



Research article

Collapsing ecosystem functions on an inshore coral reef

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ABSTRACT

Ecosystem functions underpin productivity and key services to humans, such as food provision. However, as the severity of environmental stressors intensifies, it is becoming increasingly unclear if, and to what extent, critical functions and services can be sustained. This issue is epitomised on coral reefs, an ecosystem at the forefront of environmental transitions. We provide a functional profile of a coral reef ecosystem, linking time-series data to quantified processes. The data reveal a prolonged collapse of ecosystem functions in this previously resilient system. The results suggest that sediment accumulation in algal turfs has led to a decline in resource yields to herbivorous fishes and a decrease in fish-based ecosystem functions, including a collapse of both fish biomass and productivity. Unfortunately, at present, algal turf sediment accumulation is rarely monitored nor managed in coral reef systems. Our examination of functions through time highlights the value of directly assessing functions, their potential vulnerability, and the capacity of algal turf sediments to overwhelm productive high-diversity coral reef ecosystems.

1. Introduction

Ecosystems are characterised by a dynamic suite of functions or processes that maintain equilibrium states (Holling 1973; Scheffer et al., 2001) and sustain the services upon which many people depend (Fu et al., 2013; Liu et al., 2016). Understanding the importance of specific ecosystem processes, and their role in structuring ecosystem functioning, is, therefore, a key focus of ecological research, especially in this era of global climate change (Manning et al., 2018; Bellwood et al., 2019b). Researchers have applied a wide range of functional indicators to understand how ecosystems function and respond to disturbances. These include the abundance or biomass of key taxa (Paine 1969; Banerjee et al., 2018), functional group-based approaches (Steneck and Dethier 1994; Bellwood et al., 2004; Heenan and Williams 2013), as well as traits and associated metrics (e.g. Functional Diversity, Functional Evenness) (Lavorel and Garnier 2002; Mouillot et al., 2013; McWilliam et al., 2020). However, while these proxies have provided significant advances in our understanding (McGill et al., 2006; Violle et al., 2007; Bellwood et al., 2019b), they are largely centred around the use of traits that focus on the diversity of species and communities, i.e. 'pattern traits' (sensu Volaire et al., 2020). Evidence of how specific ecosystem

processes respond to disturbance remains largely unknown (Petchey and Gaston 2006; Mlambo 2014; Bellwood et al., 2019b). This knowledge gap is particularly problematic for managers, especially if the goal is to sustain a desired level of ecosystem functioning despite environmental perturbations.

This knowledge gap is compounded by the fact that ecosystem processes are rarely quantified during ecosystem monitoring programs, with the focus generally being on the abundance and diversity of different organisms and their associated traits (Ford et al., 2018; Bellwood et al., 2019b; Volaire et al., 2020). Unfortunately, many ecosystems have already changed due to human-induced environmental stressors, with consequent shifts in our baselines (Hughes et al., 2017; Barlow et al., 2018). This creates a problem: on the one hand we need to understand how ecosystem processes have or have not changed through time, in response to environmental disturbances, yet on the other hand, the data we have is largely restricted to the abundance of organisms rather than direct measurements of specific ecosystem processes. Thus, our ability to examine how the functioning of ecosystems has changed in response to perturbations is limited, with the shifting baseline syndrome potentially compromising our perceptions (Soga and Gaston 2018), unless we can derive estimates of past functions from the data we have at

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hand.

The issues outlined above are epitomised in aquatic ecosystems such as coral reefs, where long-term data on ecosystem processes are scarce. Furthermore, while high-diversity coral reef ecosystems provide services which support millions of people (Teh et al., 2013; Woodhead et al., 2019), they are also at the forefront of environmental change (Hughes et al., 2017; Williams et al., 2019). In an effort to understand how this change impacts these ecosystems, functions are often estimated using derived relationships, such as length-weight relationships to estimate fish biomass (Kulbicki et al., 2005; Froese et al., 2014). Unfortunately, the range of functions that can be examined using this approach has been limited by the availability of derived relationships. However, recent advances in functional analysis provide a way forward by enabling us to directly estimate a broader suite of ecosystem functions, such as fish productivity (e.g. Morais and Bellwood 2018; Brandl et al., 2019b; Morais et al., 2020b). These functional analyses are based on readily available monitoring data, and permit us to quantify how ecosystem functions may have changed through time in response to perturbations.

Here we apply these approaches to examine the impacts of environmental disturbances in a model inshore coral reef system. We use a time-series dataset where key metrics and functionally informative traits are quantified across a decadal timescale. This dataset allows multiple processes, which relate to the core pillars of coral reef ecosystem functioning (Brandl et al., 2019a), to be estimated from abundance data or

basic measurements. These estimated functional values complement functions that were measured more directly. In combination, the range of functions include the provision of resources to: a) herbivorous/detrivorous fishes (e.g. algal growth and detrital yields), b) predators/scavengers (i.e. biomass lost through mortality), c) fish stocks (standing biomass) and d) potential yields to humans (e.g. biomass production). As such, we provide a process-based functional evaluation of a coral reef ecosystem incorporating processes ranging from primary production to potential human yields. Importantly, this dataset encompassed a series of major disturbance events, including extreme river runoff events and sedimentation, severe tropical cyclones and repeated coral bleaching events (Goatley et al., 2016; Torda et al., 2018). Our goal is to determine if, and to what extent, coral reef ecosystem processes change when the reef is exposed to cumulative disturbance events.

