Sediment suppresses herbivory across a coral reef depth gradient

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Sediments are a ubiquitous feature of all coral reefs, yet our understanding of how they affect complex ecological processes on coral reefs is limited. Sediment in algal turfs has been shown to suppress herbivory by coral reef fishes on high-sediment, low-herbivory reef flats. Here, we investigate the role of sediment in suppressing herbivory across a depth gradient (reef base, crest and flat) by observing fish feeding following benthic sediment reductions. We found that sediment suppresses herbivory across all reef zones. Even slight reductions on the reef crest, which has 35 times less sediment than the reef flat, resulted in over 1800 more herbivore bites (h⁻¹ m⁻²). The Acanthuridae (surgeonfishes) were responsible for over 80% of all bites observed, and on the reef crest and flat took over 1500 more bites (h⁻¹ m⁻²) when sediment load was reduced. These findings highlight the role of natural sediment loads in shaping coral reef herbivory and suggest that changes in benthic sediment loads could directly impair reef resilience.

Keywords: sediment; herbivory; reef fish; coral reef; epilithic algal matrix; depth

1. INTRODUCTION

Sediments are a ubiquitous feature of coral reefs. Calcification by benthic organisms produces the carbonate reef matrix, which is then reduced to sediment by biological and physical erosion [1,2]. While most sediment is transported off reefs [3–5], some remains trapped within the epilithic algal matrix (EAM [6]; a composite of algal turfs, detritus, infauna and sediments found on all reefs, often as the most common benthic component [7–9]). While sediments provide an important function in reef accretion, infilling crevices and cementing the reef framework [10], recent evidence suggests that EAM-bound sediments can be ecologically deleterious, reducing coral recruitment [11] and suppressing herbivory; both vital ecological functions on coral reefs [12].

Coral reefs rely on a suite of ecological functions to maintain their resilience to disturbances. Among the most important functions is herbivory, provided mainly by herbivorous reef fishes [13]. These fishes maintain algae as well-cropped turfs and help in the prevention of, or recovery from, phase-shifts to macroalgal-dominated states [13]. Reduced herbivory owing to overfishing is well documented as a driver of macroalgal phase-shifts [13,14]. However, it appears that herbivory is also suppressed by sediments [12,15], although the extent of this interaction is poorly understood. Currently, our knowledge of the ecological impacts of sediments on herbivory is limited to just one reef zone; the reef flat, where sediment loads are highest [16], and corals and herbivores least abundant [17,18]. Little is known about how sediments affect herbivory in other reef zones.

Typical coral reefs have a distinct base, slope, crest and flat (figure 1a; [16]). The reef crest is normally the zone of highest wave action, accretion, productivity and herbivore activity [18,19]. While the reef crest is one of the most dynamic, and arguably, most important reef zones in terms of resistance and resilience to the effects of disturbances [19], little is known of the effects of sediment in this zone. From a physical perspective, the high hydrodynamic activity on the reef crest should keep benthic sediments low [16], however, sediment loads can change rapidly with natural or anthropogenic disturbances [4,20] and, as such, have the potential to affect herbivory. Here, we aim to assess sediment suppression of herbivory across a coral reef depth gradient including the reef base, crest and flat.

2. MATERIAL AND METHODS

Experimental manipulations were conducted in December and January (2009–2010), across a 300 m section of exposed reef, off Lizard Island in the northern Great Barrier Reef, Australia (14°41′00″S, 145°27′45″E). The reef flat, crest and base were selected for comparisons (figure 1a). The reef flat at the study site has low complexity, few corals, a depth of 1–3 m, and is sheltered from breaking waves by the reef crest. The crest is 3–6 m deep, has the highest topographic complexity and relatively abundant corals, predominantly Acropora and Pocillopora. At the reef base, manipulations were conducted on the consolidated reef matrix just above the transition to sand at 12–15 m.

