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The functioning of future coral reefs: fishes, sediments and productivity

by

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Abstract

Globally, ecosystems are being reconfigured by a range of intensifying human-induced stressors. Coral reef ecosystems are at the forefront of this environmental transformation, with many now existing in highly altered configurations. However, as coral reefs change it is becoming unclear if, and to what extent, critical ecosystem functions and services can be sustained. Addressing this knowledge gap requires the identification of likely future reef configurations, and then within this operating space, an examination of the factors which shape critical ecosystem functions.

To gain an insight into the likely composition of future coral reefs, I compiled and analysed a global dataset composed of 24,468 observations spanning 1997-2018. This revealed that high macroalgae cover, widely regarded as the major degraded state of reefs, is a phenomenon largely restricted to the Western Atlantic. Algal turfs/crustose coralline algae was the dominant benthic cover on reefs and appears set to become increasingly prevalent as corals decline further. This global analysis was complimented by a high-resolution examination of the benthic composition on a reef shaped by climate change. By assessing the same 349 photoquadrats from 2016-2021 I revealed that bleaching in 2016 drove a ~50% reduction in coral cover, and a concomitant increase in algal turf cover. From 2018 to 2021, significant increases in coral cover (>600%) and substantial *Acropora* recruitment were detected in some areas. By contrast, other areas exhibited virtually no recovery nor *Acropora* recruitment. Given that the timeframe between disturbances is set to decrease, these results suggest that algal turf covered reefs will represent a likely future reef configuration, with some coral recovery possible between disturbances.

If the future state for coral reefs is one of high algal turf cover, this inevitably raises the question: what role will algal turfs play in the functioning of future coral reefs? To address this question, I reviewed the literature on algal turfs and the sediments they contain.

In doing so, I highlight what algal turf sediments are, how they interact with key ecosystem processes, the potential importance of algal turf sediments on future reefs, and key knowledge gaps that need to be addressed. Together, the evidence suggests that algal turf sediments could shape how future reefs function.

Importantly, in addition to high algal turf cover, it is widely expected that most future coral reef configurations will also have low structural complexity. To gain an insight into the nature of algal turf sediments on future reef configurations I examined if, and to what extent, algal turf condition and reef structure are connected. Specifically, I utilised 3D structure-from-motion technology to examine how elevation and surface angle are related to algal turf condition. Importantly, as both elevation and surface angle decreased, the state of the turfs shifted from short productive algal turfs (SPATs) to long sediment-laden algal turfs (LSATs). This suggests that on flatter coral reefs, sediment accumulation is likely to be enhanced, altering algal turf condition fundamentally.

While it appears that LSATs may typify future reefs, the implications of this for algal turf productivity, a critical function on reefs, is unclear. I therefore assessed algal turf condition and growth across a sediment load gradient. This revealed precipitous declines in both the productivity of algal turfs, and the relative nutritional value of particulates from turfs in SPAT to LSAT states. Furthermore, when I applied the models to known sediment loads, I revealed that sediment loads explain observed algal turf productivity gradients across multiple spatial scales. In an era of climate change and coral reef reconfiguration, sediments could hold the key to maintaining benthic productivity on coral reefs.

As the productivity of algal turfs is likely to be important in sustaining herbivorous fish populations on future reefs, our current understanding of turf productivity was further explored by conducting a meta-analysis. In doing so, I revealed the marked importance of depth, and turf biomass, in shaping turf productivity and turnover, respectively. However, I

also uncovered marked shortcomings in the current data on turf productivity as it was temporally, spatially, and methodologically limited. Unfortunately, this lack of knowledge may leave us ill-prepared to effectively manage the functioning of future reefs.

As it appears that effectively managing the condition of algal turfs could help maintain the productivity on coral reefs, the potential bottom-up effects of algal turf sediments on coral reef functioning warranted further examination. I therefore developed and utilised novel 'function-spaces' to link decadal time-series benthic and fish assemblage data to multiple functions on an inshore reef. The data suggested that increased sediment accumulation in algal turfs 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. This examination highlights the value of directly assessing functions and the capacity of algal turf sediments to fundamentally alter the functioning of high-diversity coral reef ecosystems.

Clearly, algal turf sediments have the capacity to shape ecosystem functions. However, as these sediments are unmonitored and unmanaged on all coral reefs globally, it is unclear how they interact with ecosystem management approaches that assume fish presence is equal to function delivery. To examine this, I assessed how a key surgeonfish species interacted with sediments across multiple spatial scales. At broad spatial scales, the presence of the surgeonfish was correlated with sediment loads, while at smaller spatial scales, function delivery by the surgeonfish was constrained by sediment distributions. These results reveal a complex dynamic between proximate agents of function delivery (fish) and the ultimate drivers of function delivery (sediments), emphasizing weaknesses in the assumed links between fish presence and function.

Overall, this thesis revealed that low-complexity algal turf dominated reefs represent a highly likely configuration in the future. Within this operating space, this thesis also revealed that managing the complex interactions between herbivory, sediments and algal turf condition is important if the productivity of reefs is to be sustained. As we progress into an uncertain future shaped by climate change, the successful management of these interactions could help sustain reefs and their capacity to support the people that depend on them.

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Chapter 1: General introduction

The notion that the Earth has left the stability of the Holocene and entered the uncertainty of the Anthropocene is being increasingly acknowledged (Lewis and Maslin 2015; Steffen et al. 2015). In this new epoch we, as a species, are set to have a marked impact on how the Earth, and its ecosystems, are composed and operate (Johnson et al. 2017a; Steffen et al. 2018; Folke et al. 2021). Indeed, declines in the state of most ecosystems, ranging from the polar regions (Stroeve et al. 2007; McClintock et al. 2008; Schofield et al. 2010) to high diversity equatorial rainforests (Zhou et al. 2014; Barlow et al. 2018; Bullock et al. 2020), have now been documented in the literature. In many cases, these ecosystem changes are underpinned by the omnipresent force of global climate change (Schofield et al. 2010; Barlow et al. 2018; Bruno et al. 2018; Nolan et al. 2018), with a swath of other human derived, or human exacerbated, stressors also shaping ecosystems at smaller spatial scales (Dudgeon 2019; França et al. 2020; Wagner et al. 2021). Unfortunately, given the magnitude of these stressors and the changes they have underpinned, it is now widely believed that returning the Earth's ecosystems to states of the recent past may no longer be an attainable goal (Seastedt et al. 2008; Chapin et al. 2010; Kopf et al. 2015; Duarte et al. 2020). The world's coral reefs provide a particularly clear demonstration of these changes, and highlight the poignancy of these sentiments (Hughes et al. 2017a; Bellwood et al. 2019a; Morrison et al. 2020).

In many ways the plight of coral reefs has become a 'poster-child' for climate change-driven ecosystem change, as these tropical, high diversity, shallow-water ecosystems are at the forefront of environmental change (Barlow et al. 2018; Bruno et al. 2019; França et al. 2020; Wulff 2021). Specifically, climate change has now resulted in three global coral bleaching events (1998, 2010 and 2014-2017) (Skirving et al. 2019), as well as numerous more localised bleaching events (Hughes et al. 2018a; Sully et al. 2019) including five (1998, 2003, 2016, 2017 and 2020) on the world's largest reef system, Australia's Great Barrier Reef (GBR) (Hughes et al. 2021; Pratchett et al. 2021). As such, bleaching events are now shaping coral reefs across far larger spatial scales than previous stressors (Eakin et al. 2019; Dietzel et al. 2021b), with these spatial scales eclipsing the scales of current management approaches (Bellwood et al. 2019a; Bruno et al. 2019; Graham et al. 2020). It appears that the status-quo of coral reefs has fundamentally changed, with the reef configurations of the recent past becoming increasingly rare (Gardner et al. 2003; Hughes et al. 2018b; Bellwood et al. 2019b). Unfortunately, these changes are coming at a time when the strength of connections between people and coral reefs are stronger than ever before, with hundreds of millions of people now directly, as well as indirectly, relying on and valuing the services that coral reefs provide (Teh et al. 2013; Spalding et al. 2017; Eddy et al. 2021; Reguero et al. 2021). This situation led to the recognition that the challenge for scientists and managers now is: "*to identify and maintain the ecosystem functions that are crucial for sustaining coral reefs, and to secure the ecosystem services that highly altered reef assemblages can provide to people in the future*" (Hughes et al. 2017a). However, addressing this challenge hinges on our conceptual understanding of 'ecosystem functioning'.