2. Methods

2.1. Study site and overview

Field data were collected from Pioneer Bay, on the leeward side of Orpheus Island on the inner-shelf of Australia's Great Barrier Reef (GBR), between 2005 and 2019. To examine long-term trends, we collected data in 2018 and 2019 to match data from previous studies at this location (Fox and Bellwood 2007; Bonaldo and Bellwood 2011;

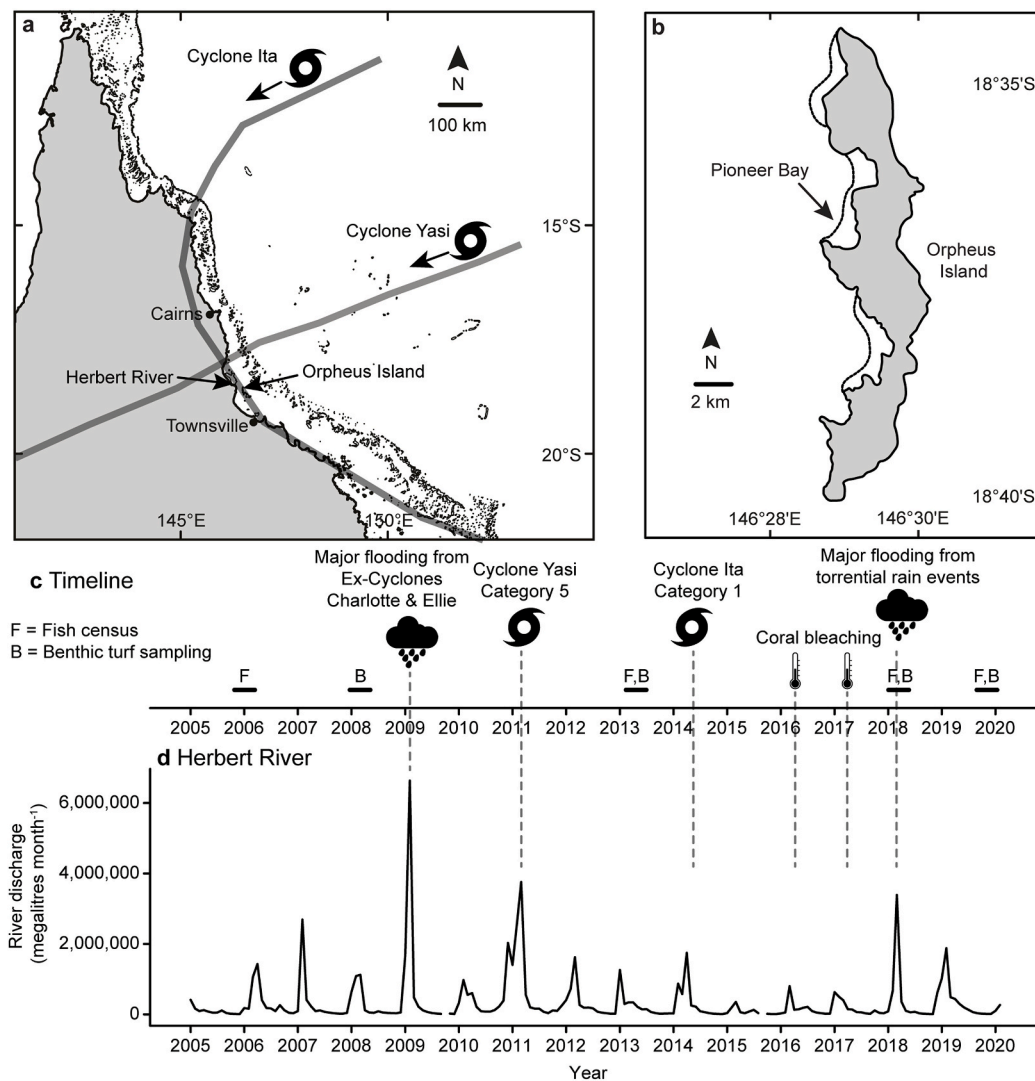


Fig. 1. Overview of study location and sampling timeline. a) Map of North Queensland, Australia, showing the location of Orpheus Island relative to the Herbert River as well as the tracks of two relevant cyclones. b) Map of Orpheus Island showing the location of Pioneer Bay where sampling occurred. c) Sampling timeline indicating when benthic algal turf sampling and herbivorous fish censuses occurred relative to major disturbance events. d) The monthly discharge from the Herbert River during the sampling period (Source: Queensland Government 2020).

Goatley et al., 2016). During this time (2005–2019) Orpheus Island has been subjected to a suite of environmental disturbances, including extreme river runoff events, sedimentation, cyclones and coral bleaching events (Bellwood et al., 2019a; Goatley et al., 2016; Gordon et al., 2016a; Torda et al., 2018) (Fig. 1).

This study focused on how the functioning of the algal turf community (in terms of its ability to provide nutritional resources to fishes) and the herbivorous fish community (in terms of its trophodynamic functioning) on this coral reef changed over time. Although collected at approximately the same time, the benthic and fish components are examined separately to reveal the production and consumption components of the ecosystem under investigation. These two communities, and the production vs consumption processes they support, were selected for examination because in terms of production: a) algal turfs are among the most abundant benthic covering on many coral reefs (Jouffray et al., 2015; Smith et al., 2016; Emslie et al., 2019), b) high algal turf coverage is expected to typify reefs of the future (Bellwood et al., 2019a; Tebbett and Bellwood 2019), and c) algal turf communities act as a reservoir of nutritional resources for fishes (Crossman et al., 2001; Wilson et al., 2003; Kramer et al., 2012). Herbivorous fishes were likewise selected to represent consumption processes because: a) most nominally herbivorous fishes utilise one or more components of algal turf communities as a nutritional resource (Choat et al., 2002; Kelly et al., 2016), b) nominally herbivorous fishes are expected to dominate future reefs with limited coral cover (Pratchett et al., 2018; Robinson et al., 2019a), and c) nominally herbivorous fishes support many fisheries around the world and are likely to continue to do so into the future (Edwards et al., 2014; Bellwood et al., 2018; Robinson et al., 2019b).

3. Benthic data: algal turfs and benthic production

3.1. Sample collection and processing

We assessed the nature of the algal turf community, and the sediments it contains, on the reef crest in Pioneer Bay in April 2018 and December 2019. This data matched equivalent samples taken in February 2008 (Bonaldo and Bellwood 2011) and April 2013 (Goatley et al., 2016). As algal turf sediment loads are remarkably stable over short temporal time scales (days to months) (Gordon et al., 2016a; Tebbett et al., 2018), these sampling time periods are representative of the years in which sampling was conducted. To sample the algal turf communities we used a submersible electronic vacuum sampler (modified after Purcell 1996), to collect 6 algal turf particulate samples from two sites ($n = 12$) on the reef crest (2–4 m) each year. Suitable sampling surfaces were outside of the territories of farming damselfishes, flat, smooth, free of sediment-retaining pits, macroalgae and encrusting organisms and were covered in algal turfs (following Tebbett et al., 2017a). Sampling areas were delineated using a 58 cm² PVC ring. Within the sampling area, we also quantified algal turf length by measuring the length of 5 haphazardly selected algal turf filaments using the depth probe of vernier callipers (following the methods outlined in Tebbett and Bellwood 2019). The collected particulates were then processed to yield: a) particulate volume, b) total dry particulate mass, c) dry inorganic sediment mass, and d) dry organic detrital particulate mass following Tebbett and Bellwood (2020). Particulate processing methods are provided in the supplemental material (see Supplemental Text S1, S2).

