Habitat-specific biogenic production and erosion influences net framework and sediment coral reef carbonate budgets

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Abstract

Carbonate budgets are increasingly being used as a key metric to establish reef condition. To better understand spatial variations in framework and sediment net carbonate budgets, we quantified biogenic carbonate production, erosion, and dissolution within and between five distinct geomorphological habitats of Heron Reef on the southern Great Barrier Reef. The protected reef slope had the greatest estimated net framework carbonate budget (22.6 kgCaCO₃ m⁻² yr⁻¹ ± 2.4 SE), driven by abundant, fast-growing acroporid corals coupled with low levels of macro- and micro-bioerosion. The estimate of the exposed reef slope was significantly lower due to localized damage from a single tropical cyclone that occurred 7 years prior to this study (9.7 kgCaCO₃ m⁻² yr⁻¹ ± 0.1 SE). Within the extensive lagoon, net framework carbonate budgets ranged from 0.24 kgCaCO₃ m⁻² yr⁻¹ (± 0.1 SE) to 3.0 kgCaCO₃ m⁻² yr⁻¹ (± 0.7 SE). The greatest net sediment carbonate budget was estimated within the reef crest (6.0 kgCaCO₃ m⁻² yr⁻¹ ± 1.1 SE) and the lowest in the shallow lagoon (1.2 kgCaCO₃ m⁻² yr⁻¹ ± 0.2 SE). Chemical dissolution of the sediments exhibited spatial variability, with reef crest and reef flat sediments in a state of net production. Considering the area of each habitat, the net reef framework and sediment budgets across Heron Reef were 4.06 kgCaCO₃ m⁻² yr⁻¹ and 2.82 kgCaCO₃ m⁻² yr⁻¹, respectively. The results of this study improve our understanding of spatial variability in carbonate production and bioerosion and provide a comprehensive reef-scale carbonate budget for a relatively undisturbed coral reef ecosystem.

The growth and persistence of coral reefs are dependent on the positive balance between calcium carbonate (CaCO₃) production and erosion. Often referred to as a “carbonate budget,” CaCO₃ production from calcifying organisms must exceed the erosion from biological, physical, and chemical (e.g., passive dissolution accelerated by ocean acidification) processes to maintain and increase coral reef structure (Chave et al. 1972; Eakin 1996; Kleyapas et al. 2001; Perry et al. 2012). The addition of CaCO₃ to a system occurs through biogenic production (e.g., hard corals, crustose coralline algae, microbial cementation) and sediment import, whereas CaCO₃ loss occurs through biological erosion, mechanical erosion, and sediment export and dissolution (Kleyapas et al. 2001). Carbonate budgets are increasingly being used as a metric to establish reef condition as anthropogenic influences exert unprecedented pressures on coral reefs (Eakin 1996; Perry et al. 2018; Hughes et al. 2018a). As climate change intensifies, determining whether reef growth can keep pace with sea level rise at local scales will be critical if coral reef ecosystem goods and services are to be secured (Beck et al. 2018).

The organisms and processes that influence production and erosion vary spatially across reef habitats and systems. Across entire reef systems, reef slope framework carbonate budgets are generally greater than those of lagoonal environments (e.g., reef flat) (Eakin 1996; Hart and Kench 2007; Browne et al. 2013; Perry et al. 2017; Ryan et al. 2019), particularly when dominated by fast-growing acroporid corals (Hart and Kench 2007; Browne et al. 2013; Perry et al. 2015; Van Woesik and Cacciapaglia 2018). Likewise, gross bioerosion is also greatest in reef slope...
environments, with lower rates of bioerosion by parrotfishes and other macrobioeroders in lagoonal habitats (Hutchings et al. 1992; Hoey and Bellwood 2008). Rates of carbonate production and bioerosion can also vary within habitats depending on depth, exposure, or history of disturbance (Brown et al. 2013; Januchowski-Hartley et al. 2017; Van Woesik and Cacciapaglia 2018; Ryan et al. 2019). Despite this variability, census-based studies that include in situ measurements for spatially adjusted rates of \( \text{CaCO}_3 \) production, bioerosion, and dissolution are rare (reviewed in Lange et al. 2020) but are essential if we are to understand reef framework production and the accretion potential of entire reef systems.

Here, we combined seasonal field-based measurements with a census-based approach to determine framework and sediment net carbonate budgets for the platform reef system Heron Reef in the Capricorn-Bunker region of the southern Great Barrier Reef (GBR), Australia (23°27′S 151°55′E). A recent review by Lange et al. (2020) highlighted that sites within the GBR represent only 5.6% of the 338 reef sites reported in the global carbonate budget literature. Many GBR studies were conducted four decades ago, using chemistry-based hydrochemical techniques (e.g., Kinsey 1979). Although chemistry-based techniques are useful for determining an integrated measurement of the net ecosystem calcification (e.g., Davis et al. 2019), these measurements do not allow for investigating the proportional importance of specific \( \text{CaCO}_3 \) producers and bioeroders. Therefore, we investigated reef framework production and bioerosion, and reef sediment production and dissolution by quantifying the individual contribution of biogenic carbonate producers, eroders and dissolvers across eight sites within the five distinct geomorphological habitats of Heron Reef (Fig. 1; Table 1) (Phinn et al. 2012). We documented seasonal and habitat-specific benthic community composition as well as: (1) framework production of two reef-building corals (\( \text{Acropora intermedia} \) and \( \text{Porites lobata} \)), (2) sediment production of the calcifying macroalge of the genus \( \text{Halimeda} \), (3) bioerosion of the excavating sponge \( \text{Cliona orientalis} \), (4) rates of microbioerosion, and (5) dissolution of the carbonate sediments. We also quantified habitat-specific rates of macrobioerosion (including by parrotfishes, worms and bivalves), and sourced the remaining framework (e.g., production of crustose coralline algae) and sediment (e.g., dissolution via sea cucumber bioturbation) carbonate contributions from the literature. In doing so, we estimate in situ, habitat-specific framework, and sediment net carbonate budgets and furthermore, integrate these data into previously established high-resolution habitat maps to estimate reef-scale framework and sediment carbonate budgets.

