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High rates of erosion on a wave-exposed fringing coral reef

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Abstract

Erosion is a key process in shaping the physical structure of coral reefs, yet due to erosion being semi-cryptic and difficult to quantify, information remains limited. Here, we investigate erosional processes along Ningaloo Reef, an extensive fringing coral reef in Western Australia. We employed both direct and indirect methods to measure erosion in wave-exposed reef slopes and protected lagoonal habitats. Direct measurements of erosion on coral blocks were among the highest found globally, with total erosion of 3.07 kg m^{-2} yr^{-1} (4% from micro, 0.6% from macro, and 94% from external), whilst indirect rates were estimated at 2.4 ± 0.20 kg m^{-2} yr^{-1} (78% from parrotfish, 22% from urchins). Indirect erosion rates were influenced by the species and size of parrotfish, with *Chlorurus microrhinos* removing 0.44 ± 0.19 kg m^{-2} yr^{-1} (22% of parrotfish erosion). Scanning electron microscopy and computed tomography show that micro and macroborer erosion contributions to direct erosion were low, most likely due to heavy grazing by parrotfish and the short deployment period of experimental substrates. A substantial portion of external erosion on blocks (0.53 ± 0.23 kg m^{-2} yr^{-1}) could not be attributed to bioeroders and was poorly correlated with wave exposure, suggesting processes not quantified contribute to this unaccounted aspect of erosion. Our results confirm that bioerosion by parrotfish is especially significant at Ningaloo Reef, and large-bodied individuals of *C. microrhinos* are key in conserving this key ecological process.

The process of erosion plays a crucial role in the maintenance and persistence of coral reefs. The breakdown of reef substrate through physical, biological, and chemical processes alters the shape and structural complexity of the reef, which has profound effects on the ecological services it provides. Changes in structural complexity, for example, can affect the diversity of fish assemblages (Graham and Nash 2013) and are an important predictor of reef resilience to disturbance (Perry and Alvarez-Filip 2019). In instances where rates of erosion exceed rates of carbonate production (e.g., Eakin 1996), the loss of reef structure may also threaten reef capacity to mediate wave exposure, thereby compromising their ability to protect coastlines and inshore habitats (Sheppard et al. 2002; Cuttler et al. 2018; Perry et al. 2018). Conversely, erosion can remove dead reef substrate, which can free up bare space for coral settlement (McCauley et al. 2014) and create sediments and rubble that contribute to the stability of shorelines and reef habitats (Bellwood 1996; Perry et al. 2011). Understanding the factors that govern erosion is, therefore, key to understanding physical, biological, and chemical processes on coral reefs.

Various methods have been established to measure erosion on reefs, leading to greatly improved knowledge of processes that drive both internal and external erosion (Pari et al. 2002; Tribollet and Golubic 2005; Yarlett et al. 2018). However, erosion remains difficult to measure, particularly when it occurs within the reef framework (i.e., internal erosion; Hutchings 1986). Furthermore, the majority of studies that have directly quantified erosion tend to focus on shallow, sheltered reef environments

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Additional Supporting Information may be found in the online version of this article.

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(reviewed by Browne et al. 2021). Given rates of erosion are highly variable across geographic regions and among reef habitats (Silbiger et al. 2017; Browne et al. 2021), it is important to investigate a range of environments to gain insights into the factors driving this variability.

Erosion on coral reefs can be classified into three primary categories: physical, chemical, and biological. Physical erosion is primarily caused by hydrodynamic forces leading to dislodgement or abrasion and is positively related to wave exposure and severe storms (Madin and Connolly 2006; Puotinen et al. 2020). Chemical erosion is the dissolution of calcium carbonate, and while it typically occurs slowly, it is positively related to factors such as water motion, microbial activity, and increased ocean acidification (Reyes-Nivia et al. 2013; Glynn and Manzello 2015; Cornwall et al. 2021). Biological erosion is the breakdown of reef carbonates due to the activities of organisms which may employ both chemical and mechanical processes. Among the three categories of erosion, bioerosion is considered the most significant on coral reefs (Browne et al. 2021), often accounting for the majority of reef erosion (Glynn and Manzello 2015).

Bioerosion on coral reefs is attributed to organisms whose actions are categorized as external or internal. External bioerosion occurs when animals scrape the surface of the reef while feeding (Glynn and Manzello 2015). External bioeroders include grazing parrotfish, pufferfish, and urchins, which play an important role in creating new substrate for coral recruitment (Mumby and Harborne 2010; McCauley et al. 2014), generating calcium carbonate sediments (Hutchings 1986), and shaping reef structure (Hutchings 1986; Hutchings et al. 2005). Grazing by parrotfish and urchins contributes up to 90% and 84% of the estimated total bioerosion in the Indo-Pacific and Caribbean, respectively (Chazottes et al. 1995; Bellwood 1996; Perry et al. 2014). Accordingly, one-time "snapshot" assessments of grazer abundance and activity have been used to indirectly estimate total rates of erosion (e.g., Graham and Nash 2013; Hoey et al. 2016), although this may not adequately capture temporal and spatial variability in grazing pressure (Perry and Hepburn 2008; Johansson et al. 2010; Lange et al. 2020). Furthermore, long-held empirical relationships between grazer abundance and rates of erosion derived from one or two locations are often used to extrapolate across regions or globally (Glynn and Manzello 2015; Perry et al. 2018), which may not adequately represent the local activity of bioeroders.