In each reef zone, 20 sediment samples were collected as a baseline by haphazardly placing a 5.8 × 10⁻³ m² PVC ring on the EAM and collecting enclosed sediments using an electric vacuum sampler [16]. Manipulations were conducted by delineating haphazardly selected areas of EAM using a 1.5 × 1.5 m PVC frame. Half of the frame was kept as a control plot and was covered in clear plastic sheeting to ensure that no sediment was disturbed. The other half was cleared of sediment using a compressed air-gun to loosen sediments from the EAM and an airlift with a 5 m outlet hose to remove them [12]. Care was taken to ensure that removed sediments were deposited down-current, preventing sediments resettling on the plots. Benthic sediment loads in manipulated plots were reduced by 79% (9.4% tested using the vacuum sampler (as above), 10 min following airlift/air gun sediment removal, to control for sediment resettlement; figure 1b). Following sediment removal, a video camera was mounted on a tripod so that both the treatment and control plots were in view. The PVC frame was removed after 30 s of recording to allow calibration of the videos. The camera was left recording for at least 4 h 30 min. Videos were viewed on a computer with the plots marked on an overlaid transparent film. Bites by herbivores (parrotfishes [scarine labrids], rabbitfishes [Siganidae] and surgeonfishes [Acanthuridae]) in both cleared and control plots were counted in 1 of 15 min of each hour, resulting in 1 h of data per replicate. Owing to logistical constraints the sampling was unbalanced between reef zones; 8, 5 and 6 replicate videos were recorded on the base, crest and flat, respectively. Overall, bite rate data and the impact of individual taxa were analysed using analyses of variances (ANOVA; Type II S.S. owing to the unbalanced design [21]), fourth-root transformations were applied to ensure assumptions were met. All data are presented as mean ± s.e. throughout.

3. RESULTS AND DISCUSSION

A total of 32 477 bites by herbivorous reef fishes were observed. Of these, 26 838 (82.6%) were in cleared plots (figure 1c, see the electronic supplementary material).
Sediment reductions resulted in higher herbivore feeding rates in all three zones \( (F_{1,108} = 5.2, p = 0.03) \), although the extent of responses among reef zones differed \( (F_{2,108} = 13.4, p < 0.0001) \). We document a general response of increasing herbivory following sediment reduction, extending beyond previous observations in high-sediment locations \( (\text{where sediment loads are over 8 kg m}^{-2}; \text{figure 1} b, c) \). The effect of sediment removal on the reef crest is particularly surprising, as the crest sediment loads were the lowest detected in any reef zone, with only 237.8 ± 3.2 g m\(^{-2}\); i.e. 35 times less than the reef flat \( (\text{figure 1} b) \). It is well known that reef crests have the highest herbivore abundances and highest rates of herbivory \( [17–19] \), explaining the high bite rates in the control plots. However, what was particularly striking was that a sediment reduction of less than 150 g m\(^{-2}\) on the crest had a comparable effect on herbivores as a reduction of over 7800 g m\(^{-2}\) on the flat. It appears that fishes may be far more sensitive to sediments on reefs than previously thought. Alongside potential feedbacks involving reduced herbivory, algal growth and sediment trapping \( [12,22] \), any changes in sediment loads, therefore, appear to have the potential to fundamentally alter vital ecological processes on coral reefs.

When considering specific taxa, the surgeonfishes were responsible for the largest number of bites, taking 82.8 per cent of all bites observed. The disparity in bites compared with the other taxa does not correspond with a faster bite rate or higher abundance of surgeonfishes on the reef studied. Both are similar to those of parrotfish in this region \( [5,23,24] \). While the proportional response of the surgeonfishes to sediment reduction did not differ from the other taxa \( (\text{see the electronic supplementary material}) \), the high number of bites by this taxon led to a considerable difference in the number of bites taken from cleared plots \( (\text{figure 2}; \text{ANOVA interaction: } F_{4,48} = 5.5, p = 0.004; \text{see the electronic supplementary material}) \). This probably corresponds with surgeonfishes’ known preference for feeding on flat reef surfaces \( [25] \), similar to those selected for this study. The surgeonfishes, it appears, are of considerable importance as herbivores of EAMs on low-complexity surfaces on the crest and flat.

With regard to the other taxa, the parrotfishes showed the largest difference following sediment removal on the crest \( (\text{see the electronic supplementary material}) \), reflecting earlier studies \( [3,18] \) and emphasizing the value of low sediment locations for these fishes. Rabbitfishes, in contrast, showed the largest response on the reef flat \( (\text{notably } Siganus argenteus \text{ and } Siganus spinus) \) and base \( (\text{predominantly } Siganus doliatus); \text{electronic supplementary material}) \), reflecting reported division within the family relating to morphological and behavioural attributes \( [26] \).

Our study revealed that herbivorous coral reef fishes are highly sensitive to changing benthic sediment loads. It is not only in high-sediment areas that sediments affect herbivory. Even on the reef crest \( (\text{with 35 times less sediment than the flat}) \), a moderate sediment reduction resulted in considerably higher bite
rates. It appears that even very slight changes in sediment loads have the potential to critically alter ecological processes on coral reefs. Natural or anthropogenic disturbances that modify benthic sediment loads (e.g., storms or dredging [27,28]) could, therefore, markedly alter patterns of herbivory, leading to reductions in reef resilience and recovery potential.

All procedures were conducted according to the ethics guidelines of James Cook University, Townsville (approval: A1522), and permitting requirements of the Great Barrier Reef Marine Parks Authority (permit: G10/33755.1).

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