**Methods**

**Study location and geomorphological habitats**

Heron Reef is composed of five distinct geomorphological habitats: reef crest, reef flat, shallow lagoon, deep lagoon, and reef slope (Fig. 1; Table 1), as described by Phinn et al. (2012). The area occupied by each geomorphological habitat was previously determined using high-resolution Quickbird-2 satellite imagery (Phinn et al. 2012), and these areas were used to determine scaled net carbonate budgets for reef frameworks and sediment. To quantify reef scale carbonate production and bioerosion, a total of eight sites were established to encompass the diverse benthic communities that distinguish each geomorphological habitat. Benthic community composition at the site-level was representative of the larger geomorphological habitat (Phinn et al. 2012). One site was established within each of the following habitats: reef crest, reef flat, shallow lagoon, and deep lagoon (Figs. 1, 2). Within the reef slope habitat, four sites were established at two different depths, 5 and 8 m, on the northeast (“Fourth Point”) and southwest (“Harry’s Bommie”) of Heron Reef to investigate any within habitat differences (Figs. 1, 2). The northeast side of Heron Reef is exposed to wave forces including those associated with cyclones, whereas the southwest rim experiences reduced wave energy intensity (Bradbury and Young 1981; Connell et al. 1997).

At each site, 3 × 15 m transects were established originating from a central reference point and running north, east, and west. Benthic community composition was measured in situ seasonally (from January 2015 to November 2016 incorporating each season twice; \( n = 8 \)) by recording percent cover for 30 \( \times 30 \) cm quadrats per transect, totalling 7.5 \( \text{m}^2 \) per transect (Brown et al. 2018). Seasonal means for benthic cover, temperature and photosynthetically active radiation (PAR) by site are reported in Brown et al. (2018). The following groups were used directly or indirectly for framework and sediment carbonate budget calculations: scleractinian corals identified to family or genera and growth form (e.g., Acroporidae-branching), \( \text{Halimeda} \) algae, crustose coralline algae (CCA), turf algae, fleshy macroalgae, sediment, coral rubble patches, and “bare” substrate (see Brown et al. 2018 for detailed methodology).

**Quantifying reef framework carbonate production and bioerosion**

To quantify net carbonate framework rates, we used an adapted version of the census based ReefBudget methodology (Perry et al. 2012, 2015, 2017). Site-specific net carbonate budgets (Eq. 20, Table S1) were calculated by subtracting gross bioerosion (Eq. 19, Table S1) from gross production (Eq. 5, Table S1). Framework rugosity was determined using the chain-and-tape method, calculated as the ratio of contour-following distance to linear distance between two points on the reef (Perry et al. 2017). The standardized transect area was defined as the transect area multiplied by the rugosity of the transect (Eq. 1, Table S1). Gross coral carbonate production was calculated by multiplying the calcification rate for each coral type by the total area that type occupied (Eq. 2, Table S1). Seasonal calcification rates for branching \( \text{A. intermedia} \) and massive \( \text{P. lobata} \) were determined in situ at HBS, SL, DL,
and FP5 through changes in buoyant weight of translocated colonies over a one-year period (Davies 1989) (Supplementary Methods, Fig. S1). Calcification rates also varied across sites for these coral species. Therefore, site-specific mean calcification rates were applied within and across comparable sites (Table 2). For the remaining corals, non-seasonal calcification rates were sourced from the literature, preferably specific from Heron Reef where available, followed by Indo-Pacific-averaged rates (Table 2). The gross coral carbonate production was the sum of all carbonates produced by each coral species (Eq. 3, Table S1). Temporal rates of carbonate production by crustose coralline algae were determined by Kennedy et al. (2017), for three habitats of Heron Reef (reef slope, reef crest, and reef flat). Therefore, habitat-specific mean calcification rates were applied within and across comparable sites (Eq. 4, Table S1) (Table 2). Gross production was then the sum of the total mass produced by corals and CCA (Eq. 5, Table S1).

Table 1. Characteristics of each geomorphological habitat at Heron Reef, southern Great Barrier Reef. The proportion of the platform area that consists of reef slope (total) is the sum of SW reef slope (protected) and NE reef slope (exposed). Coral cover, sediment cover and rugosity are averages for each habitat (±SE). Platform habitat area was determined from the data of Phinn et al. (2012).

|                      | SW reef slope (protected) | NE reef slope (exposed) | Reef slope (total) | Reef crest | Reef flat | Shallow lagoon | Deep lagoon |
|----------------------|---------------------------|-------------------------|-------------------|-----------|-----------|----------------|-------------|
| Platform habitat area (km²) | 2.36                      | 2.36                    | 4.72              | 2.24      | 18.27     | 5.74           | 4.45        |
| Percentage of platform area (%) | 6.67                     | 6.67                    | 13.33             | 6.33      | 51.57     | 16.21          | 12.56       |
| Coral cover (%)       | 75.36                     | 44.07                   | 59.71             | 53.83     | 17.46     | 2.61           | 14.85       |
| ±SE                   | 2.22                      | 18.95                   | 15.64             | 3.17      | 0.67      | 0.35           | 1.30        |
| Sediment cover (%)    | 4.65                      | 13.89                   | 9.27              | 14.34     | 43.09     | 55.60          | 46.00       |
| ±SE                   | 0.81                      | 4.79                    | 2.80              | 1.08      | 1.12      | 2.60           | 5.79        |
| Rugosity              | 1.35                      | 1.15                    | 1.25              | 1.06      | 1.09      | 1.01           | 1.07        |
| ±SE                   | 0.04                      | 0.03                    | 0.10              | 0.03      | 0.02      | 0.01           | 0.03        |
Framework bioerosion was established via several measurements. To estimate bioerosion from parrotfishes (Scaridae), the composition and abundance of parrotfish populations were assessed without the influence of divers by using standardized video assays at each site \((n = 4–6)\). Video assays were chosen over underwater visual censuses because parrotfish are among the most sensitive fishes to divers (Dickens et al. 2011). On the southwest reef slope, video assays were only performed at

**Fig. 2.** Representative images (background) and measured benthic cover (foreground) of each site \((a–h)\) surveyed at Heron Reef, southern Great Barrier Reef. Benthic cover \((\% ; \text{minimum, 25th percentile, median, 75th percentile, and maximum})\) adapted from Brown et al. (2018). The average number of sea cucumbers recorded is displayed above the sediment data. Abbreviations: ACR-TCD, Acroporidae (tabular/corymbose/digitate); ACR-BRA, Acroporidae (branching); ACR-PE, Acroporidae (plating/encrusting); POCI, Pocilloporidae; POR-MASS, Poritidae (massive); POR-BRA, Poritidae (branching); POR-ENC, Poritidae (encrusting); FAV-LOB, Favidae-Lobophyllidae; CCA, crustose coralline algae; HB8, Harry’s Bommie 8 m; HB5, Harry’s Bommie 5 m; FP5, Fourth Point 5 m; FP8, Fourth Point 8 m.
TABLE 2. Input values used to determine the habitat-specific framework and sediment carbonate production and bioerosion/dissolution. Note that production or bioerosion rates given here are standardized to the surface area (m²) of the organism in question unless otherwise specified. Reef framework production rates presented in the form of skeletal density (g cm⁻³) and linear growth rate (cm year⁻¹) were integrated following the Perry et al. (2015) methodology to estimate carbonate production rates in kgCaCO₃ m⁻² yr⁻¹. Standard error reported for values determined in this study. N/A is used when the metric or organism in question was not observed at the given site. Asterisk (*) indicates units are kg m⁻³ yr⁻¹. Indo-Pacific carbonate production rates accessed from https://geography.exeter.ac.uk/reefbudget/indopacif/.

