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Sediments ratchet-down coral reef algal turf productivity

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Abstract

Coral reefs are highly productive ecosystems, with much of this productivity arising from the algal turfs which cover the hard reef substratum. This productivity can flow up the food chain through herbivorous fishes, to be harvested by humans as fishable biomass. However, algal turfs exist on a spectrum of forms from short productive algal turfs (SPATs), to long sediment-laden algal turfs (LSATs). The latter are increasingly likely to typify Anthropocene coral reefs, however, we have a limited understanding of their nature and potential productivity. We assessed the nature of algal turfs in terms of length, biomass, relative detritus content, and productivity across a sediment load gradient, from SPATs to LSATs, at two reefs separated by more than 450 km along Australia's Great Barrier Reef (GBR). Furthermore, to assess the capacity of sediments to shape productivity, we modelled algal turf productivity, as a function of sediment load, across multiple spatial scales in a Bayesian framework. We recorded precipitous declines in both the productivity of algal turfs, and the relative nutritional value of particulates, up to sediment loads of ~100 g m^{-2}. However, algal turf biomass did not change with sediment loads. This appears to reflect a shift in algal community composition from short, high-biomass, highly-productive algae at low sediment loads, to longer, low-biomass, less productive algae at high sediment loads. Importantly, these relationships provide a robust framework for estimating algal turf productivity on coral reefs. Indeed, when we applied our models to known sediment loads, we reveal that sediment loads alone can fully explain observed algal turf productivity gradients across multiple spatial scales. In an era of global climate change and coral reef reconfiguration, algal turf sediments may hold the key to maintaining benthic productivity on coral reefs in the Anthropocene.

Key words:

Algal turf; Coral reef; Ecosystem function; Epilithic algal matrix; Herbivory; Productivity

1. Introduction

Paradoxically, coral reefs exist as highly productive ecosystems within nutrient poor waters (Adey and Goertemiller, 1986; Brandl et al., 2019b; Darwin, 1842). A paradox that is highlighted by the algae that inhabit coral reefs, which maintain high productivity under such conditions (Adey, 1998; Hatcher, 1988; Steneck, 1997). This productivity in turn supports core trophic pathways on coral reefs, including energy transfer up the food chain through herbivorous fishes (Kelly et al., 2017; Russ, 2003). Ultimately, this productivity is often harnessed by humanity, with millions of people globally relying on coral reefs to produce fishable biomass to meet basic subsistence needs (Moberg and Folke, 1999; Woodhead et al., 2019). However, coral reefs are changing fast and transitioning to lower-coral cover configurations (Bellwood et al., 2019a; Bruno et al., 2019; Hughes et al., 2017). If we are to sustain key services from these highly-altered systems, it is vital to understand, and quantify, the nature of core ecosystem functions, such as benthic productivity, in these modified systems (Bellwood et al., 2019b; Brandl et al., 2019a; Hughes et al., 2017).

Algal turfs epitomise the highly productive nature of algae on coral reefs and, in many cases, they are the primary contributors to benthic productivity in these systems (Carpenter, 1985; Hatcher, 1988; Klumpp and McKinnon, 1992). Importantly, we are likely to witness a rise, globally, in the coverage of algal turfs on climate change-modified coral reefs (Tebbett and Bellwood, 2019). This is because: a) on many coral reefs algal turfs are already a major benthic covering (Donovan et al., 2018; Smith et al., 2016; Wismer et al., 2009), b) algal turfs readily colonise dead coral substrata following primary colonisation by cyanobacteria (Diaz-Pulido and McCook, 2002), and c) they are highly stress-tolerant (Hay, 1981; Steneck and Dethier, 1994) and future climate change conditions even appear to be advantageous to algal turfs (Bender et al., 2015; Johnson et al., 2017). Understanding the capacity of algal turfs to sustain productivity on Anthropocene coral reef systems is of critical importance (Bellwood et al., 2019a; Brandl et al., 2019a). However, this capacity may be shaped by the other stressors faced by coral reefs, foremost among these is sediments.

After climate change, increased sediment inputs are widely identified as one of the major threats to coral reefs (Bainbridge et al., 2018; Fabricius, 2005; Magris and Ban, 2019), with 50% of the world's reefs at risk of increased terrestrial inputs (Burke et al., 2011). These sediments often become trapped within the complex structure of algal turfs (Connell et al., 2014; Latrille et al., 2019); an interaction that is likely to intensify as climate change reduces the topographic complexity of reefs (Tebbett et al., 2020). It is these sediments that appear to shape the nature of algal turfs, as they can reduce herbivory and lead to a transition from short productive algal turfs (SPATs) to long sediment-laden algal turfs (LSATs) (sensu Goatley et al., 2016). Recently, experimental evidence highlighted that a causal relationship exists between sediment loads in algal turfs and algal turf productivity, in terms of the potential yield to herbivorous fishes, with increasing sediments reducing yields (Tebbett et al., 2018). However, this study was experimental and undertaken on a pre-bleached coral reef. We lack a clear understanding of sediment-algal turf productivity relationships under the current scenarios on highly-altered post-bleached coral reefs.

