Tebbett, Sterling B., Goatley, Christopher H. R., Streit, Robert P., and Bellwood, David R. (2020) ***Algal turf sediments limit the spatial extent of function delivery on coral reefs.*** **Science of the Total Environment, 734 .**

Algal turf sediments limit the spatial extent of function delivery on coral reefs

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Abstract

The presence of key organisms is frequently associated with the delivery of specific ecosystem functions. Areas with such organisms are therefore often considered to have greater levels of these functions. While this assumption has been the backbone of coral reef ecosystem-based management approaches for decades, we currently have only a limited understanding of how fish presence equates to function on coral reefs and whether this relationship is susceptible to stressors. To assess the capacity of a stressor to shape function delivery we used a multi-scale approach ranging from tens of kilometres across the continental shelf of Australia's Great Barrier Reef, down to centimetres within a reef habitat. At each scale, we quantified the spatial extent of a model function (detritivory) by a coral reef surgeonfish (*Ctenochaetus striatus*) and its potential to be shaped by sediments. At broad spatial scales, *C. striatus* presence was correlated strongly with algal turf sediment loads, while at smaller spatial scales, function delivery appears to be constrained by algal turf sediment distributions. In all cases, sediment loads above ~250-500 g m^{-2} were associated with a marked decrease in fish abundance or feeding activity, suggesting that a common ecological threshold lies within this range. Our results reveal a complex functional dynamic between proximate agents of function delivery (fish) and the ultimate drivers of function delivery (sediments), which emphasizes: a) weaknesses in the assumed links between fish presence and function, and b) the multi-scale capacity of algal turf sediments to shape reef processes. Unless direct extractive activities (e.g. fishing) are the main driver of function loss on coral reefs, managing to conserve fish abundance is unlikely to yield the desired outcomes. It only addresses one potential driver. Instead, management of both the agents that deliver functions (e.g. fishes), and the drivers that modify functions (e.g. sediments), are needed.

Key words:

Algal turfs; Coral reefs; Ecosystem function; Ecosystem management; Fish; Resilience

1. Introduction

In the past it has been widely considered that maintaining the abundance of particular organisms or functional groups on coral reefs will, by proxy, maintain the ecosystem functions delivered by these taxa/groups (Bellwood et al., 2004; Graham et al., 2013; Hughes et al., 2010; Strain et al., 2018). This assumption has underpinned coral reef management approaches that usually focus on conserving the abundance of key organisms in an effort to preserve ecosystems in desired configurations that are resilient to change (Mcleod et al., 2019; Mumby and Steneck, 2008; Steneck et al., 2018). Such resilience-based management approaches are often implemented via national parks or marine protected areas (MPAs) (Chung et al., 2019; Roberts et al., 2017; Steneck et al., 2019; Williams et al., 2019). Rather than managing the realised function (i.e. the movement or storage of energy or material [Bellwood et al., 2019b]), these management approaches conserve the abundance of the agents (often fishes) that deliver key functions (Chung et al., 2019; Steneck et al., 2019; Williams et al., 2019). However, the limitations of these approaches for conserving coral reef ecosystems are becoming increasingly apparent (reviewed in Bates et al., 2019; Bellwood et al., 2019a; Bruno et al., 2019; but see Steneck et al., 2019). At the heart of these limitations lies our assumption that the presence of fish is a good proxy for the application of their specific ecosystem functions, and our limited understanding of the factors that constrain the application of these functions.

Based on the assumption that the presence of fish is equal to function, no-take MPAs are often used to manage reefs by restricting extractive activities and therefore controlling the removal of functionally-important fishes (Chung et al., 2019; McCook et al., 2010; Roberts et al., 2017; Williams et al., 2019). However, the most pervasive stressors of coral reef ecosystems often transcend MPA boundaries (Graham et al., 2020; Jones et al., 2004; Suchley and Alvarez-Filip, 2018). At the forefront of these stressors is global climate change, which indiscriminately degrades coral reefs through mass coral bleaching and subsequent habitat degradation (Bruno et al., 2019; Graham et al., 2020; Hughes et al., 2017b; Jones et al., 2004). After climate-change, a major stressor faced by reefs is increased sediment inputs via terrestrial runoff, coastal development, and related dredging activities (Bainbridge et al., 2018; Erftemeijer et al., 2012; Fabricius, 2005; Suchley and Alvarez-filip, 2018). Indeed, globally, more than 50% of reefs are at risk of increased terrestrial inputs (Burke et al., 2011). These sediment increases often have widespread impacts inside and outside of MPAs (Bégin et al., 2016; Suchley and Alvarez-filip, 2018; Wenger et al., 2016).

Increasing sediment inputs on coral reefs can have profound implications for ecosystem functions (Bainbridge et al., 2018; Fabricius, 2005; Wenger et al., 2017). This is particularly apparent when sediments become bound within algal turfs (Birrell et al., 2005; Latrille et al., 2019; Speare et al., 2019; Tebbett and Bellwood, 2020) to become part of the epilithic algal matrix (EAM: i.e. the matrix of algal turfs, inorganic sediment, organic detritus, microalgae and microbes *sensu* Wilson et al., 2003). It appears that understanding the impacts of increased sediment accumulation in algal turfs will be critical on Anthropocene reefs (Bellwood et al., 2019b; Tebbett and Bellwood, 2019). This is because algal turfs are expected to increase in cover on many climate-modified coral reefs (Bellwood et al., 2019b; Jouffray et al., 2015; Smith et al., 2016), and because algal turfs represent a critical interface that will shape key processes such as coral settlement (Birrell et al., 2005; Ford et al., 2018; Speare et al., 2019), herbivory/detritivory (Eurich et al., 2018; Kelly et al., 2016; Tebbett et al., 2017a) and benthic productivity (Tebbett and Bellwood, 2020). Any alteration of these key reef processes, by sediments accumulated in algal turfs, is likely to have important bottom-up consequences for coral reef ecosystems.

A particularly sobering example of such consequences followed a 37-fold increase in algal turf sediment loads in an MPA on the Great Barrier Reef (GBR) (Goatley et al., 2016). Despite the superficial appearance of resilience (a diverse and abundant herbivorous fish assemblage) (see Ford et al., 2018), the delivery of functions by fishes (e.g. fish feeding rates) collapsed, leading to transitions in benthic conditions (Goatley et al., 2016). These results bring to the fore a significant and ongoing problem in our study of functions on coral reefs. This was clearly noted by Steneck (1983): “it is generally assumed that the abundance of herbivores corresponds with their impact on algae. This assumption has never been tested.” For many functions, this sentiment remains as true today as it did in 1983 (see Bellwood et al., 2019b). On coral reefs, we currently lack a clear understanding of how the presence of key fishes relates to the delivery of functions, especially across varying spatial scales and when faced with degrading environmental conditions.

At within-reef scales, Streit et al. (2019) recently highlighted that feeding by herbivorous coral reef fishes is remarkably patchy. Again, this result highlights shortcomings in our commonly held assumption that fishes, when present, apply their functions homogenously across the reef at small scales (as demonstrated by our frequent application of such assumptions when estimating fish functions on reefs, e.g. Bellwood et al., 2003; Graham et al., 2018; Ruttenberg et al., 2019). Notably, Streit et al. (2019) suggested that algal turf sediment loads could be a mechanism responsible for the feeding patchiness, however, the relationship was not tested. Indeed, to-date, the effects of turf-bound sediment on the spatial partitioning of function delivery, and the sediment levels responsible for any effects, have remained largely unexplored, despite the potential importance of these sediments in shaping functions on degraded coral reefs. Essentially, we need to identify a) if algal turf sediments affect fish function delivery, b) the sediment levels (i.e. threshold levels) at which any such effects manifest themselves and c) at what spatial scales these effects operate. Is it at cross-shelf scales, cross-habitat scales, bite-scales, or, all of the above?

To address these knowledge gaps, we examined relationships between fish presence and function delivery (fish feeding) in relation to the key stressor: algal turf sediments. By focusing on a highly abundant detritivorous reef fish as the model species, we assess the effect of algal turf sediments on the spatial distribution of this species, and the spatial extent of its function delivery. In doing so, we provide a mechanistic understanding of cross-scale links between algal turf sediments and ecosystem function on coral reefs, allowing us to predict the potential ramifications of degrading environmental conditions from increasing algal turf sediment accumulation.

2. Materials and Methods

2.1 Study species

The focal fish species, the bristletooth surgeonfish, *Ctenochaetus striatus* (Fig. 1a), occurs across the Indo-Pacific from the Red Sea to the central Pacific (Trip et al., 2008). Within this broad distribution, *C. striatus* is often highly abundant (Cheal et al., 2012; Friedlander et al., 2010; Rasher et al., 2017; Samoilys et al., 2018) and in many places it is an important component of artisanal fisheries (Craig et al., 2008; McClanahan and Cinner, 2008; Russ et al., 2018). Due to its high abundance, *C. striatus* is also a key player in a number of ecosystem functions across its range including reef detritivory and sediment transport (Choat et al., 2002; Goatley and Bellwood, 2010). Indeed, the primary nutritional resource that *C.*

striatus targets and assimilates on coral reefs is detritus (Choat et al. 2002, Crossman et al. 2005; Robertson and Gaines, 1986; Tebbett et al. 2017b).

On coral reefs detritus is generally considered to be non-living organic particulate material (although it may contain living diatoms, cyanobacteria and other microbes and microalgae), that often accumulates, along with inorganic sediments, in algal turfs as part of the EAM (Crossman et al., 2001; Wilson et al., 2003). *Ctenochaetus striatus* are particularly well-suited to targetting this detrital material as they use elongated comb-like teeth (Fig. 1b), and their ability to open their jaws to nearly 180°, to brush detritus from algal turfs in a 'dustpan and brush'-like motion (Purcell and Bellwood, 1993; Tebbett et al., 2018). This particulate material is subsequently processed in a muscular gizzard-like stomach (Choat et al., 2004; Crossman et al., 2005). However, this morphology and feeding behaviour means that when targetting detrital material *C. striatus* are also exposed to the inorganic sediments, which are also bound within algal turfs. Indeed, inorganic sediments are a hindrance to feeding and if algal turf sediment loads increase, *C. striatus* feeding rates decrease. This causal relationship has been clarified in a previous experimental aquarium-based study (Tebbett et al., 2017a). This distinct reduction in feeding appears to be driven primarily by increasing total sediment load (Tebbett et al., 2017a), rather than by a decrease in the relative levels of the targeted detritus (Tebbett et al., 2017a) or by the source of the sediment (river vs. reef) (Tebbett et al., 2017c). With this clear mechanistic understanding (sediment increases cause reduced feeding rates) at hand, we are therefore able to explore the relationship between total sediment loads and feeding by this abundant and broadly distributed surgeonfish species, ultimately allowing us to assess the potential delivery of functions across multiple spatial scales.