Like external bioerosion, internal bioerosion of the reef framework by boring organisms can remove substantial calcium carbonate (Sammarco and Risk 1990; Hutchings et al. 2005; Glynn and Manzello 2015). Internal erosion, however, is logistically challenging to measure as bioeroding organisms are often small ($< 10\,\mu$m), sparsely distributed (e.g., bivalves) and only detectable using extractive (i.e., collecting and breaking open samples of reef) and/or expensive (i.e., internal scanning) methods (*see* discussion in Browne et al. 2021). Subsequently, studies have begun utilizing a combination of scanning electron microscopy (SEM) (Grange et al. 2015; Lloyd Newman et al. 2023) and micro computerized tomography (microCT) (Enochs et al. 2016; Dee et al. 2023) to accurately measure rates of internal erosion by micro and macro borers.

There are multiple environmental factors that impact erosion of reef substrates, one of which is wave-driven water movement. Wave-driven water movement can influence rates of physical, chemical, and biological erosion (Hutchings 1986), with several studies recording higher rates of (predominantly external) erosion in exposed compared with lagoonal habitats (Tribollet and Golubic 2005; Hoey and Bellwood 2008). Waves generate the physical force needed to break down and dislodge the reef framework (Puotinen et al. 2020). This process can promote the growth of microalgae and macroborers, which, in turn, may accelerate erosion by secreting chemicals that dissolve the reef framework and promote external erosion (Hutchings 1986; Rice et al. 2020). Despite the recognized importance of wave exposure, most erosion studies using experimental blocks have focused on shallow, sheltered environments (Chazottes et al. 1995; Dee et al. 2023), with notable exceptions (Sammarco and Risk 1990; Kiene and Hutchings 1994; Tribollet and Golubic 2005). As a result, our knowledge of how wave exposure influences rates of physical, chemical, and biological erosion remains a research priority.

Here, we use high-resolution CT and SEM scans to measure rates of external and internal erosion of experimental coral (massive *Porites* sp.) blocks deployed for 12–20 months within lagoon and reef slope habitats on a wave-exposed fringing coral reef. By combining direct measurements of external and internal erosion, with indirect estimates of parrotfish erosion, urchin erosion, and water velocity, we identify the prominent drivers of erosion within the World Heritage-listed Ningaloo Reef. These partitioned estimates of erosion represent the first for an exposed, fringing coral reef in the eastern Indian Ocean and provide a basis for understanding and managing spatial variation in a key ecological process.

Methods

Study region

This study was conducted along the north-western section of Ningaloo Reef (Nyinggulu) between 22°17′00″S, 113°49′00″E and 21°49′00″S, 114°03′00″E. This region of Ningaloo Reef has a well-developed fringing reef with a shallow lagoon (max depth: 4 m) extending 1.3–2.0 km from the shore and a continuous reef slope approximately 2.0–4.0 km from the shore (Thomson et al. 2020; *see* Supporting Information Fig. S1; Supporting Information Table S1).

External and macroborer erosion of coral blocks

A total of 51 blocks ($5 \times 2 \times 1$ cm) of dead *Porites* sp. (hereafter referred to as blocks) were deployed across 17 sites (10 reef slope, 7 lagoon: $n = 3$ blocks/site) in September 2020 with 17 blocks retrieved in September 2021

(12 months) and 15 blocks retrieved in May 2022 (20 months). The remaining 19 blocks were unable to be located on retrieval, presumably because they were physically dislodged during the deployment period. Blocks were cut from massive *Porites* sp. cores (75 mm diameter, $n = 2$) collected from within the study region during a previous study (Müller et al. 2001). Before deployment, each block was visually inspected to ensure there were no pre-existing boreholes, density was measured using Archimedes' principle of water displacement (mean density $\pm$ SE $= 1.44 \pm 0.02$ g cm^{-3}) and each block was mounted on an acrylic base (8 cm × 2 cm × 0.4 cm) using Sikabond 142 epoxy (following Enochs et al. 2016). Blocks were then imaged with a SkyScan 1176 microCT (Bruker-microCT) at 90 kV and 273 μA (35 μm resolution with a 0.1 mm Cu filter) before being deployed on the reef using stainless mounting plates (Mundy 2000). Blocks were deployed at the start of transects used to record parrotfish and urchins, such that they were located within the transect area (*see* Supporting Information Methods). On retrieval, blocks were rinsed in freshwater, oven-dried at 60°C for 24 h, and rescanned with the SkyScan 1176 microCT. Pre- and post-deployment scans were reconstructed using Bruker NRecon software with ring artifact reduction of 20 and beam hardening of 20% (following Dee et al. 2023), then directly compared using Data-Viewer software with a "difference" image stack (.bmp) to identify external erosion (removed exterior pixels), macroborer erosion (removed interior pixels > 35 μm) and unchanged material (pixels with no change) (Fig. 1). Volumetric analysis (cm^3) of external and macroborer erosion for each block was conducted using CTAn software (version 1.18) (*see* Supporting Information Methods).

Microborer erosion of blocks

Microborer erosion (< 35 μm) was quantified on a subset of coral blocks ($n = 6$) deployed for 12 months using a modified method from Lloyd Newman et al. (2023). Two 1 cm^3 cubes were cut from the upper facing central surface of blocks (3 × lagoon, 3 × reef slope). Cubes were cut ~ 0.5 cm from each edge of the block, soaked in diluted hydrogen peroxide ($\sim 6\%$) for 24 h and embedded with low viscosity resin (Araldite CY212) under vacuum for 3 h and cured at 60°C for 24 h. One surface of the resin cube was polished using a series of wet/dry paper grits (60–2000) until the carbonate material was exposed, then etched for 20 s in 10% HCl, rinsed in distilled water, oven-dried and splutter coated with gold for SEM examination. The first cube from each block was used to quantify the mean depth of borers, the second cube used to quantify the surface area removed by microborers (*see* Supporting Information Methods).