3.2. Benthic data statistical analysis

We initially analysed traditional metrics related to the condition of the algal turf community (inorganic sediment mass and algal turf length), and a key function (potential algal turf growth; calculation details are provided in Supplemental Text S3). It should be noted that algal turf length and growth provide different insights into the functioning of the system as the former is a static, standing stock, measure (i.

e. a measure of how much turf there is), while the latter is a process-based metric, productivity, that provides information on the rate of resource renewal (i.e. how quickly turf is replaced). Data were compared among years using Bayesian generalised linear mixed-effects models (GLMMs) fitted with a Gamma distribution and log-link (sediment mass and turf length) or lognormal distribution (turf growth). In all cases, sampling year was treated as a categorical fixed effect while site was treated as a random effect (to account for any lack of spatial independence). All models were based on weakly informative priors (see Supplemental Table S1 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. In all cases, the diagnostics suggested that the chains were well mixed and converged on a stable posterior (with all Rhat values less than 1.05) and were uncorrelated (with lag values < 0.2). In addition, our effective samples were > 1000 , and there were no patterns in the residuals. It should be noted that turf length data were based on the mean turf length in each sediment sampling location in 2008, 2018 and 2019. However, in 2013 the nature of the turf length data differed in that it was based on 30 haphazard turf measurements at each of two sites. All analyses of benthic data were performed in the software R (R Core Team 2019), using the *rstan* (Stan Development Team 2018), and *rstanarm* (Goodrich et al., 2018) packages.

3.3. Benthic algal turf function-space

Algal turf community functions were also calculated for each individual replicate unit (i.e. each algal turf sample) and then plotted in multivariate space to provide an overview of the relative levels of the benthic functions in each sample period. The resultant benthic function-space was based on five functions that were specifically selected as they, a) pertain directly to the ability of the algal turf community to provide nutritional resources to fishes, and b) were able to be quantified ([M = measured directly] or derived [C = calculated]) from the long-term data at hand (a major limitation in studies of this nature). Specifically, these five functions were: potential algal turf growth ([C]; linear growth in mm day⁻¹), algal turf biomass ([C]; g m⁻²), standing detritus mass ([M]; g m⁻²), relative detrital mass in particulates ([M]; %), and harpacticoid copepod standing biomass ([C]; µg ash-free dry weight [AFDW] m⁻²). Algal turf biomass, detrital biomass and copepod biomass were selected as functions as they relate to the storage of nutrients in the system that can be exploited directly and/or inadvertently by herbivorous fishes (Hatcher and Larkum, 1983; Purcell and Bellwood 2001; Choat et al., 2002; Kramer et al., 2017). Potential algal turf growth was also selected as a function because this process relates to the speed at which resources are generated for herbivorous fishes to exploit (Russ 2003; Kelly et al., 2017). Relative detrital mass in particulates is a measure of the trade-off nominally herbivorous fishes face when feeding on particulate matter in algal turfs, i.e. the return of nutritious detritus relative to the cost of processing inorganic sediments (Gordon et al., 2016b; Tebbett et al., 2017b). The computed benthic function-space, therefore, focuses on the ability of a critically important compartment of the benthos (i.e. algal turf communities) to directly provide nutritional resources to fish populations (i.e. herbivorous fishes).

The five benthic functions were directly measured, or calculated from the measured turf traits, during each sampling period (details of these calculations are provided in the Supplemental Material Text S3). After all of the functions were calculated and compiled into a data matrix, we constructed the benthic function-space. Initially, the data matrix was fourth-root transformed and range standardised by columns to ensure each function had an equal weighting in the analysis. Subsequently, a Euclidean distance matrix was calculated. As we wanted to examine how the individual replicate sample units were positioned in multidimensional function-space we formulated a principal co-ordinate analysis from our Euclidean distance matrix and visualised this using

'heatmaps'. Heatmaps were used to visualise the function-space because they focus on where the greatest density of points is located in multidimensional space rather than focusing on the outliers that are used to delineate polygons. To compute the heatmaps, we used the scores of the PCoA to calculate four Kernel Utilization Distributions (KUDs), one for each time period. KUDs are widely used in the field of animal movement as they describe the probability distributions of 'animal detections' in space (Worton 1989). In our context, the 'animal detections', were the individual algal turf sampling units across the multidimensional function-space. Colour gradients were subsequently informed by the bivariate KUDs, with the 'hottest' areas marking areas with the highest density of samples. Please note, this approach highlights areas in multidimensional space with more samples exhibiting the functional characteristics associated with that area, not necessarily more 'function'. Finally, significant differences between the years in terms of position in the function-space were assessed using a permutational multivariate analysis of variance (PERMANOVA). Site identity was also included as a factor to account for the lack of spatial independence. Homogeneity of variance was also examined using permutational multivariate analysis of dispersions (PERMDISPs) (Supplemental Table S2). The benthic function-space was computed in the software R (R Core Team, 2019), using the *raster* (Hijmans 2017), *adehabitatHR* (Calenge 2006) and *vegan* (Oksanen et al., 2019) packages. For discussion on the correlation and non independence of the five functions, as well as discussion on uncertainty and interpretation please see the supplemental material (Text S4).

4. Herbivorous fish assemblage: consumption of benthic production

4.1. Fish censuses

The abundance and community composition of herbivorous fishes (parrotfishes [Labridae], surgeonfishes [Acanthuridae] and rabbitfishes [Siganidae]) were initially quantified on the reef crest in Pioneer Bay in December/January 2005/2006 (Fox and Bellwood 2007) and April 2013 (Goatley et al., 2016). It is important to note that the first-time point for fish (2005) differs to that for benthic algal turfs (2008); however, no major stressors acted upon this system between these sampling periods (Fig. 1). In April 2018 and December 2019, we repeated the same methods to match this existing data by performing 12 non-overlapping censuses across the bay (each year). To minimise diver effects on fishes (Emslie et al., 2018) we used 5-min timed swims (GPS calibrated length = 46.1 ± 1.1 m [mean \pm SE]), or 45 m tape transects laying the tape as fishes were counted. All censuses were undertaken by two divers on SCUBA. The first diver counted all relevant herbivorous fishes >10 cm total length (TL) in a 5 m wide transect, while the second diver counted all fishes 5–10 cm long in a 1 m wide transect. All fishes were identified to the lowest taxonomic level (generally species) and placed into 5 cm TL size categories (fishes >10 cm TL) or 2.5 cm size categories (fishes <10 cm TL). Size data were subsequently used to calculate the biomass of each fish using Bayesian length-weight regression parameters (Froese and Pauly 2018).