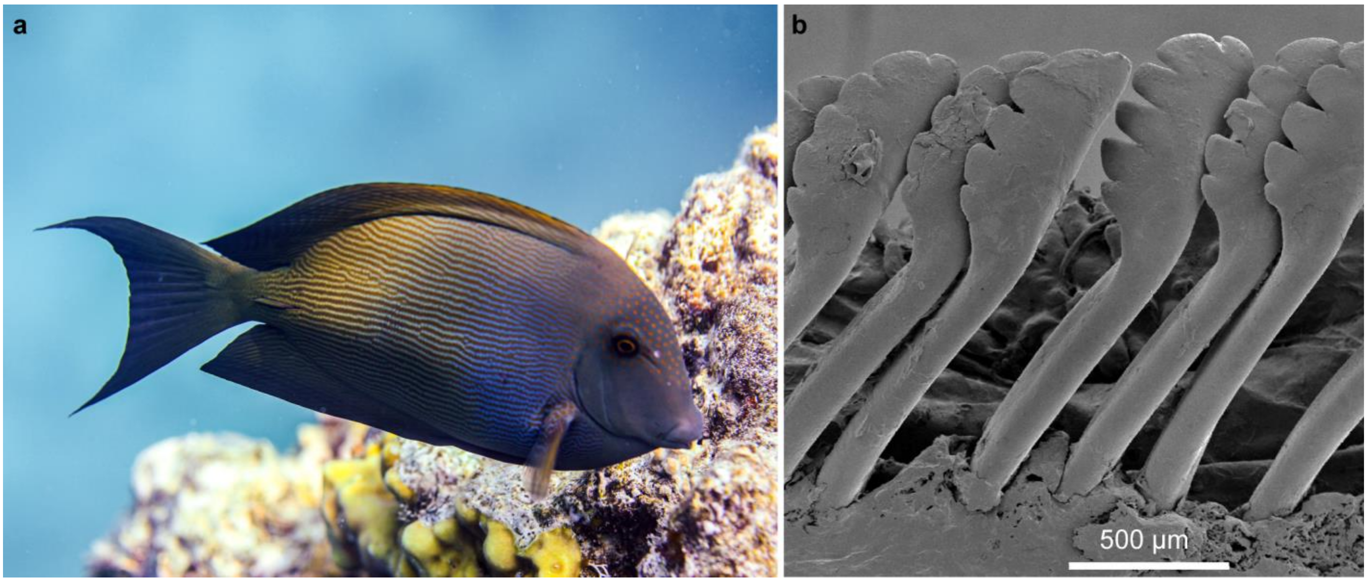

Figure 1 a) The study species *Ctenochaetus striatus* at Lizard Island, Australia (photograph V. Huertas). b) A scanning electron micrograph of the elongated comb-like teeth of *C. striatus* (anterior view of pre-maxilla).

2.2 Study design

To assess the spatial patterns of function delivery, and its relationship with algal turf sediments, this study incorporated five spatially stratified components (Table 1, Fig. 2). First, we explored the relationship between the abundance of *C. striatus* and algal turf sediment loads (hereafter expressed as the mass of sediment in algal turfs measured in g m^{-2}) across two spatial scales ([i] the entire GBR shelf and [ii] habitat zones within an individual reef) to identify a) where threshold levels of sediment that influence *C. striatus* abundance could occur and b) if the thresholds are similar at both scales (Part A). Second, within the shelf-position and habitat where *C. striatus* was most abundant, we determined the preferred feeding surface, and the cover of this preferred surface, to assess the potential spatial concentration of feeding relative to available reef area (Part B). Third, on these preferred surfaces we ground-truthed prior aquarium-based experiments to assess if *C. striatus* do indeed prefer to feed in low-sediment areas on the reef in un-manipulated conditions (i.e. under conditions where the full suite of natural abiotic and biotic factors that could structure *C. striatus* feeding behaviour were operating) (Part C). Fourth, to explore how algal turf sediments were related to the spatial delivery of function, *C. striatus* feeding rates were modelled using an observed sediment load frequency distribution from the preferred feeding surfaces (Part D). Following this, we applied this model to examine the effects of simulated increases in sediment loads on fish feeding (Part D). Fifth, the relationship between increasing sediment loads and the nature of the EAM was assessed, to explore how the EAM changes as sediment loads increase (Part E). These individual steps therefore examined the function of a detritivorous fish at progressively smaller spatial scales assessing: a) the reef/habitat scale presence of *C. striatus* relative to total sediment loads (Part A), b) the extent of within-habitat function delivery relative to benthic cover type, and surface angle (Part B) c) the within-habitat effects of algal turf sediments on spatial feeding patterns (Part C) and, finally, the implications of increasing algal turf sediment accumulation on d) fish feeding (Part D) and e) on the condition of the EAM (Part E).

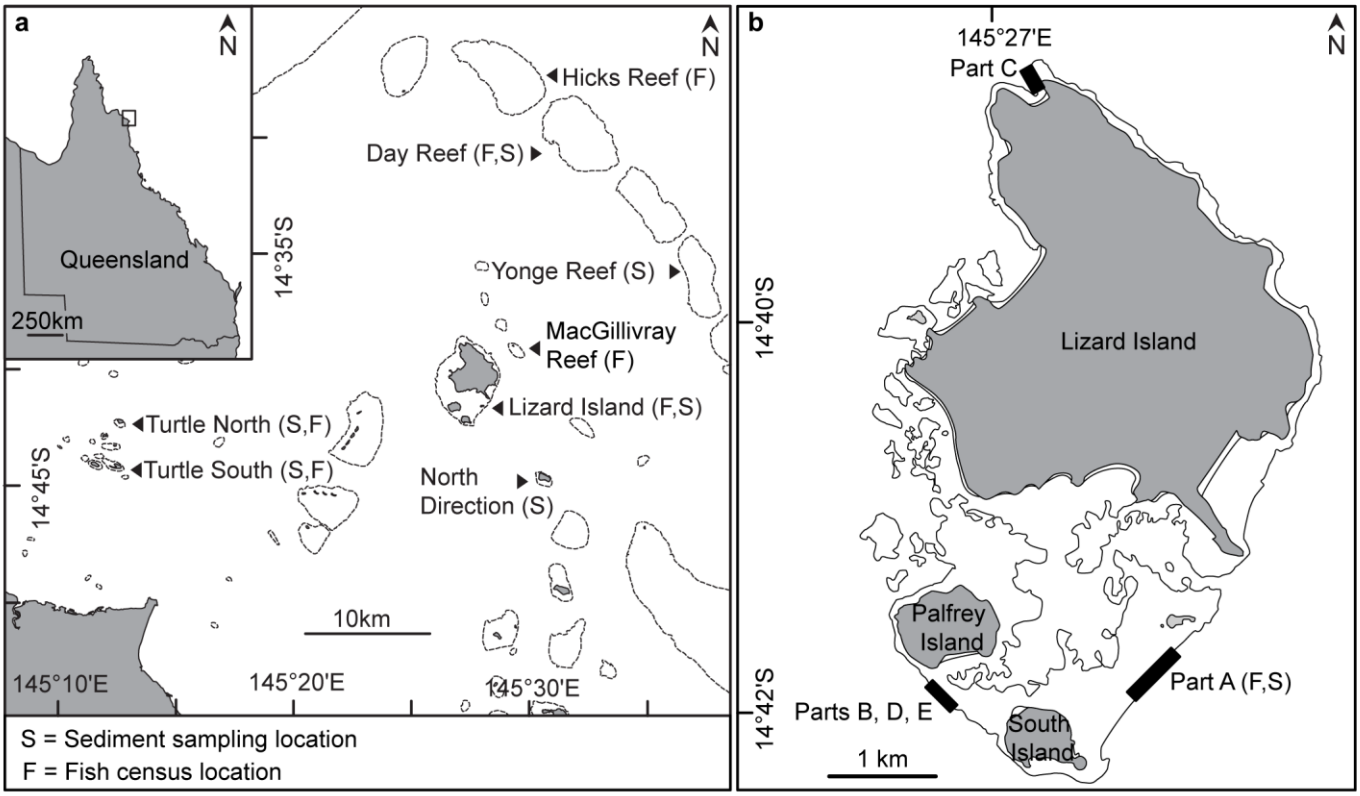

Figure 2 a) Map of the reefs around Lizard Island, Australia, showing the reefs at which the cross-shelf sediment sampling and fish censuses (part A) occurred. b) Map of Lizard Island showing the locations where different parts (A, B, C, D, E) of the study were conducted.

2.3 C. striatus vs. sediment distributions across (i) the GBR and (ii) reef habitats – Part A

We examined the relationship between the abundance (i.e. presence) of *C. striatus* and sediment loads across two spatial scales, with the aim to identify potential threshold values of sediments that correlate with decreased abundances of *C. striatus*. Such threshold levels would allow us to put the sediment levels documented in the subsequent components of this study into a broader spatial context and highlight links between relevant sediment levels, *C. striatus* feeding, *C. striatus* distributions, and ultimately the delivery of functions by this species (Table 1). The two spatial scales examined were (i) across the northern GBR shelf on inner-, mid- and outer-shelf reef crests, and (ii) in the shelf position where *C. striatus* was most abundant (mid-shelf), across reef habitats (flat, crest, slope) at Lizard Island, Australia (Fig. 2). In these analyses, fish abundance data were based on timed swims from Wismer et al., (2009). The sediment load data for this component was based on underwater vacuum sampling and was sourced from Tebbett et al., (2017d) (across shelf), and Purcell, (2000) (across habitats).