Clearly a comprehensive understanding of the interaction between sediments and productivity is necessary if we are to sustain critical ecosystem functions on Anthropocene coral reefs. The aim of this study, therefore, is to investigate the nature of algal turfs and their productivity across a range of algal turf conditions and associated sediment loads under field conditions on climate-impacted reefs. This relationship will, therefore, be investigated on two disparate reefs with recent histories of stressors that foreshadow the future of many coral reefs and, in doing so, will provide a framework for estimating algal turf productivity on such disturbed systems. We will then apply these empirical data, via a Bayesian modelling framework, to existing datasets to examine algal turf productivity, as a function of sediment load, across multiple spatial scales; from centimetres within reef habitats to among reefs spanning the entire continental shelf of the Great Barrier Reef (GBR). The overarching goal of this study is to document, and provide a framework for estimating, spatial patterns in algal turf productivity, and to explore the role that sediment may play in shaping patterns in this key process on Anthropocene reefs.

2. Materials and methods

2.1 Study sites

This study was conducted between March and April 2019 at Lizard Island in the Northern GBR, and April and May 2019 at Orpheus Island in the Central GBR (Fig. S1). Lizard Island is a mid-shelf reef located approximately 30 km from the mainland, while Orpheus Island is an inner-shelf reef located approximately 15 km from the mainland. As the influence of terrestrial sediment inputs, and the nature of sediment dynamics, varies across the continental shelf (Fabricius et al., 2014; Tebbett et al., 2017) these two islands can provide differing insights into how sediment dynamics may influence algal turf productivity. Furthermore, each island has been subject to different stressors including coral bleaching, cyclone impacts, and sediment disturbances (Goatley et al., 2016; Gordon et al., 2016; Wismer et al., 2019). At each island we had two sites, each within leeward facing bays (Fig. S1), and at each site we focused on the shallow-water (0-5 m below chart datum) habitat stretching from the crest to the mid-flat. This shallow-water habitat was selected as it represents the most productive and ecologically relevant habitat on climate-reconfigured coral reefs (Bellwood et al., 2018). For details of the herbivorous fish community at each site see supporting information (Text S1; Table S1).

2.2 Field sampling

At each site productivity was measured in terms of the change in turf length using a standard caging technique (following Roff et al., 2018; Russ, 2003). At each site, 26-32 flat (~<15° from horizontal) areas of consolidated reef matrix were selected. Selected sampling locations were covered in algal turfs, outside the territories of damselfishes, and free of sediment-retaining pits, macroalgae and encrusting organisms. Locations were each covered in herbivore exclusion cages constructed from 12 × 12 mm stainless steel mesh and measured 140 × 140 × 100 mm (L × W × H) with a 50 mm fringe. Cages of this nature have been used extensively in prior experiments (e.g. Bonaldo and Bellwood, 2011; Clausing et al., 2014; Fong et al., 2018; Latrille et al., 2019) and cage effects on the nature of algal turfs have been rigorously examined (Tebbett et al., 2018). Immediately prior to caging, 10 haphazardly selected algal turf filaments were measured using the depth probe of vernier callipers and recorded by pushing the tips of the callipers into saltwater-resistant pressure-sensitive poster adhesive (Blu-tack). Indentations were then measured in the lab using digital callipers yielding an average algal turf length for each caged location (reviewed in Tebbett and Bellwood, 2019). Cages were then positioned over the measured area and the fringe was contoured to the reef substratum and nailed to hold it in place. The distance of each cage from the reef crest was also recorded.

Cages were left in place for five days. As algal turfs can grow rapidly in the absence of herbivorous fishes (Bonaldo and Bellwood, 2011) this time was sufficient to examine changes in length while minimising potential caging effects. Following the removal of cages, algal turf length was remeasured (as above) yielding the change in algal turf length over 5 days (i.e. the average starting length of algal turf filaments was subtracted from the average length after 5 days of caging). Sediments trapped within the algal turfs were then sampled from within a 58 cm^2 PVC ring using a submersible electronic vacuum sampler (modified after Purcell, 1996). The sediment and algal turf community on an identical area of reef substratum adjacent to the caged area (i.e. open to herbivorous fishes) was also sampled, as above, during the 5 day deployment period, generally upon deployment of cages, to provide data on relationships between sediment, algal turf length, algal turf biomass and detritus levels in the presence of herbivores. Algal turf biomass was sampled after sediment collection by removing and collecting the algal turf community using the vacuum sampler. This was achieved by using a steel tube fitted to the intake hose of the vacuum sampler to scrape the substratum to a depth of ~1 mm. Dislodged algal material was then collected in a 220 µm mesh filter fitted between the tube and the electronic pump. Algal filters were then sealed and placed on ice. Once on land the material from the filters was rinsed with freshwater, placed into vials and frozen prior to laboratory processing.

2.3 Sample processing

To fix organic material, 15 ml of 4% buffered formaldehyde was added to the sediment samples. Each sample was then transferred into a 9 l container and left for 3 h, before decanting the water, to allow particulate material >10 µm to settle (Purcell, 1996). All samples were then transferred to 120 ml sample jars and wet sieved through a 2 mm stainless steel mesh so that only material <2 mm was retained (sands, silts and clays; ISO 14688-1:200). To remove salts, each sample was then rinsed with freshwater three times, leaving at least a 3 h settling period between rinses. Samples were then dried to a constant weight at 60˚C and weighed to 0.0001 g to yield total benthic particulate mass. Organic material was then removed from the samples by bleaching them for at least two weeks using 30% hydrogen peroxide (H_2O_2). Samples were stirred, and fresh solution was added on a regular basis. Samples were then re-dried and weighed, as above, yielding total sediment mass, and the proportion, by mass, of organic particulate material in benthic particulates. Each frozen algal turf sample was thawed, dried to a constant weight at 60˚C and then weighed to 0.0001

g. Organic algal material was then removed from each sample by bleaching, as above. Each sample was then re-dried and re-weighed, as above, yielding total organic algal biomass.