A large body of ecological literature has aimed to understand how ecosystems function (e.g. Walker et al. 1999; Cardinale et al. 2002; Edwards et al. 2015; van der Plas et al. 2020). However, despite this attention, a clear universal definition of the term 'function' had remained elusive (cf. Jax 2005; Farnsworth et al. 2017). In 2017 I was part of a team that embarked on a nearly two-year long journey to understand what was meant by the term 'function' in ecology, especially as it applied to coral reefs. Eventually, this work culminated in a definition of ecosystem function as: *the movement or storage of energy or material within an ecosystem* (Bellwood et al. 2019b). This universal operational definition is synonymous with an 'ecosystem process' and is useful as it works from a cellular to global level (Bellwood et al. 2019b). However, on the journey to coining this definition two major issues were exposed. Firstly, functional studies rarely measure functions as they relate to ecosystem processes, instead in most cases, easy-to-measure traits or proxies are used that are thought to have functional significance (Bellwood et al. 2019b). Secondly, a 'functionality crisis' appeared to be occurring where it was unclear if we sufficiently understood the breadth and depth of functions on coral reefs to make informed management decisions (Bellwood et al. 2019b). This became particularly apparent when we considered the changing status-quo for the world's coral reefs and recognised that the functions once considered critical may no longer be as important in new contexts (Bellwood et al. 2019b).

Clearly, understanding ecosystem functions, and identifying those that are critical to maintaining the states on coral reefs that are desired by people is seen as a key research endeavour for coral reef scientists. However, this endeavour may have been stymied by our focus on indirect estimates of functions, and by the rapidly changing nature of coral reef configurations in the Anthropocene. To address these issues, it appears that we need to identify the likely configurations of future coral reefs, and then within these configurations directly focus on interactions and processes that shape the ability of these coral reefs to deliver services to humankind. This represents the framework for this thesis, i.e. to examine the likely configuration of future reefs, and then focus on critical interactions and processes in this context.

In terms of reef configurations, the general narrative over the last two decades has been that coral reefs will degrade along an axis from high coral cover to high macroalgal cover (Hughes 1994; Bellwood et al. 2004; Graham et al. 2006; Mumby et al. 2007; Jackson et al. 2014). Such coral-macroalgae 'phase-shifts' have received a significant degree of attention in the literature (e.g. Done 1992b; McManus and Polsenberg 2004; Hughes et al. 2007; Cheal et al. 2010; Roff and Mumby 2012; Crisp et al. 2022), especially in terms of focusing on potential management interventions (e.g. Hughes et al. 2010; Graham et al. 2013; Ceccarelli et al. 2018; Steneck et al. 2019). However, although widely accepted, it has been argued that such phase-shifts are relatively uncommon (Bruno et al. 2009, 2019; Côté et al. 2013; Russ et al. 2015), and that macroalgae can be naturally abundant even on 'healthy' reefs (Vroom et al. 2006; Vroom 2011; Bruno et al. 2014; Smith et al. 2016). Indeed, Adey (1998) considered coral reefs to be "*algal structured and mediated ecosystems in shallow, turbulent, alkaline waters*". This uncertainty in the literature makes it unclear if reefs covered in high macroalgae cover should be considered as the major configuration of future coral reefs. Clearly, exploring the likely configuration of future reefs requires further investigation.

Moreover, the study of macroalgae phase-shifts on coral reefs is at least partially responsible for the recognition that nominally herbivorous fishes play a variety of critical functional roles on reefs that maintain the resilience of these ecosystems (Bellwood et al. 2004; Hughes et al. 2007; Steneck et al. 2017). Indeed, this engendered a substantial amount of research into the 'top-down' control of algae on coral reefs by fishes (e.g. Humphries et al. 2015; Loffler et al. 2015; Longo et al. 2015; Plass-Johnson et al. 2015; Bonaldo et al. 2017; Dell et al. 2020), with overfishing of herbivores often pinpointed as the primary factor leading to a loss of resilience (Hughes 1994; Bellwood et al. 2004; Hughes et al. 2017a). Interestingly, this conceptual shift went against many 'bottom-up' views that nutritional resource quality and quantity limited herbivorous fish populations (reviewed in Choat and Clements 1998; Clements et al. 2009). As one would expect, this led to disagreement in the literature over the relative importance of top-down vs bottom-up forces as they apply to herbivorous fishes (e.g. Russ et al. 2015; Clements and Choat 2018; Bruno et al. 2019; Steneck et al. 2019). However, top-down vs bottom-up forces appear to be inherently linked through positive feedback loops, with the relative strength of top-down vs bottom-up forces dependent on the context of any given reef (Burkepile and Hay 2006; Bellwood et al. 2019b;

Bruno et al. 2019). As such, while a top-down view of herbivory on coral reefs has been the primary focus in recent years, this may need to be balanced against further examination of bottom-up forces (see discussion in Bellwood et al. 2019b).

Interestingly, the top-down focus on herbivory may also point towards what interactions are important to study in the context of future coral reefs. Indeed, if the overfishing of herbivorous fishes is considered to be a major structuring force of herbivorous fish populations, and in-turn, the condition of the benthos (see discussion in Mumby and Steneck 2008; Hughes et al. 2010; Graham et al. 2013; Bruno et al. 2019), this suggests that herbivorous fishes are also valued by people as a food resource. This observation is supported by the fact that herbivorous fishes (especially parrotfishes, surgeonfishes and rabbitfishes) are regularly harvested by fishers and can make up the bulk of subsistence/artisanal fisheries catches (Houk et al. 2012; Bejarano et al. 2013; Edwards et al. 2014; Samoilys et al. 2017; Humphries et al. 2019). For example, the herbivorous surgeonfish *Naso unicornis*, is the most commercially-valuable coral reef fish species across the insular Pacific (Taylor 2019). As such, it may be concluded that maintaining the productivity of herbivorous fish populations would be critical in sustaining coral reef fisheries production for people in some areas.

The abundance and biomass of nominally herbivorous fishes on coral reefs is frequently linked to the quality, quantity and productivity of benthic nutritional resources (e.g. Russ 2003; Russ et al. 2015, 2018; Tootell and Steele 2016; Robinson et al. 2019c, 2020; Oakley-Cogan et al. 2020). Interestingly, a growing body of evidence is suggesting that these nutritional resources are closely intertwined with sediments on both inshore and offshore coral reefs and that this in-turn shapes how nominally herbivorous fishes exploit resources (Randall 1955; Bellwood and Fulton 2008; Goatley and Bellwood 2012; Tebbett et al. 2017a, 2017b, 2018a; Ng et al. 2021). Indeed, three decades ago, Choat 1991 suggested that "*most of the plant material consumed by herbivorous reef fishes are small, structurally* *simple, and occur in complex assemblages. These can trap sediment and organic detritus…Under these circumstances and especially where algal fragments are mixed with calcareous material, the return per feeding episode could be relatively small.*" If sediments are indeed shaping how herbivorous fishes exploit resources, this has the potential to have bottom-up consequences for herbivorous fish populations, with subsequent declines in fisheries yields (e.g. Orlando and Yee 2017; Delevaux et al. 2018; Wenger et al. 2020). In this respect, as factors such as deforestation and dredging have increased in the catchments/coastal waters adjacent to reefs, increased sediment inputs and declining water quality now represent one of the most substantial and widespread stressors that reefs face after climate change (Fabricius 2005; Burke et al. 2011; Erftemeijer et al. 2012; Magris and Ban 2019; Suárez-Castro et al. 2021). Indeed, Andrello et al. (2022) revealed that water pollution (via sediments or nitrogen) was the most frequent (32.3% of reefs) top-ranked non climate pressure on the world's coral reefs. As such, understanding how benthic productivity and nutritional resources are affected by sediments, and what the ramifications are for herbivorous fishes, appears to be a particularly important interaction to explore in the context of future coral reefs.