To quantify fish abundances accurately, censuses must be conducted at spatial scales of 10s-100s m^2. By contrast, to provide an overview of the sediment loads that fishes are interacting with when feeding, multiple sediment samples are taken at the scale of cm^2. Due to this mismatch of spatial scales, individual sediment load values (including a mean value) and individual fish census results cannot simply be matched one-by-one, as this would fail to account for the variability in sediment loads that fishes would be associating with in the area of each transect. Therefore, we undertook an iterative random sampling procedure to match sediment load data and fish data to account for this variability.

To match sediment and fish data, we randomly sampled (with replacement) a sediment load value from the range of sediment loads measured at each respective shelf position (inner [n = 20], mid [n = 17], outer [n = 20]) or habitat (slope [n = 30], crest [n = 30], flat [n = 30]) and matched this value to a replicate fish abundance transect within the corresponding shelf position/habitat (inner [n = 8], mid [n = 9], outer [n = 9]) (slope [n = 4], crest [n = 4], flat [n = 4]). This procedure was repeated until all fish censuses (n = 26 and n = 12 for cross-shelf and habitats, respectively) had a matching sediment load value. We then ran a regression tree on each of these compiled datasets to identify the sediment value (i.e. threshold value) at which *C. striatus* abundances differed the most. To account for variance in the dataset we repeated the above procedures 10,000 times for both across-shelf and across-habitat analyses. We then calculated the mean of each set of 10,000 values to identify average sediment threshold values across the (i) shelf locations and (ii) across habitats. Analyses were performed in the software R (R Core Team, 2018) using the *rpart* (Therneau and Atkinson, 2018) package.

The fish and sediment load data were matched relatively closely spatially as all data were collected from the same region (northern GBR) along the same latitudinal cross-shelf transect (inner-, mid- and outer-shelf reefs around Lizard Island) (Fig. 2), and from the same or nearby reefs. It should be noted that a temporal mismatch of approximately 10 years exists between the fish distribution data and the two sets of sediment load data. However, this is unlikely to be a major confounding factor since the sediment load data used herein is consistent with sediment distribution patterns that have been documented in multiple studies on different reefs across the GBR (i.e. very low sediment loads on reef crests relative to reef flat and slope habitats and higher sediment loads close to the mainland relative to mid- and outer-shelf reefs) (reviewed in Tebbett and Bellwood, 2019). It is therefore unlikely that the nature of these patterns has changed substantially. Furthermore, fish transects and sediment collection were both performed prior to the major bleaching event that impacted the northern GBR in 2016 (Hughes et al., 2017b).

As changes in benthic cover have also previously been linked to the abundance of herbivorous/detritivorous fishes (e.g. Russ et al., 2018, 2015) we also sourced data from Wismer et al., (2009) on algal turf/crustose coralline algae (CCA) coverage (i.e. the availability of feeding surfaces). These data on benthic cover were from the same time period, reefs and habitats where fish surveys were conducted and were based on benthic point transects. The relationship between *C. striatus* abundance and the coverage of algal turfs/CCA was explored graphically.

2.4 *Preferred feeding surfaces of C. striatus – Part B*

To examine the selection of feeding surfaces by *C. striatus*, a SCUBA diver, using an underwater video camera, recorded the feeding behaviour of 106 individuals on an upper reef crest at Lizard Island (Fig. 2b). Here the upper reef crest is obliquely exposed to prevailing winds, lies in approximately 1 – 3 m of water and is composed of horizontal, consolidated reef matrix. *C. striatus* are highly-abundant in this location with the majority of feeding activity occurring on the upper reef crest (Goatley and Bellwood, 2010).

From the video footage, the benthic category (algal turf/crustose coralline algae [CCA], soft coral, branching hard coral, massive hard coral, staghorn hard coral, encrusting hard coral, sand, macroalgae, anemone, hydroid or unidentifiable), and the angle of the benthic category (horizontal [< 30˚], sloping [30 – 60 ˚], vertical [60 - 90˚] or overhanging [> 90˚]) on which a fish took its first bite, was recorded. Calculating the angle of the surface was necessary as surface angles influence sediment dynamics (Duran et al., 2018; Tebbett et al., 2020b). On the same video frame (encompassing an area of reef ~4 m^2) as the first bite, 10 randomly generated points were overlaid and the benthic cover and angle under each point was categorised as above. This was necessary to calculate the relative coverage of preferred feeding surfaces on the reef.

To assess feeding surface selectivity, relative to the abundance of the surface, Ivlev's electivity indices were calculated. Ivlev's electivity indices assess preference for a particular resource on a scale from -1 to 1 (-1 would indicate total avoidance, 0 indicates the resource is used in proportion to its abundance, 1 indicates total preference). Ivlev's electivity indices were calculated both among benthic categories, and among surface angles within the preferred benthic category.

2.5 Spatial constraints of sediments on C. striatus feeding – Part C

Previous aquarium-based experiments had revealed that *C. striatus* feeding rate decreases markedly with increasing sediment loads allowing a clear feeding response curve to be generated (Tebbett et al., 2017a). Furthermore, a previous field-based study revealed that *C. striatus* feeding increased markedly when sediments were removed from algal turfs (Bellwood and Fulton, 2008). However, while these experiments simulated natural conditions in a controlled manner, both artificially manipulated sediment loads. Therefore, the assumption that *C. striatus* actually feed in areas of low sediment under unmanipulated conditions (i.e. with the full suite of natural factors operating that structure feeding rates in fishes [e.g. predator avoidance and behavioural interactions]) had to be assessed.

To do this we established three sites on the leeward reef crest in Mermaid Cove, Lizard Island (Fig. 2b). At each of these sites, a grid system of cameras covering 36 m^2 was established and a photo mosaic of each site was compiled following Streit et al., (2019). Specifically, eight underwater cameras (GoPros) were spatially arranged so that their combined field-of-view covered the 36 m^2 observation areas, recording any fish feeding over approximately 4 hours. High-resolution photomosaic maps of these observation areas were created using structure-from-motion software (Agisoft Photoscan Pro). This software uses partially overlapping images (sourced from videos taken by a diver swimming in a zig-zag pattern over the study site and recording the benthos), to create digital three-dimensional models and ‘ortho-rectified’ planar maps. The latter show the entire study site in an idealised, flattened bird’s eye view perspective, i.e. accounting for distortion from camera lenses and benthic structure (for details on this software see Streit et al., [2019] and Tebbett et al., [2020b]). Natural benthic features as well as introduced ‘location markers’ visible on these 3D models and ortho-rectified maps were used to triangulate and record the feeding location of fishes visible in the GoPro video footage (for detailed methods of visual fish tracking from video, see Streit et al., [2019]).

Video footage was examined to establish three *C. striatus* feeding ‘hot-spots’ in each site. A hot-spot was defined as a 30 cm diameter circle (the size was selected based on: a) the size of the sediment sampling ring and b) the nature of the feeding data and spatial clustering of feeding locations) that contained the most *C. striatus* feeding locations (i.e. the highest local feeding density). Hot-spots were identified on the photomosaic and within each hot-spot 4 non-overlapping sediment sampling spots were haphazardly designated. In addition, using the software (ArcGIS), 13-15 randomly located, non-hot-spot, sampling surfaces were designated within each site. These maps were then loaded onto an underwater digital camera (Nikon Coolpix W300) to allow for the identification of sediment sampling sites underwater. For each of these sampling locations, we then quantified sediment loads and the surface angle of the location (see supplemental text S1 for full details of sediment sampling and processing).

We tested for differences in sediment loads between hot-spots and random sample locations using a generalised linear mixed-effects model (GLMM) with a Gamma distribution and log-link. A Gamma distribution was used due to the continuous strictly positive nature of the sediment data. Surface angle and sample type (hot-spot or random) were initially fitted as interacting fixed effects, while site and hot-spot identity were fitted as random effects. The most parsimonious model was selected based on the corrected Akaike Information Criterion (AICc) (Table S1). Model assumptions and fit were examined using residual plots, all of which were satisfactory. Statistical modelling was performed in the software R (R Core Team, 2018) using the *glmmTMB* (Brooks et al., 2017), *MuMIn* (Barton, 2018) and *tidyverse* (Wickham, 2017) packages.

2.6 *Increasing sediment loads and C. striatus feeding – Part D*

The effect of algal turf sediments on the feeding rate (bite rate) of *C. striatus* was modelled as a function of: a) an observed sediment load frequency distribution, and then b) two scenarios of increasing sediment loads. Initially, to establish an observed sediment load frequency distribution, 111 sediment samples were collected from a reef crest at Lizard Island (Fig. 2b). Sediments were collected by haphazardly placing a 20 cm^2 PVC ring on a suitable algal turf/CCA-covered surface and then using an underwater vacuum sampler to remove the sediments. Sediments were processed following the methods outlined in supplemental text S1. The angle of each surface was also recorded using an inclinometer so that sediment loads could be matched with the preferred feeding surface angle of *C. striatus* (established in the second component of this study). In addition, the length of five haphazardly selected algal turf filaments per sample were measured using callipers (following the procedure outlined in Tebbett and Bellwood [2019]) to explore the relationship with sediment loads in the next component of this study (Part E).

From the 111 sediment samples collected, 80 were collected from preferred feeding surfaces, providing information on the range and variability of sediment loads present on these surfaces (see supplemental text S2). Using this observed sediment load frequency distribution, the bite rate (bites min^{-1}) of *C. striatus* at each of the 80 sediment loads was estimated using a published experimental aquarium-based feeding response model that related *C. striatus* feeding rates to sediment load (Tebbett et al., 2017a). From the output of this model, the potential relative reef area over which *C. striatus* may feed at a very high (8 – 10), high (6 – 8), moderate (4 – 6), low (2 – 4) and very low (0 – 2) bite rates (bites min^{-1}) on preferred feeding surfaces could be determined. These bite rate bins were established to facilitate the presentation of the results as a conceptual figure, which highlighted how sediment loads and feeding rates of *C. striatus* could be arranged spatially across an area of reef.