2.4 Statistical analysis

Initially we examined the relationship in algal turfs adjacent to caged plots between a) algal turf length, algal turf biomass and the proportion of detritus in benthic particulates (as an indication of the relative nutritional value of particulates) and b) algal turf sediment load; using Bayesian generalised linear mixed effects models (GLMMs). In all models sediment load (g m^{-2}: continuous factor, logged), and island identity (categorical factor) were fitted as fixed factors with an interaction term, while site identity was treated as a random factor to account for the lack of spatial independence among samples. The model assessing algal turf length used a lognormal distribution (gaussian with a log-link), biomass used a Gamma distribution with a log-link, while the model assessing the proportion of detritus used a Beta distribution with a logit-link. In all cases weakly informative priors were used (see Table S2 for prior details and chain specifications for each model). Model convergence, fit and assumptions were assessed using trace plots, autocorrelation plots, rhat plots, posterior predictive checks, effective sample sizes and residual plots, all of which were satisfactory. Furthermore, we checked for any effect of the distance of plots from the reef crest by regressing the residuals of each model against this factor to examine patterns. No patterns were revealed.

The relationship between algal turf productivity and initial algal turf length was also examined using a Bayesian GLMM, as above. Algal turf productivity was based on the linear extension of algal turfs (i.e. mm of growth day^{-1}). Only positive growth was considered in the model (9 of the 120 plots recorded negative growth and these were excluded from further analysis. This was because: a) these may have been due to measurement errors [departure from 0 growth was small, <0.3 mm day^{-1} in all cases], b) the inclusion of these values would have heavily limited modelling options, and c) they could have been influenced by small invertebrate grazers/small herbivorous fishes that could have entered through the 12 × 12 mm mesh). In this model initial algal turf length (mm; continuous factor, logged) and island identity were fitted as interacting fixed factors, while site was fitted as a random factor. The model was based on a lognormal distribution. Furthermore, as the driver of algal turf productivity appears to be sediments (Tebbett et al., 2018), rather than turf length, we wanted to specifically examine the relationship between productivity and algal turf sediment load. Unfortunately, exploratory data plots suggested that final sediment load in the algal turfs was a poor predictor and may have been influenced by algal growth and caging effects. We therefore built a model to predict initial sediment load as a function of initial algal turf length (see Text S2). We then used these predicted sediment loads (g m^{-2}; continuous factor, logged) in place of initial algal turf length in a second Bayesian GLMM with a lognormal distribution (as above), to examine the relationship between algal turf productivity and estimated initial sediment load. All statistical analysis were performed in the software R (R Core Team, 2018) using the *rstanarm* (Goodrich et al., 2018), *brms* (Burkner, 2017), *bayesplot* (Gabry and Mahr, 2018), *tidybayes* (Kay, 2019), *tidyverse* (Wickham, 2017) and *emmeans* (Lenth, 2019) packages.

2.5 Model application

Previous studies have shown that algal turf productivity can vary considerably across the continental shelf of the GBR and among reef habitats (Klumpp and McKinnon, 1992; Russ, 2003; Russ and McCook, 1999), while Tebbett et al., (2020) suggested that it might also be influenced by topographic complexity at small spatial scales. However, evidence suggests that while hydrodynamics and coastal influences may be the primary drivers of productivity, these patterns are mechanically linked to variation in algal turf sediment loads across the same spatial scales (i.e. the ultimate driver may be hydrodynamics, however this influences productivity by shaping the proximal driver – sediment loads) (Purcell and Bellwood, 2001; Tebbett et al., 2020, 2017). Therefore, to examine the potential impact of sediment loads on algal turf productivity across different spatial scales, we applied our model to published algal turf sediment load data across: a) topographic complexity within a reef habitat, b) across reef habitats, and c) across the continental shelf of the GBR. For variation across topographic complexity, 100 algal turf sediment loads were estimated (based on 0.13 to 0.72 m of elevation above the reef substratum for horizontal algal turf sites; data from Tebbett et al., (2020). Data on algal turf sediment loads from reef crest, fore-flat, and mid-flat habitats at Lizard Island in the northern GBR were sourced from Purcell, (2000), while data on algal turf sediment loads from reef crests on inner-, mid-, and outer-shelf reefs across the northern GBR were sourced from Tebbett et al., (2017).