4.2. Herbivorous fish data statistical analysis

Initially, we analysed more traditional monitoring data and a key function (biomass productivity; calculation details are provided in the Supplemental Text S5) related to the herbivorous fish community. Specifically, we examined how the abundance, biomass, biomass production and community composition of herbivorous fishes changed over the 14-year sampling period. Abundance, biomass and biomass production were compared among years (categorical fixed effect) using Bayesian generalised linear models (GLMs) fitted with Gamma distributions and log-links. In all cases, weakly informative priors were used (see Supplemental Table S1 for prior details and chain specifications for

each model). Model fit and assumptions were assessed as above.

To explore how the community composition of the herbivorous fish species in Pioneer Bay changed among sampling periods, we used a multivariate approach. Specifically, we computed a Bray Curtis similarity matrix for both species abundance and species biomass fourth-root transformed data, and visualised changes using constrained distance-based redundancy analysis. Significant differences between the years in terms of the position of the communities in multivariate-space were assessed using permutational multivariate analysis of variance (PERMANOVA). Variation in homogeneity was assessed as above (i.e. using a PERMDISP [Supplemental Table S2]). The statistical analyses were performed in the software R (R Core Team, 2019), using the *rstan* (Stan Development Team 2018), *rstanarm* (Goodrich et al., 2018) and *vegan* (Oksanen et al., 2019) packages.

4.3. Herbivorous fish function-space

To understand how changes in the herbivorous fish community may have influenced its functioning, we calculated a function-space based on five functions that specifically pertain to how energy is stored or cycled in fish communities. This function-space was based on individual censuses as the replicate units. The five functions were: standing biomass (g m^{-2}), rate of biomass production ($\text{g m}^{-2} \text{day}^{-1}$), consumed biomass ($\text{g m}^{-2} \text{day}^{-1}$), carbon respired ($\text{g m}^{-2} \text{day}^{-1}$) and turnover rate (%). These five functions broadly cover the three main aspects of trophodynamics: energy use (carbon respired), assimilation and conversion to biomass (biomass production and standing biomass), and transfer to other trophic levels (consumed biomass and turnover). As for the turf community above, these functions are not necessarily independent (see Supplemental Text S4 for discussion). Indeed, they are likely to be correlated with each other, a feature that is well captured in multivariate analyses. Although these functions are unlikely to capture the full extent of herbivorous fish functioning, they are likely to provide a more detailed understanding of the trophodynamic functioning of this herbivorous fish community when compared to findings based on changes in fish abundances alone (cf. Brandl et al., 2019b; Benkwitt et al., 2020; Morais et al., 2020b). The procedures to obtain standing biomass, biomass production, consumed biomass and turnover all follow Morais et al. (2020b) (full details are provided in the Supplemental Material Text S5).

After the functions had been calculated for the herbivorous fish community, the function-space for these fishes was formulated as above for the algal turf community (a PCoA with which we calculated bivariate KUDs and heatmaps). The herbivorous fish function-space was likewise analysed as above, i.e. using a PERMANOVA and PERMDISP (see Supplemental Table S2) and the same software packages.

5. Results

By examining the nature of the algal turfs (i.e. sediment loads and algal turf length) we revealed a fundamental change in the condition of the algal turf community at Orpheus Island (Fig. 2a, b, c). Indeed, the mass of inorganic sediments bound within the turfs appears to have increased 2181% (462%–6870% [95% credibility intervals]) between 2008 and 2019 (Fig. 2a; Supplemental Table S3). Concomitantly, algal turf length increased by 38% (9%–224%) from 2008 to 2019 (Fig. 2b; Supplemental Table S3). Such marked changes in the sediment load and length of algal turfs clearly had an impact on potential turf growth which had declined by 62% (54%–68%) in 2019 relative to 2005 (Fig. 2c; Supplemental Table S3). Essentially, a marked phase-shift in the condition of the turfs occurred, from short productive algal turfs to long sediment-laden algal turfs.

The herbivorous fish community exhibited similar changes with an overall decrease in abundance of nearly 70% (51%–82%) from 2005 to 2019 (Fig. 2d; Supplemental Table S3) and a similar decline in herbivorous fish standing biomass (Fig. 2e; Supplemental Table S3). However, unlike abundance which declined steadily (Fig. 2d), biomass remained