We then applied the model, as above, under two different scenarios of increasing sediment accumulation. To do this, 80 random sediment loads were generated from a normal distribution (representing a moderate ~2-fold increase in sediment loads) and a negatively skewed distribution, representing a severe, yet not unrealistic, blanketing of high sediment loads (~4-fold increase in mean sediment load) simulating the sediment-laden algal turf state described in Goatley et al., (2016). In both cases the distributions were truncated within natural bounds (i.e. between the minimum and maximum sediment loads recorded from the collected sediment samples [see text S2]), to account for natural limitations in the amount of sediment that algal turfs can accumulate (Gordon et al., 2016; Latrille et al., 2019; Tebbett et al., 2018). Due to random sampling, final sediment load frequency distributions corresponded to a 2.3-fold (moderate) and 4.5-fold (more severe) increase in mean accumulated sediment loads. Unfortunately, apart from a single study (Goatley et al., 2016) there has been no other published long-term (>1 year) data on sediment loads through time. Therefore, the two increases we have modelled are relatively arbitrary, however, they are within a realistic range of naturally occurring sediment loads, considering that the study by Goatley et al., (2016) reported a 37-fold increase in mean sediment loads over a four-year period. All modelling was performed in the software R (R Core Team, 2018).

It should be noted that our model predictions of how *C. striatus* feeding will be affected by increasing sediment loads assume that *C. striatus* will not compensate for a reef-wide increase in sediment loads by feeding more and will remain in a similar location i.e. in contrast to moving to a new, low-sediment area of reef. To-date, available evidence suggests that even if fishes only have the option of feeding on algal turfs containing high sediment loads they will feed there, but at significantly reduced rates (Goatley et al., 2016; Tebbett et al., 2017a). It is also highly unlikely that fishes will move over long distances to more favourable locations. Indeed, coral reef fishes appear to establish a sense of 'home' soon after settlement (Bellwood et al., 2016; Streit et al., 2017) and as adults many nominally herbivorous fishes, including *C. striatus*, are highly site attached with restricted home ranges (e.g. Davis et al., 2017a; Krone et al., 2008; Welsh and Bellwood, 2012). Evidence suggests that if fishes move in response to changing environmental conditions, then such movement will be limited (Ceccarelli et al., 2006; Nash et al., 2012; Wismer et al., 2019).

2.7 Relationships between sediment loads and the EAM – Part E

As inorganic sediments are just one component of the EAM, it was necessary to explore if/how increasing sediment loads were related to other components of the EAM namely: organic detrital load, relative levels of organic detritus in total particulates (i.e. organic detritus + inorganic sediment) and algal turf length. We explored these relationships in the 80 sediment samples collected at the study site (see above) from the preferred feeding surfaces of *C. striatus*. Specifically, the relationships between organic detrital load (g m^{-2}), the relative level of detritus in the benthic particulates as a proportion of total particulate mass, as well as algal turf length (mm) with inorganic sediment load (g m^{-2}) were examined using generalised linear models (GLMs). Models examining organic detrital load and algal turf length were based on Gamma distributions with a log-link due to the continuous positive nature of these data. The model examining the relative level of detritus was based on a beta distribution due to the proportional nature of these data. In all models, sediment load was fitted as a continuous fixed effect (logged to ensure data was homogenously distributed across the x-axis). Model fit and assumptions were assessed using residual plots, all of which were satisfactory. All statistical modelling was performed in the software R (R Core Team, 2018), using the *tidyverse* (Wickham, 2017), *glmmTMB* (Brooks et al., 2017), *patchwork* (Pedersen, 2019) and *emmeans* (Lenth, 2019) packages.

3. Results

3.1 C. striatus vs. sediment distributions across (i) the GBR and (ii) reef habitats – Part A

C. striatus were entirely absent from the inner-shelf reef crests where mean sediment loads were 915.2 ± 172.5 g m^{-2}, while their abundance was highest (5.8 ± 1.4 individuals 100 m^{-2}) on mid-shelf reef crests where sediment loads were lowest at 134.8 ± 31.1 g m^{-2} (Fig. 3a, c). Regression tree analysis identified the greatest change in *C. striatus* abundance corresponded to a split in the data at a sediment load of 256.3 ± 1.5 g m^{-2} (mean ± SE) (i.e. ~25% of the mean sediment load on inner-shelf reefs [Fig. 4a]). Interestingly, this threshold level aligns with average sediment loads on outer-shelf reefs (219.6 ± 52.4 g m^{-2}), where *C. striatus* occur at intermediate densities (3 ± 1.1 individuals 100 m^{-2}). On average, once sediment loads exceeded 256 g m^{-2} fish numbers were substantially lower.

A similar pattern was documented among habitats at Lizard Island. *C. striatus* were highly abundant in low-sediment reef crest habitats, but largely absent in sediment-rich slope and flat habitats (Fig. 3b, d). The regression tree suggested that, on average, splitting the data at a sediment load of 514.9 ± 3.4 g m^{-2} explained the greatest change in *C. striatus* abundance across habitats (Fig. 4b). Among habitats, therefore, fish numbers were substantially lower when sediment loads exceeded average reef crest sediment values (127.5 ± 17.5 g m^{-2}) by ~4-fold, i.e. exceeding 515 g m^{-2}.

Importantly, sediment loads provide an indication of the quality of *C. striatus* preferred feeding surfaces (see below), while algal turf/CCA coverage provides an indication of the quantity, i.e. availability, of their preferred feeding surfaces. It is interesting to note that while *C. striatus* abundance appears to correlate strongly with sediment loads across both spatial scales (shelf and habitat) (Fig. 3), the same is not the case when just algal turf/CCA coverage is considered. For algal turf/CCA coverage there appears to be some correlation with *C. striatus* abundance across the shelf, however, across habitats there appears to be no clear relationship (Fig. 3). This suggests that it is the quality of the preferred feeding surface, rather than the quantity, that may be most important in mediating the distribution patterns of *C. striatus*.

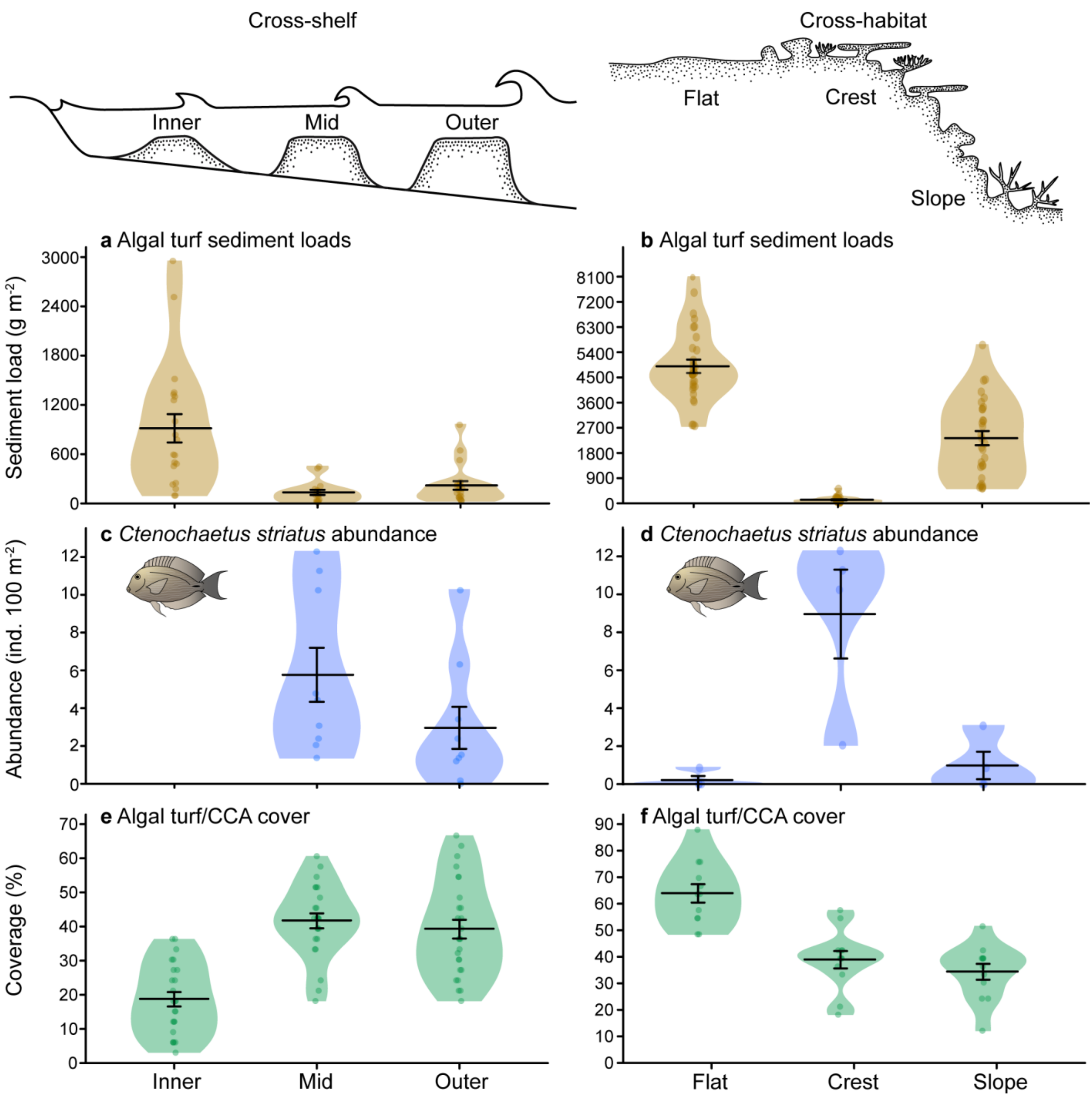

Figure 3 Sediment loads (a, b) and the abundance (c, d) of the surgeonfish *Ctenochaetus striatus* across the continental shelf of the Northern Great Barrier Reef, Australia (a, c) and reef habitats at Lizard Island, Australia (b, d). The coverage of algal turfs and crustose coralline algae (CCA) were recorded on the same reefs across the same spatial scales (e, f). Black lines denote the observed mean ± SE, dots denote the observed values, and semitransparent violin plots indicate the distribution of the observed values.

