



REPORT

High herbivory despite high sediment loads on a fringing coral reef

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Abstract Algal turfs are expected to increasingly dominate the benthos of coral reefs in the Anthropocene, becoming important sources of reef productivity. The sediments trapped within algal turfs are known to determine turf condition and influence a range of key ecological processes, particularly the feeding behavior of fishes. Yet, our understanding of the interactions between turfs, sediments and fishes is largely derived from offshore reef systems, where turfs typically contain relatively low sediment loads. Here, we expand on this knowledge by characterizing the properties of turfs and their interactions with fishes on a large, mainland fringing reef system, Ningaloo Reef. Algal turfs varied in algal biomass, height and percent of organic content in the sediment between sites, while the total inorganic and organic sediment loads were comparable. Despite being located in an arid climate with low riverine sediment inputs, turfs in Ningaloo contained an average of 3.5 kg m^{-2} of inorganic sediment, one of the highest loads reported in the literature. Yet, turf feeding rates by fishes in our study were comparable to locations

where inorganic sediment loads are substantially lower. Feeding was dominated by herbivorous fishes ($> 80\%$ of the bites on average), with surgeonfishes being the dominant herbivore feeders (72% of the herbivore bites). In particular, the sediment sucker *Acanthurus grammoptilus* and the cropper *Acanthurus triostegus*—which crops off algal filaments protruding above the sediment layer—were the dominant and most commonly observed feeders. Our results suggest that cropping and sediment-sucking surgeonfishes are able to feed on turfs with high sediment loads, an ability that may prove advantageous in sediment-laden turf-dominated-reefs of the future.

Keywords EAM · Epilithic algal matrix · Coral reef · Algal turf · Long sediment-laden algal turf · Grazing · Ecosystem function · Surgeonfish

Introduction

In the Anthropocene, coral reefs have entered an era of rapid change driven by an increase in the intensity, frequency and duration of disturbance events (Hughes et al. 2018). Many reefs in this era are expected to be characterized by low coral cover and reduced structural complexity (Alvarez-Filip et al. 2009; Hughes et al. 2017), with organisms such as algae, filter-feeders and/or cyanobacteria becoming the primary space occupiers following coral decline (Brown et al. 2017; de Bakker et al. 2017; Jouffray et al. 2019; Vercelloni et al. 2020). As reefs are increasingly shaped by human actions, algal turfs, in particular, are expected to become widespread due to their positive response to many anthropogenic drivers of change (e.g., eutrophication, acidification) and their ability to expand rapidly after disturbance (Connell et al. 2013; Johnson

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et al. 2017; Ellis et al. 2019). Algal turfs are single or multi-species aggregations of algae that form the principal structural component of the epilithic algal matrix (EAM), a term used to refer to the composite detritus, sediment, microalgae, microbes and infauna entrapped by turfs. The increasing prevalence of flatter, turf-dominated reefs is expected to fundamentally reshape ecological functions such as primary productivity, reef accretion, herbivory and coral recruitment (Arnold et al. 2010; Perry and Alvarez-Filip 2018; Tebbett et al. 2020). There is thus a clear need to better understand how the rise of algal turfs will transform reef dynamics and ecosystem services, such as benthic-dependent food chains and the fisheries they support (Bellwood et al. 2019a).

In terms of linking benthic productivity to fisheries production, herbivorous fishes represent a critical energy conduit on coral reefs (Russ and St. John 1988; Morais et al. 2020). Herbivorous fishes deliver key ecosystem functions that may promote the stability and resilience of coral reefs (Perry et al. 2014; Morgan and Kench 2016; Steneck et al. 2018). However, the nature of these functions differs considerably among different functional groups of herbivorous fishes depending on how they interact with the different benthic components across space and time (Humphries et al. 2014). For example, it is well established that browsers feed on large fleshy macroalgae shaping algae-coral competition (e.g., Burkepille and Hay 2008), and that excavators erode coral skeletons and the reef matrix making significant contributions to sediment production and island construction (e.g., Morgan and Kench 2016). Herbivorous fishes that exploit the nutritional resources contained within the EAM (e.g., algae, detritus, cyanobacteria) are the most diverse in terms of the functions that they perform (e.g., sediment, detritus and algae removal), and the ways they feed and interact with the substratum, being partitioned into scrapers; brushers; croppers; concealed croppers; and sediment suckers (Adam et al. 2015, 2018; Marshall and Mumby 2015; Bellwood et al. 2019b). As algal turfs are already a dominant component of contemporary coral reefs worldwide (healthy or degraded; Vroom et al. 2006; Smith et al. 2016; Kennedy et al. 2020), unpacking the drivers of EAM feeding pressure is key to understanding ecosystem functioning on coral reefs (Robinson et al. 2020).

Increasing evidence suggests that the sediments trapped within algal turfs are a major determinant of algal turf condition and a key driver of fish herbivory on reefs (reviewed in Tebbett and Bellwood 2019). Specifically, the quantity and quality of sediments bound within algal turfs both influences—and is influenced by—fish grazing pressure. For example, sediment-laden turfs inhibit the feeding rate of some nominally herbivorous fishes while limiting how effectively others feed (Tebbett et al. 2017a; Duran

et al. 2019), potentially reducing the yield of nutritional resources to these fishes (Choat 1991). Conversely, the grazing activity of nominally herbivorous fishes can remove sediments (Goatley and Bellwood 2010; McAndrews et al. 2019) and maintain short algal turfs with high biomass-specific productivity and low sediment loads (Carpenter 1986; Rasher et al. 2012; Clausing et al. 2014). Recently, it has been recognized that these short productive algal turfs (SPATs) represent a specific state of algal turfs, with decreased grazing and increased sediment deposition leading to transitions to an alternative algal turf state: long sediment-laden algal turfs (LSATs) (Goatley et al. 2016; Fong et al. 2018; Duran et al. 2019). As such, increases in algal turf sediment loads have the potential to impair benthic productivity with bottom-up consequences on herbivorous fish population sizes (Tebbett et al. 2021). Yet, not all herbivorous species feed and interact with algal turfs in the same way (Marshall and Mumby 2015; Gordon et al. 2016a; Tebbett et al. 2017a; Adam et al. 2018; Duran et al. 2019), and identifying which taxa are more resilient to increased sediment inputs—and specifically to what loads—requires further investigation.