3. Results

Increasing algal turf sediments loads had a clear effect on the nature of the algal turfs (Fig. 1). There was a strong positive relationship between sediment load and algal turf length (Fig. 1a). However, this relationship was dependent on the island in question with the slope of the Orpheus Island relationship being steeper than the slope of the Lizard Island relationship (as the 95% credibility intervals did not overlap zero this suggested the interaction had a clear effect; Table S3). Remarkably, in terms of algal turf biomass, there was no detectable differences between the islands and no clear relationship with sediment load (in all cases the 95% credibility intervals overlapped zero) (Table S3; Fig. 1b). However, there was a marked effect of sediment load on the proportion of organic particulate material (detritus) in the total benthic particulate mass (Fig. 1c). The proportion of detritus in benthic particulates declined rapidly from 0 until an inflexion point centred around a sediment load of ~68 g m^{-2}; Fig. 1c). As the 95% credibility intervals of the model did not overlap zero this suggested that sediment load had a clear effect on the proportion of detritus, while the models also highlighted that there were no differences between islands (Table S3). Together these results highlight that with increasing algal turf sediment loads, a) algal turf length increases, b) algal turf biomass does not change, and c) relative detritus levels within the algal turfs declines rapidly.

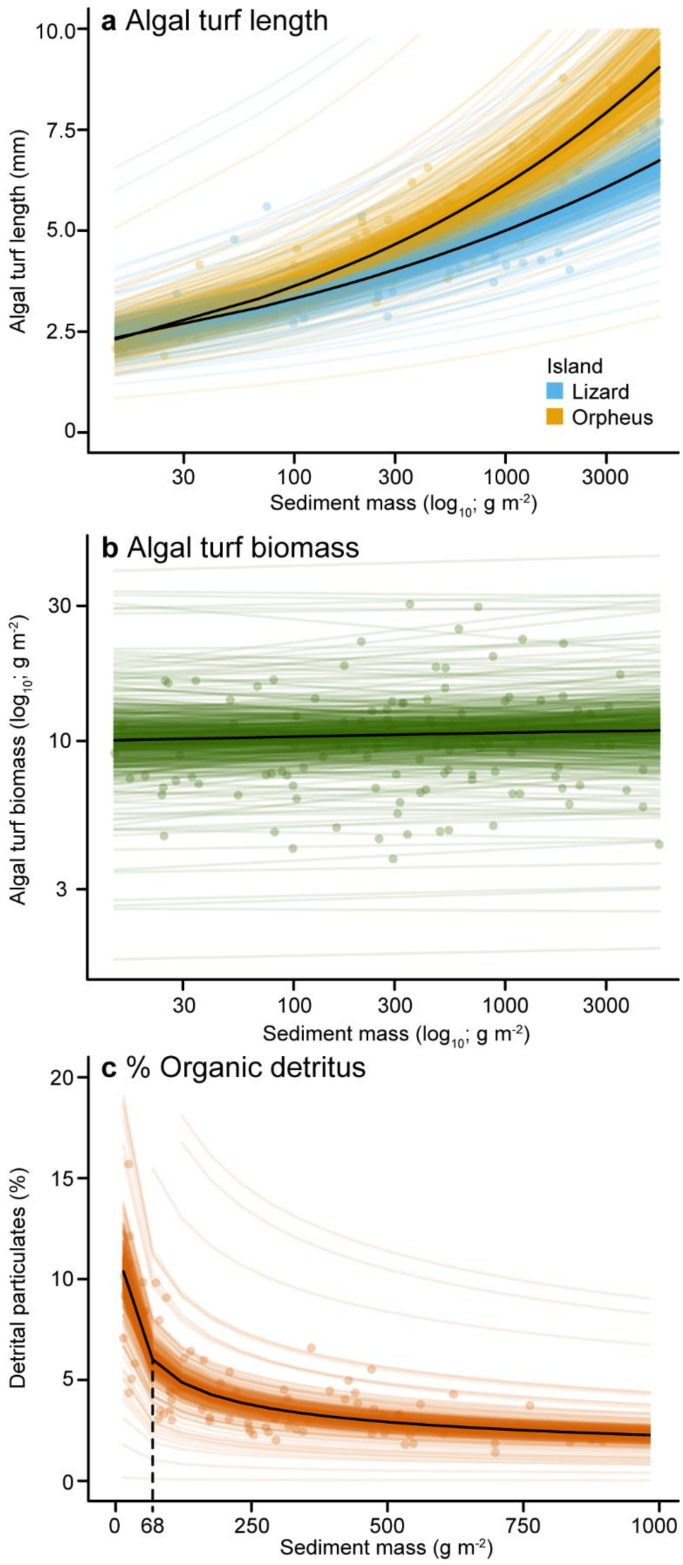

Figure 1 The relationship between algal turf sediment load and a) algal turf length, b) algal turf biomass, and c) percentage of organic detritus by mass in benthic particulates. The black lines indicate the mean predicted model fit, while the coloured lines are based on 500

randomly selected model fits sampled from the posterior distribution. The coloured dots are the raw data points. Note that for panel c) the dashed line indicates the inflexion point and the x axis has been trimmed so that the trend can be seen clearly (please refer to Fig. S2b for the full graph).

Increasing initial algal turf length and predicted initial algal turf sediment load led to precipitous declines in the productivity of algal turfs (Fig. 2). These declines levelled off at initial algal turf lengths of ~4-5 mm and sediment loads of ~100-200 g m^{-2} with a clear inflexion point at a sediment load of ~108 g m^{-2} (Fig. 2). Furthermore, the model suggested that initial algal turf length had a substantial effect on algal turf productivity as the 95% credibility intervals did not overlap zero (Table S3). Similarly, the model suggested that predicted sediment load had a substantial effect on algal turf productivity as the 95% credibility intervals did not overlap zero (Table S3). In both models the credibility intervals of the algal turf length/ predicted sediment load interaction with island identity, and the island identity factor alone, overlapped zero, suggesting that neither the interaction nor island identity had a substantial effect on algal turf productivity (Table S3). Overall, these results suggest that algal turf growth slows with linear extension, and that small changes in algal turf sediment loads can have marked effects on algal turf productivity. SPATs, therefore, can be considered algal turfs under ~5 mm in length that contain less than ~100 g m^{-2} of sediment.