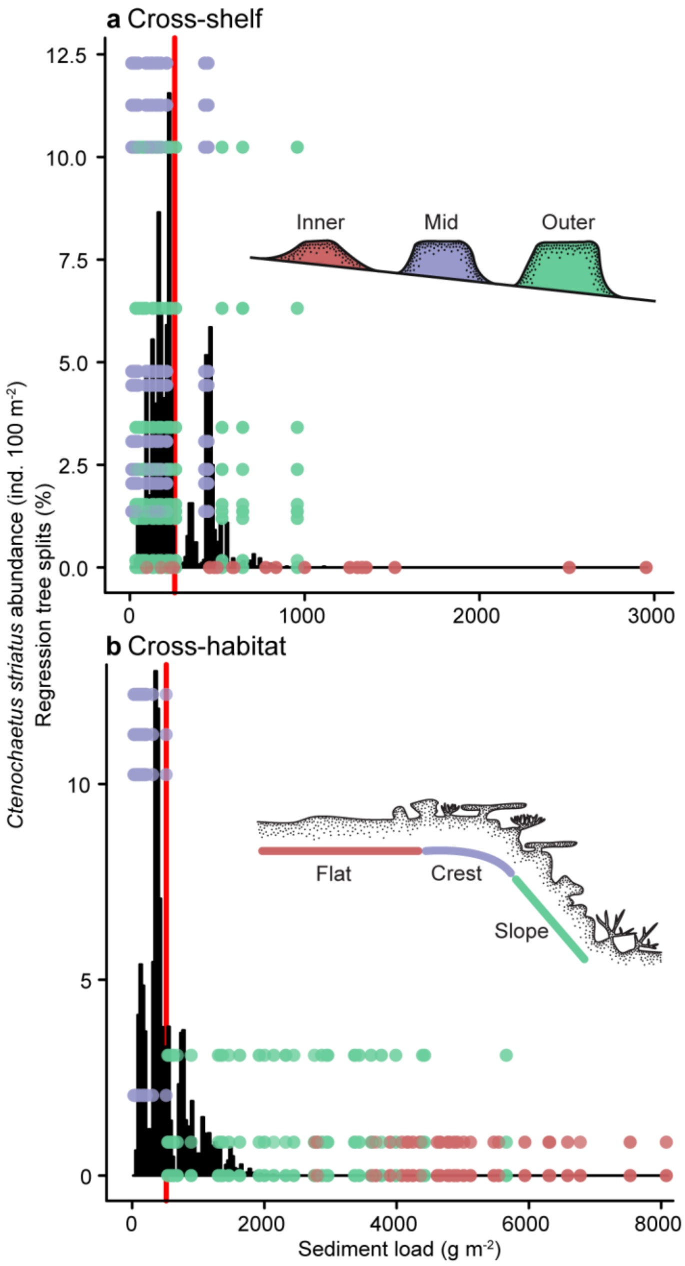

Figure 4 The relationship between the abundance of *Ctenochaetus striatus* and sediment loads across a) the continental shelf of the Great Barrier Reef, Australia and b) habitats at Lizard Island, Australia. Coloured dots were based on an iterative process whereby observed sediment load data was randomly matched to each census of *C. striatus* abundance (see Fig. 3) (1,000 randomly selected iterations are presented). The black histograms represent the frequency distribution of results from 10,000 regression trees that identified the sediment load at which the abundance of *C. striatus* changed the most. The red vertical line represents

the mean sediment load identified from the regression trees (256 g m^{-2} across the shelf, and 515 g m^{-2} across reef habitats).

3.2 *Preferred feeding surfaces of C. striatus – Part B*

On the upper reef crest at our Lizard Island site, algal turf/CCA covered 60.9% of the benthos and was selectively fed on by *C. striatus* (Ivlev's Electivity [IE]: 0.23) with 97.2% of all bites occurring on algal turf/CCA (Fig. 5a, c). On this turf/CCA covered substratum, *C. striatus* fed preferentially on horizontal surfaces (IE: 0.097) with 53.8% of all bites occurring in just 27.7% of the total area (Fig. 5b, d) (for details of how percentages were calculated see supplemental text S3, Fig. S1). This indicates that function is delivered by *C. striatus* in a concentrated manner, focussing on a restricted range of preferred surfaces.

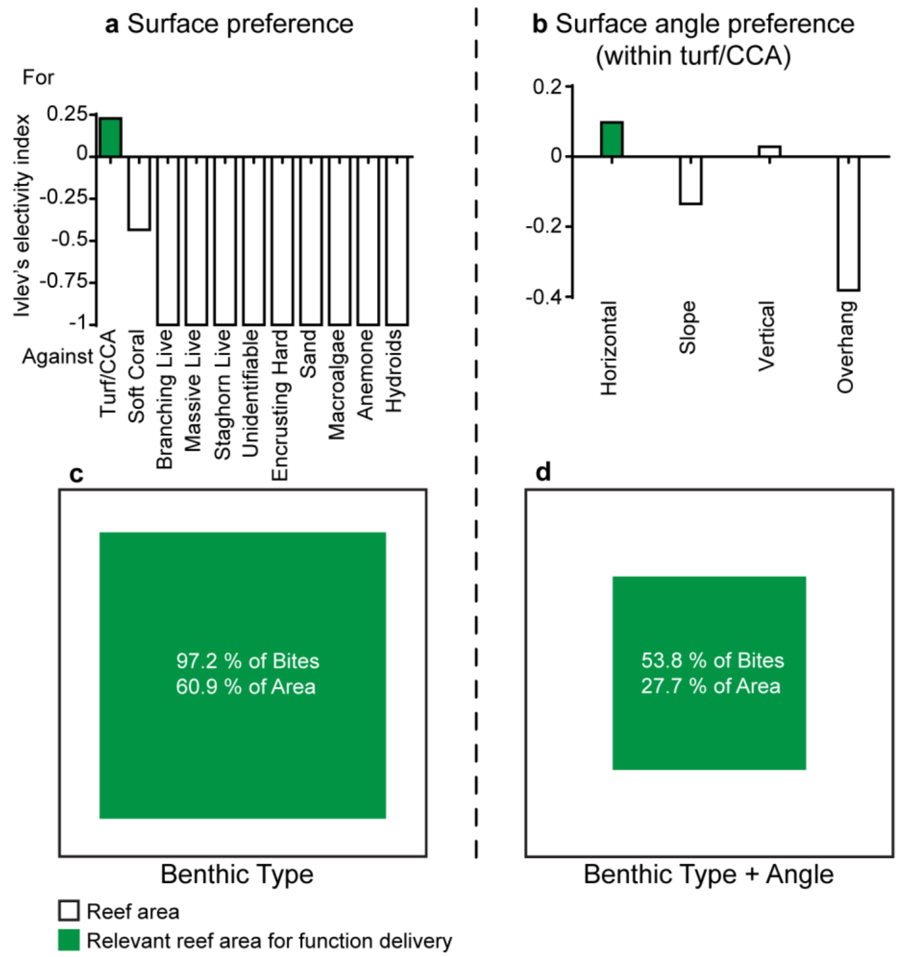

Figure 5 Ivlev's electivity indices of *Ctenochaetus striatus* feeding in response to: a) benthic cover type, and b) preferred benthic cover and the angle of the surface with that cover. The percent of reef area relevant for *C. striatus's* function delivery considering its different levels of feeding selectivity is represented as green squares (c, d). For details on percentage calculations see supplemental text S3, Fig. S1.

3.3 Spatial constraints of sediments on C. striatus feeding – Part C

Based on video recordings and 'hot-spot' mapping, sediment loads in areas identified as *C. striatus* feeding hot-spots were markedly lower (270.8 ± 37.4 g m^{-2}) than randomly sampled surfaces (931.9 ± 133.7 g m^{-2}) (Fig. 6). Note that the sediment loads of feeding hot-spots closely reflects the sediment load abundance thresholds found at larger spatial scales (Fig. 4). The model revealed that there was a significant interaction between surface angle and hot-spot vs. random locations (GLMM; $p < 0.05$, Table S2). Within feeding hot-spots, sediment loads remained consistently low regardless of surface angle. By contrast, in random samples, sediment loads decreased markedly as surface angles became steeper (Fig. 6). As sediment loads were markedly different in hot-spots, especially in horizontal locations (the preferred feeding surface), this suggests that *C. striatus* feeding is spatially related to sediment loads at a <10 cm scale. Essentially, *C. striatus* preferentially feed in low-sediment locations and/or their feeding maintains low sediment loads.

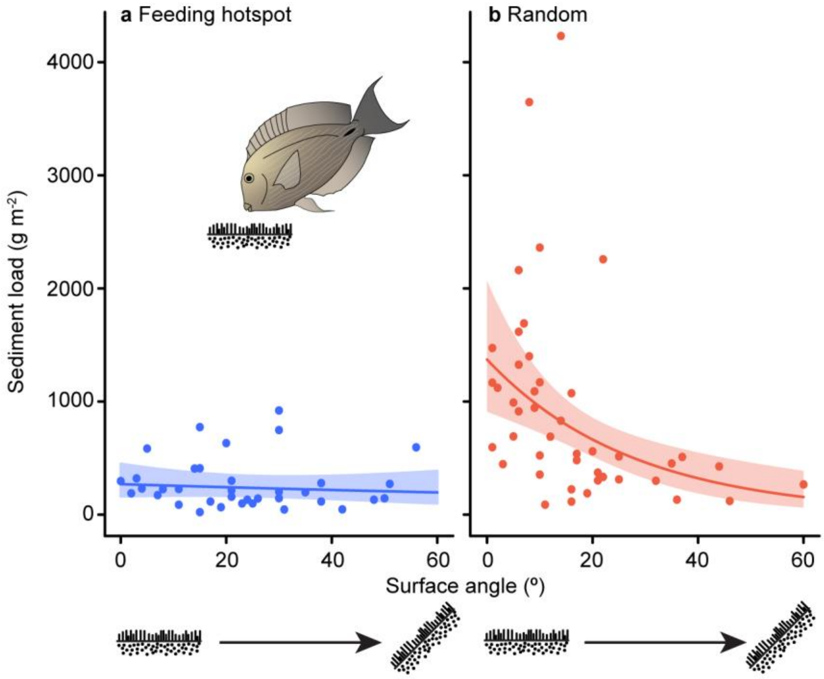

Figure 6 The relationship between sediment loads and the angle of the sampled surfaces in areas that were: a**)** *Ctenochaetus striatus* feeding hot-spots and b) randomly sampled areas from the same sites. Coloured lines are the mean predicted fit of a generalised linear mixed-effects model, shaded areas are the upper and lower 95% confidence intervals, and coloured dots are the observed data points.