Further, while we are clearly beginning to unravel the nature of the interactions between algal turfs, sediments and herbivorous fishes on coral reefs, the vast majority of work on this subject is derived from the Great Barrier Reef (GBR) (e.g., Purcell 2000; Cvitanovic et al. 2007; Tebbett et al. 2018b). There has been limited attention paid to these interactions in other geographic areas with a few notable exceptions (e.g., Florida, Duran et al. 2019; Moorea, Clausing et al. 2014; Fong et al. 2018; and Fiji, Rasher et al. 2012; McAndrews et al. 2019). This represents a substantial knowledge gap, as we do not currently understand how paradigms and insights established on the GBR apply to other reef systems. This is particularly true in the case of coastal fringing reefs, which comprise a large proportion of the world's coral reef area (Burke et al. 2011; Allen Coral Atlas 2020) and frequently contain very high sediment loads relative to offshore barrier reef systems (Field et al. 2008; Tebbett et al. 2018). To address these knowledge gaps, we quantified the nature of the algal turfs and turf feeding pressure by fishes at several sites in Ningaloo Reef, a fringing reef system in Western Australia (Fig. S1A). While previous work in this system has examined herbivory by macroalgal browsers (e.g., Michael et al. 2013), the functional makeup of herbivorous fishes feeding on the EAM and their grazing rates remains unquantified. This is surprising as algal turfs are widespread live benthic components in backreef habitats across Ningaloo (Johansson et al. 2010; van Kuelen and Langdon 2011).

Methods

Study sites

Surveys were conducted within the Jurabi no-take sanctuary zone in the Northern part of Ningaloo Reef in June 2019 (austral winter; dry season). Ningaloo Reef is one of the world's largest fringing reef systems, extending along ca. 250 km of the Western Australian coastline. The reef is exposed to strong oceanic swells across a narrow (8 km) continental shelf and has a characteristic fringing reef structure composed of a lagoon, backreef, reef flat, reef crest and slope (Collins et al. 2003). The slope falls gently from the crest to the continental shelf, and the reef crests and flat are characterized by high wave activity (Collins et al. 2003; Pomeroy et al. 2018). The back reef is either continuous or patchy on sandy substrata, and its live cover is generally dominated by corals, with algal turfs also being abundant particularly in the Northern sections (Johansson et al. 2010; van Kuelen and Langdon 2011). The lagoon features unconsolidated sand with occasional patch reefs dominated by macroalgae (e.g., *Sargassum spp.*, *Dicypoteris spp.*) and algal turfs (Johansson et al. 2010; van Kuelen and Langdon 2011).

We randomly selected five sampling sites located within the inner backreef (Fig. S1B), which is a habitat dominated by algal turfs (34.8–57.7% cover at the site level on average; Table S1). Sites were midway between the reef crest (0.7–1.7 km) and land (0.45–1.4 km) and were between 0.4 and 1.6 km apart. In addition, we selected a site proximal to the wave break and reef crest (hereafter “reef crest”), however, no other sites could be included in this habitat as sea conditions were prohibitive. Although only one reef crest location could be sampled, we included this data in the current study to help contextualise the findings with reef crest data from the GBR (discussed in more detail below).

Benthic sampling

To characterize algal turfs and their sediments at each site, we collected benthic samples of the EAM from haphazardly placed 100 cm² quadrats on flat (< 30° from horizontal) surfaces of reef pavement ($n = 5$ –8 per site). The mean height of the turf vegetation was first estimated at 5 randomly selected points within the quadrat with calipers. All the algae and sediment within the quadrat was then collected using a Venturi suction sampler with a bag attached at the end (63- μ m mesh size). Specifically, the sampler was first placed in contact with the substratum, and all the sediment particles contained within the quadrats suctioned; after 30 s, the sampler was raised ~ 2 cm from

the bottom, and all the algae was carefully scraped off the rock using a metal brush. Encrusting algae was not collected. After suctioning, divers randomly chose another sampling surface fitting the criteria above and at least 5 m apart.

EAM samples were frozen within 6 h of collection and transported to the laboratory. Upon processing, samples were carefully washed with fresh water through a sieve column (2000, 1000, 500, 250, 125 and 63 μ m) to separate the algal components and sediment fraction. All algal fragments were typically retained in the 2 mm sieve and were subsequently separated, blotted dry and weighed. To obtain the size-particle distribution and total benthic particulate load (defined here as the 63–2000 μ m fraction), the size fractions contained within each remaining sieve were then resuspended in separate glass beakers, any visible algal fragments removed, oven-dried at 60 °C for 48 h, and individually weighed. Samples were then bleached with 30% hydrogen peroxide (H₂O₂) for at least a week to remove any organic matter, with frequent stirring and fresh solution added regularly. After bleaching, samples were rinsed with fresh water to remove salts and reweighed to yield total organic and sediment inorganic loads, as well as the percentage of organics in benthic particulates. Finally, samples were treated with 5% hydrochloric acid (HCl) for at least three days and until no bubbles were produced in 24 h to remove carbonates. Samples were then rinsed, dried and weighed as above to yield the percentage of silicates in the inorganic sediment fraction. All loads were standardized to m² for comparability.

Feeding rates on the EAM at Jurabi

We used video assays to characterize the feeding pressure of reef fishes on the EAM-dominated benthos. ‘Feeding’ was deemed to occur every time a fish contacted the benthos with its jaws opened, closing its mouth subsequently, regardless of ingestion. A GoPro video camera on a weighted brick was placed on a random patch of reef substratum dominated by algal turfs (> 90% cover; Fig. S2). Divers temporarily placed two 1 m² metal quadrats to delineate a 2 m² area (ca. 2 m away from the camera), which was filmed until the camera batteries died with a mean recording time of 103 ± 25 min (mean $\pm$ standard deviation; range 71–141 min, Table S3). Five to six cameras were deployed per site (except in the site proximal to the reef crest, where feeding was not assessed due to challenging conditions), with each site being filmed on a single day between ~ 0900 and 1700 h, yielding a total of 23 videos and 39.5 h of video footage (3 cameras malfunctioned, Table S3). Individual fish > 5 cm in total length and feeding on the benthos were identified to the lowest taxonomic level possible (species or genus level)

and assigned to a trophic guild and herbivore functional group if appropriate. Trophic guilds referred to the main energy source for each species (herbivory, benthic invertivory, corallivory and omnivory), while herbivore functional groups were used to provide a more nuanced insight into how the different species of herbivorous fishes interacted with the substratum, and consequently, how sediment may influence their feeding (Table S2). The functional group classifications follow Bellwood et al. (2019b), who originally defined these functional groups based on morphological and behavioral traits which dictate how different herbivorous fishes interact with coral reefs. Feeding rates in each video replicate were standardized by area and time (i.e., bites $\text{m}^{-2} \text{h}^{-1}$), with no relationship between the total duration of video recorded and the total amount of bites recorded (Fig. S3).