Abbreviations: HB8, Harry’s Bommie 8 m; HB5, Harry’s Bommie 5 m; RC, reef crest; RF, reef flat; SL, shallow lagoon; DL, deep lagoon; FP5, Fourth Point 5 m; FP8, Fourth Point 8 m; ACR-TCD, Acroporidae (tabular/corymbose/digitate); ACR-BRA, Acroporidae (branching); ACR-PE, Acroporidae (plating/encrusting); POCI, Pocilloporidae; POR-MASS, Poritidae (massive); POR-BRA, Poritidae (branching); POR-ENC, Poritidae (encrusting); FAV-LOB, Favidae-Lobophylliidae.

| Site      | Metric                          | Skeletal density (g cm⁻³) | Linear growth rate (cm yr⁻¹) | Production or bioerosion (kgCaCO₃ m⁻² yr⁻¹) | Standard error | Input data       | Reference                                      |
|-----------|---------------------------------|---------------------------|------------------------------|---------------------------------------------|----------------|------------------|------------------------------------------------|
| HB8       | A. intermedia (ACR-BRA)        | 5.219                     | 0.211                        | This study HB5                             |                |                  |                                               |
| HB5       |                                  | 5.219                     | 0.211                        | This study                                 |                |                  |                                               |
| RC        |                                  | 5.177                     | 0.154                        | This study FP5                             |                |                  |                                               |
| RF        |                                  | 4.837                     | 0.131                        | This study SL                              |                |                  |                                               |
| SL        |                                  | 4.837                     | 0.131                        | This study                                 |                |                  |                                               |
| DL        |                                  | 5.775                     | 0.462                        | This study                                 |                |                  |                                               |
| FP5       |                                  | 5.177                     | 0.154                        | This study                                 |                |                  |                                               |
| FP8       |                                  | 5.177                     | 0.154                        | This study FP5                             |                |                  |                                               |
| HB8       | P. lobata (POR-MASS)           | 7.269                     | 0.664                        | This study HB5                             |                |                  |                                               |
| HB5       |                                  | 7.269                     | 0.664                        | This study                                 |                |                  |                                               |
| RC        |                                  | 6.516                     | 0.411                        | This study FP5                             |                |                  |                                               |
| RF        |                                  | 3.423                     | 0.947                        | This study SL                              |                |                  |                                               |
| SL        |                                  | 3.423                     | 0.947                        | This study                                 |                |                  |                                               |
| DL        |                                  | 7.285                     | 0.432                        | This study                                 |                |                  |                                               |
| FP5       |                                  | 6.516                     | 0.411                        | This study                                 |                |                  |                                               |
| FP8       |                                  | 6.516                     | 0.411                        | This study                                 |                |                  |                                               |
| HB8       | Crustose coralline algae (CCA) | 1.049                     |                               | Reef slope of Heron Reef Kennedy et al. (2017) |                |                  |                                               |
| HB5       |                                  | 1.049                     |                               | Reef slope of Heron Reef Kennedy et al. (2017) |                |                  |                                               |
| RC        |                                  | 1.244                     |                               | Reef crest of Heron Reef Kennedy et al. (2017) |                |                  |                                               |
| RF        |                                  | 0.949                     |                               | Reef flat of Heron Reef Kennedy et al. (2017) |                |                  |                                               |
| SL        |                                  | 0.949                     |                               | Reef flat of Heron Reef Kennedy et al. (2017) |                |                  |                                               |
| DL        |                                  | 0.949                     |                               | Reef flat of Heron Reef Kennedy et al. (2017) |                |                  |                                               |
| FP5       |                                  | 1.244                     |                               | Reef crest of Heron Reef Kennedy et al. (2017) |                |                  |                                               |
| FP8       |                                  | 1.049                     |                               | Reef slope of Heron Reef Kennedy et al. (2017) |                |                  |                                               |
| All sites | ACR-TCD                         | 1.429                     | 4.188                        | Average of Acropora table, corymbose and digitate | Indo-Pacific carbonate production |                  |                                               |
| All sites | ACR-PE                          | 0.940                     | 3.148                        | Montipora folioid/plating                  | Indo-Pacific carbonate production |                  |                                               |
| All sites | POCI                            | 1.230                     | 1.500                        | Pocillopora damicornis from Heron Reef slope | Anderson et al. (2017) |                  |                                               |
| All sites | FAV-LOB                         | 1.457                     | 0.981                        | Hard coral- massive                        | Indo-Pacific carbonate production |                  |                                               |

(Continues)
| Site      | Species Type | Production | Growth Rate | Notes |
|-----------|--------------|------------|-------------|-------|
| POR-BRA   | Porites      | 2.197      | 1.447       | Porites-branching | Indo-Pacific carbonate production |
| POR-ENC   | Porites      | 1.267      | 1.175       | Porites-encrusting | Indo-Pacific carbonate production |
| OTH-HARD  | Average of Menulina, Hydnophora, and Galaxea | 1.517 | 1.370 | Indo-Pacific carbonate production |

**HB8**

- **C. orientalis bioerosion rate (external)**
  - HB8: 5.374, 0.248
  - This study: HB8

**RC**

- N/A

**RF**

- N/A

**SL**

- N/A

**DL**

- N/A

**FP5**

- 3.589, 0.271
  - This study: FP5

**FP8**

- 3.589, 0.271
  - This study: FP8

**HB8**

- Microbioerosion rate
  - 0.000, 0.0006
    - This study

**HBS**

- 0.002, 0.0008
  - This study

**RC**

- -0.001, 0.0008
  - This study

**RF**

- -0.003, 0.0005
  - This study

**SL**

- -0.006, 0.0006
  - This study

**DL**

- -0.006, 0.0010
  - This study

**FP5**

- -0.003, 0.0004
  - This study

**FP8**

- 0.000, 0.0006
  - This study: HB8

**All sites**

- Sponge bioerosion minimum (internal)
  - 7.043, 0.959
    - Average of published rates of beta-stage C. orientalis (suitable alpha-stage rates not available)
    - Schönberg (2001); Schönberg (2002); Fang et al. (2014); Achlatis et al. (2017); and the present study