3.4 Increasing sediment loads and C. striatus feeding – Part D

With the link between the spatial distribution of sediments and *C. striatus* feeding established, the variability of sediment loads on preferred *C. striatus* feeding surfaces could be considered. When factoring in the observed sediment load frequency distributions, function delivery was concentrated even further, beyond the constraints imposed by preferred feeding substrate and substrate angle (Fig. 4c, d). Based on the observed frequency distribution of sediments, *C. striatus* feeding was maximised (> 8 bites minute^{-1}) in just 10.4% of the total reef area (Fig. 7a, d). This means that 26.1% of all feeding by *C. striatus* would occur in just 10.4% of the total reef area (for details of how percentages were calculated see supplemental text S3, Fig. S1).

A modelled 2.3-fold increase in mean sediment load, from 173.7 to 399.2 g m^{-2}, on preferred feeding surfaces (i.e. horizontal Turf/CCA, Fig. 5a, b), resulted in a 44.3% reduction in total *C. striatus* feeding, relative to observed levels (Fig. 7). A 4.5-fold increase in sediment load from 173.7 to 773.2 g m^{-2} resulted in a 78.0% reduction in total *C. striatus* feeding. Under this scenario, the percentage of total reef area which was likely to experience high and very high feeding by *C. striatus* (> 6 bites min^{-1}) fell by 99.6% from 20.5% to just 0.7% of total reef area (Fig. 7c, f). This highlights the potential of sediments to impair *C. striatus* feeding, limiting function delivery to specific locations on the reef.

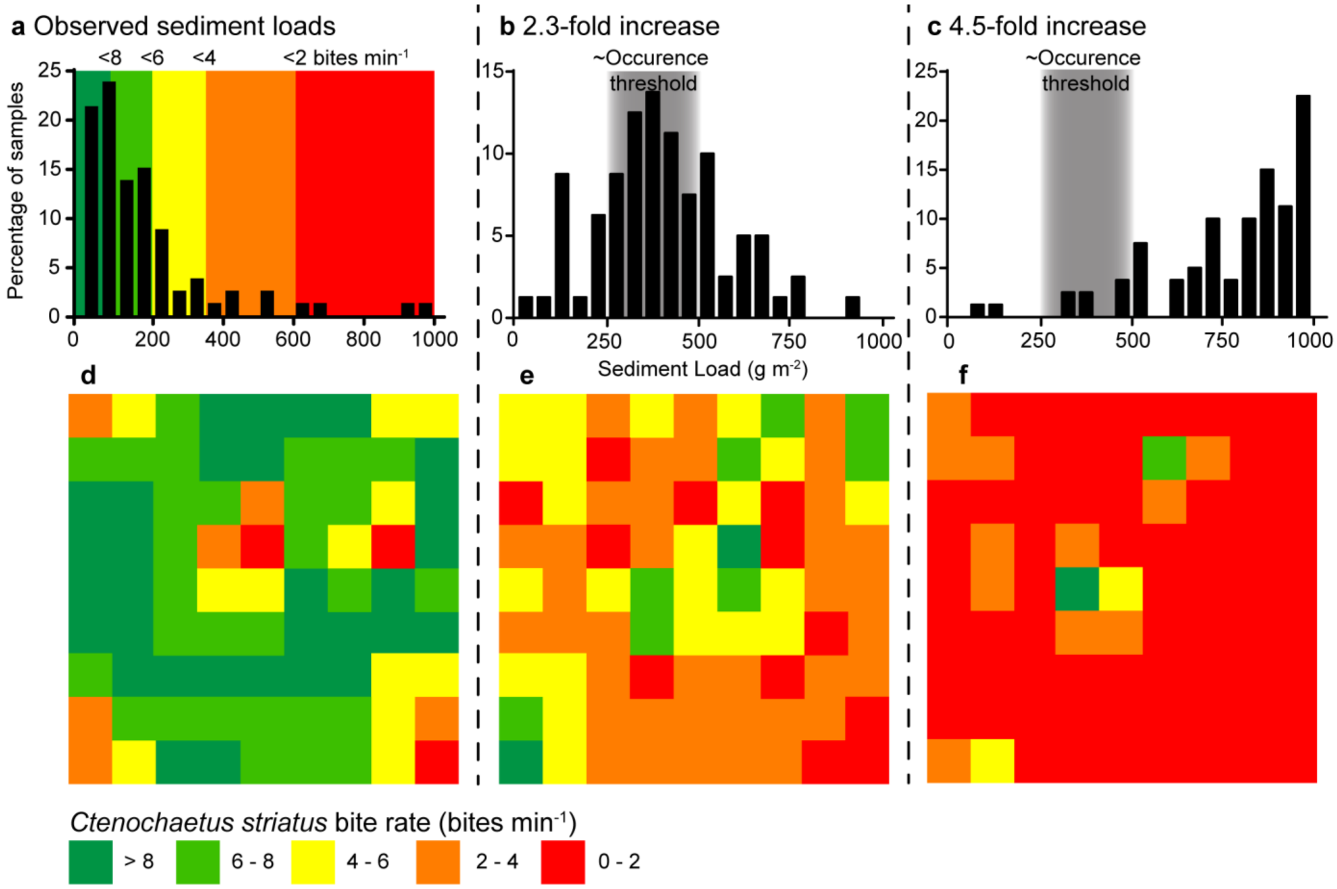

Figure 7 Frequency distributions of sediment loads on horizontal algal turf/crustose coralline algae covered surfaces. a) shows the observed frequency distribution of sediment loads on a mid-shelf reef crest on the Great Barrier Reef, b) represents a projected 2.3-fold increase in mean sediment load with a normal frequency distribution, and c) represents a more severe 4.5-fold increase in mean sediment load with a negatively skewed frequency distribution (the vertical grey bars indicate approximate sediment load thresholds determining the occurrence of *Ctenochaetus striatus*, see Fig. 4). The coloured squares in (d-f) show the predicted potential feeding rate (0 – 10 bites min^{-1} in 2 bites min^{-1} bins) of *C. striatus* on areas of horizontal turf/CCA covered by the three different sediment regimes. The coloured areas of a) show the feeding rate bin cut-offs and the range of sediment loads within the frequency distribution that fall within those feeding rates.

3.5 *Relationships between sediment loads and the EAM – Part E*

Clear relationships existed between sediment loads and the nature of the EAM (Fig. 8). Specifically, as sediment loads increased in the EAM so did the standing mass of organic detritus, with a significant positive relationship between these two variables (Fig. 8a; Table S3). However, interestingly, the mass of organic detritus did not appear to accumulate at the same rate as inorganic sediments because as sediment loads increased the proportion of detritus in total particulates (i.e. organic detritus + inorganic sediments) decreased significantly (Fig. 8b; Table S3). Essentially, this suggests that as sediment loads increase they ‘water-down’ the relative amount of organic detritus in particulates, therefore reducing relative yields of organic detritus to detritivorous fishes. Furthermore, as sediment loads increased, the length of algal turf filaments also increased significantly (Fig. 8c; Table S3), although it should be noted that as detritus levels are co-linear with sediment loads, detritus loads could also contribute to this increase in algal turf length. Overall, these relationships suggest that increasing sediment loads would facilitate the development of longer algal turfs, which offer lower relative nutritional returns (i.e. organic detritus relative to inorganic sediment) per bite for detritivorous particulate feeding fishes such as *C. striatus*.

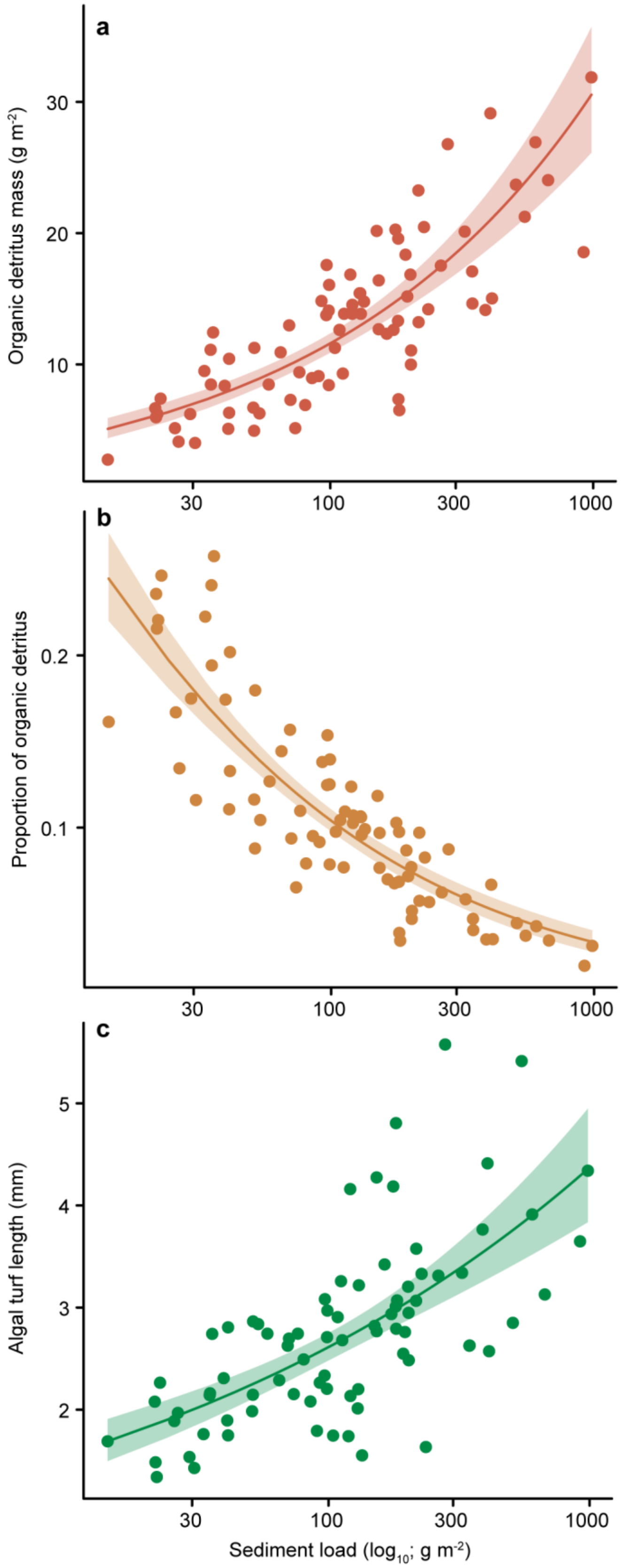

Figure 8 The relationship between inorganic sediment loads and a) organic detrital loads, b) the relative level of organic detritus in benthic particulates by mass and c) algal turf length.

