate production. The methodology is presently designed only for Caribbean sites, but has potential to be adapted for use in other regions. Rates are calculated using data on organism cover and abundance, combined with annual extension or production rate measures. Set against this are estimates of the rates at which bioeroding species of fish, urchins and internal substrate borers erode reef framework. Resultant data provide a

measure of net rates of biologically driven carbonate production ($\text{kg CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$). These data have potential to be integrated into ecological assessments of reef state, to aid monitoring of temporal (same-site) changes in rates of biological carbonate production and to provide insights into the key ecological drivers of reef growth or erosion as a function of environmental change. Individual aspects of the budget methodology can also be used alongside other census approaches if deemed appropriate for specific study aims. Furthermore, the methodology spreadsheets are user-changeable, allowing local or new process/rate data to be integrated into calculations. Application of the methodology is considered at sites around Bonaire. Highest net rates of carbonate production, $+9.52$ to $+2.30 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$, were calculated at leeward sites, whilst lower rates, $+0.98$ to $-0.98 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$, were calculated at windward sites. Data are within the ranges calculated in previous budget studies and provide confidence in the production estimates the methodology generates.

Communicated by Geology Editor Prof. Bernhard Riegler

Electronic supplementary material The online version of this article (doi:[10.1007/s00338-012-0901-4](https://doi.org/10.1007/s00338-012-0901-4)) contains supplementary material, which is available to authorized users.

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Keywords *ReefBudget* · Carbonate production · Bioerosion · Ecological change · Environmental monitoring

Introduction

Coral reefs are undergoing major transitions that threaten their natural functioning and resilience (Nyström et al. 2000). These changes may modify reef ecology and geomorphology in various ways, but especially through (1) altered benthic community composition and species interactions (McManus and Polsenberg 2004); (2) changed abundance of key reef-associated species, especially fish and urchins (Mumby 2006); and (3) reduced topographic complexity (Alvarez-Filip et al. 2009). A critical question is what implications do these changes have for the maintenance of coral reef structures? Specifically, how does ecological change impact upon the geomorphic role of a coral reef as a focal point for carbonate production and thus for reef framework accumulation? This issue has direct relevance for understanding the nature and rates of change that can occur with respect to the structural complexity of a reef (and its long-term persistence as a 3-dimensional topographic structure) but also, conversely, for those reef-associated species most strongly influenced by habitat complexity.

The production and accumulation of reef framework carbonate is controlled by the relative rates of, and the interactions between, a range of ecologically, physically and chemically driven production and erosion processes (Perry et al. 2008; Montaggioni and Braithwaite 2009). Corals are typically the primary (and dominant) constructional (i.e. framework producing) components on a reef, adding significant carbonate per unit area (Vecsei 2004), with additional carbonate being deposited by calcareous encrusters (especially crustose coralline algae, CCA; Payri 1997). Post-depositionally, carbonate is also added through physicochemical and biologically mediated lithification. Offsetting carbonate production are processes that erode reef framework either through dissolution or through conversion to sediment. Bioerosion (biological substrate erosion) is facilitated by a wide range of reef-associated faunas, including by specific fish and echinoid taxa (Peyrot-Clausade et al. 2000), and endolithic macro- and microboring organisms (Vogel et al. 2000; Perry and Hepburn 2008). Episodic physical disturbances also influence reef development, largely through the generation of coral rubble, the deposition of which can be an important reef-building process. Carbonate dissolution, resulting from organic matter oxidation (Tribble et al. 1990), can also occur post-depositionally, although the volumes of cements

observed in Holocene reefs suggest that over prolonged periods, precipitation may dominate over dissolution (Vecsei 2004).

The relative roles of these production and erosion processes strongly influences reef-building potential, a concept encapsulated within the carbonate budget approach to conceptualising and quantifying reef development: in its entirety a reef carbonate budget reflects the sum of gross carbonate production from corals and calcareous encrusters, and sediment produced within or imported into the reef, less that lost through biological or physical erosion, dissolution or sediment export (Chave et al. 1972). These are clearly disparate and complex parameters to quantify, but three different methods have most commonly been employed: hydrochemical measures, census-based measures and sediment accumulation rate based measures. Each provide different estimates of, and insights into, the processes and rates of carbonate production, differ in the spatial and temporal scales over which they can be applied and yield different types of data (Electronic Supplementary Material, ESM Table 1). Thus, their merits depend upon the research questions being asked.

Here, we describe a new ‘rapid’ census-based methodology (*ReefBudget*) that quantifies rates of biologically driven carbonate production and erosion, and which has been adopted because: (1) it allows examination of the relative importance of different biological carbonate producers and eroders in different environments; and (2) because these can be examined in the context of reef ecological change. Whilst several studies have previously utilised census-based approaches to quantify reef carbonate production (Bak 1976; Hubbard et al. 1990; Eakin 1996; Harney and Fletcher 2003; for a review of rates, see Montaggioni and Braithwaite 2009), and resultant data used to estimate regional (Vecsei 2001) and global scale reef carbonate production rates (Kleypas 1997; Vecsei 2004), the lack of standardised approaches has hampered between site comparisons and limited the number of broader integrated budget studies thus far undertaken. The method we describe can be applied both to individual reef zones (reef flat, reef slope, etc.) or at whole reef scales and can allow same-site temporal changes in ecologically driven carbonate production rates to be determined where episodic or more permanent changes occur in the abundance of individual carbonate producers and eroders (Eakin 2001). Such dynamics are fundamental for understanding phases of reef construction and degradation and should, as various studies have suggested, form a logical aspect of reef ‘health’ assessments (Rose and Risk 1985; Edinger et al. 2000; Risk et al. 2001). It is also possible that individual aspects of the methodology can be utilised alongside other census-based approaches where these are deemed appropriate. For example, managers may wish to include

coral production estimates alongside standard survey monitoring protocols. Here, we describe the rational and methodologies underpinning *ReefBudget* and consider its merits through its application at sites around Bonaire. Results are compared with previous carbonate budget data from other sites in the Caribbean and globally.

‘*ReefBudget*’: rationale and field methodologies

The *ReefBudget* methodology follows the *framework production states* approach discussed by Perry et al. (2008) and focuses on quantifying the relative contributions made by different carbonate producer/eroder groups to net biologically driven carbonate production ($\text{kg CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$): production and erosion rates are calculated using data on organism cover and abundance, combined with published extension or production rate, or erosion rate data. Although important to the development of reefs as geological structures, sediment production and post-depositional lithification are not directly quantified. At present, the protocol and on-line data entry spreadsheets

(<http://www.exeter.ac.uk/geography/reefbudget>) are Caribbean focused, but potential exists to extrapolate the approach to Indo-Pacific sites. Within each survey site (habitat, environment or depth zone) census data, with the exception of parrotfish data (discussed in the following sections), are collected along the same transect lines: the methodology recommending six fixed 10 m transects. These are established either along depth contours parallel to the reef front (spaced 10 m apart) or along discrete (depth consistent) reef structures (e.g. spurs) as deemed most appropriate. We marked transects with 0.5 m long, PVC sand pegs (labelled with numbered acrylic tags), allowing data to be collected over sequential days where necessary. Permanent transects can also be established in this way for temporal monitoring. Within each site, the following were also collected for site characterisation: (1) data on the ratio of reef framework to sediment along the depth contour in question; and (2) gross scale measures of reef topographic complexity. Methods used in the budget are described in the following sections, and the production and erosion equations shown in Tables 1 and 2.