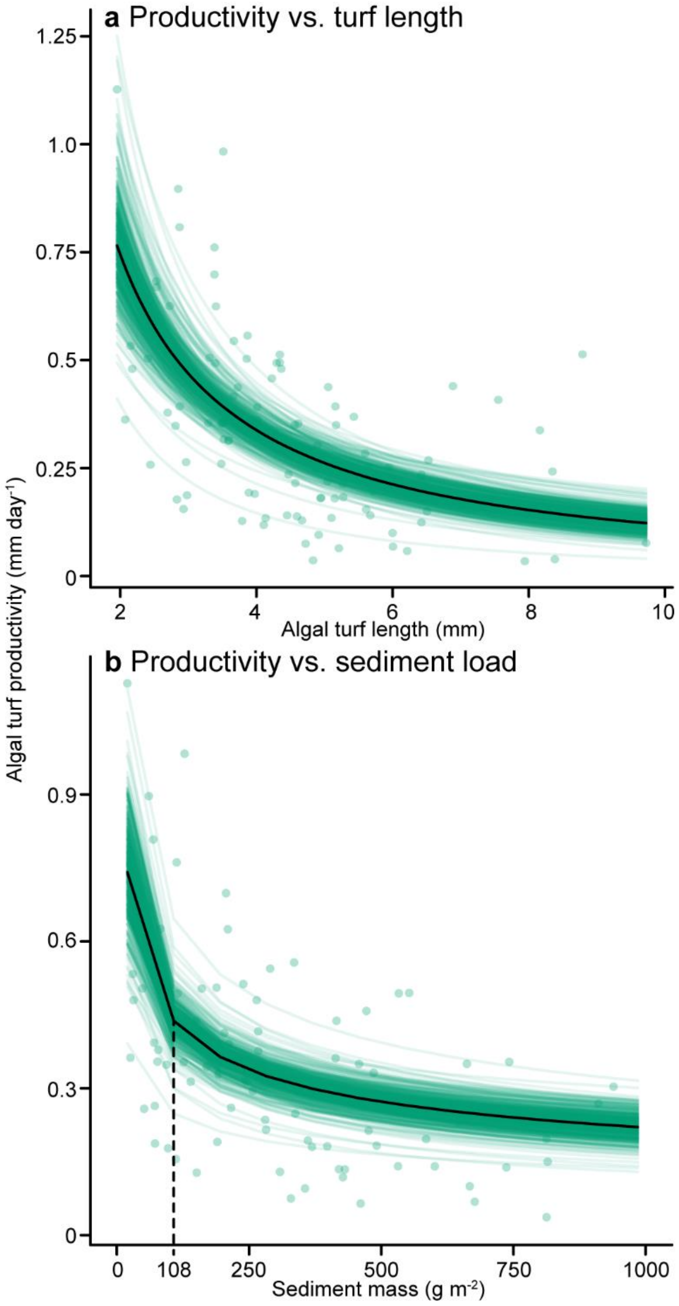

Figure 2 The relationship between algal turf productivity and a) initial algal turf length, and b) predicted initial algal turf sediment load. The black line indicates the mean predicted model fit, while the green lines are based on 500 randomly selected model fits sampled from the posterior distribution. The green dots are the raw data points. Note that for panel b) the dashed line indicates the inflexion point and the x axis has been trimmed so that the trend can be seen clearly (please refer to Fig. S2c for the full graph).

Clear patterns emerged when the model relating algal turf productivity to algal turf sediment loads was applied to data describing algal turf sediments across the three spatial scales (Fig. 3). Firstly, at the smallest spatial scale, productivity clearly increased with increasing substratum elevation, suggesting that algal turfs on flatter reefs would be less productive (Fig. 3a). Furthermore, marked differences in estimated algal turf productivity occurred across reef habitats, with the highest productivity on the reef crest followed by a marked decline across the reef flat (Fig. 3b). Finally, at the largest spatial scale, estimated algal turf productivity varied substantially across the continental shelf of the GBR, with noticeably higher levels on mid- and outer-shelf reef crests compared to inner-shelf reef crests (Fig. 3c). Taken together, these patterns highlight the potential of algal turf sediments to drive variation in algal turf productivity across multiple spatial scales.