Thesis outline

Clearly, a major challenge for coral reef scientists is to understand the critical functions on coral reefs that sustain the services that people require. The key priority is to quantify processes directly, in the context of future reefs. In this context, a focus on the interactions between benthic resources/productivity, herbivorous fishes, and sediments is likely to yield particularly useful insights. The primary aim of this thesis, therefore, was to explore the functioning of future coral reefs with a specific focus on the interactions between herbivorous fishes, productivity and sediments. This overarching aim was addressed in eight separate data chapters.

Firstly, in **Chapter 2** I explored what the likely configuration for coral reefs in the future could be by using a macroecological approach. Specifically, I compiled and examined trends in a global benthic composition time series dataset that spanned 22 years and covered all major coral reef realms. This macroecological approach was complimented in **Chapter 3** by a high-resolution examination of benthic dynamics at a coral reef location shaped by climate change. In this chapter I explored how back-to-back coral bleaching events, which occurred following back-to-back cyclones, shaped benthic composition. In addition, the short-term recovery capacity of this location was assessed to provide an insight into the potential benthic composition of this location into the future.

With a working conceptual framework for future coral reef configurations, in **Chapter 4,** I considered the potential importance of sediments trapped within algal turfs on these reefs. To do this I reviewed the literature and answered a series of key questions, while also considering the potential importance of these sediments on future reefs. This was followed by a field-based study on an offshore reef to determine how algal turf sediments are likely to influence future reef states, especially on lower-complexity flatter systems. This study **(Chapter 5)** used 3D photogrammetry to specifically examine the interaction between coral reef complexity and the nature of algal turfs. In **Chapter 6** I then focused more closely on how sediments were related to benthic nutritional resource quality, and productivity, across two islands with markedly different environmental contexts (i.e. at an inshore vs an offshore reef location). In doing so, Bayesian models that related sediment loads to algal turf growth were developed, and these were utilised to explore algal turf productivity across various spatial scales. This examination of algal turf productivity was complemented in **Chapter 7** by a meta-analysis of previous algal turf productivity studies on coral reefs. In this meta-analysis I utilised boosted regression trees to explore how key environmental factors relate to algal turf productivity on coral reefs. To place herbivorous fishes into the context of Chapters 2-7, in **Chapter 8,** I utilised a decadal timeseries dataset of sediment loads, algal turf condition and herbivorous fishes from an inshore reef. By combining this dataset with previously derived empirical relationships, I was able to explore processes using novel ‘function-scape’ analyses to quantify changes in the ability of the benthos to provide nutritional resources to herbivorous fishes, and the productivity of the herbivorous fish assemblage, through time as sediment loads increased. Finally, in **Chapter 9** I assessed shortcomings in our current approach to ecosystem-based management on coral reefs. By focusing on a highly abundant surgeonfish species, I was able to explore how the assumption that presence is equal to function delivery applied in the wake of increasing sediment inputs on coral reefs. I then assessed what this means for the direct management of ecosystem functions.

Chapter 2: Benthic composition changes on coral reefs at global scales

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Abstract

Globally, ecosystems are being reconfigured by a range of intensifying human-induced stressors. Coral reef ecosystems are at the forefront of this environmental transformation. If we are to secure key reef ecosystem functions and services, it is important to understand the configuration of future reefs, especially in terms of their benthic composition. However, the composition and trajectory of global coral reef benthic communities is currently unclear. My global dataset of 24,468 observations spanning 22 years (1997-2018), revealed that marked declines in coral cover have occurred in the Western Atlantic and Central Pacific. Furthermore, the data suggests that high macroalgae cover, widely regarded as the major degraded state on coral reefs, is a phenomenon largely restricted to the Western Atlantic. By contrast, in the Central Pacific, coral loss has largely been associated with increased cover of low-lying algal communities (mainly algal turfs and crustose coralline algae). Indeed, on reefs outside of the Western Atlantic, the primary axis of coral reef change lies between hard coral cover and low-lying algal communities, not macroalgae. For most reefs, understanding this configuration, typified by high cover of low-lying algal communities, will be key to maintaining their functional capacity.

Introduction

The pace and spatial extent of ecosystem transformations is set to increase in the Anthropocene as the strength of human modified stressors intensifies (Betts et al. 2017; Dudgeon 2019; Arrigo et al. 2020). Such is the magnitude of these stressors, that it has led to the suggestion that returning ecosystem configurations to those of the recent past may now be an unattainable goal (Seastedt et al. 2008; Chapin et al. 2010; Kopf et al. 2015; Duarte et al. 2020). Instead, the primary goals now are to maintain the functions that sustain these ecosystems, and to secure the services that these ecosystems deliver to people, even in highly altered configurations (Seastedt et al. 2008; Chapin et al. 2010; Kopf et al. 2015). A prerequisite to these goals is the recognition and understanding of the operating space, or configuration, of these highly altered ecosystems at a global scale.

These challenges are epitomised by coral reefs, an ecosystem at the forefront of environmental transformations (Graham et al. 2014; Hughes et al. 2017a; Bellwood et al. 2019a). Coral reefs are now being modified by a range of stressors (Harborne et al. 2017; Hughes et al. 2017a). Foremost among these is climate change, which has resulted in repeated mass coral bleaching events at global spatial scales (Hughes et al. 2018a; Sully et al. 2019). It now appears inevitable that coral reefs in the near future will continue to change. These changing coral reef configurations may have far-reaching consequences given the disproportionate amount of marine biodiversity (Fisher et al. 2015a) and productivity (Hatcher 1990) that coral reefs support, as well as the extent to which hundreds of millions of people rely on coral reefs (Teh et al. 2013; Ferrario et al. 2014). Clearly, if we are to manage reefs through these transformations, we need to understand the likely configuration of coral reefs in the near future. Given the spatial and temporal scope of the stressors currently acting upon coral reefs this understanding must come at a global spatial scale.

To gain an insight into likely coral reef configurations of the near future, and to identify the most pressing future research endeavours, we need to answer two relatively straightforward questions: 1) how is the benthic composition of coral reefs changing at a global scale? and 2) how, and to what extent, do these changes vary among major realms? To explore these questions, I compiled an extensive, global, dataset composed of 24,468 site-level observations of coral reef benthic composition. These observations spanned 13,802 sites (unique GPS coordinates) and 22 years from 1997 (i.e. immediately prior to the first global mass-coral bleaching event [Skirving et al. 2019]) until 2018 (i.e. a year after the most recent global coral bleaching event [Skirving et al. 2019]), and encompassed all major reef regions across 60° of latitude (Fig. 2.1a).

Methods

Benthic composition dataset compilation

To examine how benthic composition varied across coral reefs globally I compiled an extensive timeseries dataset. I limited my definition of 'coral reefs' to between ±30° of latitude from the Equator following Allen Coral Atlas (2020) and from 0 – 30 m water depth. The individual datapoints in my dataset were mean site level (i.e. a unique latitude, longitude and depth) benthic community composition data. Mean site level data were used as this was the finest resolution of data that could be reliably sourced.