Table 1 Equations used in the calculation of carbonate production rates in the *ReefBudget* methodology

Variables (units)	Equation
Coral production ($\text{kg m}^{-2} \text{ year}^{-1}$)	$\sum_i (R \times ((X_i/100) \times ((D_i \times G_i \times 10,000)/1,000)))$
Calcareous encruster production ($\text{kg m}^{-2} \text{ year}^{-1}$)	$\sum_i (R \times ((X_i/100) \times ((C_i \times 10,000)/1,000)))$
Where: R = Rugosity of transect	
X_i = Mean % cover of i th species	
D_i = Density (g cm^{-3}) of the i th species	
G_i = Growth rate (cm year^{-1}) of the i th species	
C_i = A mean calcification rate ($0.018 \text{ g cm}^{-2} \text{ year}^{-1}$) for secondary carbonate producers calculated from published Caribbean data	

Example for coral carbonate production rates based on data from site NDR-5, transect 3

M. annularis: $\sum_i (1.86 \times ((22.06/100) \times ((1.31 \times 1.175 \times 10,000)/1,000))) = 6.3 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$
M. mirabilis: $\sum_i (1.86 \times ((3.27/100) \times ((1.28 \times 1.64 \times 10,000)/1,000))) = 1.28 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$
M. cavernosa: $\sum_i (1.86 \times ((2.58/100) \times ((0.703 \times 1.483 \times 10,000)/1,000))) = 0.51 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$
A. agaricites: $\sum_i (1.86 \times ((0.59/100) \times ((0.258 \times 1.825 \times 10,000)/1,000))) = 0.05 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$
D. strigosa: $\sum_i (1.86 \times ((0.27/100) \times ((0.53 \times 1.2 \times 10,000)/1,000))) = 0.03 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$
Millepora spp.: $\sum_i (1.86 \times ((0.21/100) \times ((1.238 \times 2.27 \times 10,000)/1,000))) = 0.11 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$
Crustose CA: $\sum_i (1.86 \times ((5.48/100) \times ((0.018 \times 10,000)/1,000))) = 0.02 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$
Gross carbonate production for Site NDR-5, transect 3 = $8.3 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$

Data input notes: Density (D_i) and growth rate (G_i) data based on the following for each species:

M. annularis— D_i and G_i based on Caribbean average data for species
M. mirabilis— D_i and G_i based on pooled data for Caribbean massive/sub-massive taxa
M. cavernosa— D_i based on Caribbean average data for species, G_i based on pooled Caribbean data for family
A. agaricites— D_i and G_i based on Caribbean average data for species
D. strigosa— D_i based on Caribbean average data for species, G_i based on pooled Caribbean data for family
Millepora spp.— D_i and G_i based on pooled Caribbean data for genera

Table 2 Equations used in the calculation of erosion rates in the *ReefBudget* methodology

Variables (units)	Equation		
Parrotfish bioerosion (kg CaCO ₃ m ⁻² year ⁻¹)	$\Sigma sp \left((((B_r \times (\% B_{ls}) \times M_e) \times nsp) \times 365)/1,000 \right)$ where: Σsp = The sum of erosion rate for each size class and life phase within each species B_r = Bite rate (per day)—based on data in Mumby et al. (2006) B_{ls} = Bites leaving scars—based on data in Bruggemann et al. (2006) M_e = Mass (g) eroded per bite—based on data in Bruggemann et al. (2006) nsp = Abundance of parrotfish in a particular size class and life phase of a species		
Example of parrotfish bioerosion rate calculations for Site NDR-5 (for exemplar purposes only data for terminal phase <i>Sparisoma viride</i> shown)			
<i>S. viride</i> —abundance (no m ⁻²) by size class: 15–24 cm = 0.0007; 25–34 cm = 0.0017; 35–44 cm = 0.006			
Fork Length (cm)	15–24 cm	25–34 cm	35–44 cm
<i>Sparisoma viride</i>	$((((5565 \times 0.58 \times 0.0182) \times 0.0007) \times 365)/1000)$	$((((4256 \times 0.74 \times 0.0614) \times 0.0017) \times 365)/1000)$	$((((2946 \times 0.8 \times 0.1456) \times 0.006) \times 365)/1000)$
Bioerosion (kg CaCO ₃ m ⁻² year ⁻¹)	0.015	0.120	0.752
Thus, the total erosion due to terminal phase <i>Sparisoma viride</i> , for Site NDR-5, is 0.89 kg CaCO ₃ m ⁻² year ⁻¹			
Urchin bioerosion (kg m ⁻² year ⁻¹)	<i>Diadema antillarum</i> —Bioerosion = $\Sigma_s (0.0029x^{1.6624} \times n_s \times 365)/1000$ <i>Echinometra</i> spp.—Bioerosion = $\Sigma_s (0.0007x^{1.7309} \times n_s \times 365)/1000$ Other urchin <i>s</i> —Bioerosion = $\Sigma_s (8 \times 10^{-5}x^{2.4537} \times n_s \times 365)/1000$ Where: Σ_s = The sum of bioerosion rates for all size classes x = Median test size for an urchin within a size class n_s = Abundance of urchins within a size class (no m ⁻²)		
Example of bioerosion rate calculations for <i>D. antillarum</i> for Site NDR-5, transect 6			
Abundance by size class: 0–20 mm = 0; 21–40 mm = 3; 41–60 mm = 0; 61–80 mm = 0; 81–100 mm = 0			
Thus $\Sigma_s (0.0029x^{1.6624} \times n_s \times 365)/1000 = (0.0029 \times 30^{1.6624} \times 0.15 \times 365)/1000 = 0.04$ kg m ⁻² year ⁻¹			
Clionid sponge bioerosion (kg m ⁻² year ⁻¹)	0.0231 <i>x</i> Where: <i>x</i> = % cover of sponge tissue on the available substrate within the transect		
Example of sponge bioerosion rate calculation for Site NDR-5, transect 4			
Transect rugosity 1.82; available substrate = 77.5%; Available area for potential bioerosion = 14.11 m ²			
Sponge cover = 649 cm ² ; cover of sponges = 0.46 %			
Thus, sponge bioerosion rate = 0.0231 × 0.46 = 0.01 kg m ⁻² year ⁻¹			
Microbioerosion (kg m ⁻² year ⁻¹)	Shallow fore-reef sites (0–5 m) = <i>R</i> × % available substrate × 0.27/100 Deeper fore-reef (5–10 m) = <i>R</i> × % available substrate × 0.27 Where: <i>R</i> = rugosity of the transect		
Example of microbioerosion rate calculation for Site NDR-5, transect 4			
Rugosity = 1.82; Available substrate = 77.5 %			
Thus microbioerosion rate = (1.82 × 77.5) × 0.27 = 0.38			

Benthic cover and carbonate production by corals and coralline algae

Most reefs are naturally 3-dimensional (rugose), and thus, accurate census-based surveys must account for a reef's topographic complexity to determine the actual surface area covered by calcifying biota. To quantify carbonate production by corals and calcareous encrusters, *ReefBudget* integrates benthic cover and surface rugosity data collection, using a modified version of the standard line intercept methodology. Along each transect, a 10-m 'guide' tape is pulled taut between the fixed marker stakes. The distance covered by benthic species, for each linear 1 m of transect, is then recorded along the surface of the reef, immediately beneath the 10 m transect line. This should integrate data from all crevices and overhangs, and a short (1 m) flexible tape is most suitable for this. The distance covered by the following benthic groups is recorded: coral (to species or morphological group level); CCA and other calcareous encrusters (we also investigated areas of macroalgal cover to determine where living CCA occurred under the algal canopy); turf algae; macroalgae; non-encrusting calcareous algae (*Halimeda* sp., etc.); sediment; and rubble. Survey codes for groups/species are given on the survey sheets downloadable from the *ReefBudget* website. Substrate rugosity (as a function of total reef surface relative to linear distance) and % benthic cover are automatically calculated in the data sheets. Although this methodology is more time-consuming than standard survey methods (especially in highly rugose habitats), it provides more accurate data on the actual surface area covered by each benthic component (Goatley and Bellwood 2011) and ensures that benthic cover on cryptic surfaces is integrated into budget measures.

To calculate rates of coral carbonate production, the methodology integrates mean per cent cover of each coral species with species-specific (or nearest equivalent species) measures of skeletal density (g cm^{-3}) and linear growth (cm year^{-1}). The collection of new data on coral linear extension rates and density is clearly problematic since it requires significant destructive coral sampling. *ReefBudget* thus uses published data from sites (and water depths) as proximal and comparable with those under study (see *ReefBudget* website for Caribbean coral growth and density data). This allows, where possible, same species (or at least same coral morphological group) data to be used from comparable water depths. These data are combined with rugosity measures to yield a value for coral carbonate production ($\text{kg CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$) relative to actual transect surface area, using the equations in Table 1.