Coloured lines are the mean predicted fits of generalised linear models, shaded areas are the upper and lower 95% confidence intervals, and coloured dots are the observed data points.

4. Discussion

Using a hierarchical multi-scale approach, ranging from patterns across a continental shelf down to centimetres within a single reef habitat, we show that: a) *C. striatus* abundance (presence) appears to be correlated with sediment loads and decreases substantially when specific sediment levels are surpassed across both (i) GBR shelf positions and (ii) reef habitats; b) on the shelf-position and reef habitat where *C. striatus* are most abundant they predominantly feed over a small area of the reef (~50% of feeding in ~25% of reef area) characterised by horizontal algal turfs/CCA; and c) at small <10 cm scales the spatial delivery of function (feeding) by *C. striatus* was related to sediment loads in un-manipulated conditions. In all the above cases, sediment loads above ~250-500 g m^{-2} resulted in decreased abundance or feeding, suggesting a distinct ecological threshold lies within this range. Furthermore, d) a predictive model highlighted how feeding rates could be spatially constrained by increased sediments, and e) relationships examined between sediments and other components of the EAM suggest that as sediment loads increase algal turfs will become longer and that sediment loads and organic detritus levels are closely related, with increasing sediment levels reducing the relative yield of detritus to *C. striatus* when feeding.

At every spatial scale examined, *C. striatus* responded negatively to sediments, ultimately leading to decreased function delivery, with consistent thresholds explaining where and how *C. striatus* fed. Sediment loads can explain not only the abundance/presence of *C. striatus*, but also where function is delivered when *C. striatus* are present (although the exact mechanism underlying these affects may be related to how sediments and detritus interact in the EAM e.g. sediments ‘watering-down’ relative organic detrital yields to *C. striatus*). The latter observation highlights that function cannot be assumed based on fish presence alone.

4.1 Presence versus function

In the past it was often assumed that fishes would apply their functions relatively homogenously across the reef scape wherever they were present (although a number of studies have suggested that feeding may be far more selective e.g. Clements et al., 2017; Davis et al., 2017a; Streit et al., 2019). Indeed, this assumption has underpinned our approaches to estimating reef functions such as grazing rates and bioerosion rates, as these are generally estimated by simply multiplying fish species abundance and feeding rates by bite size/volume data (e.g. Bellwood et al., 2003; Graham et al., 2018; Ruttenberg et al., 2019). In essence, we often calculate how much of a function may occur in a particular area but we pay relatively little attention to where it actually is delivered within the area (a potential limitation of many functional studies [reviewed in Bellwood et al., 2019b]). Indeed, in our study we demonstrate that *C. striatus* deliver their function through feeding unevenly across the reef-scape, with more than 50% of feeding occurring in less than 28% of the area (Fig. 5). This supports the findings of Streit et al. (2019), who found a similar concentration (50% of bites in 14% of area) across multiple groups of herbivorous fishes in a diverse fish assemblage, showing that herbivorous fish feeding, in general, may be exceedingly patchy with high levels of selectivity (also see Bruggemann et al., 1994; Carlson et al., 2017; Clements et al., 2017; Streit et al., 2019; Welsh and Bellwood, 2012). It is clear that we cannot assume homogeneity of function delivery.

This patchiness, therefore, adds another level of complexity when we want to estimate or conserve functions on reefs. While the absence of fishes inhibits any function delivery (if a fish is not present, it cannot deliver a function [although this is also dependent upon our ability to detect fishes using traditional censusing techniques and our understanding of the functions they perform (Fox and Bellwood, 2008; Tebbett et al., 2020a)]), the inverse is not assured. We cannot assume that just because a fish is present it will deliver its purported functions. Indeed, presence does not equal function because presence itself merely offers the potential for the function to be delivered, but the expression of this potential is conditional on additional factors. In the case of *C. striatus*, if these fishes are present on the reef, where and to what extent they feed (and ultimately deliver their function) appears to depend on the distribution of sediment loads (Fig. 7). In a management context, therefore, trying to conserve function, by solely managing the abundance of *C. striatus*, could fail (see Williams et al., 2019). In this particular example, function is a product of both fish presence and sediment distributions. Managing for fish presence alone only addresses one component of the 'functional equation'. To effectively manage for a consistent function, it is critical to know at what scales this functional equation becomes important. Or in other words, at what scale do sediments influence fish feeding activity and other major reef processes?

4.2 Functional interpretations: the influence of scale

We examined relationships between *C. striatus* and sediments across multiple spatial scales spanning several orders of magnitude. At every spatial scale, we found *C. striatus* responded negatively to similar levels of sediments. Across the broader scales examined, (i) shelf-position and (ii) reef habitats, the relationships were correlative; more *C. striatus* occurred where sediments were low (i.e. *C. striatus* were absent on inner-shelf reefs where sediment loads are highest and most abundant on mid-shelf reefs where sediment loads were lowest). These results are strongly supported by the existing literature, as several previous studies have found similar distribution patterns for *C. striatus* (e.g. Cheal et al., 2013, 2012; McClure et al., 2019; Russ, 1984), with previous suggestions that sediment may influence such distribution patterns (Cheal et al., 2013, 2012; Samoilys et al., 2019). Our direct comparison of *C. striatus* and sediment loads strongly support these suggestions. At these scales, sediments appear to be a significant driver of *C. striatus* abundance, however, it remains to be determined if this correlative relationship between sediment and fish abundance is a causal relationship. For example, does sediment inhibit feeding of *C. striatus* and is it thus, in-turn, responsible for reduced fish abundance? If yes, fish feeding should respond similarly to the sediment thresholds that appear to drive fish abundances.

This need to determine mechanistic links and reveal potential explanations for broader-scale correlative patterns, highlights the value of small-scale functional assessments. Our small-scale, detailed assessments of *C. striatus* function delivery revealed, in increasingly fine grain, that *C. striatus* feeding locations are characterised by low sediment loads, highlighting a direct connection between sediment loads and *C. striatus* feeding. Thus, at these fine spatial scales, sediments appear to influence *C. striatus* feeding behaviour, rather than presence/absence, i.e. once *C. striatus* are present, algal turf sediments can structure where *C. striatus* actually deliver their bites. Importantly, these observed relationships are supported by prior experiments, which established a causative link between increased sediment loads and decreased *C. striatus* feeding rates in an experimental aquarium setting (Tebbett et al., 2017a) and on the reef (Bellwood and Fulton, 2008).

In combination, the previous experimental evidence with our detailed field observations allows us to move beyond correlative speculations towards a more mechanistic understanding of observed patterns, highlighting the links between sediment, feeding behaviour and fish absence across multiple spatial scales. Interestingly, fish feeding behaviour and absence appear to be governed by common sediment thresholds; i.e. if average sediment loads exceed ~250-500 g m^{-2}, then *C. striatus* cannot feed effectively and are likely to not occur. Perhaps this is best demonstrated by the fact that the average sediment load on inner-shelf reefs (915 g m^{-2}) is higher than that used (773.2 g m^{-2}) in scenario three of our modelled *C. striatus* feeding patterns (Fig. 7). The lack of *C. striatus* in sediment-rich habitats seems intuitive and inevitable, given that such high sediment loads would dramatically compress nutritionally exploitable space (Fig. 7). Sediments play a major role in the feeding ecology of this species, to the extent of potentially structuring both their feeding and distribution patterns. If sediment loads remain consistently high, viable feeding surfaces will be rare or non-existent, with energetic constraints (Fig. 8b) preventing the long-term persistence of *C. striatus* in these areas.

4.3 Algal turf sediments and consideration of other explanatory drivers

Our study focused on how sediment loads mediate the abundance and feeding behaviour of *C. striatus* across multiple scales. However, there are a number of other abiotic and biotic factors that have been found to structure herbivorous fish abundance and feeding behaviour including the nature of algal turfs (Russ, 2003; Tootell and Steele, 2016), topographic complexity (Emslie et al., 2014; Graham and Nash, 2013), hydrodynamic exposure (Bejarano et al., 2017; Bellwood et al., 2018; Fulton et al., 2005) and turbidity (Mallela et al., 2007; Moustaka et al., 2018) and social drivers such as competition (Davis et al., 2017b; Francini-Filho et al., 2010) and predation (Catano et al., 2016; Rasher et al., 2017; Rizzari et al., 2014).