Comparison of total sediment loads

To place the algal turf inorganic sediment load data of our study into context, we sourced data obtained through similar methodologies from several published sources. Comparable studies had to (i) collect sediments from natural reef surfaces and (ii) collect similar sediment size fractions to the ones in this study (so comparisons of total load were accurate). All available comparable studies had been conducted on reefs on the Great Barrier Reef (Fig. S1C) (Goatley et al. 2016; Tebbett et al. 2017b, 2018, 2020; Latrille et al. 2019). In all cases, algal turf sediment data were based on samples collected in shallow-water (< 5 m) coral reef habitats including broadly comparable outer reef flats and leeward crests (i.e., back reefs on the GBR) but also exposed crests. Sediments were collected from flat, smooth surfaces (as above), using an electronic vacuum sampler. All samples had been bleached to remove organic matter using the same or a similar process to that outlined above and sieved through a sieve stack (2000, 1000, 500, 250, 125, 63 μm). To ensure the data were comparable to samples taken from Ningaloo, we did not include the < 63 μm size fraction from these datasets. Where available, algal turf length data were collected using the same methods as outlined above.

Statistical analyses

All analyses were conducted within the R statistical environment (R Development Core Team 2016). We tested for differences in turf algal biomass, mean turf height, benthic particulate load, total organic and inorganic sediment loads between sites within Jurabi in Ningaloo Reef using general linear models (GLMs) with a Gaussian error distribution. Site was considered as a fixed effect because we were interested in seeing if the turf characteristics differed

between sites. The proportion of organics in the benthic particulates and the proportion of silicates in the inorganic sediment between sites were compared using beta regression models due to the proportional nature of the data (*betareg* package; Cribari-Neto and Zeileis 2010). To compare the inorganic sediment loads found within turfs in the Jurabi study area with those from other reefs in the GBR, we used a generalized linear model with reef shelf position (coastal, inner-, mid- and outer-shelf), reef identity (nested within shelf position, 13 levels) and reef habitat type (crest, leeward crest and outer flat, crossed factor) as fixed factors and a Gaussian error distribution. Assumptions of the models were assessed by plotting residuals against fitted values and via quantile–quantile plots. Turf algal biomass for the Jurabi comparison and total inorganic sediment load for the GBR comparison were log-transformed (natural logarithm) to achieve homoscedasticity and normality of the residuals.

To test for differences in feeding pressure (bites $\text{m}^{-2} \text{h}^{-1}$) between trophic groups, herbivore functional groups and species in Jurabi, we used three independent generalized linear mixed models with zero-inflated negative binomial distributions (intercept-only model for the zero-inflation) using the *glmmTMB* package (Brooks et al. 2017). This was done due to the absence of bites by different groups in our data. For the species model, only species feeding on turf regularly (i.e., > 1 mean bite $\text{m}^{-2} \text{h}^{-1}$ at a given site) were included (14 out of 26 species). Sampling site was incorporated as a random effect in all models, to control for unmeasured factors that might affect herbivory and facilitate inferences for our Ningaloo study area beyond the particular sites studied. The simulated residuals and dispersion were then checked with the *DHARMa* package (Hartig 2020).

Results

Benthic sampling

Average turf algal biomass ranged from 1 to 260 g fresh weight (FW) m^{-2} between samples and was significantly higher at JB2 and JB4 (one-way ANOVA, $F_{5,25} = 40.9$, $p < 0.001$). Turfs at all sites were dominated by filamentous algae (100% of biomass) except at JB4 where the corticated algae *Lobophora variegata* and *Dictyota dichotoma* were also present and contributed substantially to the biomass (50–99%). There was no relationship between turf biomass and turf sediment load across sites (Fig. S4). Mean algal turf height in Jurabi ranged from 0.11 to 1.33 cm between samples, with JB2 and JB4 having significantly higher, and JB3 significantly lower, heights than the rest of the sites (Fig. 1B). Total benthic particulate