Parrotfish bioerosion rates

To estimate the bioerosion rates of parrotfishes at each survey site, we used size and species-specific estimates of parrotfish abundance, bite rates, bite volume, and proportion of bites leaving scars. Parrotfish abundance was quantified along a single 100 m × 10 m belt transect at each of 17 sites. Transects were located immediately adjacent to coral blocks (< 1 m) with surveys conducted in September 2020, September 2021, and May 2022 ($n = 3$ transects per site) during daylight hours (07:00–16:00 h), following Sale (1980). Along each 100 × 10 m transect, observers identified and recorded all parrotfishes to species and estimated total length (TL) to the nearest 10 cm. Parrotfish bite rates (bites min^{-1}), bite volume (cm^3) and proportion of bites leaving scars were estimated using focal individual observations (following Bellwood 1996, Bruggemann et al. 1996; *see* Supporting Information Results). The mean bite mass for each parrotfish species was calculated by multiplying the mean bite volume by the mean substrate density for Indo-Pacific coral reefs (1.47 g cm^{-3}, Perry et al. 2011).

Urchin bioerosion rates

Urchin bioerosion was based on *Echinometra mathaei*, the most abundant urchin at Ningaloo (Langdon 2012). Bioerosion rates were estimated as the product of average urchin densities and published individual bioerosion rates of *E. mathaei* at Ningaloo (0.13 kg m^{-2} yr^{-1}; Langdon 2012). Urchin densities were quantified using a 25 m photo transect conducted between 07:00 h and 16:00 h at each of the 17 sites in September 2020, September 2021, and May 2022 ($n = 3$ transects per site; *see* Supporting Information Methods).

Total (net) erosion and unaccounted erosion

To estimate rates of erosion not accounted for by biological processes, we combined directly measured rates of internal and external erosion on blocks and subtracted our indirect estimates of biological erosion from parrotfish and urchin surveys.

$$\text{Total (net) erosion} = \text{internal erosion} + \text{external erosion},$$

$$\text{Unaccounted external erosion} = \text{external erosion (from blocks)} - (\text{parrotfish erosion} + \text{urchin erosion}).$$

Structural complexity of reef (rugosity)

Structural complexity of the substrate at each site was estimated using a rugosity index derived from a 10-m chain (chain link dimensions: 22 × 12 mm) laid alongside the transect tape used for surveys of urchins. The chain was placed on the substrate, covering all crevices and gaps within the substrate. We measured the linear distance covered by the chain along the transect tape and calculated the rugosity index by dividing 10 m by the recorded linear distance (adapted from Risk 1972). Consequently, a higher rugosity index indicated a substrate with greater structural complexity. A mean rugosity was calculated for each site by