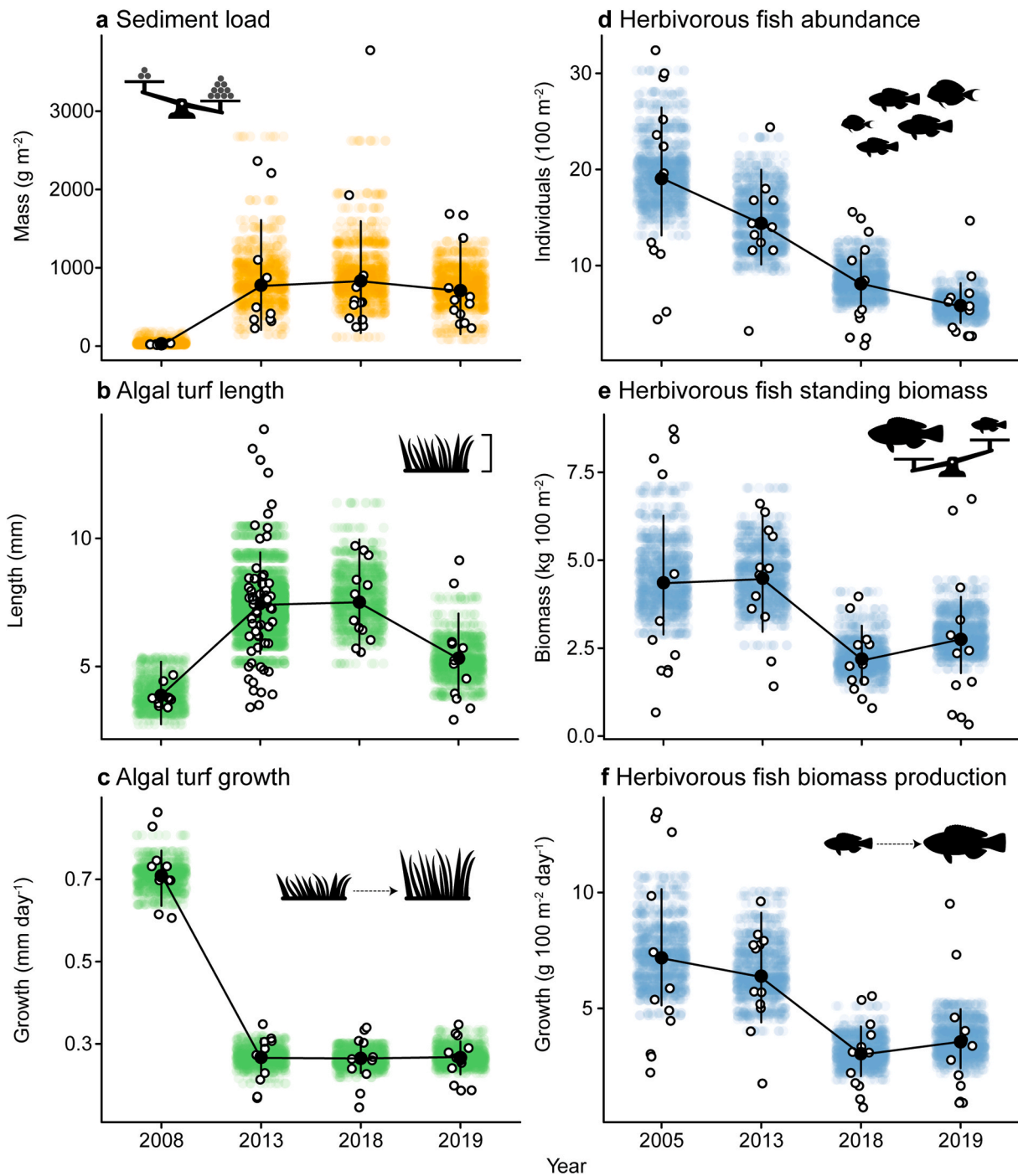


Fig. 2. Changes in the algal turf and herbivorous fish communities on the reef crest in Pioneer Bay, Orpheus Island. There was a marked shift in the algal turf community in terms of (a) sediment load, (b) length and (c) potential growth. Similarly, there were concomitant changes in the herbivorous fish community (parrotfishes, rabbitfishes and surgeonfishes), with decreases in (d) abundance, (e) standing biomass and (f) growth rate. The black points and range bars indicate the predicted mean and 95% credibility intervals from Bayesian generalised linear mixed-effects models (a, b, c) and generalised linear models (d, e, f), the coloured points are 100 randomly selected model fits from the posterior distribution and open circles are the raw data points.

relatively stable from 2005 to 2013, before declining by nearly 50% (16%–71%) in 2018, and remaining 37% (–1% - 63%) below 2005 levels in 2019 (Fig. 2e; Supplemental Table S3). Furthermore, it appears that the ability of the herbivorous fish community to replace biomass also collapsed as biomass production rates declined by 50% (19%–70%) from 2005 to 2019 (Fig. 2f; Supplemental Table S3). Overall, from 2005 to 2019 70% of the individual fish and 37% of the herbivorous fish biomass was lost from this coral reef system, while the capacity to produce new biomass was reduced by 50%. Analysis of the community

composition of herbivorous fishes (weighted by both abundance and biomass) revealed that the declines occurred across all species and that the herbivorous fish communities in 2018 and 2019 appeared to represent a depauperate version of that present in 2005 (Supplemental Figure S1; Table S4).

It is clear that the algal turf and herbivorous fish communities changed substantially across the study period with flow-on effects on ecosystem functions. Our calculated function-spaces reveal the strength of multiple functions, simultaneously, and provide a broad overview of

how the functional configuration of the two communities changed through time.

Firstly, the benthic function-space revealed a clear temporal shift in the ability of the algal turf community to provide nutritional resources to herbivorous fishes. The community occupied significantly different areas of function-space in 2013, 2018 and 2019 relative to 2008 (Fig. 3; Supplemental Figure S2; Table S4). Indeed, in 2008 the composition of

the benthic functions were characteristic of a high-productivity system that could readily provide nutritional resources to herbivorous fishes (i. e. high algal turf growth rates and a high proportion of organic detritus relative to inorganic sediments in the turfs) (Fig. 3). However, by 2013 the growth of algal turfs had reduced, while the standing biomass of algal turfs, copepods and detritus had increased, leading to an alternative functional configuration in 2018/2019. This new functional