Based on an initial examination of available data I settled on six benthic categories to represent benthic composition: 1) hard corals, 2) soft corals, 3) macroalgae, 4) low-lying algae, 5) other organisms, and 6) sand. Hard corals were made up of corals from the order Scleractinia while soft corals were from the order Alcyonacea. Macroalgae were generally considered fleshy and calcareous algae >~20 mm in height (Bruno et al. 2009; Tebbett and Bellwood 2019) (see Fig. A4 in Appendix A). The low-lying algal category included algal turf/crustose coralline algae[CCA]/rubble/cyanobacteria/dead coral/bare substratum/rock (as benthic composition data rarely discriminated among these different benthic categories a single category was used (following Nugues and Bak 2008; Gilmour et al. 2013; Toth et al. 2014; Tsounis and Edmunds 2017) to maximise data retention; see Text A1 in Appendix A for an extensive discussion on this as well as Chapters 4 and 6). The other organisms category was composed of other biotic organisms that are found on reef but are often not major constituents such as sponges, ascidians, seagrass, bivalves. It is critical to note that in all cases, I ensured the ‘other’ category did not comprise benthic categories often classed as ‘abiotic’ but are invariably covered in a constituent of the low-lying algal category (Diaz-Pulido and McCook 2002; Harris et al. 2015; Smith et al. 2016; Wolfe et al. 2021). Likewise, I ensured that all data had specifically monitored for ‘other’ biotic benthic components such as sponges and ascidians to ensure these were not pooled together as constituents of the low-lying algal category. With these six benthic categories I was able to capture 100% of the coral reef benthic community composition (i.e. I did not just focus on a subset of the biotic benthic community). I relied on these major divisions to maximise the resolution in the dataset, while minimising the amount of data that had to be excluded because it was collected at a coarse resolution.

Initially, I compiled benthic composition data from six major publicly available monitoring databases: Caribbean Coastal Marine Productivity (CARICOMP), Mo’orea Coral Reef Long Term Ecological Research, National Oceanic and Atmospheric Administration (NOAA), Reef Check, Reef Check Australia and Reef Life Survey (see Text A2 in Appendix A for a full list of data sources and links). Where necessary, these data were pooled into the relevant benthic composition categories, and site level means were calculated. In all cases, spurious data categories (e.g. transect tape, mobile fauna and unclassified) were excluded from calculations as they did not represent sessile benthic substrata. Data from these databases were also excluded if the metadata (namely depth, latitude, longitude, and sampling year) were missing or spurious.

To complement the data from these databases and ensure that my dataset was comprehensive, I then undertook an extensive formal search of the literature for available data. My search and filtering process was based on PRISMA protocols (Moher et al. 2009), and a flow diagram outlining each step is provided (Fig. A6 in Appendix A). This was achieved using the search engine Google Scholar and the search terms: "coral reef" AND benthic AND percent AND (transect OR quadrat). This search yielded 14,900 total results on the 20th of May 2020 (not including patents or citations). Note that, in contrast to searches in databases such as Web of Science and Scopus, these search terms take advantage of Google Scholar's default setting to search within the full text of documents. Therefore, for example, the use of terms such as 'transect' do not limit the papers returned to methods papers containing this term in the title, abstract or keywords of documents.

I initially filtered these 14,900 documents based on their title and abstract for any potentially relevant documents. This process resulted in a subset of 1,748 potentially relevant documents for further investigation. Each of these potentially relevant documents were then examined in detail and the suitability of their data for inclusion in my dataset were assessed against a set of criteria. These criteria were: a) sampling was conducted on a coral reef system within my definition of a coral reef (i.e. ±30° of latitude from the Equator and 0 – 30 m water depth), b) the document contained benthic community composition data at sufficiently fine resolution to fit into my six benthic categories in a form that I could extract (i.e. raw data, tables or from figures), with no missing data/benthic categories (note that if a study stated that the cover of a benthic category was quantified, but this category was found to have zero cover, then this study was still included in the dataset), c) the data were pooled at the site scale or a finer spatial scale (i.e. data across sites were not pooled and presented together), d) the data presented in the manuscript had not already been included in my database from another source, e) sufficient detail was presented in the document that outlined the sampling location, depth, time and methods used, and f) there was no clear selection of study sites to meet a pre-defined criteria (e.g. if a study selected for 'high coral cover' sites it was not included).

I relied on the criteria above to ensure that: a) the ecosystem sampled was consistent across data, b) the data covered the entire coral reef benthos, c) among site level variation was not averaged out, d) I did not include the same data twice, e) I had sufficient metadata from the past studies to explain potential patterns in benthic community composition, and f) I did not add bias to my dataset due to a sampling focus. After this second extensive filtering process I was left with a subset of 83 studies that contained relevant data for my dataset (see Text A2 in Appendix A for a full list of references). The vast majority of documents (1,449) simply did not contain the necessary data (i.e. most only reported 'coral cover' or 'algae cover' rather than complete benthic community composition). The widespread limitation of coral reef benthic data to just these two categories is best highlighted by the recent (2020) Status of Coral Reefs of the World report which was constrained to examining 'coral cover' and 'algae cover' at a global scale (Souter et al. 2021).

From each relevant document I then extracted data on the benthic cover (mean percent) of each of my six benthic categories at the level of individual sites. In most cases these data were sourced from raw data files, or tables in the main document. However, in some cases, it was necessary to extract the relevant data from figures in the document using WebPlotDigitizer (Rohatgi 2019). In addition, I also extracted information on the location of each study site (latitude and longitude), the depth of each habitat (where a range was given the median depth was used), the method used to quantify the benthos, the year sampling was conducted, and the habitat which was sampled. In terms of the depth data, note that authors in past studies are likely to have presented depth at the time of sampling, rather than depth below chart datum, which means there could be 1-2 m of error associated with these depth values.

Database cleaning and checking

With the compiled database at hand, I undertook a quality control procedure to check the data contained within my dataset. To do this I manually checked each data point. Specifically, I ensured a) the six benthic categories were standardised (i.e. they added up to 100%), b) the latitude and longitude data were accurate (I checked this by examining each individual set of coordinates in Google Earth), c) each data point had a corresponding depth (in meters) and year sampled value, d) the method used to collect each data point was categorised (line intercept transect, point intercept transect, chain intercept transect, photo quadrats along a transect, in-situ quadrats, or analysis of individual frames from a video), e) the habitat sampled was categorised as either reef flat, lagoon, slope, back reef, crest, or submerged reef (where this information was not presented I placed the datapoint into a category based on its depth and satellite imagery in Google Earth), and f) the location of each datapoint was categorised into a biogeographic realm and ecoregion (based on the latitude and longitude of the sampling site) following the classification scheme presented in Kulbicki et al. (2013) as well as a finer scale geographic unit based on the country/state/island/island group. Following this final quality control procedure my timeseries dataset contained 24,674 unique datapoints representing mean site level coral reef benthic community composition spread across more than 40 years of sampling (1977 – 2018).

Data analyses

All statistical analyses and data handling were performed in the software R (R Core Team 2020). Initially, I filtered my data to retain data from 1997-2018. Even though my dataset spanned 1977-2018 there was very little data prior to 1997 (only 0.83% of all data in the dataset were from the 20-year period from 1977-1996 [Fig. A7 in Appendix A]) making any inferences based on this early data difficult. Following this, I then recorded which benthic category was the most abundant at each reef site in each year. To explore how the dominance of the three primary benthic coverings (hard coral, macroalgae, and low-lying algal communities) varied over time at a global spatial scale, I used separate generalised additive mixed effects models (GAMMs) in the *mgcv* (Wood 2017) package. Specifically, I treated time (year sampled) and depth (to account for any depth-related patterns) as continuous fixed effects using thin plate splines. In addition, I also fitted habitat and geographic unit as random effects using random effects smoothers. Method and ecoregion were not included in the models as they had a high level (>0.8) of concurvity with the other factors already included. For all three models I used a binomial distribution and logit-link. After fitting the models, I checked that a sufficient number of knots were used by checking if k and edf were close to each other, while considering the values of the k-index and simulated p value in gam.check (Wood 2017). In addition, I examined the residuals of both models for temporal autocorrelation. No significant patterns of temporal autocorrelation were detected. I also assessed the residuals of both models for spatial autocorrelation using variograms (package: *gstat* [Gräler et al. 2016]), and also compared these to variograms of the residuals from models containing only the fixed effects structure as well as variograms of the raw data. In all cases my models accounted for spatial correlation and there were no clear patterns in the residuals. I also examined model residuals using simulation-based model-checking (package: *DHARMa* [Hartig 2020]). In all cases this indicated that the fit was satisfactory.