**All sites**

- Sponge bioerosion maximum (internal)
  - 541.748*, 73.742
    - Estimated from average of published rates of beta-stage C. orientalis, assuming an average sponge penetration depth of 13 mm
    - Schönberg (2001); Schönberg (2002); Fang et al. (2014); Achlatis et al. (2017); and the present study

**All sites**

- Worm bioerosion (external and internal)
  - 0.00001
    - Average rates of erosion from sipunculans and polychaetes
    - Osorno et al. (2005)

**All sites**

- Bivalve bioerosion (external and internal)
  - 0.00041
    - Lithophaga
    - L.M. Valentino and R.C. carpenter, unpubl

**HB8**

- Halimeda production
  - 0.002, 0.002
    - This study

**HBS**

- 0.254, 0.241
  - This study

**RC**

- 1.611, 0.072
  - This study

**RF**

- 1.526, 0.035
  - This study

**SL**

- 1.657, 0.099
  - This study
HB5. As there is no significant difference in benthic community between 5 and 8 m sites (Brown et al. 2018), it was assumed that roaming parrotfish populations would visit these proximate sites comparably. Video assays were performed in spring only (October 2018). Previous investigation at Heron Reef has suggested negligible differences in total abundance of parrotfishes across seasons, but the relative abundance of species may vary; of the three species most relevant to this study, *Chlorurus spilurus* and *Scarus rivulatus* are reportedly more abundant in spring, whereas *Chlorurus microrhinos* is less abundant in spring than winter (Castro-Sanguino et al. 2016). High-definition digital video cameras (GoPro Hero 4 Silver in underwater housing) were attached to a surfboard mount on a dive weight. Cameras were deployed randomly within the transect area recording 69–129 min per deployment. All deployments were conducted within 3 h of high tide to minimize any confounding effects of tide.

Each video was examined in full by the same experienced observers (SBM and KTB) to determine the abundance of parrotfishes. When a parrotfish was encountered, the species, life history stage (juvenile, initial, terminal) and size class (total length; < 10, 10–20, 20–30, 30–40, 40–50, 50–60 cm) were scored for each parrotfish captured in each video. A 30 cm calibration marker was present in each video to better estimate parrotfish sizes. Care was taken not to re-census fish that left and subsequently re-entered the sampling area. Bioerosion rates were then determined for each parrotfish species by applying the model developed by Perry et al. (2015), which uses size and life phase to predict bite rate and volume of carbonate removed. A set of equations were used to estimate the area captured by the camera’s view (Fig. S2) in order to determine parrotfish biomass (kg hectare⁻¹), based on published length–weight relationships (FishBase, www.fishbase.org), and density of the parrotfishes (individuals hectare⁻¹) following Perry et al. (2015). Appropriate adjustments were made to consider local species encountered at Heron Reef, as this model has not previously been applied to the Great Barrier Reef region.

Bioerosion rates of sponges, worms and bivalves were determined both for eroding species with protruding surface tissues (hereafter termed “externally visible” or simply “external” bioerosion), and for species that are fully endolithic (but only inside coral rubble) and are barely, or not, visible macroscopically on the surface of the substrate (hereafter termed “internal” bioerosion). Our assessment for eroding species did not include cryptic species (i.e., hidden in cavities or overhangs). For external bioerosion, intensive visual surveys were performed along the same three 15 m transects previously described to quantify the area covered by macroscopic sponges (m²), mostly clionaidas) as well as the abundance of worms (e.g., sipunculans, polychaetes) and bivalves (e.g., *Lithophaga* spp.). Seasonal bioerosion rates for the most abundant externally-visible sponge (in this case beta-stage *C. orientalis* [Schönberg et al. 2017]) were determined in situ at HB5, SL,
DL, and FP5 via changes in buoyant weight of translocated experimental cores over a one-year period (Supplementary Methods, Fig. S1). Because bioerosion rates varied by site, site-specific mean bioerosion rates were applied within and across comparable sites (Table 2). For the worms and bivalves, bioerosion rates per individual were sourced from the literature (Osorno et al. 2005). Standardized bioerosion rates were determined by multiplying by the area covered for sponges (Eq. 7, Table S1), and by the number of individuals for worms (Eq. 8, Table S1) and bivalves (Eq. 9, Table S1). Gross external bioerosion was the sum of the total mass eroded by sponges, worms and bivalves (Eq. 10, Table S1).

To determine internal bioerosion rates, 30 roughly cylindrical fragments of coral rubble measuring approximately 2 cm diameter by 15 cm long were randomly collected from rubble patches at each site. Samples from the reef slope comprised species of staghorn Acropora whereas samples from the lagoon comprised species of Isopora and pocillopora. The total number of coral rubble fragments per square meter of rubble patches was quantified by sampling 0.25 m² quadrats along the same three 15 m transects described above. Fragment abundance per area was multiplied by the relative cover of rubble patches (%) along these transects to establish a standardized quantification of rubble per site (Eq. 11, Table S1). Each cylindrical rubble sample was divided into four sub-cylinders, thus yielding three pairs of complimentary, previously internal, cross-sectional samples. For each of these three complementary pairs, the area (cm²) occupied by sponges on one of the surfaces was quantified under magnifying glass. A minimum and a maximum sponge presence were estimated for each rubble sample. The minimum (cm²) is the sum of the cross-sectional sponge surface areas of each sub-cylinder (assuming individual sponges do not extend throughout the length of the sub-cylinder). To estimate maximum sponge presence (cm²), the sponge surface area in each sub-cylinder was multiplied by the length of the sub-cylinder, and the four products were summed (assuming the observed surface area extends throughout the entire length of the fragment). The number of worms and bivalves were also quantified per rubble fragment. For each site, the minimum total internal bioerosion from sponges was estimated by multiplying the standardized abundance of rubble fragments by the average minimum occupancy of sponges in the fragments and the planar bioerosion rate (Eq. 12, Table S1). The maximum internal bioerosion from sponges was determined by multiplying the standardized rubble amount by the maximum presence of sponge and volumetric bioerosion rate (Eq. 13, Table S1). Gross internal bioerosion rate from sponges was then reconciled for each site by averaging the estimated minimum and maximum (Eq. 14, Table S1). The equivalent rates for worms (Osorno et al. 2005) and bivalves (L.M. Valentino and R.C. Carpenter, unpubl.) were sourced from the literature and multiplied by the standardized rubble abundance and the average count of individual worms (Eq. 15, Table S1) and bivalves (Eq. 16, Table S1) inhabiting the same cylindrical rubble samples. Finally, the gross internal bioerosion is thus the sum of the total estimated mass eroded by sponges, worms, and bivalves (Eq. 17, Table S1).