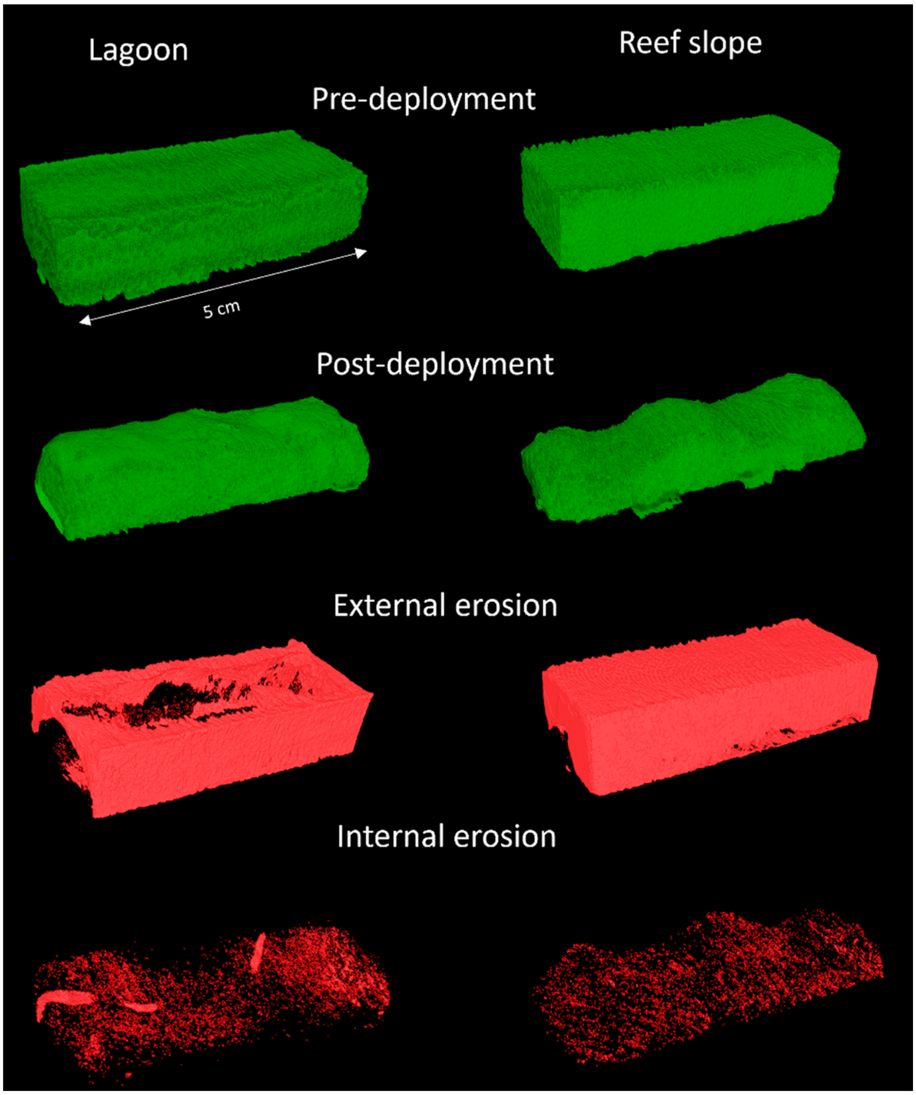

Fig. 1. Micro-computerized tomography (microCT) scans of experimental *Porites* sp. blocks deployed in the lagoon and on the reef slope Ningaloo Reef for 20 months (605 d). Block images show representative scans of two individual blocks (**a**) pre- and (**b**) post-deployment in green, and areas of (**c**) external and (**d**) internal erosion post-deployment in red.

averaging values from surveys conducted in September 2020, September 2021, and May 2022.

Water velocity estimates

Estimates of wave-induced water velocity at the seafloor (daily mean and max) at each study site were derived using the "simulating waves near shore" model (Booij et al. 1999) on a 30 × 30 m grid encompassing the study area. To validate model estimates of water velocity, water velocity loggers (Hobo onset Mat-1) were deployed for 3 months (September 2020–November 2020) at 10 of the 17 sites (6 × reef slope, 4 × lagoon) and the daily mean and maximum water velocities of the model compared with those of the loggers using linear regression. Comparisons between the model and in situ logger daily mean and maximum water velocities revealed a high correlation between predicted and observed values (*see* Supporting Information Results: Mean water velocity $R^2 = 0.7$, maximum water velocity $R^2 = 0.9$).

Statistical analyses

Differences in rates of block erosion (microborer, macroborer, external, total), parrotfish (biomass and estimated erosion of six species), and urchin erosion (estimated erosion) among lagoon and reef slope habitats were examined using analysis of variance (ANOVA "stats" package). ANOVA assumptions of homogeneity of variances and normality were initially tested using Levene's ("car" package) and Shapiro–Wilk tests ("stats" package). In cases where ANOVA assumptions were not met, data were log-transformed. The a priori ANOVA design included deployment length (fixed, 2 levels) × reef position (fixed, 2 levels), with sites a random factor nested within reef position. However, as there were no differences in erosion rates (kg m^{-2} yr^{-1}) between deployment lengths (12 and 20 months), blocks within each deployment length were pooled to improve the level of replication within the reef position. To determine the strength and direction of the relationships among erosion sources and environmental variables (water velocity, reef rugosity, and visible bite marks), Pearson correlation coefficients were calculated (r^2) and significant relationships visualized ("corrplot" package). Differences in the composition of parrotfish assemblages among habitats was tested using PERMANOVA on log-transformed data and a Bray–Curtis similarity matrix. All statistical tests and plots were performed in R version 4.2.2.

Results

Internal and external erosion of blocks

Overall, rates of external erosion on the blocks were 20 times greater than rates of internal erosion (Fig. 2; Table 1). Rates of external erosion were significantly lower and less variable in the lagoon than on the reef slope ($F_{1,31} = 14.53$, $p < 0.01$; Figs. 1, 2). In comparison, rates of internal erosion (micro and macroborer) did not differ between the lagoon and reef slope ($F_{1,2} = 0.069$, $p = 0.79$; $F_{1,31} = 0.031$, $p = 0.84$), however, microborer erosion rates were five to six times higher than macroborer erosion rates (Table 1). The number of visible bite marks on blocks were significantly higher on those deployed on the reef slope than on the lagoon (slope: 7.23 bites/block vs. lagoon: 4.75 bites/block; $F_{1,25} = 4.6$, $p = 0.04$), but did not differ between deployment lengths (12 vs. 20 months: $F_{1,31} = 0.31$, $p = 0.59$).

Parrotfish bioerosion

The estimated rate of parrotfish erosion averaged across all locations was 1.88 ± 0.34 kg m^{-2} yr^{-1}. Parrotfish biomass and indirect estimates of parrotfish erosion were fivefold to sixfold greater on the reef slope than on the lagoon (biomass: $F_{1,16} = 23.25$, $p < 0.01$; erosion: $F_{1,16} = 23.25$, $p < 0.01$; Fig. 3; Table 1). The composition of parrotfish assemblages differed among habitats ($F_{1,24} = 13.83$, $p < 0.001$; *see* Supporting Information Table), with *Chlorurus spilurus* accounting for the majority (40%) of estimated parrotfish erosion within the lagoon and *Chlorurus microrhinos* the majority (84%) of estimated parrotfish erosion on the reef slope (Fig. 3).

Urchin bioerosion

The estimated rate of *E. mathaei* erosion averaged across all locations was 0.52 ± 0.11 kg m^{-2} yr^{-1} (Fig. 2). *E. mathaei* densities and indirect estimates of erosion were 20- and 25-fold higher on the reef slope than on the lagoon, respectively (density: $F_{1,16} = 9.15$, $p < 0.01$; erosion: $F_{1,16} = 9.15$, $p < 0.01$; Fig. 2; *see* Supporting Information Table). Although not measured, the vast majority of *E. mathaei* were estimated to be of a similar size (30–40 mm test diameter).

Physical environmental variables

Reef rugosity was significantly higher on the reef slope than at lagoon sites (Table 1; $F_{1,25} = 25.23$, $p < 0.01$). Similarly, both mean water velocity ($F_{1,25} = 234$, $p < 0.01$) and max water velocity ($F_{1,25} = 1046$, $p < 0.01$), were greater on the reef slope than in the lagoon (Table 1).