The data entry sheets that accompany the methodology auto-calculate production rates and are preset with average

regional rates of linear extension and skeletal density for each coral species (or nearest morphologically and ecologically similar species). Users can select spreadsheets using data stratified into the following depth groups: 0–5 m and 5–10 m. However, data can be manually modified where site (or depth)-specific rates are available, or as new data become available. In our applications, we used extension and density data in the following order of preference: (1) same species, same depth, same-site; (2) same species, same depth, regional average; (3) same genus, same depth, regional average; (4) same family, same depth, regional average; and (5) similar morphological group, same depth, regional average. Far fewer data are available on CCA growth and density rates (see Payri 1997), making quantitative estimates using these parameters less reliable. We thus base estimates of CCA production on published (and recently collected) rates of calcification per unit area of substrate (data derived from experimental settlement tiles).

Determining rates of reef framework bioerosion

Bioerosion is the corrosion of hard substrates by living agents and a wide variety of organisms contribute, including specific species of fish and urchins, and various endolithic organisms, the most important being certain species of sponges, bivalves, worms and endolithic microborers. *ReefBudget* uses a census-based approach to quantify erosion by urchins, parrotfish and endolithic sponges and integrates published erosion rates for endolithic microborers to estimate biological substrate erosion.

Bioerosion: urchins

The main echinoid bioeroders belong to the genera *Diadema*, *Echinometra*, *Echinostrephus* and *Eucidaris* and, in general, urchin erosion rates vary with species and size (Bak 1990, 1994). *ReefBudget* thus censuses the number and size class of urchins (to species) by examining the substrate 1 m either side of each transect (total 20 sq m), with the number of individuals in the following test size classes recorded: 0–20, 21–40, 41–60, 61–80 and 81–100 mm etc. To determine erosion rates by different species, we utilised published data on test size and erosion rate relationships: published data suggesting a relatively tightly correlated plot regardless of species (Fig. 1a). For the Caribbean, data exist for the two dominant species, *Diadema antillarum* and *Echinometra viridis*, indicating that bioerosion rates for *D. antillarum* are ~3 times those of *E. viridis* of similar test size (Fig. 1b). We thus used separate equations to calculate bioerosion rates ($\text{kg m}^{-2} \text{ year}^{-1}$) for *D. antillarum*, *Echinometra* and all 'other' urchins (Table 2).

Bioerosion: fish

The feeding techniques of several families of fish cause CaCO_3 ingestion, however, only a few species actively erode reef substratum whilst feeding, of which parrotfish are the most important. *ReefBudget* uses a methodology based on quantifying parrotfish erosion as a measure of fish bioerosion. In these estimates, consideration is given to species and body size as controls on erosion rate (Scoffin et al. 1980; Bellwood 1995; Bruggemann et al. 1996), and to life phase as a control on feeding rate (Bruggemann et al. 1994a, b; Mumby et al. 2006). To assess parrotfish abundance, we conducted 10 belt transect surveys (30 m by 4 m wide) in the vicinity of the study transects. All observations were made between 1100 and 1700 hours (period of maximum feeding activity). Species, life phase and fork length (in the following size classes 5–14, 15–24, 25–34, 35–44 and >45 cm) of each parrotfish were recorded. To calculate bioerosion rates, we employed a model based on fork length as a predictor of bite rate (bites/hour) derived from two parrotfish species (*Sparisoma viride* and *Scarus vetula*) at different life-phase stages (Bruggemann et al. 1994a, b, c). We made the assumption that relationships between fork length and bite rate and bite size can be extrapolated within genera (Mumby et al. 2006). For each species, life phase and size class, a bioerosion rate per parrotfish per day (g) can then be established (see Table 2). Details of the calculations, which incorporate factors relating to daylight hours, feeding rates, bite size, life phase and species, are provided in the online methodology. In Bonaire, we used the bite rate data of Bruggemann et al. (1994b, c), but at other sites additional bite verification data collection is recommended (see online methodology for approaches).

Bioerosion: macroborers (sponges, bivalves and worms)

Macroborers produce boreholes with diameters >1 mm and include endolithic sponges, bivalves, and polychaete and sipunculid worms. Of these, sponges have received the greatest attention because, on a reef-wide basis (and especially within the Caribbean), they typically dominate—comprising up to 90 % of the macroboring community in terms of substrate infestation (Goreau and Hartman 1963; Perry 1998). To avoid destructive coral sampling to assess endolithic bioerosion (e.g. Kiene 1988), *ReefBudget* adopts the non-destructive methodology of Ward-Paige et al. (2005) as a census-based approach to quantifying endolithic sponge abundance. Estimates of worm and bivalve bioerosion, which are typically less significant in Caribbean fore-reef environments, are excluded. Whilst we acknowledge that this results in a conservative estimate of endolithic macroboring, thus far suitable census and supporting rate data for these two groups (for the Caribbean region) do not appear to exist. We determined area coverage by individual colonies of bioeroding sponges (cm^2), using a transparent 5×5 cm grid, within an area encompassing 0.5 m either side of each transect (total 100,000 cm^2). From this, % surface area covered by sponge tissue can be determined. To estimate sponge bioerosion rates from census data, we utilised published datasets to derive a relationship between sponge tissue cover and bioerosion rate, as discussed theoretically by Rose and Risk (1985) and Schönberg (2001), and similar to a recently employed method to quantify sponge bioerosion in the Adriatic (Calcinai et al. 2011). Specifically, we employed published data to establish: (1) the relationship between % surface area of sponge tissue/papillae cover and the % volume of substrate removed by

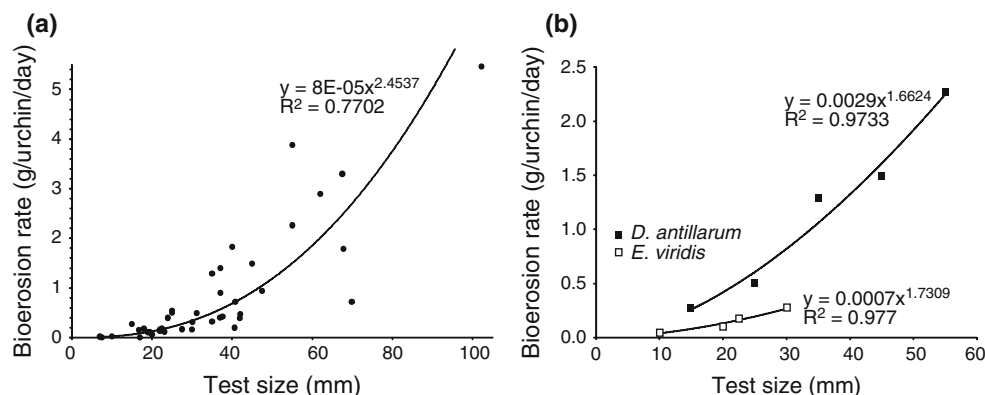


Fig. 1 a Bioerosion rates ($\text{g urchin}^{-1} \text{ day}^{-1}$) relative to test size based on Caribbean and Indo-Pacific data. Data from: Scoffin et al. (1980), Brown-Saracino et al. (2007), Carreiro-Silva and McClanahan (2001), Griffin et al. (2003), Conand et al. (1997), Bak (1990), Russo (1980), Downing and El-Zahr (1987), McClanahan and Muthiga

(1988), Mokady et al. (1996), Mills et al. (2000), Appana and Vuki (2006), Herrera-Escalante et al. (2005). **b** Bioerosion rates ($\text{g urchin}^{-1} \text{ day}^{-1}$) for two Caribbean species relative to test size, *Diadema antillarum* (Scoffin et al. 1980) and *Echinometra viridis* (Griffin et al. 2003)

endolithic sponges (Rose and Risk 1985; Fig. 2a); and (2) the relationship between % volume of substrate removed by macroborers and bioerosion rate in $\text{kg CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$ (Scoffin et al. 1980; Chazottes et al. 1995; Tribollet and Golubic 2005; Fig. 2b). Using these data, it is then possible to derive a relationship between % surface area of sponge papillae (as a function of volume removed) and bioerosion rate, whereby bioerosion rate = % surface area of sponge tissue/papillae $\times 0.0231$ (Fig. 3; Table 2).