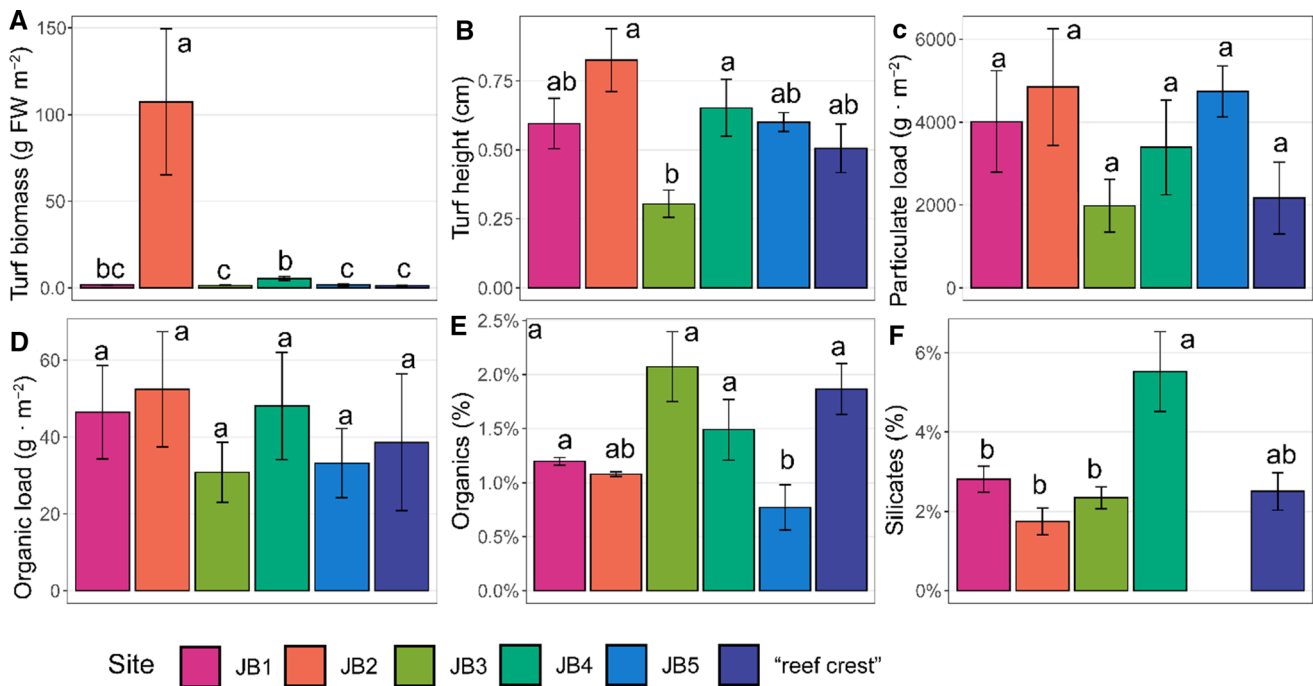


Fig. 1 **a** Algal turf biomass, **b** Mean turf height, **c** benthic particulate load, **d** organic load, **e** percent of organic material in the benthic particulates and **f** percent of silicates in the inorganic sediments from the epilithic algal matrix at 5 study sites on the Jurabi backreef (JB) sanctuary and “reef crest” within Ningaloo Reef. Error bars denote

standard errors while letters denote significant differences between sites. Percent of silicates in the sediments in JB5 could not be determined. $n = 5$ except for JB3 ($n = 8$) and JB4 ($n = 7$) and the reef crest site ($n = 6$)

loads contained within the EAM varied by an order of magnitude within sites (e.g., 206.7–8615.9 g DW m⁻² at JB4), although were comparable among all study sites (one-way ANOVA, $F_{5,25} = 1.57$, $p = 0.19$; Fig. 1c). The average particulate load was 3586 ± 2569 g DW m⁻². The total organic loads ranged from 0.1 to 103.0 g DW m⁻² (average 41 ± 28 g DW m⁻²) and also did not differ among sites (one-way ANOVA, $F_{5,25} = 0.46$, $p = 0.80$; Fig. 1d), constituting between 0.0 and 4.1% (average $1.4 \pm 0.7\%$) of the benthic particulate mass, with JB5 having a significantly lower percentage of organics than the other sites (Fig. 1e). The inorganic sediment from Jurabi was mostly from biogenic origin (i.e., dominated by carbonates; average $96.8 \pm 2.0\%$), with silicates only constituting between 0.1 and 10.6% of the inorganic sediment weight. Notably, JB4 had a significantly higher percentage of silicates than the other sites (5.7%; Fig. 1f).

The algal turfs from Jurabi contained the highest mean inorganic sediment (i.e., particulate – organic) loads of all the reefs examined (3545 ± 2545 g DW m⁻²), being significantly higher than most offshore reefs on the GBR (Fig. 2a). Notably, mean algal turf sediment loads in Jurabi were on average ca. 500, 2500 and 1500% higher than those reported on inner-, mid- and outer-shelf reefs of the GBR, respectively. This was also supported by the relationship between sediment load and algal turf length, which

was positive at both locations but showed a significantly steeper slope in Ningaloo (GLM, Sediment $\times$ Location interaction, $F_{1,100} = 21.05$, $p < 0.0001$), suggesting that long turfs had more sediment in Jurabi (Fig. 2b). Overall, coastal reefs on Ningaloo and the GBR supported higher sediment loads than reefs further offshore (Table 1).

Feeding rates on the EAM at Jurabi

In total, 71 fish species were identified interacting with the EAM at Jurabi, although many did so only rarely. Substratum fish bites were dominated by herbivorous fishes (246.5 ± 234.0 bites m⁻² h⁻¹, GLMM, Wald Chi-square test = 358.8, $df = 3$, $p < 0.0001$) followed by benthic invertivores (58.2 ± 48.8 bites m⁻² h⁻¹), with relatively few bites by corallivores and omnivores (1.1 ± 3.0 and 0.7 ± 1.7 bites m⁻² h⁻¹, respectively; Fig. 3a). Within the herbivorous guild, grazing pressure varied considerably across video assays (30.9 – 1071.8 bites m⁻² h⁻¹) and species (GLMM, Wald Chi-square test = 62.7, $df = 13$, $p < 0.0001$). A total of 26 herbivorous species were observed biting the EAM, although only 14 species had bite rates > 1 bite m⁻² h⁻¹ (Fig. 3b). Indeed, three fish species alone contributed ca. 68% of the total bites on average: *Acanthurus triostegus*, *Ctenochaetus* sp. and