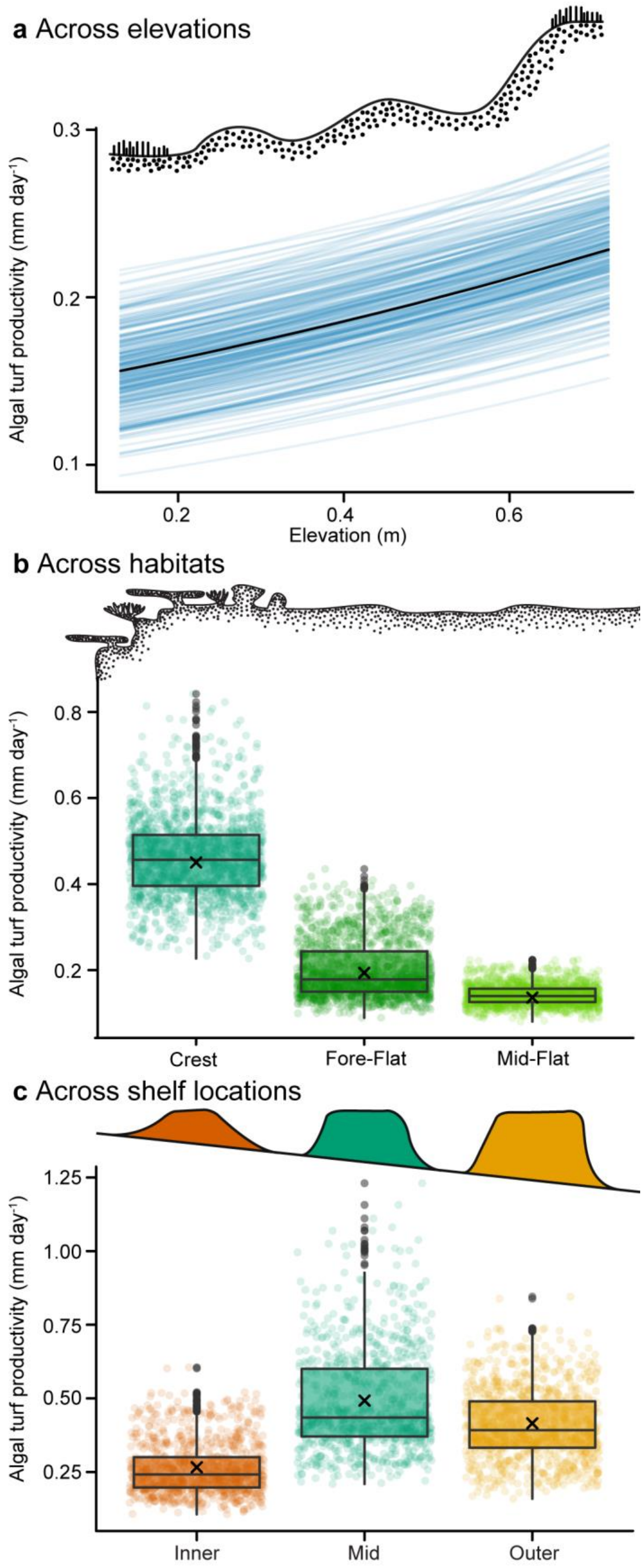

Figure 3 Predicted algal turf productivity across varying a) substratum elevations at Lizard Island, Australia, b) reef habitats at Lizard Island, and c) shelf positions across the Great

Barrier Reef, Australia. a) the black line indicates the mean predicted fit of a Bayesian model relating algal turf productivity (mm day^{-1}) to algal turf sediment load, while the blue lines are based on 250 randomly selected model fits from the posterior distribution. b) and c) boxplots show the median, 25th percentiles and outliers, the crosses show the mean value, and dots are based on 50 randomly selected predictions from the posterior distribution of a Bayesian model relating algal turf productivity (mm day^{-1}) to algal turf sediment load.

4. Discussion

Coral reefs in the Anthropocene are expected to be typified by lower coral cover, lower topographic complexity, and a higher coverage of algal turfs (Bellwood et al., 2019a; Tebbett and Bellwood, 2019). These algal turfs form an interface that is closely connected with essential coral reef ecosystem processes including coral settlement (Birrell et al., 2005; Speare et al., 2019), herbivory (Duran et al., 2019; Kelly et al., 2017; Streit et al., 2019) and, importantly, benthic productivity (Hatcher, 1988; Klumpp and McKinnon, 1992; Steneck, 1997). However, the state of algal turfs can range along a spectrum of sediment loads from short productive algal turfs (SPATs) to long sediment-laden algal turfs (LSATs) (Goatley et al., 2016). Across this spectrum, we examined the capacity of sediments to shape the nature of algal turfs and the functions they provide (Fig. 4). Unexpectedly, we found that even at relatively low sediment levels, there was precipitous declines in the productivity of algal turfs, with a concomitant decrease in the relative amount of detrital particulates. As such, even small shifts in the state of algal turfs towards LSATs, brought on by stressors such as enhanced sediment fluxes or overfishing (Fong et al., 2018; Goatley et al., 2016; Tebbett et al., 2018), may have considerable bottom-up effects on coral reef ecosystem processes.