Bioerosion: microborers

Carbonate substrate degradation by endolithic microorganisms is associated with a range of photosynthetic cyanobacteria, chlorophytes and rhodophytes and heterotrophic fungi and bacteria. Microbioerosion assessments have relied heavily on experimental substrates, but few have used them to determine rates. Although data on this process are not extensive, it is questionable whether carbonate budgets can ignore the process, since published rates are often within the ranges calculated for macroborers (Tribollet and Golubic 2005). In our calculations, we used the Caribbean rate data of Vogel et al. (2000) for sites between 0 and 10 m depth at a rate of $0.27 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$. These rates were applied to all areas of reef substrate within each reef zone (excluding areas of sand cover) (Table 2).

Confidence ratings for different census-based budget estimates

Because of the necessary use of published data on parameters such as calcification rate and bioerosion rate, different budget assessments using the *ReefBudget* methodology will inevitably vary in the level of confidence that can be given to different budget components. This rating will vary with experience of the surveyor, and the availability of local datasets to underpin budget estimates. We thus recommend that a confidence rating be assigned to both the methodological component of each study and the

data entry component employed in calculating individual production/erosion rates at each study site (Table 3).

Field application of the methodology: a case study from Bonaire

Study area

To examine application of the *ReefBudget* methodology, we quantified biological reef framework production and erosion rates at 5 sites (2 windward, 3 leeward) around Bonaire, southern Caribbean (Fig. 4), in November 2010. Reef development is restricted on the exposed windward side of Bonaire, both spatially and in terms of actual framework accumulation. In contrast, well-developed fringing reefs occur along much of the leeward coast, with the submarine terrace extending offshore between ~ 20 – 250 m and with a pronounced drop-off at ~ 5 – 15 m . Study sites were selected that exhibited marked inter-site differences in benthic cover and topographic complexity (gross substrate rugosity) and documented differences in

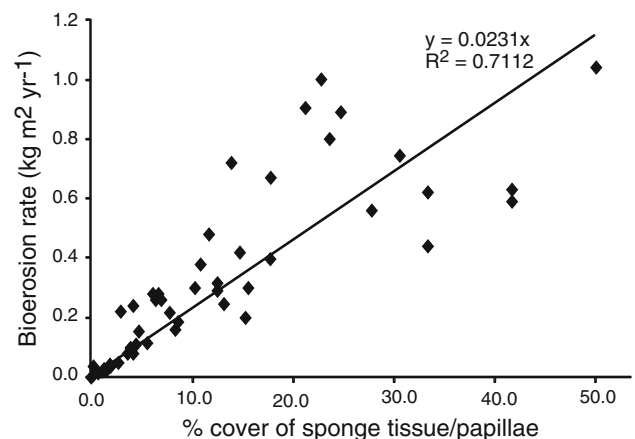


Fig. 3 Plot showing relationship between % sponge tissue/papillae cover and bioerosion rate (data in Scoffin et al. 1980; Chazottes et al. 1995; Tribollet and Golubic 2005)

Fig. 2 **a** Data from Rose and Risk (1985) showing the relationship between % surface area of sponge tissue/papillae and the % volume of coral colony removed by sponge boring. **b** Relationship between the % colony volume removed by borers and the rate of bioerosion (data from Scoffin et al. 1980; Chazottes et al. 1995; Tribollet and Golubic 2005)

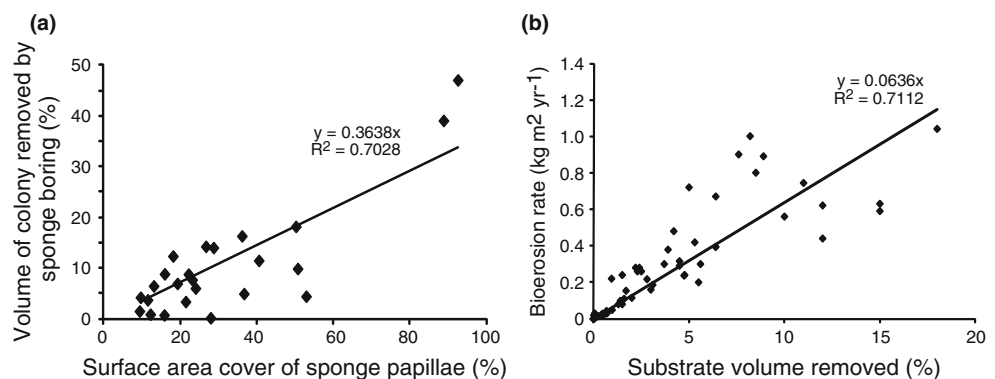


Table 3 Recommended confidence rating scheme for assessing reliability of both the survey methods (high, medium or low) and supporting input data (high, medium or low) for each component of the budget calculations

	Methodology rating—High ^a	Methodology rating—Medium ^b	Methodology rating—Low ^c
Input data rating—High ^d	H/H High confidence in survey method and high confidence in supporting datasets	M/H Reasonable confidence in survey method but high confidence in supporting datasets	L/H Low confidence in survey method but high confidence in supporting datasets
Input data rating—Medium ^e	H/M High confidence in survey method and reasonable confidence in supporting datasets	M/M Reasonable confidence in survey method and reasonable confidence in supporting datasets	L/M Low confidence in survey method but reasonable confidence in supporting datasets
Input data rating—Low ^f	H/L High confidence in survey method but low confidence in supporting datasets	M/L Reasonable confidence in survey method but low confidence in supporting datasets	L/L Low confidence in survey method and low confidence in supporting datasets

^a High (methodological)—considered to provide an accurate reflection of the abundance of the budgetary component under consideration. This may be the appropriate rating for the following: (1) census studies of benthic coral cover (especially in low topographic complexity systems); or (2) for census studies of readily visible benthic substrate eroders, for example, urchins

^b Medium (methodological)—considered to provide a reasonably good estimate of the abundance of the budgetary component under consideration. This may be an appropriate rating for the following: (1) surveys of non-benthic (mobile) faunas (e.g. fish); (2) for census estimates of often cryptic benthic components, for example, CCA or sponge borers; or (3) coral census estimates where there is a high proportion of branched coral cover

^c Low (methodological)—considered to provide an approximate estimate of the abundance of the budgetary component under consideration. This would be the appropriate rating for estimates of microbioerosion because the census methods do not employ in-site assessments of species abundance

^d High (data)—supporting data considered to be accurate and reliable for the reef under study. This may be the appropriate rating where (1) a high proportion of the supporting data on coral production (especially for the main coral species present) is derived from the country or area under study; or (2) where the use of relatively well constrained size/rate data is employed, for example, for the relationship between urchin size and erosion rate

^e Medium (data)—supporting data considered to provide a reasonably good underpinning for the reef under study. This may be the appropriate rating where (1) use is made of the regional average datasets for determining production rates by corals; (2) where some assumptions are required regarding size/rate data relationships, for example, for the relationships between size and erosion rate in different parrotfish species

^f Low (data)—supporting data considered to provide an approximate underpinning for the reef under study. This may be the appropriate rating where (1) limited data exists generally for the dominant coral species within the survey area and/or there is a reliance on data from other regions or only from similar morphological groups; (2) where there is at present a general paucity of production/erosion rate data, for example, for CCA or sponge boring; or (3) a reliance on rate data employed independently of in-site surveys e.g., for microbioerosion

NB. It would be expected that these ratings may change over time as new datasets become available

the extent of Holocene reef development (Focke 1978). On the leeward (western) side, two sites were established in the ‘no dive reserve’ at 5 m (NDR-5) and 10 m (NDR-10) depths, and at dive site ‘Calabas’ at 10 m depth (CAL-10) (Fig. 4; see ESM Fig 1.). On the windward side, survey sites were established at two sites along the south-east coast: Cai at 5 m depth (CAI-5) and White Hole at 10 m depth (WH-10). Details of site characteristics (hard substrate cover, rugosity, coral species abundance and diversity) are given in Table 4.