Microbioerosion, defined as bioerosion by cyanobacteria, chlorophytes, rhodophytes, fungi, and bacteria (Golubic et al. 1981), was determined using a CaCO3 block assay (Tribollet and Golubic 2005). Blocks were cored from non-living massive colonies of species of Porites. Each core was an average depth of 2.2 cm and diameter of 4.5 cm. A total of eight cores were deployed at each site, excluding FP8, for 1 yr. Microbioerosion rates were determined via changes in buoyant weight of translocated cores over a 1-yr period and standardized to the available area index for bioerosion, which is defined by Perry et al. (2015) as all benthic cover, including area covered by turf and macroalgae, but not including sediment (Eq. 18, Table S1).

Urchins can also contribute to framework bioerosion, but none were observed during the surveys (from 2014 to 2018). Urchins are relatively rare on the GBR (Hutchings 1986; Hutchings et al. 2005) but are also mostly nocturnal (Young and Bellwood 2011) and therefore difficult to detect in transects. Published studies on the density of urchins and associated erosion impacts in habitats at Heron Island are non-existent. The erosion activities of urchins were consequently presumed to be negligible and therefore not included. Likewise, any erosion due to mechanical forces (e.g., storms, waves) was not considered in this study.

The reef-scale net framework carbonate budget was determined via weighted average. A weighting factor was determined by dividing the area that each habitat covers by the total area of Heron Reef. The weighting factor was then multiplied by the average framework budget determined per site and summed to produce the reef-scale framework carbonate budget estimate for Heron Reef. In total, the net framework carbonate budget was determined by 50% of data either determined in this study (28%) or for Heron Reef (22%), with the remaining input values sourced from Indo-Pacific literature (50%) (Table 2).

Quantifying sediment production and dissolution

Sediment production was determined using a methodology adapted from Perry et al. (2017). Although many calcifying algae (e.g., species of Amphiroa and Lithothamnion) can contribute to carbonate sediment production, only species of Halimeda were considered in this study given that they were the most abundant and are often the most significant contributor to sediment production (Maxwell et al. 1964, Drew 1983). Sediment production by species of Halimeda was estimated for each site and season using Halimeda spp. abundance data (percent cover) from transects (Brown et al. 2018). Any Halimeda that was hidden beneath vertical surfaces or overhangs was not estimated. Cover of Halimeda algae was not separated by species but included a wide range of species common across Heron Reef, including: H. discoidea, H. heteromorpha, H. macroloba, H. macrophysa, H. opuntia,
H. tuna, etc. (Schmidt et al. 2004; Castro-Sanguino et al. 2016). Cover of Halimeda algae was converted to biomass (g m\(^{-2}\)) based on the relationship observed between these two parameters at the western, shallow reef slope of Heron Reef (C. Castro-Sanguino, unpubl.). Biomass of Halimeda species was then converted to carbonate production (g CaCO\(_3\) m\(^{-2}\) d\(^{-1}\)) based on seasonal growth rate parameters and 86% average carbonate content of ash-free dry weight, as estimated by Castro-Sanguino et al. (2016) from two Halimeda species (H. heteromorpha and H. macrophylla) at Heron Reef. The rates of production derived from H. heteromorpha and H. macrophylla likely capture the variability in Halimeda productivity among habitats as they are morphologically distinct types; H. heteromorpha is highly calcified with small segments that grow fast, whereas H. macrophylla is lightly calcified (showing 11–15% less carbonate content than H. heteromorpha, C. Castro-Sanguino, unpubl.) with larger-sized segments that grow much slower (Castro-Sanguino et al. 2016). Annual sediment production from Halimeda algae (g CaCO\(_3\) m\(^{-2}\) yr\(^{-1}\)) was estimated by summation of monthly production across seasons (Eq. 21, Table S1). In calculating the sediment portion of the carbonate budget, consideration was also afforded to excretion of carbonate as sediment by parrotfishes; all that consumed was assumed to convert to sediments (Eq. 22, Table S1). Similarly, all external and internal sponge bioerosion was converted to sediment, minus a loss of 20% from chemical dissolution from within the chamber excavation process (Nava and Carballo 2008; Perry et al. 2017), and all mass eroded by worms and bivalves was assumed to be excreted as sediment (Eq. 23, Table S1). The gross sediment production was the sum of the total mass produced by Halimeda algae, parrotfish excretion, and macrobioeroders (Eq. 24, Table S1).

At two sites, HB5 on the reef slope and DL in the lagoon, seasonal sediment dissolution was directly measured over a 24-h period using in situ respirometry chambers and the alkalinity anomaly technique (Chisholm and Gattuso 1991) (Supplementary Methods). Measurements took place between August 2015 and May 2016, incorporating each season once (winter: August 2015, spring: October 2015, summer: February 2016, autumn: May 2016). For the reef flat, rates were previously estimated by Lantz et al. (2017) using similar methodology. Because rates varied among sites, site-specific mean production or dissolution rates were applied within and across comparable sites (Table 2). Post-depositional sediment production or dissolution rates were multiplied by the cover of sediment (%) and standardized to area (Eq. 25, Table S1) (Perry et al. 2017). Sediment bioturbation by sea cucumbers may be a significant contribution to reef carbonate sediment budgets (Schneider et al. 2011; Vidal-Ramirez and Dove 2016). In the current study, bioturbation was quantified by counting sea cucumbers along the same three 15 m transects as described above. Holothuria edwardsiana was the predominant species encountered. A dissolution rate for H. edwardsiana at Heron Reef was sourced from the literature and applied per individual, multiplied by the percentage cover of sediment and standardized to area (Eq. 26, Table S1) (Vidal-Ramirez and Dove 2016) (Table 2). Any import/export of carbonate rubble or sediments between habitats was not accounted for in this study. The gross sediment dissolution was the sum of the total mass dissolved by post-depositional sediment dissolution and sea cucumber bioturbation (Eq. 27, Table S1). Site-specific net sediment budgets (Eq. 28, Table S1) were calculated by subtracting gross dissolution (Eq. 27, Table S1) from gross production (Eq. 24, Table S1). In total, the net sediment carbonate budget was determined by 100% of data either determined in this study (60%) or for Heron Reef (40%) (Table 2). The reef-scale net sediment carbonate budget was determined via the same weighted average method described previously.