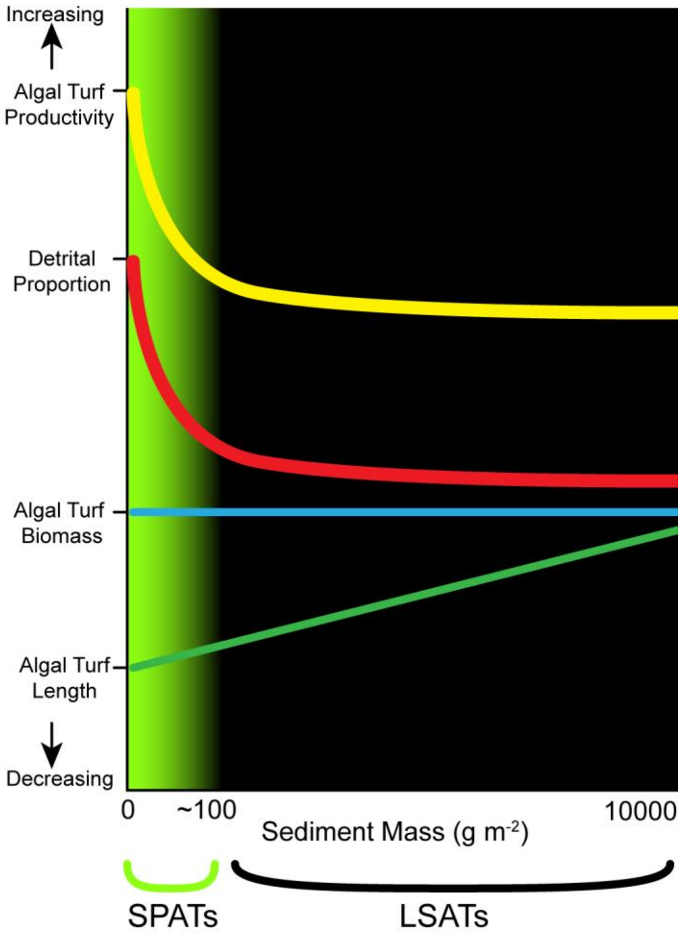

Figure 4 A conceptual diagram summarising the major changes in the nature of algal turfs on coral reefs across a spectrum from short productive algal turfs (SPATs) to long sediment-laden algal turfs (LSATs). Note that the nature of algal turfs in terms of productivity, and the relative nutritional value of particulates, appears to decline rapidly from 0 to about 100 g m^{-2} of sediment (see Figs. 1, 2 for more details). SPATs therefore appear to end when algal turf length exceeds ~5 mm and sediment loads exceed ~100 g m^{-2}

Our results support previous studies which have highlighted the positive relationship between algal turf length and sediment load on coral reefs (Fong et al., 2018; Gordon et al., 2016; Purcell, 2000), giving rise to the terms SPATs and LSATs (Goatley et al., 2016). However, the effect of this sediment on algal turf processes, such as productivity, has remained relatively unexplored, particularly across large spatial scales. In exploring this effect of various sediment loads, we highlight a fundamental shift in the productivity of algal turfs, with rapid changes at very low sediment levels <100 g m^{-2} (Fig. 4). Such low sediment levels can accumulate in algal turfs in less than three days (Latrille et al., 2019; Tebbett et al., 2018). Importantly, we also found that algal turf biomass did not change across this SPAT-LSAT spectrum, supporting the results of previous studies on coral reefs (Purcell and Bellwood, 2001), and subtropical rocky reefs (Airoldi and Virgilio, 1998). This lack of change in biomass potentially offers a mechanistic explanation for the fundamental decline in productivity. It is likely that at low sediment loads algal turf assemblages are composed of short, high unit biomass (mass per mm), high-productivity algal taxa. By contrast, with increasing sediment loads >~100 g m^{-2}, the composition may shift towards longer, low unit biomass, less productive algal taxa. Visually algal turfs appear to transition from a low dense complex algal turf community to etiolated algal filaments. Such changes in algal turf community composition across sediment loads has been shown on subtropical rocky reefs (Airoldi et al., 1995; Stewart, 1983), and further investigation on coral reefs, as suggested by Harris et al., (2015), appears warranted. However, regardless of the actual mechanistic basis, when sediment loads exceed ~100 g m^{-2} it appears algal turfs enter a critical transition zone, beyond which low productivity and low particulate nutritional value persist.

In addition to identifying changes in the nature of algal turfs across the SPAT-LSAT spectrum, a clear outcome of our study is that it provides a way forward in terms of estimating algal turf productivity on coral reefs, utilising a single ‘universal trait’. Specifically, a universal trait, is a trait that can be directly related to a range of organismal functions (Bellwood et al., 2019b). Perhaps the best example in coral reef ecology is fish body size. Fish size is related to every known fish function (Bellwood et al., 2019b), and quantifying this trait permits the estimation of a range of core ecosystem processes including nutrient cycling (Allgeier et al., 2014) and storage and production of fish biomass (Morais and Bellwood, 2018). In our case, algal turf length appears to be a similar 'universal trait' for benthic algal turfs (Fig. 4). This one trait appears to be related to many facets of algal turf condition (Flower et al., 2017; Goatley et al., 2016; Steneck et al., 2018), including accumulated sediment mass (the underlying driver of most processes related to algal turfs [Clausing et al., 2014; Fong et al., 2018; Goatley et al., 2016]). Importantly, we can now estimate productivity as a function of algal turf length and/or sediment load. This is a key step forward in the study of benthic productivity on coral reefs. This is because length is by far the easiest algal turf trait to measure, with established methods allowing direct quantification rapidly across broad spatial scales (reviewed in Tebbett and Bellwood, 2019).