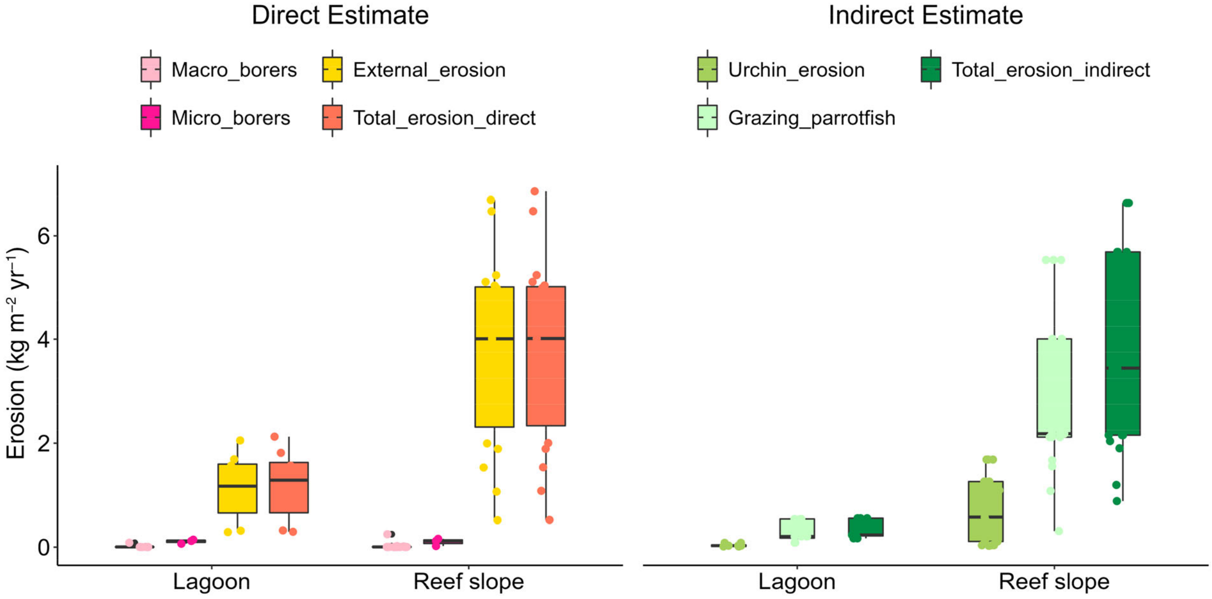

Fig. 2. Direct estimates of erosion by macroborers (light pink), microborers (dark pink), external erosion of blocks (yellow), total erosion (orange), and indirect estimates of erosion by urchins (green), parrotfish (light green) and total indirect erosion (dark green) (kg $CaCO_3$ m^{-2} yr^{-1}) in the lagoon and reef slope habitats at Ningaloo Reef. Box panels represent the interquartile range (IQR) and whiskers the range of values.

Table 1. Mean rates of erosion (kg m^{-2} yr^{-1}) and environmental and biological variables (mean ± se) at lagoon ($n = 7$) and reef slope sites ($n = 10$) at Ningaloo Reef. Direct (blocks) and indirect estimates (census-based) of erosion are shown separately. The percentage of total erosion (direct and indirect) represented by each erosion source within lagoon and reef slope habitats is shown in brackets. Estimates of microborers are based on subsamples from lagoon ($n = 3$) and slope ($n = 3$) blocks.

	Erosion source	Lagoon	Reef slope	Combined
Direct	Internal macroborers (kg m^{-2} yr^{-1})	0.01 ± 0.01 (1%)	0.02 ± 0.01 (0.5%)	0.02 ± 0.01 (0.6%)
	Internal microborers (kg m^{-2} yr^{-1})	0.12 ± 0.04 (9%)	0.11 ± 0.03 (2%)	0.12 ± 0.03 (4%)
	External erosion (kg m^{-2} yr^{-1})	1.13 ± 0.22 (89%)	3.70 ± 0.41 (97%)	2.93 ± 0.37 (94%)
	Total (direct) erosion (kg m^{-2} yr^{-1})	1.26 ± 0.25	3.83 ± 0.43	3.07 ± 0.39
Indirect	Grazing parrotfish (kg m^{-2} yr^{-1})	0.28 ± 0.07 (87%)	2.38 ± 0.35 (76%)	1.88 ± 0.34 (78%)
	Grazing urchins (kg m^{-2} yr^{-1})	0.04 ± 0.01 (13%)	0.73 ± 0.14 (24%)	0.52 ± 0.11 (22%)
	Total (indirect) erosion (kg m^{-2} yr^{-1})	0.32 ± 0.04	3.11 ± 0.24	2.4 ± 0.20
	Unaccounted erosion (kg m^{-2} yr^{-1})	0.81 ± 0.18	0.59 ± 0.33	0.53 ± 0.23
Environmental	Mean water velocity (cm s^{-1})	6.21 ± 2.60	56.83 ± 1.83	41.83 ± 4.76
	Max water velocity (cm s^{-1})	20.05 ± 5.10	155.57 ± 1.66	115.78 ± 12.27
	Depth (m)	3.10 ± 0.06	8.36 ± 0.20	6.96 ± 0.49
	Rugosity ratio	1.19 ± 0.02	1.46 ± 0.03	1.38 ± 0.03