Statistical analyses
All statistical analyses were done using R version 3.5.2 software (2014), and graphical representations were produced using the package ggplot2 (Wickham 2016). Linear mixed effects models (package lme4) were used to test the effect of site on gross framework and sediment production, gross framework and sediment erosion, and net framework and sediment budgets (Bates et al. 2015). The effect of site on parrotfish species composition was analyzed using a permutational MANOVA (PERMANOVA), with random effect of transect using the "adonis" function from the vegan package (Oksanen et al. 2007). Resemblance matrices were obtained using Bray–Curtis dissimilarity and 9999 permutations. The factor site had eight levels: HB8, HB5, RC, RF, SL, DL, FP5, and FP8. Significant interactive effects were followed by pairwise comparison of estimate marginal means using the emmeans package with Tukey HSD adjusted p-values. Data were tested for homogeneity of variance and normality of distribution through graphical analyses of residual plots for all models. For all analyses, transects (n = 3) were used as replicates and included as a random effect.

Results
Framework production, bioerosion and net carbonate budget
Gross framework production was significantly different between sites, with greater gross production at reef slope sites HB5 (25.8 kgCaCO\(_3\) m\(^{-2}\) yr\(^{-1}\) ± 3.4 SE), HB8 (24.7 kgCaCO\(_3\) m\(^{-2}\) yr\(^{-1}\) ± 1.4 SE), and FP5 (19.2 kgCaCO\(_3\) m\(^{-2}\) yr\(^{-1}\) ± 2.6 SE) when compared to the reef crest (15.1 kgCaCO\(_3\) m\(^{-2}\) yr\(^{-1}\) ± 2.6 SE), deep lagoon (3.2 kgCaCO\(_3\) m\(^{-2}\) yr\(^{-1}\) ± 0.8 SE), reef flat (2.3 kgCaCO\(_3\) m\(^{-2}\) yr\(^{-1}\) ± 0.16 SE) and shallow lagoon (0.5 kgCaCO\(_3\) m\(^{-2}\) yr\(^{-1}\) ± 0.07 SE) (F = 228.12, p < 0.0001, df = 7, post hoc: HB5 = HB8 > FP5 > RC > DL = FP8 = RF = SL) (Fig. 3a). Overall, acroporid corals were the most significant contributor to gross carbonate production (χ\(^2\) = 27.0, p < 0.0001, df = 1, post hoc: acroporid corals > all other calcifiers), contributing between 74% and ~89% of gross production on the reef slope and reef crest (Fig. 3b). All other calcifiers were proportionally more significant at sites in the reef flat, deep lagoon, and shallow lagoon, reflecting the shift in the dominant coral genera and contributing 55, 91, and 99%, respectively (Figs. 2, 3).
Gross framework bioerosion was generally low across Heron Reef (range: 0.19–4.11 kgCaCO₃ m⁻² yr⁻¹), with significant differences found only between the reef crest (4.1 kgCaCO₃ m⁻² yr⁻¹ ± 0.6 SE) and shallow lagoon (0.21 kgCaCO₃ m⁻² yr⁻¹ ± 0.05 SE) or deep lagoon (0.19 kgCaCO₃ m⁻² yr⁻¹ ± 0.16 SE) (χ² = 26.8, p = 0.0004, df = 7, post hoc: RC > SL = DL) (Fig. 3a). Overall, the highest rates of bioerosion were driven by parrotfishes (χ² = 29.8, p < 0.0001, df = 1, post hoc: parrotfish > all other bioeroders), with parrotfishes contributing 91–99% of gross bioerosion on the reef slope and reef crest (Fig. 3b). A total of 17 species of parrotfishes were encountered across Heron Reef, with significant differences in species composition (pseudo-F(6,6) = 3.018, p < 0.0001) and biomass (χ² = 32.7, p < 0.0001, df = 6, post hoc: RC = HB5 = FP5 = FP8 > RF = SL = DL) between sites (Figs. S3; Table S2). The most abundant parrotfishes on the reef crest and reef slope were C. spilurus and S. rivulatus, however, C. microrhinos, a large, excavating parrotfish was the greatest contributor to increased bioerosion (Fig. S3). Within the lagoon, S. ghobban was both the most abundant (Fig. S3) and most significant contributor to bioerosion, although parrotfish bioerosion was comparatively negligible there. Across all sites, sponges, worms, bivalves, and microbioeroders contributed little (<0.01 kgCaCO₃ m⁻² yr⁻¹, proportionally less than 5%) to gross bioerosion rates due to their low abundance and low rubble cover (“all other bioeroders” Fig. 3b).

Net framework carbonate budgets varied significantly between sites, with most reef slope sites significantly higher than sites in the lagoon (χ² = 114.7, p < 0.0001, df = 1, post hoc: HB5 = HB8 = RC > DL = FP8 = RF = SL) (Fig. 3a). The highest net carbonate budgets were recorded at the protected reef slope sites HB5 and HB8, with 23.1 (±4.2 SE) and 21.9 (±2.5 SE) kgCaCO₃ m⁻² yr⁻¹, respectively. These sites were characterized by having very high rates of carbonate production and comparatively low rates of bioerosion (2.69 and 2.70 kgCaCO₃ m⁻² yr⁻¹ ± 0.65 and 0.09 SE), as well as due to reduced coral cover, not increased gross rates of bioerosion (Figs. 2, 3). The lowest net carbonate budget was recorded within the shallow lagoon (Table 3), which is attributable to sediment cover (Fig. 2) and, again, not explained by high gross rates of bioerosion (Fig. 3). The platform-scale net framework carbonate budget of Heron Reef, accounting for the area of each habitat, was 4.06 kgCaCO₃ m⁻² yr⁻¹. Mean, standard deviation, standard error, and confidence interval values of framework carbonate production and bioerosion by site are presented in Table S3.

### Sediment production, dissolution, and net sediment budget

Gross sediment production differed among sites, with significant differences found only between the reef crest (5.7
kgCaCO$_3$ m$^{-2}$ yr$^{-1}$ ± 0.6 SE) and shallow lagoon (1.8 kgCaCO$_3$ m$^{-2}$ yr$^{-1}$ ± 0.1 SE) ($\chi^2 = 25.1, p = 0.0007, df = 7$, post hoc: RC > SL) (Fig. 4a). Overall, *Halimeda* algae and parrotfish excretion were the most significant contributors to gross sediment production ($\chi^2 = 31.8, p < 0.0001, df = 2$, post hoc: *Halimeda* = parrotfish > all macrobioeroders) (Fig. 4b). Production by *Halimeda* algae was proportionally more significant in the lagoon and northeast reef slope sites (between 67% and 93%), whereas parrotfish excretion was more significant at the southwest reef slope sites and reef crest (between 63% and 95%). Sediment produced by all other macrobioeroders (e.g., sponges, bivalves) proportionally accounted for only 0.3% of sediment production across Heron Reef (Fig. 4b).