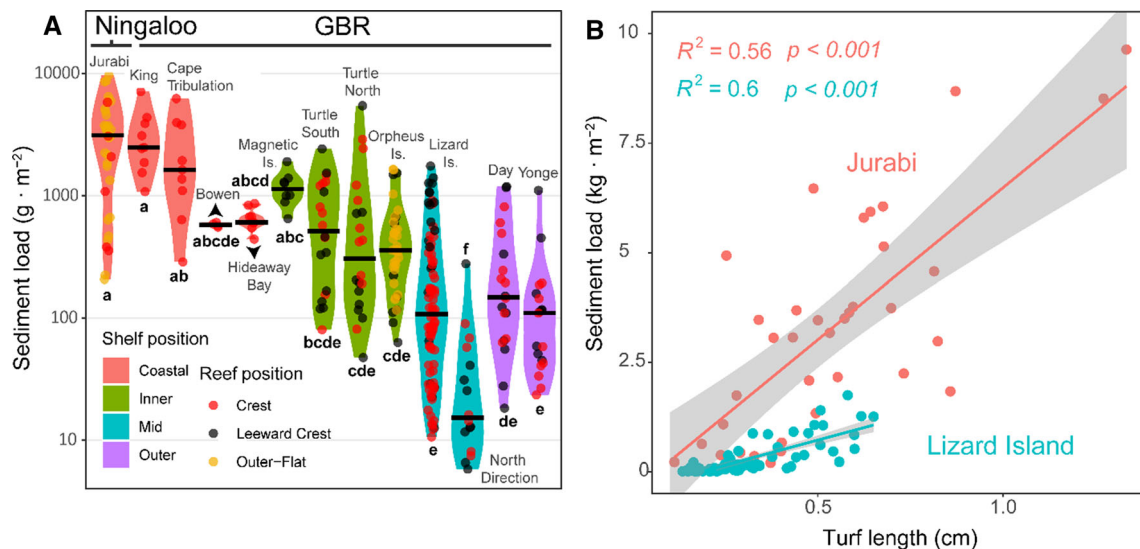


Fig. 2 **a** Total sediment loads (63–2000 μm) in algal turfs within the Jurabi study area in Ningaloo Reef and across the continental shelf of the Great Barrier Reef. The shelf position is indicated by the coloured violin plots, while the habitat sampled within each reef is indicated by the coloured dots **(b)** The relationship between algal turf length and

total sediment load at Jurabi and Lizard Island. Solid lines are predicted values from a linear model, and grey shaded areas denotes the 95% confidence interval. Note the logarithmic scale on the y-axis in panel B

Table 1 Generalized linear model results testing for the effects of reef shelf position, reef identity and reef habitat on inorganic sediment loads (63–2000 μm) across Jurabi (Ningaloo Reef) and reefs in the Great Barrier Reef

Effect	df	Mean SQ	F-value	p-value
Shelf Position	3	129.6	116.7	< 0.0001
Reef identity	9	7.6	6.8	0.001
Reef habitat	2	4.0	3.6	0.030
Shelf position $\times$ Reef habitat	3	5.6	5.0	0.002
Reef identity $\times$ Reef habitat	3	3.3	2.9	0.033
Residuals	276	1.1		

Significant ($\alpha < 0.05$) p-values are indicated in bold

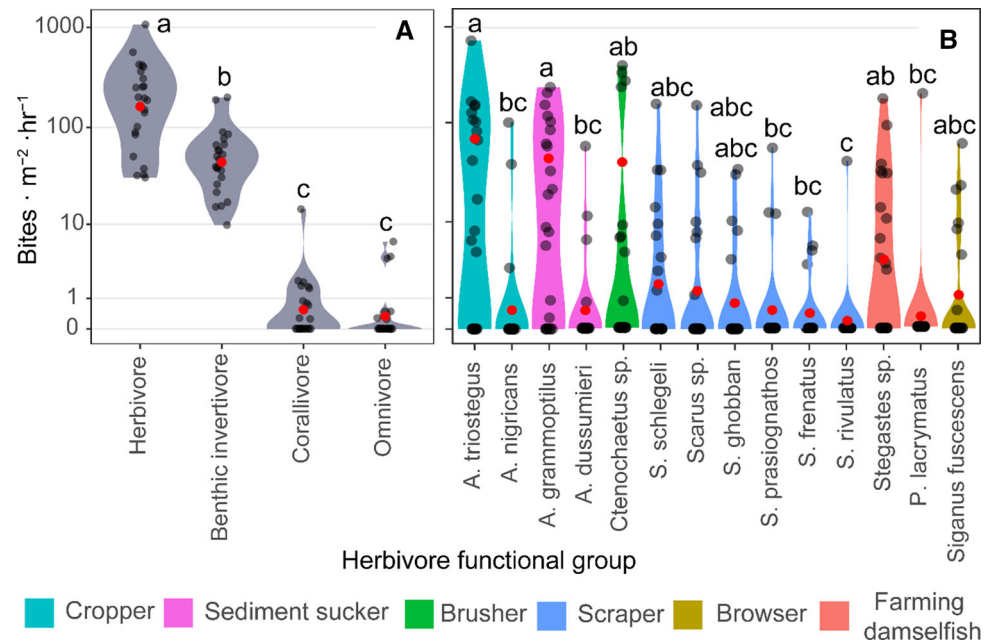
Acanthurus grammoptilus (71.6 ± 134.6 ; 49.6 ± 109.4 and 47.4 ± 67.3 bites $\text{m}^{-2} \text{h}^{-1}$ per video replicate, respectively). *Ctenochaetus* sp. was not observed feeding at two of the sampled locations, however. Overall, surgeonfishes were responsible for the bulk of herbivory (72% of the bites on average; 178.4 ± 191.5 bites $\text{m}^{-2} \text{h}^{-1}$). While parrotfishes and rabbitfishes contributed relatively few bites (32.3 ± 65.5 and 5.7 ± 13.8 bites $\text{m}^{-2} \text{h}^{-1}$, respectively), the mean herbivory rates of several species of parrotfish and rabbitfish (e.g., *Scarus ghobban*, *S. schlegeli*, *Siganus fuscus*) were comparable to some surgeonfish species (Fig. 3b), albeit their contribution to herbivory across samples was highly variable. Bites by benthic invertivores were dominated by the goatfish *Parupeneus barberinoides* and the wrasses *Stethojulis* spp., *Thalassoma*

lunare and *T. lutescens*). *Acanthurus grammoptilus* and *A. triostegus* were the most common herbivores observed feeding (5 and 4 out of 5 sites; 16 and 14 out of 23 videos, respectively), while *Stethojulis* sp. and *Parupeneus barberinoides* were the most commonly observed invertivores (5 and 5 out of 5 sites; 19 and 15 out of 23 videos, respectively).