To visualise variation in benthic composition of all six benthic components through time I extracted data from 1997, 2007, and 2017 from the four focal realms (Central Pacific, Indian Ocean, Indo-West Pacific and Western Atlantic). I based the visualisation on these 3 years as 1997 represented the earliest year in my retained dataset, while 2007 and 2017 were equidistantly spaced apart, and covered the vast majority of the temporal scope in my dataset. A ten-year period was chosen to limit any influence of temporal autocorrelation on the visualisation. Based on these three years of data, I then calculated a dissimilarity matrix based on the Morisita-Horn index (as it is robust when sample sizes differ [Jost et al. 2011]), and plotted the data using a constrained CAP ordination (package: *vegan* [Oksanen et al. 2019]). I constrained the ordination by year and realm to clearly visualise differences along these axes. To ensure the axes were directly comparable, the multivariate analysis was conducted as one analysis (i.e. all three years together) and only the results were plotted separately by year. To aid interpretation I then calculated 50% kernel density estimates for each realm in each year (package: *adehabitatHR* [Calenge 2006]). Calculating kernel density estimates is a technique that has been popularised in the field of animal movement to describe the probability of animal detections in a space and to delineate core areas as this technique is not sensitive to outliers (Worton 1989). Therefore, in my case, the 50% kernels indicate the core areas of the ordinations (i.e. a multivariate space) occupied by the sites from each realm in each year.

Based on the ordinations, the examination of hard coral, macroalgae and low-lying algal community dynamics in the Western Atlantic, Indo-West Pacific and Central Pacific through time appeared warranted, especially given the history of comparing these realms in the coral reef literature (e.g. Bellwood et al. 2004; Roff and Mumby 2012; Siqueira et al. 2019; Roff 2021). The Indian Ocean was not included in the analysis due to the relatively small size of the dataset from this realm compared to the other three (Fig. A7 in Appendix A). To do this, I utilised GAMMs (package: *mgcv* [Wood 2017]) to examine temporal variation in the proportional cover of the three benthic components, separately, in the three realms. I treated time (year sampled) as a continuous fixed effect with separate splines for each realm. In addition, to account for depth-related patterns, I fitted depth as a continuous fixed effect with separate splines for each realm. In all cases I used thin plate splines for the fixed effects. As above, I also fitted habitat and geographic unit as random effects using random effects smoothers. Again, method and ecoregion were not included in the models as they had a high level (>0.8) of concurvity with the other factors already included. For both models I utilised a tweedie distribution with a log link function. A tweedie distribution was superior to a betabinomial distribution here due to the nature of the data in all cases (i.e. the data contained a large number of exact zeroes and the nonzero observations were continuous and positively skewed [and with very few observations at the upper bounds of the proportional dataset – i.e. close to 100% cover]). Model fit and assumptions were assessed as above and where necessary the number of knots was increased for the fixed effects splines. In all cases no significant patterns were detected in the residuals and model fit was satisfactory. Additional packages used for graphical representation of the data included *emmeans* (Lenth 2020), *tidyverse* (Wickham et al. 2019), *sf* (Pebesma 2018), *maps* (Becker et al. 2018), *ggtern* (Hamilton and Ferry 2018), and *patchwork* (Pedersen 2020).

Results and discussion

Reef benthic composition

At the global scale, reef-building scleractinian corals (i.e. hard corals), which are the principal structure formers of coral reefs (Graham and Nash 2013; Cornwall et al. 2021), were never the most abundant benthic covering at the majority of sites (Fig. 2.1b). Moreover, macroalgae, widely considered to be the major alternative degraded state on coral reefs (Bellwood et al. 2004; Hughes et al. 2017a), were also never the most abundant benthic covering over the 22-year period considered (Fig. 2.1b). Instead, throughout the entire 22-year period, the most abundant benthic category at the majority of sites was the low-lying algal community category (Fig. 2.1b). Such low-lying algal communities are composed of a continuum that spans from relatively bare substratum with a thin biofilm, through crustose coralline algae (CCA), to long sediment-laden algal turfs (see Chapters 4 and 6 as well as Text A1 and Figs A1-A5 in Appendix A for a comprehensive discussion of these constituent algal groups, and a justification for pooling them in this analysis). However, despite this prevalence, low-lying algal communities have been poorly captured in most existing coral reef data, frequently being lumped together as ‘dead coral’, ‘rubble’, ‘pavement’, ‘rock’ or even ‘bare space’ (Fig. A1 in Appendix A), limiting my capacity to divide them further at present (e.g. Brown et al. 2017; Benkwitt et al. 2019; Russ et al. 2021) (also see Text A1 in Appendix A). Nevertheless, once corals are lost, it is low-lying algal communities, especially algal turfs and cyanobacteria, that generally fill the vacated space (Goatley and Bellwood 2011; Gilmour et al. 2013), with such reef conditions often being perceived as a ‘degraded’ condition (i.e. low coral cover) (Bellwood et al. 2004; Jouffray et al. 2019). Indeed, these data suggest that low-lying algal communities have replaced corals on reefs at global scales, and their dominance is increasing (Fig. 2.1b; Table A1 in Appendix A), mirroring a steady decline in the dominance of hard corals, especially in the last decade (Fig. 2.1b; Table A1 in Appendix A).