Rates of biological framework production and erosion around Bonaire

Based on census data, net rates of reef framework carbonate production by biological calcifiers and eroders, at the study sites around Bonaire, ranged from +9.52 to

−0.98 kg CaCO₃ m^{−2} year^{−1} (Fig. 5). Highest rates were calculated at sites on the leeward side of the island (range +9.52 to +2.30 kg CaCO₃ m^{−2} year^{−1}; Fig. 5), lowest rates at sites on the exposed (windward) south-east side (range +0.98 to −0.98 kg CaCO₃ m^{−2} year^{−1} (the latter being the only site where the budget was negative, i.e. net erosional). The relative importance of different budget contributing processes (both production and erosion related) varied between sites, but at all sites corals were the dominant carbonate producers, and parrotfish the most important substrate eroders (Fig. 6).

Highest measures of gross carbonate production by corals occurred in the two ‘no dive reserve’ sites (NDR-5 +6.73 kg CaCO₃ m^{−2} year^{−1}, NDR-10 +12.07 kg CaCO₃ m^{−2} year^{−1}), where live coral cover (LCC) is relatively high (24.1 and 28.2 %, respectively) and the substrates were relatively rugose (1.64 and 3.01 respectively)

(Table 4). *Montastraea annularis* and *Madracis mirabilis* were the most important coral carbonate producer at both depths (contributing up to 53.9 and 31.7 %, respectively to total coral carbonate production. *Diploria strigosa* and *Montastraea cavernosa* (at the 5 m site) were also quantitatively important (Table 4). Lowest rates of coral carbonate production ($+0.2 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$) were calculated at site CAI-5, where LCC was $<3 \%$ and substrate rugosity low (1.17): the only significant coral carbonate producer being *D. strigosa* (Table 4). At most sites, measures of the relative contribution of calcareous encrusters to carbonate production are low ($<2.5 \%$), the exception being at CAI-5 where CCA accounted for $\sim 32 \%$ of estimated gross production. Most of this is associated with the calcareous algae *Ramirusta* sp. (Peyssonneliaceae, Rhodophyta) (Eckrich et al. 2011) which overgrows dead substrate in this area.

Parrotfish make the largest relative contribution ($>65 \%$) to substrate erosion at all sites, although erosion estimates vary between sites. Highest estimates were at leeward sites (range: -2.10 to $-2.75 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$), the lowest actual measure ($-0.95 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$) being at CAI-5. At the three leeward sites, *Sparisoma viride* and *Scarus vetula* (Table 4) were the main bioeroders, with *S. viride* alone contributing to between 53.9 and 69.1 % of total parrotfish erosion. At the windward sites, *S. viride* was the dominant bioeroder at Site WH-10 and *S. rubripinne* at Site CAI-5 (Table 4). Most other bioeroders make a limited contribution to total substrate erosion. Urchins were essentially absent from a budgetary perspective, with only a few specimens of small *D. antillarum* and *E. lucunter* encountered at NDR-5 and NDR-10, and *D. antillarum* and *E. viridis* at Site CAL-10 (Table 4). No bioeroding urchins were encountered at the windward sites. Endolithic sponges

play a limited role in substrate erosion, and calculated bioerosion rates are low at all sites ($<0.1 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$). This, however, reflects the sparse coverage of bioeroding sponges recorded in surveys. A limitation with these estimates is the difficulty of quantifying tissue cover on the most cryptic surfaces at sites with complex relief (e.g. site NDR-10). Thus, our estimates at this site may underestimate the true level of sponge boring. At the three leeward sites, the dominant sponge borers were *Cliona delitrix*, *C. aprica* and *C. caribbaea*. At the windward sites, only *C. delitrix* was observed in abundance. Rates of microbioerosion range from 0.2 to $0.6 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$ (Table 4).

Key drivers of biological carbonate production and erosion around Bonaire

The relative importance of different biological carbonate producers and eroders to net biologically derived carbonate production varies between sites around Bonaire and can provide important information on the key processes driving carbonate budget states at individual sites and at individual points in time. At our sites, coral carbonate production and parrotfish erosion are the primary drivers of the budget estimates and provide independently reliable indicators of both gross biological carbonate production and gross substrate erosion (Fig. 7a, b), although it is apparent that marked differences in net production can occur between sites with similar LCC, this occurring as a function of individual coral species abundance and substrate rugosity. This suggests that for these reefs even small ecological shifts may drive major changes in net biologically driven carbonate production. For example, whilst total live coral cover is clearly important, at most sites *M. annularis* is responsible for a significant proportion of calculated production. Even partial loss of this species would significantly impact the budget. Similarly, much of the biological erosion occurs through the activities of one parrotfish species, *S. viride*. Removal of this key species may both immediately change gross substrate erosion rates, but also subsequently change coral cover as ecological dynamics on a reef change (e.g. Mumby 2006). Other reef framework measures (specifically rugosity; Fig. 7c) and of reef community structure (specifically coral diversity; Fig. 7d) are less reliable indicators of reef carbonate production.

Discussion: considerations of accuracy and data limitations

Census-based estimates indicate clear inter-site differences in gross and net rates of biological carbonate production and erosion around Bonaire. These reflect variations in coral cover, topographic complexity (rugosity) and in the

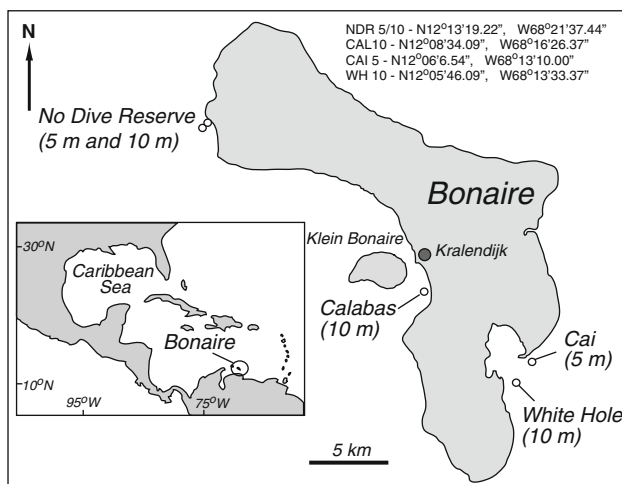


Fig. 4 Location of the five study sites (water depths in parentheses) around Bonaire

Table 4 Summary of site characteristics and of individual biologically derived carbonate production and erosion rates (± 1 sd) calculated for the five sites in Bonaire ($n = 6 \times 10$ m transects per site); NDR—no dive reserve (west coast), CAL—Calabas (west

coast), CAI—Cai (east coast), WH—White Hole (east coast). A confidence rating for each budget component based on the approach described in Table 3 are in parentheses