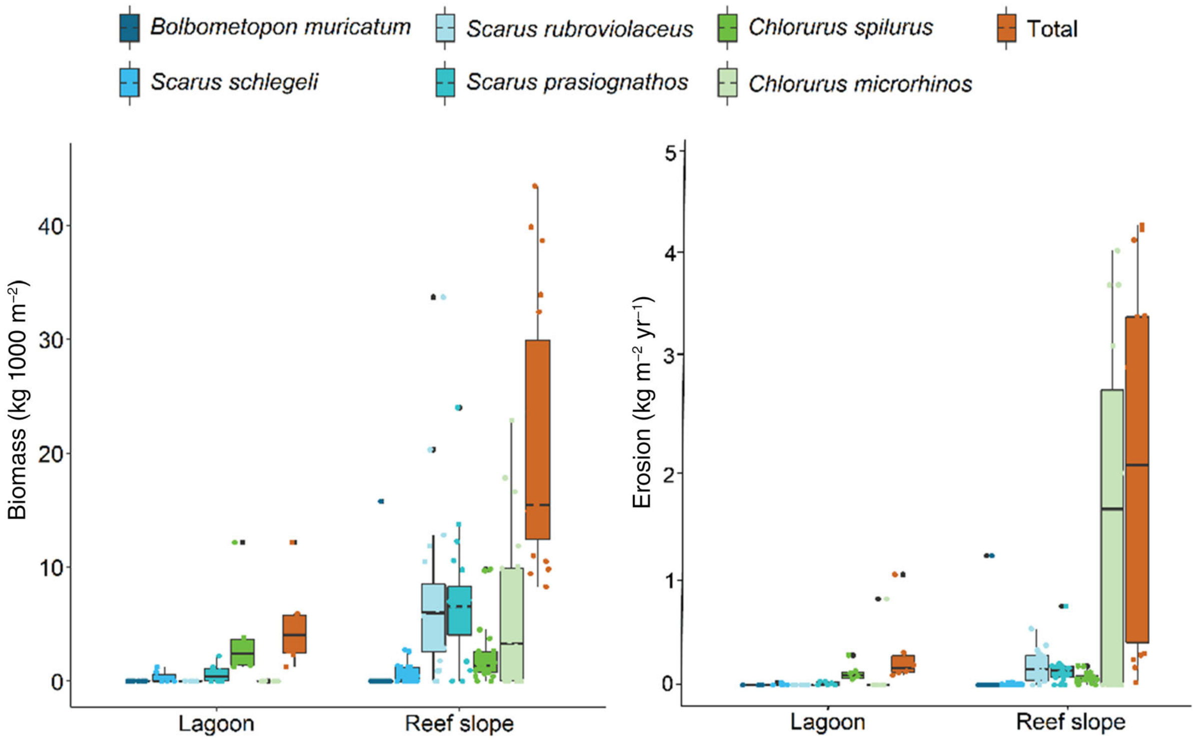

Fig. 3. Parrotfish biomass (kg 1000 m^{-2}) and predicted rates of erosion (kg m^{-2} yr^{-1}) for the six most abundant species of parrotfish in lagoon and reef slope habitats at Ningaloo Reef. Total represents the sum of biomass or erosion by all parrotfish spp. Box panels represent the interquartile range (IQR) and whiskers the range of values.

Predictors of erosion

External erosion was positively correlated ($p < 0.05$) with estimated parrotfish erosion ($r^2 = 0.49$), urchin erosion ($r^2 = 0.50$), maximum water velocity ($r^2 = 0.61$), reef rugosity ($r^2 = 0.47$), and visible bite marks on blocks ($r^2 = 0.44$). Internal erosion by macroborers was not correlated with any variable, including external erosion (*see* Supporting Information Results 2). There was no significant effect of deployment length (12 vs. 20 months) on annual rates of external ($F_{1,31} = 1.08$, $p = 0.3$), internal ($F_{1,31} = 0.46$, $p = 0.5$) or total erosion on blocks ($F_{1,31} = 1.14$, $p = 0.29$).

Table 2. Erosion rates of experimental coral blocks on coral reefs for similar length deployments. Bold values represent the deployment lengths corresponding with erosion rates shown.

Locality	Erosion rate (kg m^{-2} yr^{-1})	Habitat type	Deployment length (months)	Reference
Lizard Island, Great Barrier Reef, Australia	0.69–1.78*	Lagoon, reef flat, reef slope, offshore	**12**	Davies and Hutchings (1983)
Lizard Island, Great Barrier Reef, Australia	0.30–1.96	Lagoon, reef flat, reef slope, offshore	12, **24**, 48	Kiene and Hutchings (1994)
Northern Great Barrier Reef, Australia	0.46–3.6 0.74–2.13	Nearshore, midshore, offshore	**12** **36**	Tribollet and Golubic (2005)
Reunion Is, Indian Ocean	1.64–4.31	Eutrophic, offshore	**12**	Chazottes et al. (1995)
French Polynesia	0.03–6.77	Lagoon	**24** 6, **24**, 60	Pari et al. (1998) Pari et al. (2002)
Inshore, Great Barrier Reef, Australia	0.18–0.27	Lagoon, nearshore	12, **24**, 48	Kiene and Hutchings (1994)
Papua New Guinea	0.8–1.23*	Nearshore, high islands	**24**	Enochs et al. (2016)
Hawaii, Kaneohe Bay	0.02–0.91	Reef flat, reef slope nearshore	**12**	Silbiger et al. (2016) Silbiger et al. (2017)
Exmouth Gulf, Australia	0.152 ± 0.012	Turbid nearshore	**12**	Dee et al. (2023)
Ningaloo Reef	2.95 ± 0.37	Lagoon, reef slope	**20**	This study

*Erosion estimate did not include external grazers.