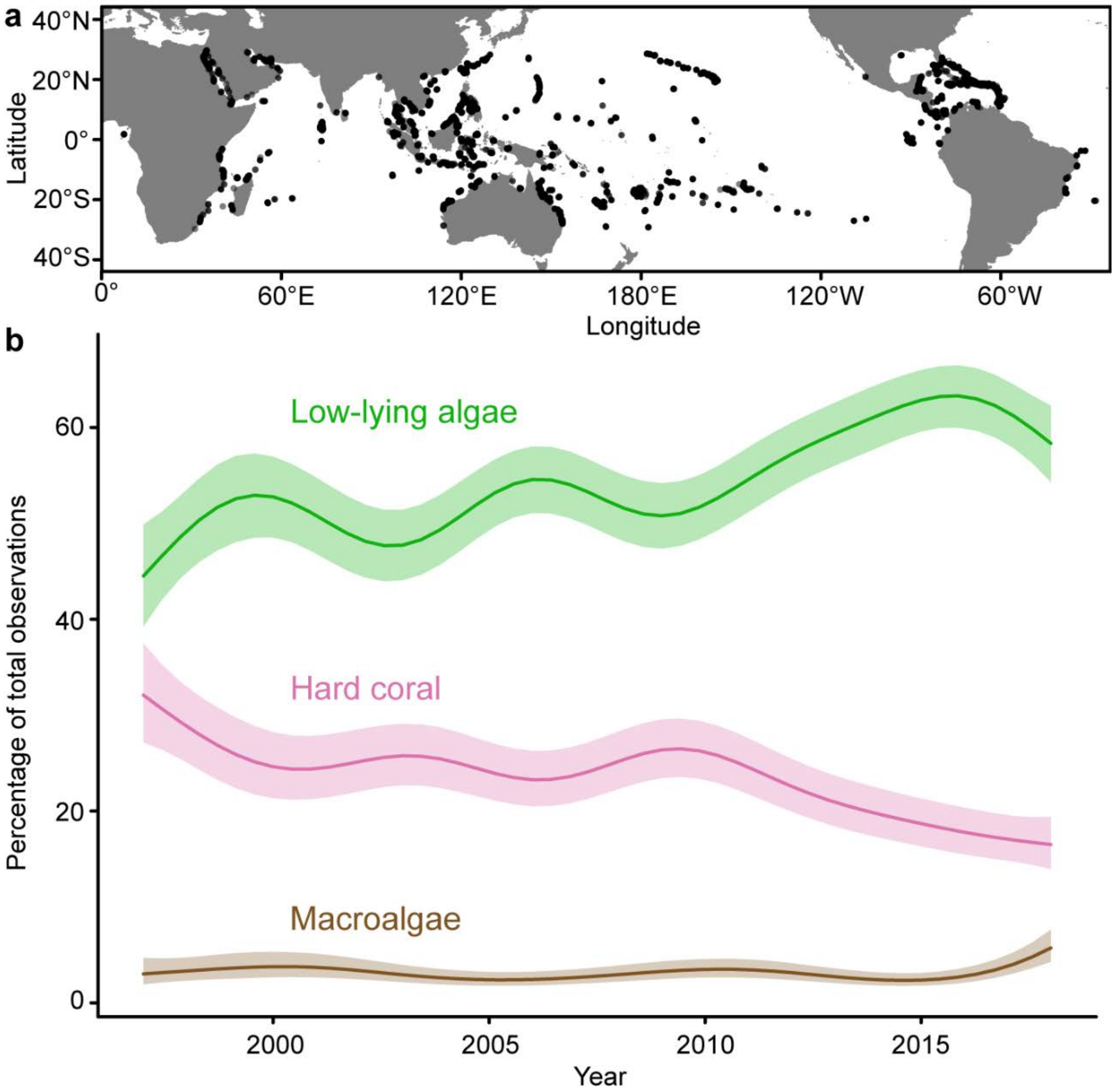

Figure 2.1 Benthic composition of the World's coral reefs. a) World map showing the spatial extent of coral reef benthic composition data (n = 24,468 data points). b) The percentage of reef sites on which hard corals, macroalgae or low-lying algal communities were the most abundant benthic covering (i.e. the highest % covering of the benthos). Solid lines denote the mean fit from generalised additive mixed effects models, while the shaded areas denote the 95% confidence intervals. For a plot based on a subset of the data but with the low-lying algal community divided into algal turfs and crustose coralline algae see Fig. A2 in Appendix A.

However, this global-scale estimate of benthic dominance does not reveal variation in composition among the world's major coral reef realms. I therefore used multivariate ordinations to explore how coral reef benthic composition differed among the four major coral reef realms (Central Pacific, Indian Ocean, Indo-West Pacific, Western Atlantic) at three different equidistant points (1997, 2007, 2017). The data revealed three distinct patterns. Firstly, from 1997 to 2017 the Western Atlantic has occupied an increasingly distinct area of multivariate space compared to the other realms, characterized by a relatively high cover of macroalgae and 'other' organisms (predominantly sponges and ascidians) (Fig. 2.2). Secondly, the Central Pacific appears to have become increasingly restricted to an area of multivariate space typified by a high relative coverage of low-lying algae (Fig. 2.2). Notably, the Central Pacific appears to have shifted away from the high hard coral cover area of multivariate space that it encompassed in 1997 (Fig. 2.2). Thirdly, despite numerous large-scale disturbances in the 20-year period (Cheal et al. 2017; Hughes et al. 2018a; Sully et al. 2019), reefs in the Indian Ocean and Indo-West Pacific have consistently occupied an area of multivariate space typified by relatively high hard coral cover (Fig. 2.2).

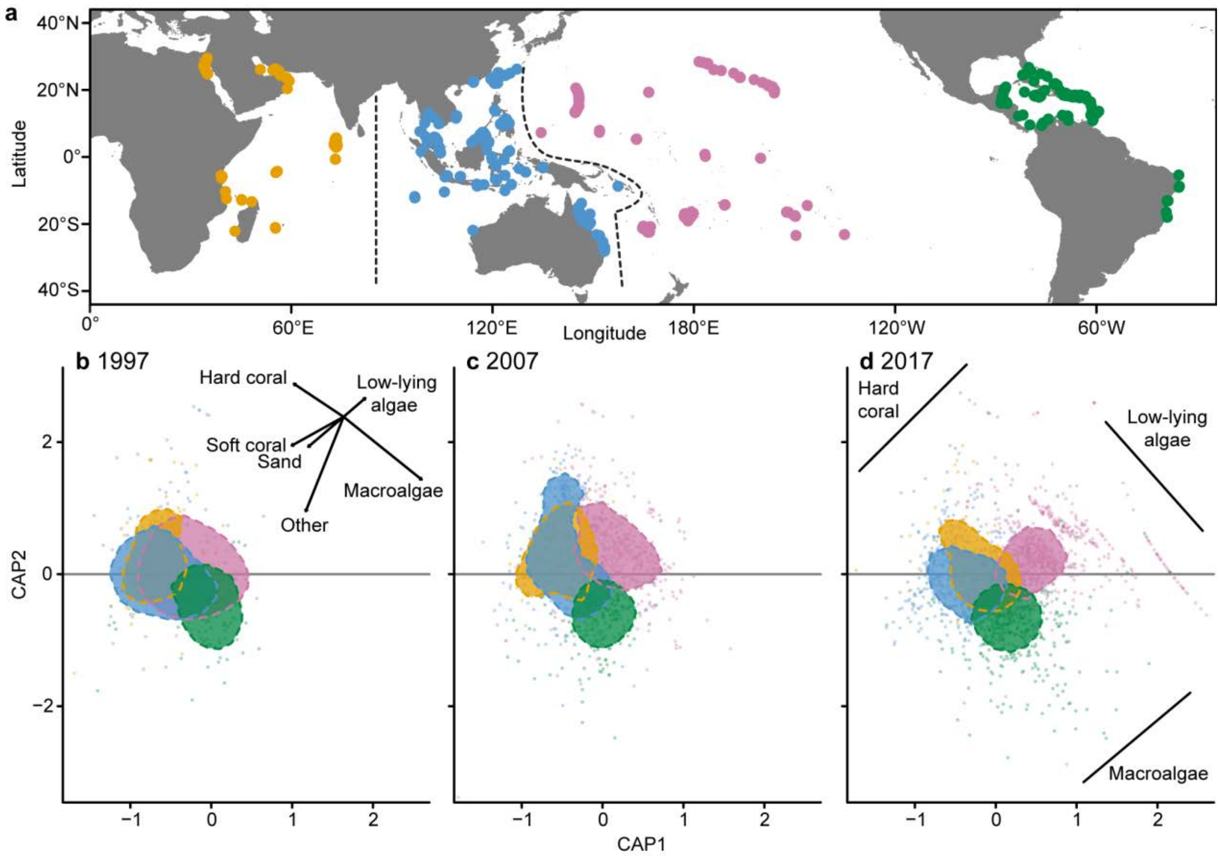

Figure 2.2 Coral reef benthic composition among major realms. a) World map showing the delineation of the major reef realms based on the data from 1997, 2007 and 2017 used in the ordination plots (n = 424, 1102, 1924, respectively). Constrained multivariate ordination plots based on the Morisita-Horn index showing coral reef benthic composition in the four realms in b) 1997, c) 2007, and d) 2017. The coloured polygons in the ordinations are based on 50% kernel density distributions, denoting where the data points are concentrated in multivariate space. Note the vectors in b) show the relationship between the benthic categories and how they influence the site level benthic composition data points in the ordination plots. The lines in d) denote the areas of multivariate space typified by the three major benthic coverings.