Discussion

Coral reefs are changing rapidly, and systems dominated by algal turfs are increasingly viewed as one of the most prevalent configurations for reefs in the Anthropocene (Smith et al. 2016; Brown et al. 2017; Jouffray et al. 2019). On such reefs, previous research has suggested that the sediments bound within the algal turfs will be critical in shaping a range of ecosystem functions and interactions between organisms (Birrell et al. 2005; Ricardo et al. 2017; Speare et al. 2019; Tebbett and Bellwood 2019; Evans et al. 2020). In particular, the interactions between nominally herbivorous fishes and algal turfs appear to be closely intertwined with sediments (Bellwood and Fulton 2008; Clausing et al. 2014; Adam et al. 2018; Duran et al. 2019; McAndrews et al. 2019), although much of this understanding has been based on a few reefs from a single reef system—the GBR (Cvitanovic et al. 2007). Here, we show that despite being located in an area with low riverine sediment inputs and strong hydrodynamic activity, turfs in Ningaloo contained notably high sediment loads. However,

Fig. 3 **a** Total number of bites by major fish trophic groups on substrata dominated by algal turfs at Jurabi (JB1–5). Data from our 5 study sites were pooled. **b** Total number of bites by herbivorous fish species (the dominant biters). Herbivorous species with fewer than 1 mean bite $\text{m}^{-2} \text{h}^{-1}$ at any given site are not shown. Red dots denote mean values, while black dots indicate observations of a given camera replicate at a given site. Note logarithmic scale on the y-axis



despite these high sediment loads, feeding rates on algal turfs by nominally herbivorous fishes at our study area are broadly comparable to other reefs systems (Bellwood and Fulton 2008; Rasher et al. 2013; Goatley et al. 2016; Lefcheck et al. 2019), many of which had substantially lower sediment loads. These results shed new light on the context-specificity of interactions between algal turfs, sediments and herbivorous fishes on coral reefs.

Algal turf sediment loads within our Ningaloo sampling area were among the highest reported in the literature, with maximum loads approaching 10 kg m^{-2} . By contrast, McAndrews et al. (2019) reported loads of 0.11 ± 0.03 and $0.07 \pm 0.02 \text{ kg m}^{-2}$ (means $\pm$ SE) for the lagoon slope and reef flat of a reef in Fiji, Kendrick (1991) found $0.04 \pm 0.01 \text{ kg m}^{-2}$ in coralline turfs from the Galápagos Islands, while Logan et al. (2008) reported loads between 0.3 and 6.3 kg m^{-2} in turfs growing on coral rubble. Only other mainland-attached fringing reefs (coastal reefs) in the GBR (e.g., Cape Tribulation, King reef) had comparable average loads to those documented in Jurabi. As turf sediments in the GBR were collected using a similar method, they can be used to contextualize our findings. However, prior to this discussion it is important to note that sediment accumulation in algal turfs on coral reefs results from a complex interplay among hydrodynamic activity, reef complexity, benthic composition, biological activity (e.g., reworking by parrotfishes), and geomorphology (Steneck 1997; Purcell 2000; Tebbett et al. 2017b; Pomeroy et al. 2018). The observed similarities and differences in the amount, granulometry and source of sediments trapped within the turfs of reefs in Ningaloo and GBR could thus be driven by a variety of context specific factors.

Specifically, it is well established that the loads and grain size composition of sediments within algal turfs vary across reef geomorphology (Purcell 2000; Tebbett et al. 2018), substratum elevation and surface angle (Duran et al. 2018; Tebbett et al. 2020), as illustrated by the large within site variation of our samples. Generally, high elevation and reef crest habitats contain less sediment, with sediment increasing with distance from the reef crest (Purcell 2000; Gordon et al. 2016b). While we tried to sample similar habitats and substrata at each of the sampled reefs, it is possible that differences in reef habitat and complexity played a key role in driving the differences observed here. Even so, collection of a few samples in the site proximal to the wave break in Jurabi (“reef crest”) revealed substantial ($> 2 \text{ kg m}^{-2}$) sediment loads (Fig. 2a). Such loads are still an order of magnitude higher than found on broadly comparable reef crests on the GBR (Fig. 2a). In addition, it is important to note that the sediment budgets on individual reefs are also markedly influenced by larger-scale hydrodynamic forcing, which vary substantially depending on the relative position of a reef with respect to the shelf (Wolanski 1994).

Beyond habitat differences it is interesting to note that coastal reefs on the GBR are exposed to regular terrestrial runoff and high suspended sediment concentrations, while experiencing relatively reduced hydrodynamic activity (e.g., oceanic swells), but high wind-driven sediment resuspension due to their shallow depth and position on the shelf (Orpin et al. 1999; Fabricius et al. 2016; Whinney et al. 2017). As a result, turf sediment loads tend to decrease with distance from the shore and can have very-fine-skewed grain size distributions and high silica content

(Tebbett et al. 2018). While the reefs of Ningaloo are also very close to shore (0.2–5 km, Collins et al. 2003), they are located on a much narrower continental shelf and are subject to higher exposure to oceanic swells and relatively less wind-driven sediment resuspension (Collins et al. 2003; Cassata and Collins 2004; Pomeroy et al. 2018), which may explain their relatively coarser sediment size (Fig. S5). Indeed even the relatively sheltered back reef is exposed to strong hydrodynamic activity (Pomeroy et al. 2018).

Ningaloo Reef is also located within an arid climate featuring little rainfall and large evaporation (Cassata and Collins 2004), resulting in low riverine and siliceous sediment inputs. Instead, most of the sediments in this reef system appear to be formed on the reef and are of biogenic origin (i.e., carbonate-dominated), with coral fragments of eroded old (> 1000 yrs) reef framework being the major sediment constituent (Cuttler et al. 2015, 2019). In contrast to fringing reefs located in tropical climates where the majority of sediment is fluvially-derived (e.g., coastal GBR; Moloka'i, Field et al. 2008), the high sediment loads encountered in our study area probably result from sustained landward sediment delivery (Pomeroy et al. 2018), whereby the algal turf matrix essentially acts as a trap when sediment reaches the EAM-dominated backreef, with the mucilaginous nature of the turf matrix potentially promoting sediment retention and reducing flow speeds (Carpenter and Williams 1993; Latrille et al. 2019).

Some of the observed differences in sediment loads between reef systems could also be due to slight methodological variations in the way sediments were collected (electronic vs air-suction sampler). The finer sediment fractions (i.e., < 63 μm), which correspond mostly to siliceous material (Gordon et al. 2016a), could not be collected in the air-suction sampling method used in Ningaloo as it is limited by the mesh size of the bag where sediments accumulate. These minor methodological disparities are however unlikely to account for the large differences observed between Ningaloo and most GBR reefs) as (i) we excluded the < 63 μm fraction from all the GBR samples and (ii) other studies considering that fraction found that it represents a minor percentage of the total sediment load in Ningaloo (Cuttler et al. 2015).