Discussion

As coral cover decreases worldwide, accurately measuring erosion across a wide range of coral reefs environments is essential. Erosional processes are expected to become disproportionately more important to overall reef carbonate budgets, highlighting the need for improved measurements (Silbiger et al. 2017; Browne et al. 2021). Here we provide the first partitioned estimates of erosion rates across multiple reef habitats at the World Heritage-listed Ningaloo Reef with direct erosion rates of blocks after 20 months representing one of the highest measured erosion rates on experimental coral substrates to date. Erosion rates were approximately four times higher than similar length deployments on offshore reefs of the Great Barrier Reef (Davies and Hutchings 1983; Tribollet and Golubic 2005) and French Polynesia (Pari et al. 2002), and more than 10 times higher than similar length deployments on turbid inshore reefs of the Great Barrier Reef, Hawaii and nearby Exmouth Gulf (Kiene and Hutchings 1994; Silbiger et al. 2017; Dee et al. 2023) (Table 2). Erosion rates often exhibit marked regional variability (Bellwood et al. 2003; Yarlett et al. 2018; Browne et al. 2021) with higher rates of erosion characteristic of offshore reefs with high biomass of grazing parrotfish, urchins and high wave exposure (Madin and Connolly 2006; Hoey and Bellwood 2008; Cheal et al. 2013). Consistent with this expectation, direct external erosion on blocks was highest on the reef slope where indirect estimates of erosion by parrotfish and grazing urchins were also highest.

Parrotfish were a key contributor to erosion at Ningaloo, accounting for 78% of estimates of indirect erosion. Parrotfish are widely recognized as important bioeroders (Bruggemann et al. 1996; Hoey and Bellwood 2008; Ong and Holland 2010), however, there is often a lack of context in how much they contribute to total erosion (Bellwood 1995; Bruggemann et al. 1996). Here, we adopt a more comprehensive approach to evaluating erosion by comparing indirect estimates of parrotfish bioerosion with direct estimates of erosion on experimental blocks. Estimated parrotfish erosion was greater than the combined estimates of the other three sources of erosion in our study: micro and macroborers, grazing urchins, and unaccounted erosion. This disproportionately large contribution of parrotfish erosion was most evident within complex reef slope habitats, where parrotfish erosion was strongly positively correlated with reef rugosity ($r^2 = 0.82$; Supporting Information Results). Our results are consistent with previous studies, which found that grazing parrotfish are the primary bioeroders in exposed, complex, shallow reef environments, contributing between 79% and 84% of total bioerosion (Perry et al. 2012). Caution is needed, however, when comparing parrotfish erosion estimates derived from small experimental blocks made from one coral type (*Porites* sp.) with those on natural reef surfaces, as likely differences in skeletal density, surface morphologies, and the age and composition of the organisms on experimental blocks vs. natural surfaces may result in different rates of grazing (Taylor et al. 2020; Molina-Hernández et al. 2022). Nonetheless, the high rates of external erosion on blocks, combined with high estimates of parrotfish erosion and the positive correlation between these two estimates among sites ($r^2 = 0.49$), supports the theory that grazing parrotfish were the dominant source of erosion at Ningaloo.

Parrotfish erosion was only moderately correlated with parrotfish biomass ($r^2 = 0.55$; *see* Supporting Information Results), indicating sites with high parrotfish biomass did not necessarily have high parrotfish bioerosion rates or vice versa. Rather, the bioerosion rate was determined by the sizes of a few parrotfish species present at each site. The highest contributions to bioerosion were found in the "excavators" *C. microrhinos* and *C. spilurus*, with large individuals of *C. microrhinos* (> 60 cm TL) and *C. spilurus* (> 30 cm TL) most common on the reef slope and lagoon, respectively. As a result, *C. microrhinos* accounted for approximately 84% of all estimated parrotfish erosion on the reef slope, while in the lagoon, where large individuals of *C. microrhinos* were absent, *C. spilurus* accounted for 40% of estimated parrotfish erosion. There are, of course, other bioeroding groups that may not have been adequately accounted for in our estimates, including *Bolbometopon muricatum*, the largest and potentially most important bioeroding parrotfish (Hoey and Bellwood 2008; Bellwood et al. 2012) that was rarely encountered in our surveys. Large individuals of *B. muricatum* occur in ecologically relevant densities throughout our study area (2.38 ind/ha; Thomson et al. 2021), with potential estimated erosion rates an order of magnitude greater than we have estimated (0.3 kg m^{-2} yr^{-1}). The comparatively low estimated erosion rates for *B. muricatum* in our study are likely due to the survey method we used (100 × 10 m UVC transects), which is less reliable for detecting highly mobile, sparsely distributed reef taxa like *B. muricatum*, than the timed swim surveys that cover larger areas (mean length of timed swim transects in Thomson et al. 2021 = 785 × 20 m). In addition, *B. muricatum* are typically found in shallow reef flat and crest habitats (Bellwood et al. 2003; Thomson et al. 2021), which were not surveyed during our study. Nevertheless, the combined estimates of erosion by excavating parrotfish (*C. microrhinos*, *B. muricatum*, and *C. spilurus*) in this study were comparable with combined estimates of erosion for *C. microrhinos* and *C. spilurus* in previous studies at Ningaloo Reef (1.18–2.30 kg m^{-2} yr^{-1}; Johansson 2012) and suggests most bioerosion in reef slope and lagoon environments at Ningaloo Reef is due to grazing by just three species of excavating parrotfishes: *C. microrhinos* and *B. muricatum* on the reef slope and *C. spilurus* in the lagoon.