The most striking pattern in the multivariate ordinations is the fundamentally different area of space occupied by the Western Atlantic (green region), the Indo-West Pacific (blue region) and the Central Pacific (pink region) (Fig. 2.2). To explore this in more detail, I used generalised additive mixed effects models (GAMMs) to specifically focus on the dynamics of hard corals, macroalgae and low-lying algal communities in these three realms from 1997-2018. These models revealed substantially decreasing hard coral cover in the Western Atlantic and Central Pacific, with limited net change in the Indo-West Pacific (Fig. 2.3a; Table A2 in Appendix A). In the Western Atlantic, along with coral loss, there appears to have been a significant concomitant increase in macroalgal coverage (Fig. 2.3b; Table A2 in Appendix A). By contrast, macroalgal coverage has remained consistently low in the Indo-West Pacific and Central Pacific (Fig. 2.3b), with only a small net increase apparent in the Central Pacific (Fig. 2.3b). Unlike in the Western Atlantic, coral loss in the Central Pacific has largely been associated with a significant concomitant increase in the cover of low-lying algal communities (Fig. 2.3c; Table A2 in Appendix A). Given that many reefs in the Indo-West and Central Pacific have been repeatedly subjected to a wide array of stressors, including repetitive mass coral bleaching events and widespread coral mortality (Hughes et al. 2018a; Sully et al. 2019), a more detectable signal in the data would have been expected if macroalgae were going to increase in these realms. I conclude that the dynamics between hard coral and macroalgae cover differ markedly between the Western Atlantic vs Indo-West and Central Pacific realms.

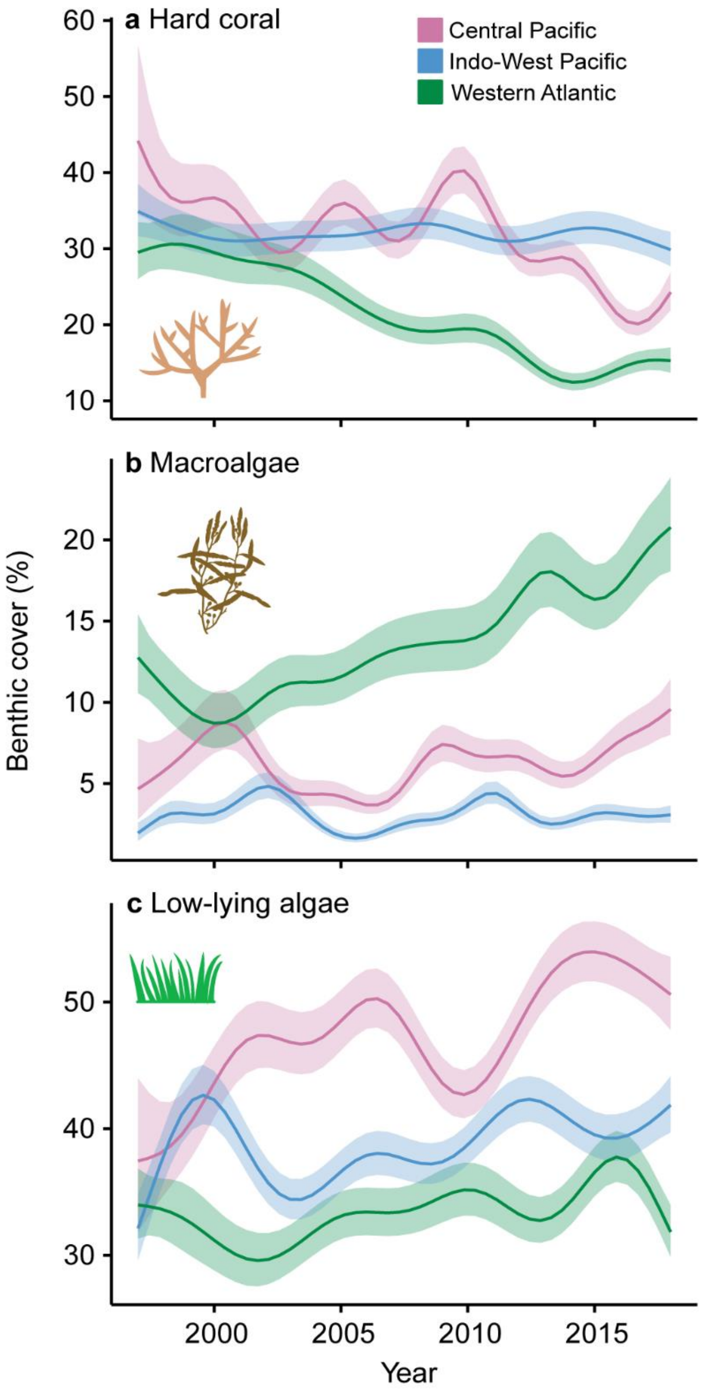

Figure 2.3 Hard coral, macroalgal and low-lying algal community dynamics in major reef realms. The benthic cover of a) hard corals, b) macroalgae and c) low-lying algal communities at coral reef sites in the Western Atlantic (n = 5071), Indo-West Pacific (n = 8382) and Central Pacific (n = 8786). Solid lines denote the mean fit from generalised additive mixed effects models, while the shaded areas denote the 95% confidence intervals. Note that the y-axis ranges differ across panels to better illustrate among realm variability.

Much of our understanding about coral reef decline and alternative stable states is based on reefs in the Western Atlantic realm (Hughes 1994; Bellwood et al. 2004; Mumby et al. 2007). However, these analyses strongly support the hypothesis that the Western Atlantic is functioning in a fundamentally different manner to other coral reef realms, and calls into question the extent to which insights gleaned in this realm can inform our understanding of ongoing change in other realms (see Bruno et al. 2009, 2019; Roff and Mumby 2012). Indeed, it has previously been highlighted that many top-down (e.g. herbivory) and bottom-up (e.g. macroalgal growth rate) factors differ fundamentally between reefs in the Western Atlantic vs Indo-West Pacific, with potential implications for their respective resilience (Roff and Mumby 2012). For example, many fast growing *Acropora* coral growth forms, which drive early coral recovery (Bellwood et al. 2004; Roff 2021) (also see Chapter 3), as well as functional groups of key herbivorous fishes (e.g. crevice cleaning surgeonfishes/rabbitfishes and browsing rabbitfishes/nasine surgeonfishes) (Roff and Mumby 2012; Siqueira et al. 2019), are completely lacking in the Western Atlantic, potentially pre-disposing these reefs to much higher macroalgal cover following coral loss.

In other realms, coral loss and reef change appears to be independent of macroalgal cover. In this respect, the Central Pacific could represent a harbinger of the future Indo-West Pacific realm as it has experienced a significant degree of coral loss over recent decades; similar coral loss is widely expected on Indo-West Pacific reefs in the future (Hughes et al. 2017a, 2018a). Interestingly, Central Pacific and Indo-West Pacific reefs may respond to disturbance in a broadly similar manner, as they share critical functional groups of hard corals (Bellwood et al. 2004; Roff 2021) and herbivorous fishes (Roff and Mumby 2012; Siqueira et al. 2019), yielding similar response diversity and resilience mechanisms, especially when compared to the Western Atlantic (Bellwood et al. 2004; Roff and Mumby

2012; Siqueira et al. 2019; Roff 2021). As such, the changes on Central Pacific reefs over the recent past may provide a more meaningful insight into the future of Indo-West Pacific reefs.