	Site/depth (m)				
	NDR-5	NDR-10	CAL-10	CAI-5	WH-10
Substrate rugosity	1.6 \pm 0.3	3.0 \pm 0.7	1.7 \pm 0.2	1.2 \pm 0.1	1.4 \pm 0.2
% sand versus hard substrate along depth contour	57.4	4.2	49.5	3.9	1.2
Live coral cover	24.1 \pm 14.6	28.2 \pm 11.9	25.0 \pm 4.5	2.9 \pm 1.8	16.6 \pm 4.1
Number of coral species and coral species diversity (H')	11 species $H' = 1.43$	18 species $H' = 1.93$	14 species $H' = 2.00$	4 species $H' = 0.63$	15 species $H' = 1.83$
Coral production ($\text{kg m}^{-2} \text{ year}^{-1}$)	6.73 \pm 6.53 (H/M)	12.07 \pm 4.89 (H/M)	4.65 \pm 0.99 (H/M)	0.20 \pm 0.13 (H/M)	2.97 \pm 1.61 (H/M)
Dominant coral species and % contribution to total carbonate production	<i>M. annularis</i> 53.9 <i>M. mirabilis</i> 25.7 <i>D. strigosa</i> 3.4 <i>M. cavernosa</i> 13.4	<i>M. annularis</i> 38.8 <i>M. mirabilis</i> 31.7	<i>M. annularis</i> 35.0 <i>M. cavernosa</i> 18.1 <i>M. faveolata</i> 17.8	<i>D. strigosa</i> 72.2	<i>S. siderea</i> 15.4 <i>D. strigosa</i> 11.4
CCA production ($\text{kg/m}^2/\text{yr}$)	0.02 \pm 0.01 (M/L)	0.20 \pm 0.14 (M/L)	0.03 \pm 0.05 (M/L)	0.06 \pm 0.03 (M/L)	0.06 \pm 0.01 (M/L)
Urchin erosion ($\text{kg m}^{-2} \text{ year}^{-1}$)	0.01 \pm 0.01 (H/H)	0.02 \pm 0.02 (H/H)	0.01 \pm 0.02 (H/H)	0.0 \pm 0.0 (H/H)	0.0 \pm 0.0 (H/H)
Parrotfish erosion ($\text{kg m}^{-2} \text{ year}^{-1}$)	2.75 \pm 1.39 (M/M)	2.17 \pm 1.56 (M/M)	2.10 \pm 1.06 (M/M)	0.95 \pm 0.62 (M/M)	1.75 \pm 0.81 (M/M)
Dominant parrotfish species and % contribution to total parrotfish erosion	<i>S. viride</i> 69.1 <i>S. vetula</i> 12.0 <i>S. aurotrenatum</i> 9.1	<i>S. viride</i> 53.9 <i>S. vetula</i> 10.6 <i>S. taeniopterus</i> 5.1 <i>S. aurofrenatum</i> 4.6	<i>S. viride</i> 63.3 <i>S. vetula</i> 20.9 <i>S. aurotrenatum</i> 11.9	<i>S. rubripinne</i> 49.5 <i>S. viride</i> 20.0 <i>S. chrysopterus</i> 11.6	<i>S. viride</i> 45.1 <i>S. aurofrenatum</i> 21.1 <i>S. chrysopterus</i> 15.4
Sponge erosion ($\text{kg m}^{-2} \text{ year}^{-1}$)	0.03 \pm 0.03 (M/L)	0.01 \pm 0.002 (M/L)	0.07 \pm 0.02 (M/L)	0.002 \pm 0.004 (M/L)	0.005 \pm 0.004 (M/L)
Dominant sponge species	<i>C. delitrix</i> <i>C. aprica</i> <i>C. caribbaea</i>	<i>C. delitrix</i> <i>C. aprica</i> <i>C. caribbaea</i>	<i>C. delitrix</i> <i>C. aprica</i> <i>C. caribbaea</i> <i>C. lampa</i>	<i>C. delitrix</i>	<i>C. delitrix</i>
Microborer erosion ($\text{kg m}^{-2} \text{ year}^{-1}$)	0.33 \pm 0.05 (L/L)	0.55 \pm 0.20 (L/L)	0.20 \pm 0.06 (L/L)	0.29 \pm 0.01 (L/L)	0.29 \pm 0.06 (L/L)
Net biological carbonate production ($\text{kg m}^{-2} \text{ year}^{-1}$)	+3.63	+9.52	+2.30	−0.98	+0.98

abundance of visually obvious key substrate bioeroders (parrotfish, urchins) between sites. For example, highest estimates of gross and net biological carbonate production are from sites inside the no dive reserve where LCC is relatively high (~ 30 % of total reef surface area), there is clear evidence of net reef framework accumulation and rugosity values (~ 3) at the 10 m depth site are equivalent to those characteristic of the most structurally well-developed Caribbean reefs (Alvarez-Filip et al. 2009). In contrast, at site CAI-5, which returns a negative budget

estimate, LCC is low (<3 %), with small, isolated coral heads colonising a relatively planar erosional limestone surface. Measures of rugosity are low (~ 1.1) and comparable with the lowest relief Caribbean reefs. Relative differences in contemporary biological carbonate production, generated by the *ReefBudget* methodology, thus seem intuitively reasonable at the site level, and are reflected in the current observed state of the reefs at each site.

However, census-based budget estimates are only as good as the individual data collection methods, and

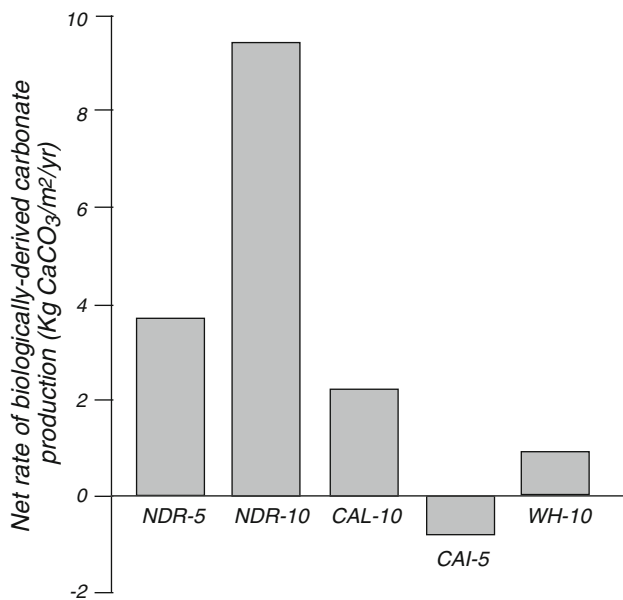


Fig. 5 Net rates of biologically driven carbonate production ($\text{kg m}^{-2} \text{ year}^{-1}$) estimated at sites around Bonaire

the input data that inform subsequent calculations. In terms of field census methods, *ReefBudget* is based on well-established methodologies that have been previously utilised to determine abundance and size frequency data for a range of species. Furthermore, the assumptions that underpin most production and erosion estimates (in terms of the parameters needed to calculate coral and CCA production, and urchin and fish erosion) are well established. Thus, these aspects of the methodology can be considered robust. Relevant rate data are more variably available. There is, for example, a relative wealth of coral growth/calcification data from the Caribbean to inform budget estimates. To account for variations with depth/site the coral production data entry spreadsheets are stratified by depth (0–5, and 5–10 m), and the data entry system is user-changeable such that the default regionally averaged, depth-specific production rate data can be modified to include locally available or acquired (in situ measured) rates. Similarly, rate data to inform parrotfish erosion estimates have been widely tested in previous studies and can be verified locally using established methods to determine bite rates, etc. Other aspects of the data input are less well constrained: in particular estimates of CCA production and endolithic bioerosion are necessarily based on a relatively few rate/process datasets and, as outlined in the following sections, these are key areas where important new contributions to our understanding of reef budget dynamics are required. The assumptions that underpin the sponge bioerosion estimates also require further testing, especially across species. The confidence ratings approach (Table 3) is designed to allow resultant uncertainty to be reported. In this context, we regard the in-built flexibility of