Gross sediment dissolution differed significantly among sites, with the greatest dissolution in the shallow (0.69 kgCaCO$_3$ m$^{-2}$ yr$^{-1}$ ± 0.07 SE) and deep lagoon (0.60 kgCaCO$_3$ m$^{-2}$ yr$^{-1}$ ± 0.2 SE) ($\chi^2 = 291.2, p < 0.0001, df = 7$, post hoc: SL = DL > FP8 = HB8 = FP5 = HB5 > RC > RF) (Fig. 4a). Sediments in the reef crest (~0.24 kgCaCO$_3$ m$^{-2}$ yr$^{-1}$ ± 0.1 SE) and reef flat (~0.75 kgCaCO$_3$ m$^{-2}$ yr$^{-1}$ ± 0.02 SE) exhibited net production. Dissolution of the sediments and bioturbation by sea cucumbers were not significantly different ($\chi^2 = 0.11, p = 0.74$, df = 1) (Fig. 4b). Net sediment carbonate budgets were significantly different among sites, with the highest budget recorded at the reef crest (5.96 kgCaCO$_3$ m$^{-2}$ yr$^{-1}$ ± 0.6 SE) ($\chi^2 = 30.7, p < 0.0001, df = 7$, post hoc: RC > DL = SL) (Fig. 4a; Table 3). The platform-scale net sediment carbonate budget of Heron Reef, accounting for the area of each habitat, was 2.82 kgCaCO$_3$ m$^{-2}$ yr$^{-1}$. Mean, standard deviation, standard error, and confidence interval values of sediment carbonate production and dissolution by site are presented in Table S4.
Discussion

Framework carbonate production and bioerosion varied significantly between geomorphological habitats at Heron Reef, with net carbonate budgets generally lower within the lagoon compared to reef slope sites. The protected reef slope exhibited the highest net carbonate budget, regardless of depth, due to high production and low bioerosion (Table 3). Indeed, coral cover on the protected reef slope ($C^2_2475\%$; Table 2) is among the highest values since the earliest records from 1962 (Connell et al. 2004). The reef slope communities were composed primarily of fast-growing tabular, branching, and plating acroporid corals, which contributed to the majority of the framework production. Grazing parrotfishes were the main contributor to framework bioerosion rates and despite estimating a suite of habitat-specific biological erosion processes, the remaining macro- and micro-bioeroders contributed negligibly.

Low contributions of these bioeroders to reef-scale CaCO$_3$ budgets have also been found elsewhere in the Indo-Pacific (Perry et al. 2017; Van Woesik and Cacciapaglia 2018), but data remain scarce and inconclusive especially due to the difficulty of determining the abundance of endolithic organisms accurately and in detail (Lange et al. 2020). Little beta-stage clionaid cover was observed across our sites (and almost entirely C. orientalis), with a maximum abundance observed on the protected reef slope. Our estimates of gross bioerosion were lower than previous studies from the northern and central GBR (Tribollet et al. 2002; Hutchings et al. 2005; Hoey and Bellwood 2008). This may be partially explained by the composition of the parrotfish community, particularly the absence of the giant coral-eating parrotfish Bolbometopon muricatum (Bellwood et al. 2003; Hoey and Bellwood 2008; Bellwood and Choat 2011). Although the abundance of macro- and micro-bioeroders were
low across our transects, future studies on other reef systems, particularly those affected by anthropogenic disturbances (e.g., thermal stress, eutrophication), should continue to evaluate the contributions of multiple bioeroding organisms, as their abundance is typically higher on present-day disturbed reefs and may increase in the future (e.g., Ward-Paige et al. 2005).

On the exposed reef slope, the net framework carbonate budget was significantly less productive at the 8 m site than at the 5 m site, likely due to the lasting impacts of cyclone Hamish (March 2009). Similar reductions in net carbonate budgets have been observed 4 yr after cyclones elsewhere in the western Pacific (Van Woesik and Cacciapaglia 2018). Coral cover at this “deep” exposed reef slope (~20%), although historically less than the shallow slope, can reach ~40% (Connell et al. 1997; Connell et al. 2004), suggesting this location is gradually recovering. Connell et al. (1997) reports that Heron Reef experienced 35 cyclones between 1946 and 1992, 21 of which were defined as damage-inducing. Although the spatial extent of the cyclone impacts on Heron Reef have historically been confined to single habitats over small spatial scales (<200 m) (Connell et al. 1997, 2004), damage from cyclone Hamish was significant and homogeneous across much of the exposed reef slope at neighboring One Tree Island (Woolsey et al. 2012). It is believed that by bringing deeper cooler waters to the surface, storm activity has been critical in sparing the southern reefs of the GBR from the thermal stress that recently caused mass coral bleaching and mortality in the central and northern GBR (Hughes et al. 2017, 2018a).

Averaging across the protected and exposed reef slope geomorphological habitat, including the cyclone affected site, yields a carbonate budget of 16.1 kgCaCO3 m−2 yr−1 (Table 3). Thus, although the reef slope is proportionally only 13% of the reef platform (Table 1) (Phinn et al. 2012), it contributes ~50% to reef-scale carbonate production—more than any other geomorphological habitat on Heron Reef (Table 3). As with the surrounding reefs of the Capricorn-Bunker region, Heron Reef represents a rare instance where contemporary growth rates are comparable with historical levels (Davis et al. 2019). The highest estimates of the net production of CaCO3 are approximately 10 kgCaCO3 m−2 yr−1 (Smith and Kinsey 1976; Kinsey and Hopley 1991; Montaggioni and Braithwaite 2009; Perry et al. 2018) and values greater than 5 kgCaCO3 m−2 yr−1 are considered “optimal reef production” (Vecsei 2004; Perry et al. 2018). Although our estimates are higher than previous approximations from Kinsey and Hopley (1991), these authors based their measurements on reefs with a 50 m wide reef slope, and variations may be due to differences in the size and shape of the examined Heron Reef. More recent studies using census-based methodologies at comparable Indo-Pacific reef slope environments have estimated net carbonate budgets of 12.3 kgCaCO3 m−2 yr−1 in the central GBR (Browne et al. 2013), 12.7 kgCaCO3 m−2 yr−1 elsewhere in the western Pacific (Van Woesik and Cacciapaglia 2018), and 8.6 kgCaCO3 m−2 yr−1 in the southern Maldives (Perry and Morgan 2017). Buddemeier and Kinzie III (1998) suggested that massive reef production may be the result of the system remaining under good conditions for an extensive period of time. Indeed, Heron Reef has largely been spared from recent disturbances suffered elsewhere on the GBR, such as the thermal stress events in 2016–2017, crown-of-thorns starfish outbreaks, and water quality degradation (De’ath et al. 2012; Hughes et al. 2017, 2018a; Mellin et al. 2019). It is improbable, however, that reefs like Heron Reef will be able to maintain coral cover and carbonate production at current levels due to predicted increases in storm intensity, intensifying ocean warming, and acidification on near-future reefs (Dove et al. 2013; Hughes et al. 2018b).