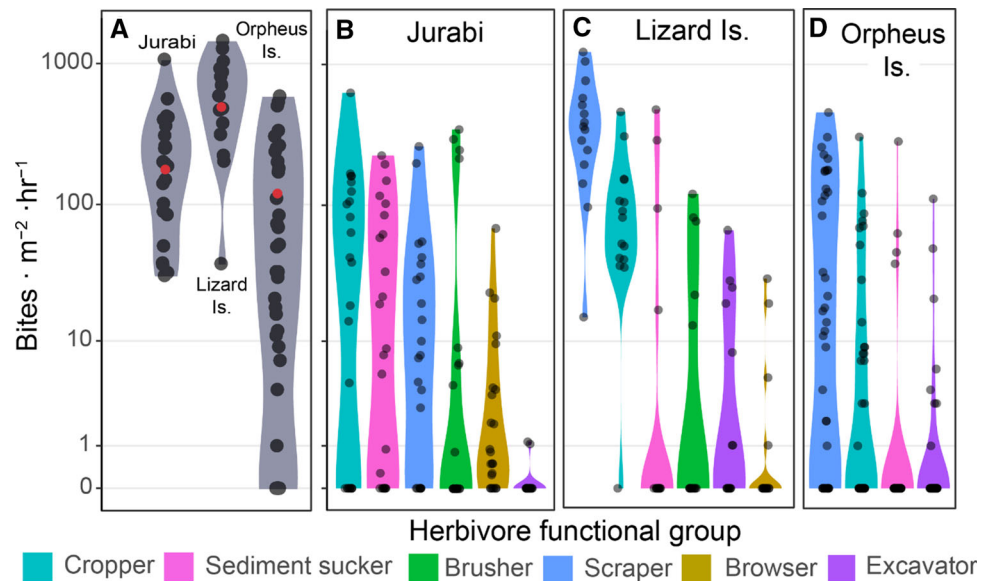
Additional potential drivers of the high sediment loads at Jurabi could be related to the organisms that generate and rework the sediment that accumulates in algal turfs. Sediment generation can be driven by reef bioerosion by sea urchins and parrotfishes, both of which are abundant at Ningaloo (Johansson et al. 2010). Sea urchins are largely restricted to the outer slope (Johansson et al. 2010), and may be responsible for generating up to $\sim 0.55 \text{ kg m}^{-2} \text{ yr}^{-1}$ of eroded material, that largely contributes to lagoon and beach sediment (Cuttler et al.

2019). In contrast, sea urchins are generally rare on the GBR and only play a minor role in bioerosion (Sammarco 1985). On the GBR parrotfishes represent the primary bioeroders, although this is dependent on shelf position, with relatively low parrotfish sediment production rates on inner-shelf reefs (Hoey and Bellwood 2008). At Ningaloo, parrotfishes also play a clear role in bioerosion and sediment production as they remove $1.18\text{--}2.3 \text{ kg m}^{-2}$ of reef matrix annually (Johansson et al. 2010), with grain size analysis suggesting that they may contribute to the sediment loads of the reef flat (Cuttler et al. 2019). Overall, however, it is clear that variation in a range of abiotic and biotic factors may be responsible for varying algal turf sediment loads among the different reef locations.

Whether the sediment loads encountered here are representative of the entirety of Ningaloo Reef remains to be investigated. The mechanisms of sediment delivery in this system are, however similar across its length, being largely dependent on reef geomorphology (Pomeroy et al. 2018; Cuttler et al. 2019), which suggests that high loads may occur in other backreef areas. Previous studies show that sediment delivery and transport in Ningaloo occurs cross-reef, with wave energy becoming weaker and sediments become finer shoreward with increasing distance from the reef crest (Cuttler et al. 2015). This is consistent with the grain size spectra of our sampling sites, which were dominated by fine sands (Fig. S5). While we found some differences in turf composition (e.g., presence or absence of corticated algae) and algal biomass between sites, these was no relationship with particulate or inorganic sediment loads. The only important predictor of sediment load was turf algal length, which aligns with previous findings in other reefs (Purcell 2000; McAndrews et al. 2019; Tebbett and Bellwood 2019).

Interestingly, despite the relatively high sediment loads encountered at Jurabi, total feeding rates by herbivorous fishes ($246.5 \pm 234.0 \text{ bites h}^{-1} \text{ m}^{-2}$; means $\pm$ SD) were similar to those registered on other coral reefs (e.g., Lakshadweep, $60\text{--}150 \text{ bites h}^{-1} \text{ m}^{-2}$, Karkarey et al. 2020; Fiji, ca. $270 \text{ bites h}^{-1} \text{ m}^{-2}$, Rasher et al. 2013; American Samoa, ca. $308 \text{ bites h}^{-1} \text{ m}^{-2}$, Craig 1996; Dominican Republic, $15\text{--}408 \text{ bites h}^{-1} \text{ m}^{-2}$ Lefcheck et al. 2019). Total feeding rates were also broadly comparable to reefs on the GBR where turf sediments have been well-characterized, and herbivory assays were conducted using a similar protocol (e.g., Orpheus Island, $110.7 \pm 159.2 \text{ bites h}^{-1} \text{ m}^{-2}$; Lizard Island, $653.9 \pm 410.5 \text{ bites h}^{-1} \text{ m}^{-2}$, Supplementary text, Fig. 4a), albeit the functional composition of herbivorous fishes involved in feeding appears to be different between the two biogeographic regions (Fig. 4b–d). Feeding pressure on the EAM in Ningaloo was dominated by cropping, sediment-sucking and brushing surgeonfishes ($69 \pm 26\%$ of the bites per video replicate),