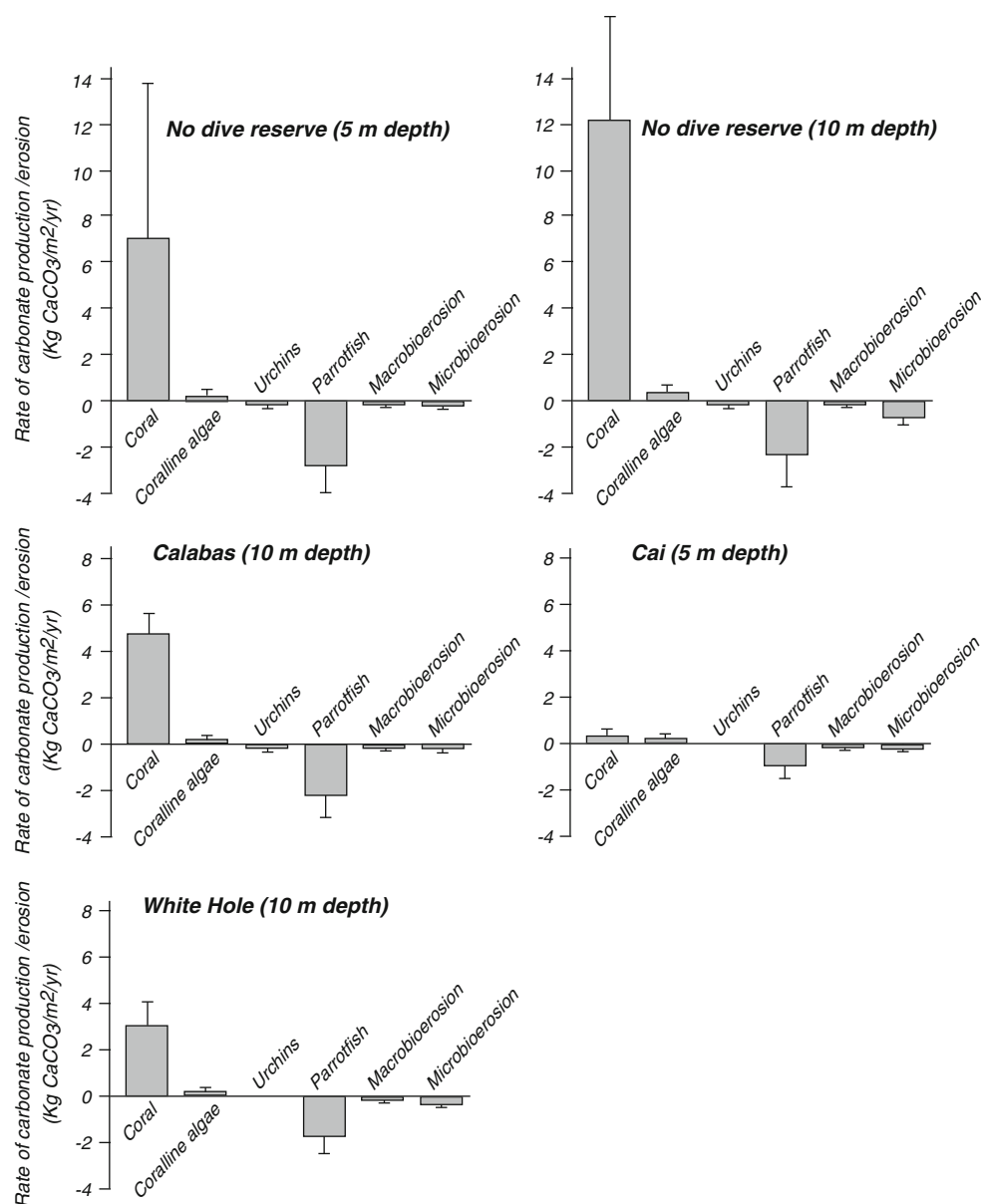
the methodology as one of its key benefits. Specifically, the ability of users to modify the data input sheets as new process or rate data become available for individual species, provides a degree of ‘future proofing’ and means that datasets can be re-calculated retrospectively to account for improved understanding of individual rate/process data.

Given, these differences in data input quality, it is appropriate to consider how production rates generated by *ReefBudget* compare with other reef carbonate production estimates. Direct comparisons between studies are clearly problematic because of differences in measured parameters (e.g. census- vs. hydrochemical methodologies) and because of inter-site differences in species types and abundance. However, in the following section, we compare our Bonaire data against: (1) individual production/erosion rate measures in other Caribbean census-based studies; (2) regional estimates of gross carbonate production based on combined hydrochemical and census-based datasets; and (3) estimates of net carbonate production from other census-based studies in the Caribbean and globally.

Comparisons at the individual process level

Allowing for between site variations in species presence and abundance, there is a reasonably good correspondence in the biological production rate estimates generated using *ReefBudget* compared with those determined in the classic Caribbean census-based studies of Stearn et al. (1977) and Hubbard et al. (1990). At Bellairs Reef, Barbados, gross carbonate production averaged $\sim 15 \text{ kg m}^{-2} \text{ year}^{-1}$ with LCC averaging $\sim 34 \%$, compared with a rate of $12.1 \text{ kg m}^{-2} \text{ year}^{-1}$ at site NDR-10 in Bonaire where LCC was $\sim 28 \%$, and $6.7 \text{ kg m}^{-2} \text{ year}^{-1}$ at site NDR-5 where LCC averaged $\sim 24 \%$. In St. Croix, gross coral carbonate production measures ranged up to $1.0 \text{ kg m}^{-2} \text{ year}^{-1}$ at around 5 m depth (although coral cover averaged only 0–11 % and included abundant, slow-growing *Agaricia* sp. and *Porites astreoides*), and 1.7 to $2.4 \text{ kg m}^{-2} \text{ year}^{-1}$ at around 10 m depth (with coral cover ranging from 10 to 25 %, again with a significant abundance of slower growing species). In terms of biologically driven carbonate erosion, highest rates in Bonaire are attributed to parrotfish, and the *ReefBudget* estimates are relatively consistent with those of Bruggemann et al. (1996) from similar depth sites at other leeward sites ($\sim 2.4 \text{ kg m}^{-2} \text{ year}^{-1}$ at 5 m depth and $\sim 1.4 \text{ kg m}^{-2} \text{ year}^{-1}$ at 10 m depth). Our data from the no dive reserve, where parrotfish biomass/numbers are higher, return higher erosion rate estimates (2.7 and $2.2 \text{ kg m}^{-2} \text{ year}^{-1}$, respectively; Table 4). Urchin erosion is of negligible significance around Bonaire at present, but our erosion estimates are consistent with those at other sites with low urchin population densities (Carreiro and McClanhan 2001; Griffin et al. 2003; Brown-Saracino et al.

Fig. 6 Relative contributions by different biological producers and eroders to carbonate budgets at sites around Bonaire. Error bars are standard deviations. $n = 6 \times 10$ m transects per site ($n = 10 \times 30$ m transects for parrotfish)



2007). The *ReefBudget* methodology employs a new approach to quantifying sponge bioerosion which, in Bonaire, returned low rate estimates of $<0.1 \text{ kg m}^{-2} \text{ year}^{-1}$ (Table 2). These are difficult to compare with published studies because of methodological differences, but erosion rates calculated in Barbados averaged $\sim 0.2 \text{ kg m}^{-2} \text{ year}^{-1}$ (Scoffin et al. 1980), and in French Polynesia ranged from 0.02 to $1.04 \text{ kg m}^{-2} \text{ year}^{-1}$ (Pari et al. 2002).

Comparisons with regional estimates of gross carbonate production

Vecsei (2001) provided a detailed synthesis of carbonate production rates within Caribbean and Indo-Pacific fore-reef environments based on data from studies using both

hydrochemical and census-based approaches (these integrating measures of production by corals, other calcifying biota and early cements). Results suggest that production rates, expressed as reef community metabolic performance (G) in $\text{kg m}^{-2} \text{ year}^{-1}$, have distinct modes in different environments and differ between the Caribbean and Indo-Pacific. However, within shallow (0–10 m depth) Caribbean fore-reef environments, $10.1 \text{ kg m}^{-2} \text{ year}^{-1}$ was considered a low production rate for reefs dominated by robust branched corals (acroporiids), whilst a high production estimate was $17.3 \text{ kg m}^{-2} \text{ year}^{-1}$ (Fig. 8a). Gross carbonate production rate estimates from our sites (all 0–10 m depth), and which omit estimates of early cementation, range from 12.1 to $0.2 \text{ kg m}^{-2} \text{ year}^{-1}$ (Fig. 8a). Our highest rates from Site NDR-10 are thus

Fig. 7 Scatter plots showing the relationships between: **a** coral cover (%) and gross carbonate production; **b** parrotfish erosion rates and total bioerosion; **c** rugosity and gross carbonate production; and **d** coral species diversity (H') and gross carbonate production. Data points are from individual transects with the exception of parrotfish erosion rate data which, because of the different survey methodology, can only be presented as an average for each site