Differences between reef slope framework production presented here and previous studies may also be attributable to methodological differences. For example, our study estimated framework production from benthic cover data (percent of each taxon), whereas Perry and Morgan (2017) treat each coral colony separately from other colonies of the same taxon due to variance in individual colony size and morphology. Over-estimation may arise in evaluating production from cover data as opposed to individual colonies, particularly for large thickets of branching Acropora that are common at Heron Reef. However, utilizing regional specific growth rates, as done in many previous studies including the aforementioned study, can result in estimates of carbonate production of up to three times greater (Kuffner et al. 2019). Previous studies in the Indo-Pacific have estimated production rates of branching Acropora to be between 10.8–27.6 kgCaCO3 m−2 yr−1 (Hart and Kench 2007). These estimates differ considerably from the measured calcification rates of A. intermedia across four sites at Heron Reef (mean 5.25 kgCaCO3 m−2 yr−1). Similarly, if rates were borrowed for Acropora (branching) and Porites (massive) from the Indo-Pacific carbonate production rates (https://geography.exeter.ac.uk/reefbudget/indopacific/), estimates of carbonate production for these organisms would have been between 10–12 and 2–4 times greater, respectively. Our values are therefore conservative on the side of the production estimate for two abundant reef-builders. Even though 50% of the data we used to construct our net framework carbonate budgets were determined at Heron Reef, the remaining data were borrowed from the Indo-Pacific literature, introducing an unavoidable degree of uncertainty to the overall budget outputs. In future studies, current, site-specific calcification rates should be integrated with more complex field measurements to best estimate reef framework carbonate production.

The reef crest and lagoonal environments exhibited significantly lower net framework carbonate budgets. On the reef crest, the net carbonate budget was almost half that of the protected reef slope (Table 3). This reduction was likely due to: (1) a reduction in carbonate production as a result of limited space for vertical growth due to tidal extremes and (2) an
increase in the abundance, biomass, and diversity of parrotfishes resulting in the highest rate of bioerosion across Heron Reef. The spatial variation in parrotfish communities observed in this study, where abundance was greater at the reef crest and reef slope than within the lagoon, is consistent with patterns observed across other reef systems (Hoey and Bellwood 2008; Perry et al. 2017; Van Woesik and Cacciapaglia 2018). Unlike at reef crest and reef slope, framework production within the lagoon was driven by species of *Isopora*, *Pocillopora* and massive *Porites*, reflecting the shift in benthic community structure (Brown et al. 2018). Kinsey and Hopley (1991) estimated that enclosed lagoons of "lagoonal reefs" on the GBR produce approximately 2 kgCaCO$_3$ m$^{-2}$ yr$^{-1}$. By investigating geomorphological habitats discretely, we improve on this previous estimate, revealing that net framework carbonate budgets varied from 0.24 kgCaCO$_3$ m$^{-2}$ yr$^{-1}$ ($\pm$ 0.10 SE) within the sediment dominated shallow lagoon, to 1.53 kgCaCO$_3$ m$^{-2}$ yr$^{-1}$ ($\pm$ 0.06 SE) within the reef flat, to 3.01 kgCaCO$_3$ m$^{-2}$ yr$^{-1}$ ($\pm$ 0.69 SE) in the deep lagoon patch reef habitat (Table 3). Similar small-scale (10–100 s m$^2$) patterns in framework carbonate production and bioerosion across habitats have been reported in the central GBR (Browne et al. 2013) and the Indian Ocean (Perry et al. 2017; Ryan et al. 2019). The combined contribution of reef crest, reef flat, shallow lagoon and deep lagoon, which represent 87% of the Heron Reef platform, amounted to almost half (47%) of the platform-scale carbonate budget.

Similar to framework production and bioerosion, sediment production and dissolution varied significantly between geomorphological habitats. The highest net sediment budget was recorded at the reef crest, where both sediment production by *Halimeda* algae and parrotfish excretion were high. Our estimates of sediment production by *Halimeda*, however, should be treated with caution. Quantifying rates of sediment generation directly from rates of carbonate accumulation may be inaccurate if, for example, the impact of herbivores on *Halimeda* growth dynamics is not accounted for (Castro-Sanguino et al. 2020). Recent estimates of carbonate sediment production by *Halimeda* at one of our reef slopes sites suggest that only 37% of the annual carbonate stored in the standing crop of *Halimeda* thalli was deposited as sediments, but this figure is likely to vary considerably among habitats (Castro-Sanguino et al. 2020). In addition, while we combined carbonate production rates from two morphologically distinct *Halimeda* species to characterize the carbonate production of the total *Halimeda* community, habitat-specific rates of sediment production at Heron Reef are likely dependent on the relative abundance of individual *Halimeda* species (Castro-Sanguino et al. 2020).

Sediment dissolution and sea cucumber bioturbation were the greatest within the lagoon. Although the reef crest displayed the highest net sediment budget by habitat (Table 3), the reef flat was the biggest contributor to the platform scale sediment budget (55%). Some recent studies have considered post-depositional sediment dissolution by applying a singular dissolution value across habitats (Courtney et al. 2016; Perry et al. 2017). However, the results presented here indicate that these processes vary between geomorphological habitats and shallow, permeable carbonate sediments can exhibit gross carbonate production (Lantz et al. 2017). Considering that the reef flat makes up to >50% of the Heron Reef platform (Table 1) and sediment covers ~45% of the habitat, applying the dissolution rate determined within the reef slope, for example, could have implications for the total sediment budget of Heron Reef.

The results of this study emphasize that net carbonate budgets exhibit significant spatial variation within and between geomorphological habitats across a single platform reef system. Our assessment of Heron Reef reinforces the importance in using current, site-specific data to calculate biogenic net carbonate production, erosion, and dissolution. Although this study provides a better understanding of biogenic production, erosion and chemical dissolution, future studies should consider habitat-specific sediment import and export as well as mechanical erosion to comprehensively understand if future growth rates will be able to track changes associated with our current rate of CO$_2$ emissions.

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Conflict of Interest
None declared.