Rates of microborer erosion after 12 months were five to six times higher than rates of macroborer erosion, although the contribution of both micro and macroborers to block erosion was generally low. Over short timescales (< 3 yrs) bioerosion by internal borers has been shown to undergo ecological succession (Kiene and Hutchings 1994; Tribollet and Golubic 2005; Schönberg et al. 2017), with rates of internal erosion increasing as initially microborers (e.g., bacteria, fungi, algae), then macroborers (e.g., sponges, bivalves, sipunculids) colonize, and consequently weaken the internal reef structure (Chazottes et al. 1995; Pari et al. 2002). Although borer erosion did not increase over the length of our study (12 vs. 20 months), higher rates of micro vs. macroborer erosion in blocks after 12 months suggests longer deployment periods may have resulted in continued ecological succession and greater rates of macroborer erosion (Kiene and Hutchings 1994). However, it is important to note that rates of micro and macroborer bioerosion were likely underestimated during our study, with heavy grazing by parrotfish potentially removing borers in the outer layers of the blocks. Hence, what we effectively measured as micro and macroborer erosion may be better defined as the "residual" borer erosion (as discussed in Chazottes et al. 1995).

Despite very high densities of urchins at several reef slope sites (range 0.11–12.95 ind/m^2), the relative contribution of the grazing urchin *E. mathaei* to indirect erosion was limited (22%). *E. mathaei* is the most abundant grazing urchin at Ningaloo Reef (Babcock et al. 2009; Johansson et al. 2010; Langdon 2012) and on many coral reefs throughout the Indo-Pacific (Keesing 1992; Mokady et al. 1996; Mills et al. 2000). *E. mathaei* have previously been recorded at densities of between 2 and 73 ind/m^2 on reefs in Kenya, Moorea, Eilat, and the Marshall Islands, with estimated rates of erosion rates of between 0.01 and 15.3 kg m^{-2} yr^{-1} (Mokady et al. 1996; Peyrot-Clausade et al. 2000). The cryptic nature of *E. mathaei*, meant our method may have underestimated their abundance, however, *E. mathaei* spine tips were readily visible in the photos used to quantify individuals in burrows (*see* Supporting Information Methods) and previous estimates of erosion by *E. mathaei* at Ningaloo are broadly comparable with our estimates (0.00–0.55 kg m^{-2} yr^{-1}, Johansson 2012; 1.00–4.50 kg m^{-2} yr^{-1}, Langdon 2012). Variation in estimates of erosion by urchins among studies is likely driven by spatial and temporal fluctuations in abundance (Uthicke et al. 2009), although the consistently low estimates of erosion from *E. mathaei* compared to parrotfish indicate urchins are an important but secondary source of reef erosion at Ningaloo Reef.

Interestingly, we found estimated *E. mathaei* erosion to be positively correlated with reef rugosity ($r^2 = 0.48$), indicating reef complexity was higher at sites with high rates of urchin erosion. *E. mathaei* grazing differs to that of parrotfishes in that *E. mathaei* prefer to feed on algae within concave reef structures (furrows), moving back, and forth along the furrow as they feed (Langdon 2012). In contrast, parrotfish preferentially feed on convex surfaces (Bellwood 1996). At high densities (> 3 ind/m^2), *E. mathaei* can create extensive furrow networks, which may enhance small scale reef complexity (Pari et al. 2002; Langdon 2012). The positive correlation we observed between urchin erosion and reef rugosity may then be partially attributable to the actions of *E. mathaei* themselves, rather than just the underlying complexity of the reef. Importantly, *E. mathaei*'s preference to feed exclusively within furrows and only leave the protection of these furrows to defend against neighboring urchins (Langdon 2012) means they are unlikely to have grazed directly on our experimental coral blocks.

Unaccounted erosion, which totaled 0.53 ± 0.23 kg m^{-2} yr^{-1}, probably included components of biological, chemical, and physical erosion. Our direct estimates of water velocities (daily mean and maximum) showed higher water velocities were linked with higher rates of both external block erosion ($r^2 = 0.61$) and estimated parrotfish erosion ($r^2 = 0.71$). However, water velocities were not correlated with unaccounted erosion (non-significant). This suggests that increased water flow might enhance block erosion by facilitating biological (i.e., parrotfish grazing), and/or chemical erosion, rather than by physical abrasion. Alternatively, it could be that parrotfish preferentially feed on blocks due to their prominent location and shape, leading to higher erosion rates on these blocks than our indirect estimates predicted.

Conclusion

This study presents in situ measurements of reef erosion rates across multiple sites and habitats at Ningaloo Reef in the eastern Indian Ocean. By providing detailed, site-specific data on rates of erosion and water movement, we provide valuable information for future erosion estimates and carbonate budget studies on wave-exposed reefs. Direct erosion rates on blocks observed after 20 months are among the highest recorded using this method. The study highlights the significant role of excavating parrotfish, which accounted for approximately 78% of estimated indirect erosion. Furthermore, indirect erosion rates were strongly influenced by the species and sizes of parrotfish present within each reef habitat, rather than the biomass of parrotfish, with one species (*C. microrhinos*) responsible for most bioerosion. The grazing urchin *E. mathaei* was found to have a relatively low contribution to total indirect erosion (22%) despite their occasional high densities at some sites, and internal erosion by micro and macroborers was generally low, likely due to heavy grazing by parrotfish and the relatively short study duration. A substantial portion of external erosion remained unaccounted for, highlighting the importance of improved methods for evaluating erosional processes across different reef environments.

Data availability statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Conflict of Interest

None declared.

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