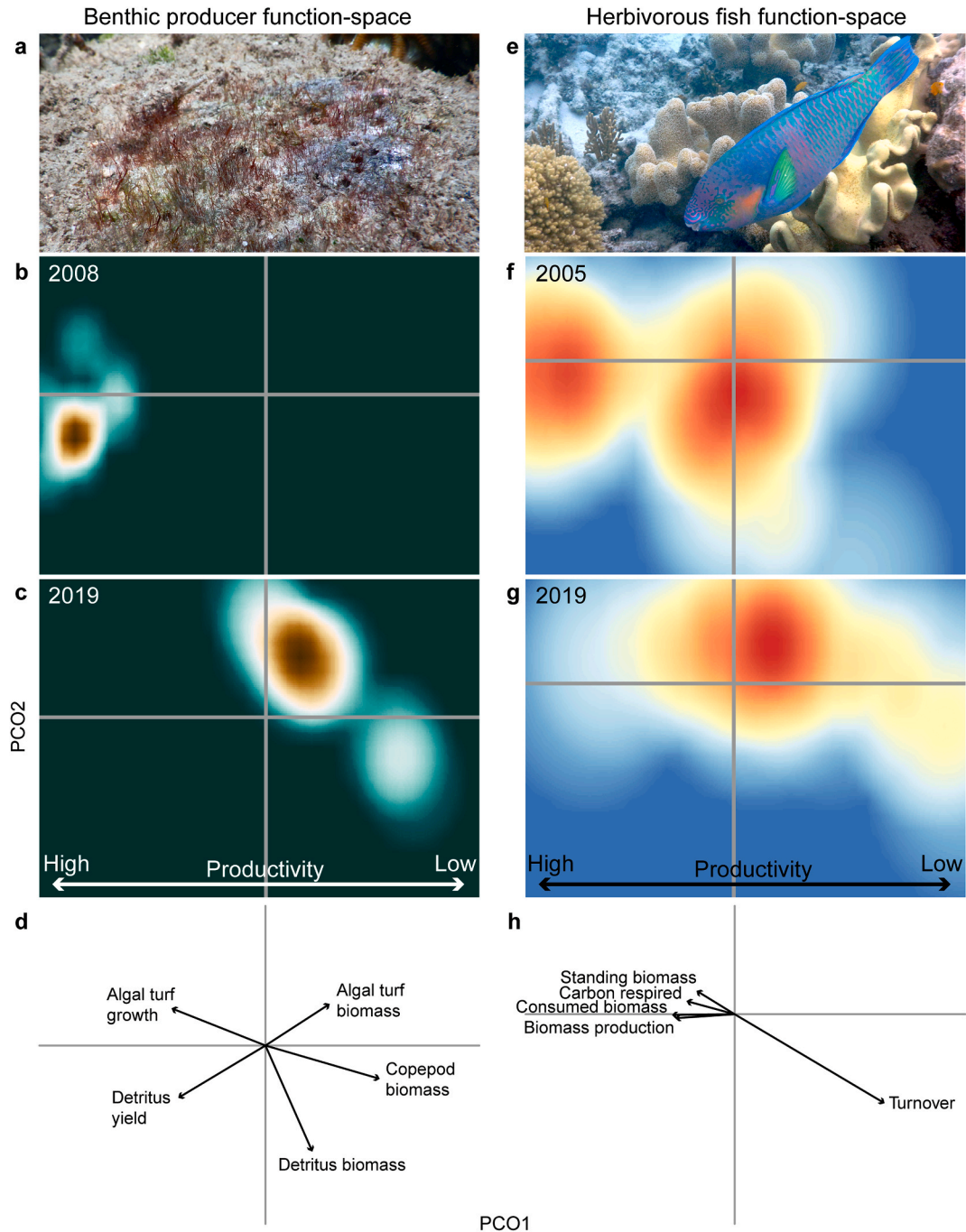


Fig. 3. Function-spaces of the benthic algal turf community and the herbivorous fish community. The benthic function-space is a multivariate space that provides an overview of the ability of the algal turf community to provide nutritional resources to herbivorous fishes from 2008 to 2019 (b, c) based on 5 specific functions (d). The herbivorous fish function-space is a multivariate space that examines the trophodynamic functioning of the herbivorous fish assemblage from 2005 to 2019 (f, g) based on 5 specific functions (h). The occupation of the function-space is represented as a heat map based on kernel utilization densities (note brown areas [b, c] and red areas [f, g] indicate more samples with that particular combination of function levels, not necessarily more ‘functions’ per se). See Supplemental Figure S2 for function-spaces from 2013 to 2018 and see Supplemental Figure S3 for specific levels of each individual function. Photographs of a benthic algal turf community (a) and the herbivorous parrotfish *Scarus rivulatus* (g) (Photographs: SB Tebbett). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

configuration represents an algal turf community that has a high standing biomass of nutritional resources (abundant algal turf, detritus, copepods), but a limited ability to replace these resources (e.g. reduced algal growth rates). This new configuration also poses a challenge for detritivorous fishes due to low relative yields of detritus. Ultimately, the new functional composition represents a relatively high biomass-low productivity benthic algal turf community.

Reflecting changes in the ecosystem-level functioning of the benthic algal turf community, the functioning of the herbivorous fish community also changed substantially (Fig. 3), eventually occupying a significantly different area of function-space in 2019 compared to 2005 (Supplemental Table S4). In 2005, the herbivorous fish community occupied an area of function-space that was typified by high standing biomass, and high relative rates of biomass production, biomass consumption and energy use (i.e. a high-productivity position) (Fig. 3). However, over time the functioning of the herbivorous fish community shifted into an area of function-space that was characterised by higher relative rates of turnover but low standing biomass, biomass production, biomass consumption and energy use (Fig. 3). These shifts mirror the benthic algal turf community. Together, these results reveal a fundamental shift over time from a high productivity/high consumption state to an alternate low-productivity functional configuration.

6. Discussion

Coral reef ecosystems have been subjected to an increasing range and intensity of stressors which have led to extensive changes in the communities that inhabit these ecosystems and, presumably, to the functions that operate within the ecosystem (Kennedy et al., 2013; Hughes et al., 2017; Bruno et al., 2019; Williams et al., 2019; Vercelloni et al., 2020). However, changes in ecosystem functioning are often only inferred from proxies; rarely are they informed by estimates of, or data on, the processes themselves (Ford et al., 2018; Bellwood et al., 2019b). By directly calculating key processes, we revealed a collapse in the abundance and biomass of herbivorous fishes, and in algal turf production as the turfs shifted towards a long sediment-laden state. In addition to patterns based on traditional metrics, we were able to examine and track ecosystem functions (i.e. the relative composition and strength of multiple functions). In doing so, we revealed that the functional status of both the algal turf community and the herbivorous fish community shifted, fundamentally, towards an alternate low-productivity configuration. Such marked shifts in the status of these components of coral reef food webs are concerning as they suggest that the ability of this ecosystem to sustain key services may be compromised.

To understand the mechanistic basis of changes and shifts in key functions, we need to consider both the nature of the communities involved, and the context of the ecosystem in question. In doing so, it is important to note that the substantial declines in herbivorous fish abundance and biomass that we documented almost certainly occurred independent of fishing effects (see Morais et al., 2020a). Our study site is part of a relatively well-enforced no-take zone within the Great Barrier Reef Marine Park, with less poaching than in other no-take areas nearby (Bergseth et al., 2017). Furthermore, in contrast to most other tropical regions, herbivorous fishes are rarely targeted on the Great Barrier Reef (Rizzari et al., 2014; Casey et al., 2017). The limited role of fishing-pressure was emphasised by the overall pattern of declining abundance and biomass across all herbivorous fish species examined (Figure S1), rather than impacts on specific species (e.g. selective fishing pressure [Russ and Alcala 1989; Hamilton et al., 2016; Morais et al., 2020a]). Together, these impacts highlight that the system responded with limited response diversity and that there was a generalised impact on fish herbivory.