Fig. 4 **a** Absolute herbivore feeding pressure on algal turfs at our study sites in Jurabi (Ningaloo Reef), Lizard and Orpheus Islands (GBR). **b–c** Herbivore feeding pressure by main functional groups across locations (see Table S2 for details on the groupings). Bites by fish < 10 cm total length were not counted at Orpheus Island. Note logarithmic scale on the y-axis



while scrapers dominated grazing pressure on the EAM at Orpheus and Lizard Island (68 ± 37 and $65 \pm 20\%$ of the bites per video replicate, respectively). Differences among reef areas in the herbivorous fish groups responsible for the majority of feeding pressure may reflect the local fish assemblage, as species-specific feeding pressure is usually correlated with fish abundance and biomass (Karkarey et al. 2020). Indeed, previous studies have found surgeonfishes (and particularly the cropping *Acanthurus triostegus*) are generally the dominant herbivores on Ningaloo reefs (Johansson et al. 2010), while the coastal and inshore reefs of the GBR have high abundances of scraping parrotfishes (Hoey and Bellwood 2008; Cheal et al. 2012; McClure et al. 2019). Yet, parrotfishes can be as abundant as surgeonfishes in Jurabi and other Ningaloo sites, and their densities are also comparable to that of Orpheus and Lizard Island (Johansson et al. 2010; Edgar and Stuart-Smith 2014, 2021; Tebbett et al. 2021), Fig. S6). The lower contribution of parrotfishes to herbivorous fish feeding pressure at Jurabi, despite their abundance, is therefore intriguing.

Beyond biogeographical differences in herbivorous fish community composition, the herbivory rates documented at Jurabi may be due to a range of other factors. For example, the relative availability of substrata and habitat structural complexity are important controls of herbivory on coral reefs (Robinson et al. 2020). Furthermore, the relative absence of parrotfish feeding, yet overall high herbivory rates despite the relatively high sediment loads at Jurabi, could also be explained by the way herbivorous fish functional groups interact with the EAM when feeding. For example, croppers such as *A. triostegus* generally have multi-denticulate teeth that allow them to selectively crop filamentous algae that protrudes above the layer of

sediment bound within the EAM (Randall 1961; Hatcher 1981), with experimental evidence showing that they are relatively resilient to increasing sediment loads. In laboratory experiments, Randall (1961) mixed fine sand with a finely-branched filamentous algae and observed *Acanthurus triostegus* meticulously picking out the filaments projecting above the sand, while Tebbett et al. (2017a) found that the cropper *Acanthurus nigrofusus* continued feeding despite increasing sediment loads. Importantly, however, the sediment loads encountered in our study are an order of magnitude higher than those used experimentally in the laboratory (i.e., ca. $75\text{--}450 \text{ g m}^{-2}$; Tebbett et al. 2017a), which reinforces evidence that croppers can continue feeding even at very high sediment loads. By contrast, the fused, beak-like teeth of scraping parrotfishes means that they interact closely with the substratum, scraping and ingesting sediment when feeding (Bruggemann et al. 1996), potentially making them sensitive to sediment loads (Gordon et al. 2016a). Still, some parrotfishes are able to feed on long turfs with deep sediments (Adam et al. 2018), and some *Scarus spp.* had comparable feeding rates to the surgeonfish species in our video assays. It is also important to note that the relatively high feeding rates of *C. striatus* at the study site, despite their sensitivity to sediments on the GBR (Tebbett et al. 2017a), is intriguing and warrants further investigation in the future. Indeed, studies examining the relationships between sediment load, fish abundance and identity and feeding pressure across larger spatial scales in the Ningaloo region are likely to help shed new light on the patterns described here.

It should be noted that a limitation of our study is that the sediment loads were not directly measured in the same plots where herbivory was measured, which could result in herbivory varying as a function of sediment load on a plot-

to-plot basis (e.g., low herbivory in high sediment plots). However, this is unlikely to have biased our observations as all the turf and video assays at each site were conducted within a small area (ca. 50 m²). Furthermore, we still recorded minimum, mean and maximum bite rates that were comparable or higher than those from other reefs, despite the minimum possible sediment load (i.e., the minimum value registered in any of the samples taken) at our sites still being high (Table 2). For example, surgeonfish and parrotfish bite rates upwards of 390 and 40 bites h⁻¹ m⁻², respectively, were documented in some video replicates at JB1, where the minimal sediment load was 2.2 kg m⁻². In comparison at Orpheus Island, where the mean sediment load is 0.5 kg m⁻² (maximum of 1.6 kg m⁻²) mean bite rates ranged from 93–107 bites h⁻¹ m⁻² across sites. Therefore, despite the potential for among plot variability in our data, the overall inference that herbivory rates were high, and sediment loads were also high, holds.

Into the future, algal turfs are predicted to accumulate more sediment as reefs lose complexity, even when sediment inputs remain unchanged (Tebbett et al. 2020), which has been suggested to lead to suppressed herbivory and decreased reef resilience (Bellwood and Fulton 2008; Goatley and Bellwood 2012; Goatley et al. 2016). The patterns described herein, however, suggest that croppers and sediment suckers may persist on reefs that are increasingly dominated by sediment-laden turfs, as they appear to be able to continue feeding from the EAM (as long as there is algal material protruding above the layer of sediments). It is important to note, however, that prior evidence highlights these fishes still preferentially feed on turfs with low sediment loads (Duran et al. 2019), and increase their feeding when sediments are removed (Bellwood and Fulton 2008). Nevertheless, our results highlight the context-specific nature of algal turf sediment loads, and interactions between herbivorous fishes and algal turfs. Overall, our results suggest that high sediment loads can occur on reefs where terrestrial inputs are minimal, and that

herbivory can still continue in areas with sediment-laden turfs. Expanding the biogeographical contexts under which the interactions between algal turfs, sediments and fishes are characterized represents a critical step forward in our understanding of turf-dominated Anthropocene coral reefs.

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Table 2 Minimum, mean and maximum bite rates by herbivorous fishes on the epilithic algal matrix and turf sediment load at our study sites in Jurabi (JB)

Site	Bite rate (bites h ⁻¹ m ⁻²)			Sediments (kg m ⁻²)		
	Min	Mean	Max	Min	Mean	Max
JB1	102	234	403	2.2	4.0	8.7
JB2	38	172	364	1.8	4.8	9.6
JB3	142	345	566	0.2	1.9	4.9
JB4	259	586	1072	0.2	3.3	8.5
JB5	31	55	89	3.6	4.7	6.5

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