In the past, research into benthic productivity has been limited by the methodologies that required expensive or technical respirometry chambers (e.g. Klumpp and McKinnon, 1992, 1989), caging techniques over extended temporal scales (e.g. Russ, 2003; Russ and McCook, 1999), and/or relied on artificial tiles that may not be representative of natural substrata (Hixon and Brostoff, 1985) and are likely to accumulate lower sediment loads than natural algal turfs (Tebbett et al., 2018). Furthermore, at larger scales the application of different methods precludes reliable comparative analysis. Due to these limitations when 'productivity' is included in large-scale coral reef studies, pelagic primary productivity or other proxies such as chlorophyll-A concentration is often used (Cinner et al., 2018; Taylor et al., 2018). However, the links with benthic productivity are often tenuous or unknown, seriously limiting the strength of inferences relating to benthic processes (Gove et al., 2013; Taylor et al., 2018). Our modelling framework, derived from readily measured algal turf traits across a spectrum of naturally occurring SPATs to LSATs, permits a direct estimation of algal turf productivity that operates at any scale. This utility is exemplified when we applied our models to estimate productivity at various spatial scales.

Our estimated multi-scale patterns of algal turf productivity, as a function of sediment load (based on models derived from our response-curves), are strongly supported by previous empirical data. Specifically, previous studies have highlighted far higher algal turf productivity on reef crest habitats relative to reef flats (Klumpp and McKinnon, 1989; Russ, 2003), but generally far lower productivity on inner-shelf reefs relative to mid-, and outer-shelf reefs on the GBR (Russ and McCook, 1999; Williams et al., 1986). Furthermore, our results support the suggestions of Tebbett et al., (2020), that enhanced algal turf sediment accumulation on flatter, low-elevation, climate-modified coral reefs could reduce algal turf productivity. Based on our models, it appears that gradients in algal turf sediments are able to explain gradients in algal turf productivity across shallow water coral reef habitats. This conclusion is underpinned by previous experimental work that established a causal relationship between sediment loads and algal turf productivity (Tebbett et al., 2018). Although other factors, such as light intensity, and hydrodynamic activity (an ultimate driver of algal turf sediment loads), are undeniably important and are likely to contribute to observed gradients in algal turf productivity (Carpenter, 1985; Hatcher, 1990; Klumpp and McKinnon, 1989; Roff et al., 2018), our results show that, in addition to a causal relationship, algal turf sediments are able to influence productivity to the full extent seen in natural and disturbed systems.

Remarkably, we found limited between-island differences in the nature of algal turfs across the range of sediment loads examined, especially in terms of algal turf productivity. This is despite the two locations being exposed to a markedly different suite of biological (e.g. herbivorous fish assemblages [see Table S1]) (Cheal et al., 2012), physical (e.g. sediment resuspension, and oceanic flushing) (Brodie et al., 2012; Woolfe et al., 2000), and anthropogenically enhanced (e.g. terrestrial inputs of nutrients) (Fabricius et al., 2014; Kroon et al., 2012), drivers. Many of these drivers, especially nutrients, have been linked to algal productivity on coral reefs (Graham et al., 2018; Hatcher, 1990; Russ and McCook, 1999; Smith et al., 2001; Williams and Carpenter, 1988). The variation in these drivers would have been captured in our ‘island identity’ factor. However, we found minimal between-island effects, strongly supporting studies which have suggested a limited role for top-down processes, such as herbivory, or bottom-up processes based on nutrients (Burkepile and Hay, 2006; Russ et al., 2015). By contrast, algal turf sediment loads alone had, by far, the largest effect on productivity. Algal turf sediment loads may therefore represent the primary driver of algal turf productivity on coral reefs.

Unfortunately, 50% of the world’s coral reefs are at risk of increased terrestrial sediment inputs (Burke et al., 2011). As algal turfs can represent the major reservoir of sediments on coral reefs (Latrille et al., 2019), increased sediment fluxes to reefs may lead to increased algal turf sediment accumulation. A process that will intensify as climate-change reduces coral reef topographic complexity (Tebbett et al., 2020). As such, our study carries particularly serious implications for coral reefs that are both at risk of increased sediment accumulation and are heavily relied upon by people in subsistence fisheries. This is because catches in many subsistence coral reef fisheries can be predominantly composed of herbivorous and detritivorous fishes (Edwards et al., 2014; Robinson et al., 2019). Unfortunately, if increasing algal turf sediment loads lead to declines in algal turf productivity and particulate nutritional value, this may impose significant bottom-up effects on the herbivorous and detritivorous fishes that rely on these nutritional resources. This conclusion is supported by studies that have highlighted the close relationship between coral reef herbivorous and detritivorous fish populations and algal-based nutritional resources (Purcell and Bellwood, 2001; Russ et al., 2015; Tootell and Steele, 2016). Together, this evidence highlights the potential capacity of algal turf sediments to shape food chains by limiting nutritional resources.

While fisheries productivity may be sustained on algal covered coral reef systems (Bellwood et al., 2018; Morais and Bellwood, 2019; Robinson et al., 2019), this fishable biomass productivity may be intimately linked to the ability of the algae to provide nutritional resources to these fishes (Kelly et al., 2017; Russ, 2003). However, we have highlighted that the capacity of algal turfs to provide these nutritional resources is heavily dependent upon accumulated sediment loads. These findings come at a time when global climate change has driven profound losses of coral cover on the world's coral reefs, with many reefs now covered primarily by algal turfs (Bellwood et al., 2019a; Bruno et al., 2019; Hughes et al., 2017). As such, sustaining the functioning and productivity of coral reefs in the Anthropocene, may be intimately intertwined with the nature of algal turfs and the sediments they contain.

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