This lack of a fishing effect is particularly interesting as one of the most widely held paradigms in coral reef ecology is that overfishing of herbivorous fishes results in reduced grazing pressure on the benthos and therefore increased algal coverage and coral collapse (reviewed in

Bellwood et al., 2004; Bruno et al., 2019). However, based on the available evidence, and considering the context of the stressors impacting our system, the most parsimonious explanation for the changes we have documented appears to be a sediment-driven bottom-up collapse of trophic interactions in this coral reef system (cf. Russ et al., 2015, 2018). Indeed, the >2100% increase in accumulated sediments from 2008 to 2019 is notable and may be a result of the acute river runoff events that have impacted this system, particularly in 2009 (Fig. 1; see Supplemental Text S6 for further discussion on the source of sediments). It should also be noted that cyclones can directly impact reef fishes in the short term (Cheal et al., 2017; Khan et al., 2017) and this may also have been a contributing factor to the documented population declines. However, such cyclone impacts represent an acute disturbance that does not match the chronic, protracted declines in herbivore populations documented herein, leaving increased sediment loads alone as the most parsimonious explanation.

Sediment accumulation in algal turfs has previously been causally linked to the development of longer algal turfs (Goatley and Bellwood 2013; Fong et al., 2018), marked decreases in algal turf productivity (Clausing et al., 2014; Tebbett et al., 2018), and declines in herbivorous fish feeding activity (Goatley and Bellwood 2012; Tebbett et al., 2017b). This latter point is particularly important as sediments appear to represent a bottom-up control on a top-down force (herbivorous fishes feeding), that may facilitate the development of longer algal turfs and enhanced sediment trapping in a positive-feedback (reviewed in Tebbett and Bellwood 2019). Importantly, such a positive-feedback may compromise a variety of key ecological services including the settlement of corals (Speare et al., 2019; Ricardo et al., 2017), reductions in algal removal rates (Goatley et al., 2016) and shifts in bioerosion patterns (Hutchings et al., 2005). Consistent with this prior evidence, we revealed the extent to which increasing sediment accumulation also correlates with declines in algal turf growth (Fig. 2c) and shifts in the functional configuration of the algal turf community (Fig. 3). Top-down control of turfs by herbivorous fishes is also possible (Smith et al., 2010; Tebbett et al., 2017c; Fong et al., 2018; McAndrews et al., 2019), however, as fish abundances were slow to change and biomass changes were delayed, the most parsimonious explanation, in this case, appears to be bottom-up (although in all cases the top-down and bottom-up effects are clearly linked). As the dynamics of herbivorous fish communities are tightly linked to their food supply (Russ et al., 2015; Tootell and Steele 2016; Graham et al., 2018; Taylor et al., 2020), it is logical to conclude that a sediment-driven collapse in resource yields represents the most plausible mechanism for the marked declines in herbivorous fish biomass and biomass production documented in this system. It is likely that the strengthening of positive feedbacks by sediments (see Tebbett and Bellwood 2019) has maintained the long sediment-laden algal turf state in this system since 2013; this may reflect some degree of hysteresis (Goatley et al., 2016; Hughes et al., 2017).

Declines in the ability of coral reefs to sustain key functions and services also have clear implications for people. Notably, from a human perspective, reefs are often valued for their high productivity, which underpins fisheries and in turn supports the people that depend on these systems (Teh et al., 2013; Lau et al., 2019). Our results suggest that if people were relying on herbivorous fishes for food provision in this system, as they do in many areas of the world (Edwards et al., 2014; Robinson et al., 2019b; Wenger et al., 2020), then these people would be confronted with a herbivorous fish stock 37% smaller in 2019 relative to 2005. Furthermore, the extraction of fisheries resources requires biomass to be produced and replenished (Allen 1971; Hilborn and Walters 1992). As such, the rate of production of new biomass provides a more relevant metric for assessing the sustainability of this critical ecosystem service than standing biomass (Morais et al. 2020a, 2020b). It is sobering to note that the observed declines in herbivorous fish biomass production exceed those seen in standing biomass, with decreases in the order of 50% or more between 2005 and 2019 (Fig. 2f). Furthermore, beyond compromising potential fisheries productivity,

this loss of herbivorous fishes is also likely to compromise other key services, such as the perceived aesthetic value of the reef, due to the loss of large colourful fishes that people find attractive (Woodhead et al., 2019; Bellwood et al., 2020). Clearly, the magnitude of the changes documented may have serious implications for the sustained provision of services to humans.

Importantly, a clear discrepancy between herbivorous fish abundance and biomass declines appeared to exist in this system (Fig. 2d, e) and this is likely to be the result of a storage effect (e.g. Morais et al., 2020b). Essentially, the discrepancy reflects a change in the size structure of the herbivorous fish community, with relatively more larger fishes in 2013 compared to 2005 (Supplemental Figure S4). The aging of fishes already present in this community appears to have sustained standing biomass levels up to 2013, thus masking background declines in abundance. However, beyond 2013 the apparent limited recruitment of new fishes into the system and eventual loss of the larger cohorts overwhelmed the buffering capacity of this storage effect.

Importantly, the change in herbivore size structure also suggests that the recruits of these herbivorous fishes were disproportionately impacted by the increased algal turf sediment loads compared to adults. Unfortunately, how algal turf sediments impact recruit/juvenile herbivorous reef fishes is currently unclear. However, we do know that parrotfishes (the main herbivorous fishes in this system) recruit to coral reefs at a smaller size than most other reef fishes and form a close association with algal turfs (often lying on or within the algal turf canopy, especially in damselfish territories or in short, well-grazed turfs; both of which contain low sediment loads) (Bellwood, 1985; Bellwood and Choat, 1989). As such, any alteration of algal turfs by sediments could impact parrotfish recruits directly and certainly warrants further investigation. Furthermore, previous studies have revealed a second mechanism by which sediments may impact juvenile parrotfishes. Specifically, high sedimentation may impact the juvenile habitat (namely branching corals) of some parrotfish species, with flow-on consequences for adult populations (DeMartini et al., 2013; Hamilton et al., 2017). Regardless of the exact mechanisms, the documented population declines represent a delayed response to disturbance, which is unlikely to be detected during immediate post-disturbance monitoring (cf. Bellwood et al., 2006).