While these drivers are highly varied, many of them, nonetheless, are related to sediment loads, which we have already established are directly linked to *C. striatus* feeding rates (see Tebbett et al., 2017a; Bellwood and Fulton, 2008). Specifically, a) algal turf sediments directly mediate the length (Fig. 8c), productivity, and composition of algal turfs (Airoldi et al., 1995; Clausing et al., 2014; Goatley and Bellwood, 2013; Purcell, 2000; Tebbett and Bellwood, 2020) and b) the rate and extent of sediment accumulation in algal turfs is mediated by topographic complexity (Tebbett et al., 2020b), hydrodynamic activity (Bodde et al., 2014; Purcell, 2000; Tebbett et al., 2017d), and sediment deposition (from suspended sediments that cause turbidity) (Latrille et al., 2019; Whinney et al., 2017). Sediment loads therefore represent a variable that has not only been linked to *C. striatus* feeding, but also represents a suite of other, diverse variables, which are often considered to be drivers of herbivorous fish distributions. In this respect, sediment loads may be an indicator variable that incorporates the cumulative influences of a range of biotic and abiotic factors that all mediate fish behaviour through their influence on sediment.

In addition to the above suite of factors, there are two factors directly related to sediment loads that warrant specific mention. The first of these is detritus. As detritus is the primary nutritional resource targeted by *C. striatus* (Choat et al., 2002; Crossman et al., 2005), it was previously assumed that the mechanism by which sediments impacted *C. striatus* feeding rate was via diluting the relative level of detritus in the EAM (e.g. Fig. 8b). However, in two prior experiments conducted in Tebbett et al., (2017a) the relative level of organic detrital material in particulates was explicitly manipulated in algal turfs to test for effects on *C. striatus* feeding. No such effects were apparent, suggesting that total sediment load alone, rather than its interaction with detritus levels, influenced feeding rates. As such the current study focused on total sediment load. Nevertheless, the results of the current study demonstrate that inorganic sediment loads are closely connected to both the total standing mass of organic detritus (Fig. 8a) and the relative amount of detritus in particulates (Fig. 8b).

These results suggest that inorganic sediments do ‘water-down’ the organic detritus in the EAM. Thus, while total detrital mass increases, the proportion per bite decreases, reducing the effective yield to *C. striatus*. Despite prior aquarium-based experiments suggesting that this ‘watering-down’ of detritus has a minimal influence on *C. striatus* feeding, the influence of such diluting processes could play a more important role under natural circumstances and could therefore explain how and why sediments have such a marked impact on *C. striatus*. However, regardless of the exact mechanism by which sediments influence *C. striatus* (i.e. indirectly via their relationship with detritus, or via more direct affects) sediments appear to be the underlying driver in both circumstances.

The second factor is sediment grain size distributions. Prior experimental evidence demonstrated that finer sediments reduced *C. striatus* feeding more than coarser sediments (Tebbett et al., 2017c). However, as this interaction was only investigated at a single sediment load (225 g m^{-2}), the influence of grain size was not incorporated in the present study as the interaction between varying sediment loads and grain size distributions on *C. striatus* feeding are not currently clear. Nonetheless, it is likely that increased levels of finer sediments would impact feeding to a greater extent than coarser sediments. Importantly, this means that the results presented herein are likely to be conservative. This is because, on coral reefs increases in sediment loads are likely to be driven by the accumulation of finer sediment grain size fractions (see Goatley et al., 2016) as fine sediments are readily transported to and deposited on reefs (Cunning et al., 2019; Jones et al., 2019; Latrille et al., 2019; Wolanksi et al., 2008). Therefore, if *C. striatus* feeding decreased more when loads of finer sediments increased, feeding rates would decline even more markedly than in the model predictions in the present study.

There are also some key factors that may shape fish distribution patterns and fish feeding rates that appear to be largely independent of sediment loads. For example, variability in water temperature has been linked to altered feeding rates (Ferreira et al., 1998; Longo et al., 2019). However, as the present study was largely conducted at the same reef, or across reefs at the same latitude, temperature is unlikely to be a significant driver in the current study. Furthermore, the abundance and distribution of nominally herbivorous fishes is often linked to dead substratum cover (i.e. hard substratum covered in algal turfs/crustose coralline algae) (Robinson et al., 2019; Russ et al., 2018, 2015). However, *C. striatus* abundance, again, appeared to be largely independent of this in the current study (Fig. 3), with distribution patterns forming a tighter relationship with sediment loads. This supports previous studies that have suggested that it is the quality of feeding substratum, rather than just its quantity, that is a stronger driver of nominally herbivorous fish distributions (Bellwood et al., 2018; Russ, 2003; Tootell and Steele, 2016).

Feeding may also be influenced by the surrounding fish community, including competition, facilitation and potential predation. However, it is important to note that in Part C of the present study (Table 1) we demonstrated that *C. striatus* feeding was concentrated in areas of low sediment in un-manipulated conditions even when these other factors were operating. Therefore, regardless of the effect of these social drivers, *C. striatus* still concentrated their feeding in areas of low sediment on the reef.

In terms of competition structuring feeding on the reef, the strength of interactions appear to be context- (especially in terms of nutritional resource availability) and species-specific (Davis et al., 2017b; Francini-Filho et al., 2010), including for the study species *C. striatus* (Choat and Bellwood, 1985; Robertson and Gaines, 1986). How predation structures *C. striatus* feeding specifically, requires further investigation. More generally, however, the nature of herbivory/detritivory on coral reefs appears to be influenced by predation (Atwood et al., 2018; Catano et al., 2016; Randall, 1965; Rasher et al., 2017; Rizzari et al., 2014). To maximise predation avoidance and feeding efficiency, *C. striatus* might utilise topographic complexity by feeding on elevated algal turf/CCA covered surfaces. Such surfaces are not only a nutritionally beneficial place to feed, as they accumulate lower sediment loads and contain higher relative detrital loads (Tebbett et al., 2020b), but these elevated surfaces may also provide a greater field of view over the surrounding reef environment, facilitating detection of predators (Brandl and Bellwood, 2015; González-Rivero et al., 2017). Therefore, incorporating other factors such as topographic complexity, as a proxy for predation risk, offers a fertile future avenue for understanding the nature of function delivery. Indeed, when considering additional factors – beyond sediment loads – it is likely that function delivery will be found to be even more constrained and heterogenous than suggested herein.

4.4 Ecological ramifications of algal turf sediments

Finally, this study highlights the role of algal turf sediments as a pervasive stressor on coral reefs. In areas where algal turf sediments are substantially impairing fish feeding (as in scenario 3 of our model [Fig. 7]), there may be a number of flow-on effects for the reef benthos and the broader ecosystem that extend beyond *C. striatus*. This is because feeding by most nominally herbivorous fishes both modifies, and is modified by, sediments in the algal turfs (Fong et al., 2018; Goatley and Bellwood, 2010; Krone et al., 2011; McAndrews et al., 2019; Tebbett et al., 2017a). Where nominally herbivorous fishes feed, they can maintain low sediment loads, and keep algal turfs cropped close to the substratum (Fong et al., 2018; Tebbett et al., 2017a). However, as sediments can constrain the spatial extent of feeding, this increases the spatial concentration of these functions being delivered to the reef (Fig. 7). In areas where algal turf sediments accumulate, and feeding is reduced, previous studies would predict: a) the development of longer algal turfs (Fig. 8c) (Fong et al., 2018; Goatley et al., 2016), b) reduced coral settlement (Birrell et al., 2005; Ricardo et al., 2017; Speare et al., 2019), and c) reduced benthic productivity (Tebbett and Bellwood, 2020). These changes may culminate in the transition of the reef from a short productive algal turf (SPAT) state, to a long sediment-laden algal turf (LSAT) state (*sensu* Goatley et al., 2016). Such transitions carry negative implications for the functioning of coral reef systems, and their ability to support key ecosystem services (Bellwood et al., 2019b).

4.5 Algal turf sediment thresholds and management implications

The data herein suggest that there are key threshold levels of algal turf sediments that impact fish abundance and feeding behaviour. For *C. striatus*, the relevant sediment levels appear to be around 250 – 500 g m^{-2}. These levels are remarkably low considering that average sediment loads on the reef crests of inner-shelf and coastal fringing reefs of the Great Barrier Reef regularly exceed 1000 g m^{-2} (reviewed in Tebbett and Bellwood, 2019). Unfortunately, it is hard to place these levels in a broader geographic context, because for most coral reef regions we do not know how much sediment is bound within the algal turfs. Indeed, it is sobering to note that, at present, algal turf sediments on the vast majority of coral reefs globally remain unmonitored and are rarely considered in coral reef management. As such, despite widespread reports of sediment impacts on coral reefs (e.g. Bégin et al., 2016; Hamilton et al., 2017; Jones et al., 2019; Wenger et al., 2016), we have only a limited understanding of how such impacts relate to algal turf sediment dynamics. Considering the clear ecological effects of algal turf sediments outlined herein, and the relatively low sediment levels over which these effects manifest themselves, increased monitoring and management of algal turf sediments may be warranted.

4.6 Conclusion

To-date, in our efforts to manage functions on coral reefs, we have generally focused on conserving the agents of function (often fishes) (Chung et al., 2019; Williams et al., 2019), by managing their abundance, biomass or biodiversity. However, using a multi-scale approach, we demonstrate how the link between presence and function delivery can be disrupted by sediment loads; algal turf sediments impair and constrain the spatial extent of function delivery. Unless direct extractive activities (fishing) are the main driver of function loss, managing to conserve fish abundance is unlikely to yield the desired outcomes in such scenarios; it only addresses one potential driver (direct extraction). Ultimately, in an era of global change leading to the degradation of coral reefs (Bruno et al., 2019; Hughes et al., 2018), managing ecosystem functions has been proposed as a particularly important endeavour (Bellwood et al., 2019a; Hughes et al., 2017a). However, this may require more than just managing fish populations. The functional equation in the present study requires management of both the agents of function (fish) and the drivers that modify this function (sediments).

Acknowledgements

We thank: C. Hemingson and the Lizard Island Research Staff for field support; M. Mihalitsis and R. Morais for helpful comments and statistical advice; C. Hemingson for the *C. striatus* vectors; anonymous reviewers for insightful and thought-provoking comments; and the Australian Research Council (DRB: CE140100020 and FL190100062), the Lizard Island Research Foundation (RPS) and an Australian Government Research Training Program Scholarship (SBT) for financial support.

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