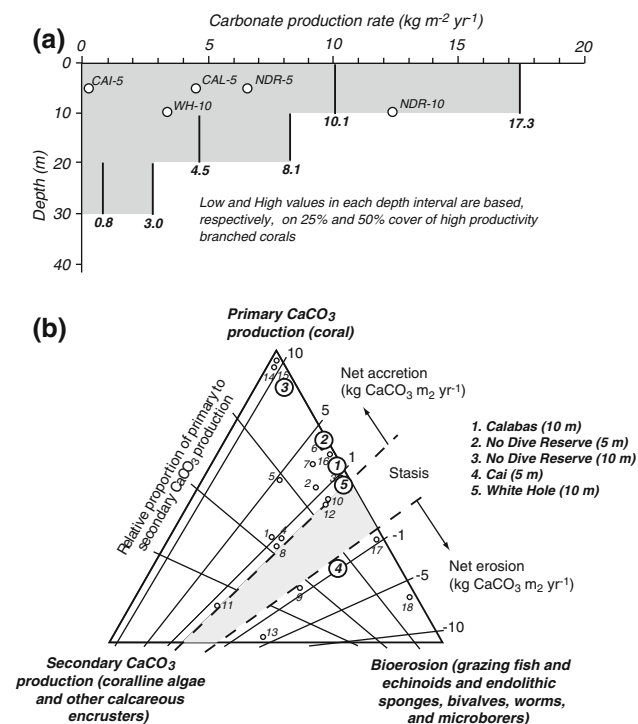
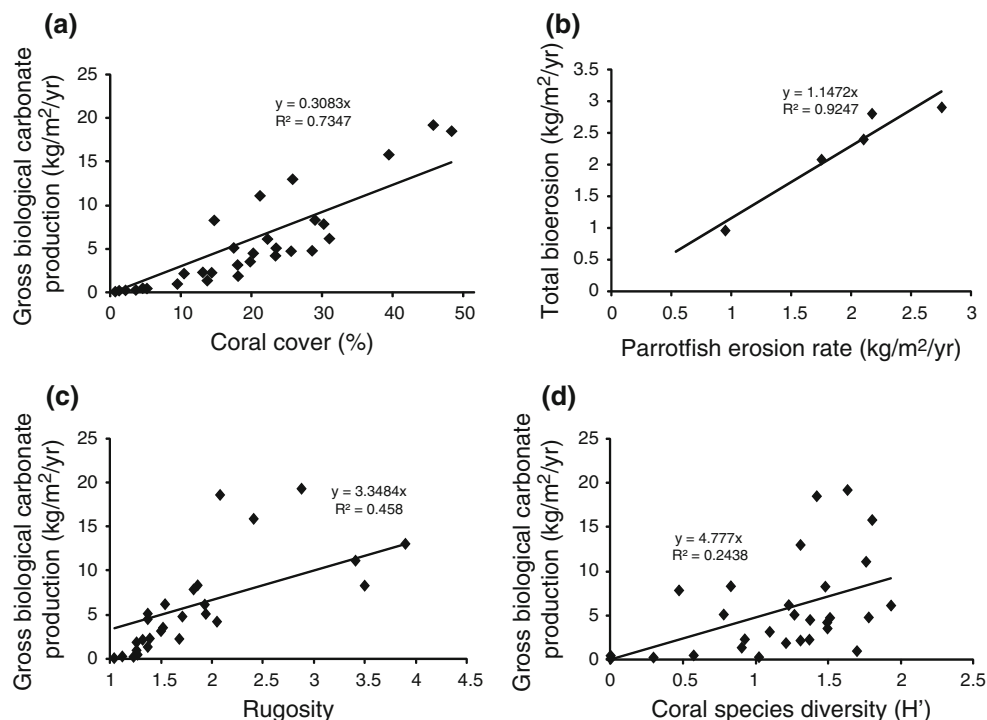


Fig. 8 **a** Gross carbonate production data from Bonaire (white filled circles) compared against range estimates of framework-dominated fore-reef carbonate production in the Caribbean across different depth intervals (integrating data on coral, calcifying biota and cement production) (from Vecsei 2001); **b** Net rates of reef carbonate production from the study sites in Bonaire (bold, circled numbers) plotted against other published reef carbonate budget data in the budget 'ternary space' of Perry et al. (2008). See Perry et al. (2008) for details of other studies

within the range previously calculated for the most productive shallow fore-reef sites when they were dominated by high productivity branched corals. Whilst these high production sites in Bonaire are dominated not by branched corals, but by large *M. annularis* colonies, they are regarded as being relatively 'healthy' compared with other Caribbean reefs and have been designated as the 'most pristine' reefs in the Caribbean (Kramer 2003), and thus, the high rates generated in our study seem reasonable in the context of past carbonate production estimates.

Comparisons with other census-based estimates of net reef carbonate production

Estimates of net biological carbonate production at the Bonaire sites range from +9.52 to -0.98 kg CaCO₃ m⁻² year⁻¹. These plot within the range of previous census-based estimates of net reef carbonate production (Fig. 8b), which range from around +5 to -1 kg CaCO₃ m⁻² year⁻¹, but with extremes ranging from ~+10 kg at a few high coral cover and high coral productivity sites to ~-7 kg at highly degraded and erosional sites (data from high eutrophication/sedimentation sites in Indonesia; Edinger et al. 2000). The most productive site in Bonaire (NDR-10) is thus at the upper range of estimates of biological carbonate production for 'normal' (a subjective term) healthy reefs, whilst the least productive (slightly erosional) site (CAI-5) is similar to the ranges reported from other low-productivity systems (Fig. 8b). Interestingly, those previous studies which have generated net erosional budget

estimates have been reported from reefs that were undergoing varying degrees of environmental disturbance (Eakin 1996; Edinger et al. 2000). The low positive and net erosional estimates generated at our windward sites cannot obviously be explained in this way, and instead seem indicative of the general state of framework accumulation which appears localised and subdued. This may be because reef productivity is itself actually very low (a seemingly valid suggestion given the low coral cover), or because what framework carbonate is produced, is exported under the high wave energy conditions that characterise this side of the island. Either way, the low/negative budget figures seem indicative of a long-term ecological or physical state on this side of Bonaire, rather than a response to recent environmental perturbations.

Concluding thoughts and future research needs

Census-based carbonate budget studies provide invaluable data on the relative contributions made by different biological carbonate producers and eroders and generate datasets that move beyond standard ecological abundance measures to provide quantitative data on the functional state of reefs in terms of biologically driven carbonate production. Such studies can tell us how much and at what rate different benthic components are producing carbonate, and which species are eroding it and at what rate. Whilst one must accept that such methodologies, along with alternative hydrochemical approaches (Vecsei 2004), will never deliver budget measures that are 100 % accurate, the budget methodology developed here provides sensible production rate estimates that are: (1) intuitively reasonable in terms of the observed depositional environments at the reefs under study (in terms of coral cover and reef framework accumulation); and (2) comparable with measures of both gross and net biological carbonate production determined in other census-based and hydrochemical studies (Vecsei 2001; Montaggioni and Braithwaite 2009). Further refinement of census-based budget estimates is clearly possible (and desirable) and to this end further studies that can provide additional data in the following areas are most urgently needed: (1) calcification and extension rates for CCA and/or net rates of CCA production in different reef environments; (2) rates of bioerosion as a function of surface area cover for different endolithic sponge species (in the Caribbean data for *Cliona delitrix*, *C. caribbaea* and *C. aprica* would be most useful) and data on how rates for these species vary across substrate types; (3) rates of bioerosion for endolithic worms and bivalves, and ideally rates that can be tied to an appropriate field census methodology; (4) rates of endolithic microbioerosion in different types of substrate and in different reef environments and depths; and (5)

rates of framework lithification and post-depositional dissolution in different environments.

Analysis of the datasets arising from census-based budget studies thus provide an opportunity to quantify which are the important ecological components influencing reef carbonate production rates at individual reef sites. This raises the possibility of using such approaches both to monitor temporal changes in biologically driven carbonate production as environmental conditions change and to model different scenarios of ecological change to understand the resilience of individual reefs as focal points for carbonate production. In other words, at what point along different trajectories of ecological change do reefs move from positive (accretionary) to negative (erosional) budgetary states, and which species are most important in controlling this? Given the documented declines in coral cover around Bonaire since the mid-1970s, it seems inevitable that whilst most sites studied presently exist in positive budgetary states they are probably not as productive as they were in the past, especially at the shallowest sites where species such as *A. palmata* have essentially disappeared. The *ReefBudget* methodology has potential as a tool for assessing and monitoring reef biological carbonate production states at a range of time and space scales, and because of the rationale underpinning the methodology, to be integrated (either in its entirety or through selected use of individual measures) into both reef management and reef survey programmes to produce quantitative measures of reef condition based on ecological data.

Acknowledgments This project was funded through a Leverhulme Trust International Research Network grant (F/00426/G). We thank Ramón de León, Bonaire National Marine Park (STINAPA), for his assistance with research permits and with arranging site access. Christine Schönberg is thanked for comments on the sponge bioerosion methodology. The constructive comments of Lucien Montaggioni and an anonymous reviewer for Coral Reefs helped tighten the focus of the paper.

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