The findings outlined above also have implications for our understanding of how coral reef functioning responds to disturbances, as these findings contrast markedly with prior results from other coral reefs. Indeed, it is generally accepted that following disturbances, especially coral bleaching events, the abundance, biomass and productivity of herbivorous fishes will increase as a result of an increasing food supply (i.e. higher algal turf cover) (Russ et al., 2015; Cheal et al., 2017; Pratchett et al., 2018; Robinson et al., 2019a, 2019b). Increased algal resources are also expected to enhance the somatic growth of herbivores (Morais et al., 2020b; Taylor et al., 2020). This has provided a glimmer of hope that herbivorous fish assemblages can sustain high fishing pressure on Anthropocene reefs (Robinson et al., 2019b; Morais et al., 2020a). However, in our study system, despite a general increase in algal turf cover over the last 15 years (Supplemental Text S7; Figure S5), there has been a prolonged decline in herbivorous fishes (Fig. 2d) and a marked shift in the trophodynamic functioning of the herbivorous fish community (Fig. 3). These results highlight how the different types of disturbance exert their effects. Most studies report a decrease in coral cover without evaluating the responses of the non-coral benthos in detail (Russ et al., 2015; Robinson et al., 2019a; Morais et al., 2020b). By contrast, we show a decline in benthic algal turf condition that occurred with only limited hard coral loss (and presumably a limited loss of structural complexity associated with hard corals, although this was not assessed) (Supplemental Text S7; Figure S5). Our results, therefore, pertain to changing algal turfs, not coral loss.

Our data suggests that if the quality of nutritional resources is compromised by sediments, then this could overwhelm any potential short-term benefits that increased resource abundance might offer

herbivorous fishes. Sediment accumulation in algal turfs could be the 'Achilles-heel' to sustaining productive herbivorous fish assemblages and may explain the declining yields of fisheries on other sediment-impacted coral reefs (Orlando and Yee 2017; Delevaux et al., 2018; Wenger et al., 2020). Importantly, this sediment accumulation would not have been detected by evaluating patterns of benthic cover alone, be it coral or algal turf cover. Moreover, it is unlikely that traditional fisheries management tools such as marine protected areas would provide much resilience against the documented productivity loss, as sediments can transcend the boundaries of these areas (Bégin et al., 2016; Wenger et al., 2016; Suchley and Alvarez-filip 2018). Management of sediment impacts requires an approach that addresses both marine and terrestrial drivers of change (Brodie et al., 2012; Bartley et al., 2014; Oleson et al., 2017; Comeros-Raynal et al., 2019; Wenger et al., 2020).

Although based on just one reef system on the Great Barrier Reef, our findings may have a broad application to coral reefs around the world, as a large proportion of the world's coral reefs occur in close vicinity to land (Burke et al., 2011; Maire et al., 2016). These nearshore coral reefs, and the herbivorous fishes that occupy them, are heavily relied upon by subsistence fisheries (Edwards et al., 2014; Wenger et al., 2020). However, they are also at particularly high risk of sediment accumulation. Indeed, evidence suggests that more than 50% of the world's coral reefs are at risk of increased terrestrial sediment inputs (Burke et al., 2011), with far-reaching impacts (reviewed in Fabricius 2005; Bainbridge et al., 2018; Magris and Ban 2019). Unfortunately, there are currently no monitoring programs on any reef system globally that assess the amount of sediments accumulated in algal turfs (reviewed in Tebbett and Bellwood 2019), nor many of the other critical hydrodynamic and geological parameters associated with these sediments (Elliff et al., 2019). Without such quantitative baseline information, our ability to evaluate systems may be compromised by shifting baselines (Soga and Gaston 2018).

Even on the highly managed and monitored GBR, our study site is the only location where algal turf sediments have been sampled repeatedly over time. Indeed, this study site is one of only four inner-shelf reefs on which turf sediments have been quantified (with total sediment loads approximately comparable in all cases [Tebbett and Bellwood 2019]). As such, we cannot quantitatively determine how widespread the problem of turf-bound sediments and their flow-on effects for critical ecosystem processes is likely to be (reviewed in Tebbett and Bellwood 2019). However, there do appear to be clear critical thresholds. Growing evidence suggests that when turf-bound sediment loads exceed approximately 100 g m^{-2} the growth of algal turfs slows markedly (Tebbett and Bellwood 2020) and the feeding activities of some nominally herbivorous fishes are impacted (Tebbett et al., 2017b). In addition, sediment loads of approximately $250\text{--}500 \text{ g m}^{-2}$ can correlate strongly with the absence of key fish species (Tebbett et al., 2020). This suggests that if sediment loads exceed these levels (approximately half the levels reported herein during 2013, 2018 and 2019) the functioning of the reef community is likely to be directly impacted by sediments. It should be noted, however, that further long-term, spatially replicated work, is required to confirm these threshold levels. Clearly, the lack of monitoring of turf-bound sediments represents a significant knowledge gap that may stymie our endeavours to secure and sustain the key ecosystem services that reefs provide (Hughes et al., 2017).

Overall, our study emphasises the importance of functional evaluations in understanding how disturbances shape ecosystems. We highlight how turf-bound sediments potentially disrupt the functioning of coral reefs through core trophic interactions. Our results, as well as other lines of evidence (Ricardo et al., 2017; Fong et al., 2018; McAndrews et al., 2019; Speare et al., 2019; Evans et al., 2020; Tebbett et al., 2020), suggest that turf-bound sediments pose a considerable risk to ecosystem processes on coral reefs. Unfortunately, increasing accumulation of such turf-bound sediments is likely to be prevalent on many coral reefs globally, although often cryptic and unmonitored. As the strength of connections between people, the land, and marine ecosystems grow, the

impacts of sediment are likely to increase. Our study provides a functional understanding of how the impacts of these sediments could reverberate up through the food chain and affect both critical ecosystem functions and human populations that rely on coral reefs.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jenvman.2021.112471>.

Author contributions statement

Sterling B. Tebbett: Conceptualisation, Data curation, Formal analysis, Investigation, Writing – original draft, Visualisation, Funding acquisition. Renato A. Morais: Conceptualisation, Formal analysis, Writing – review & editing. Christopher H.R. Goatley: Conceptualisation, Investigation, Data curation, Writing – review & editing. David R. Bellwood: Conceptualisation, Resources, Writing – review & editing, Funding acquisition.

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