Key axes of change

The hypothesis that the principal axis of change outside the Western Atlantic is hard coral to low-lying algal communities is supported by several lines of evidence. Firstly, over recent decades, low-lying algal communities have represented the most abundant benthic cover on the vast majority of coral reefs globally (Fig. 2.1). Secondly, the multivariate ordination plots (Fig. 2.2) as well as the GAMMs (Fig. 2.3) revealed a clear loss of hard coral cover and an increase in low-lying algal community cover on Central Pacific reefs (Fig. 2.3). Finally, for each of the four realms, I produced a ternery plot of benthic cover data for the three major benthic components on coral reefs (hard coral, macroalgae, and low-lying algae), for the most recent two years in the dataset (2017/2018). These plots clearly reveal that, outside the Western Atlantic, the vast majority of data points fall along the axis between high hard coral cover and high low-lying algal community cover (Fig. 2.4a, c), or exclusively within an area typified by very high low-lying algal community cover (Fig. 2.4d). Virtually no data fell along the axis purely defined by high hard coral and high macroalgal cover (Fig. 2.4). By contrast, in the Western Atlantic, the data largely fell on the macroalgae – low-lying algal community axis, with more data than in any other realm also falling along the macroalgae – hard coral axis (Fig. 2.4b). Consequently, given this current status (Fig. 2.4), as well as the evidence for increasing low-lying algal community cover on coral reefs globally (Fig. 2.1b), it would appear likely that in the future it will be the interaction between hard coral cover and low-lying algal cover that is the key axis for coral reef composition and change outside the Western Atlantic.

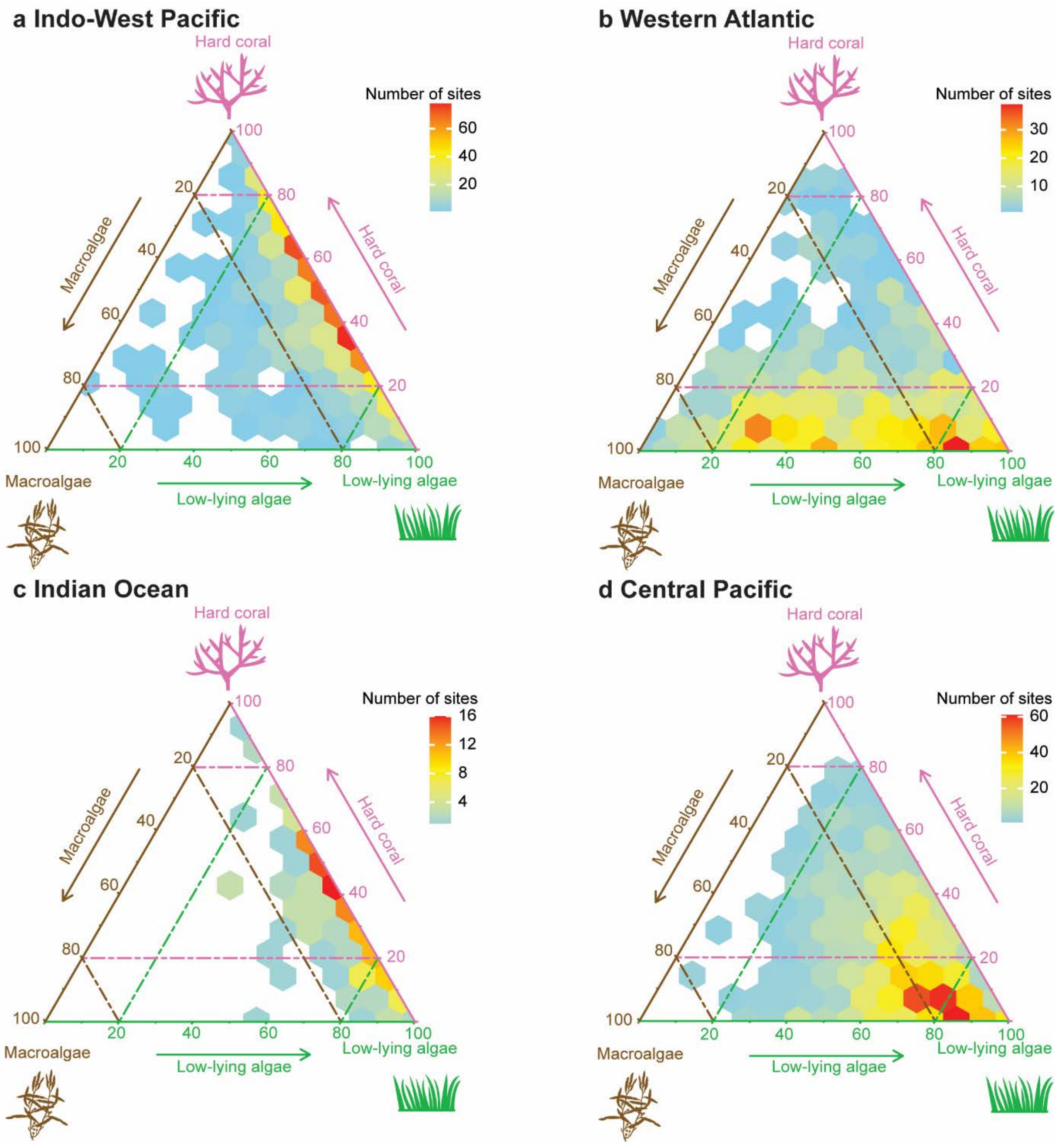

Figure 2.4 The cover of hard corals, macroalgae and low-lying algal communities on the world's coral reefs. Ternery plots of hard coral, macroalgae and low-lying algal community cover on the world's coral reefs in 2017/2018 in the a) Indo-West Pacific (n = 981), b) Western Atlantic (n = 934), c) Indian Ocean (n = 153), and d) Central Pacific (n = 1085). Colouring of the hexagons corresponds to the number of data points that fall within each hexagon.

Comparison with past studies and other ecosystems

Change on coral reefs is generally associated with the loss of hard scleractinian coral cover (Bellwood et al. 2004; Hughes et al. 2017a; Bruno et al. 2019). In this respect, my results are consistent with previous studies. For example, the long history of declining hard coral cover in the Western Atlantic, especially in the Caribbean, is well established in the literature (Hughes 1994; Gardner et al. 2003; Schutte et al. 2010). My results suggest that the declines documented in earlier studies in this realm (Gardner et al. 2003; Schutte et al. 2010), have continued, with the low levels of 10-15% coral cover in my study aligning well with recent reports (Souter et al. 2021). Moreover, the relative stability of hard coral cover during this period (1997-2018) in the Indo-West Pacific (Bruno and Selig 2007) as well as in the Indian Ocean (with the notable exception of the 1998 bleaching event) (Ateweberhan et al. 2011), has been previously documented, with my levels of 25-30% also aligning well with recent reports from these regions (Souter et al. 2021). However, it is important to highlight that my study, along with the previous studies, all represent realm-wide average trends, with changes within specific locations potentially diverging from these trajectories (Schutte et al. 2010; Souter et al. 2021).

Nevertheless, given a situation of relatively low, and in some cases decreasing, hard coral cover on reefs in recent decades, this raises the question: what benthic category is replacing corals? This is where my study differs from many previous studies from coral reefs, particularly those at a similar spatial scale, as I specifically endeavoured to separate large (i.e. >2 cm tall) macroalgae from low-lying algal forms (CCAs and turfs). Previous global scale data compilations have largely focused on ‘algae’ cover, with the constituent algal groups (be it tall macroalgae, turf algae, CCA etc) often being unclear (Souter et al. 2021). Indeed, it is because of this lack of resolution that data from numerous past studies could not be included in the present study, and why my division of algal categories was limited to macroalgae versus low-lying algae (problems with the historical quantification of low-lying algae in coral reef monitoring are discussed in Text A1 in Appendix A). However, this division between macroalgae and low-lying algae is important because it revealed that while ‘algae’ may be increasing on many reefs globally (Souter et al. 2021), in most cases this is not tall macroalgae but rather low-lying algae, such as turfs.

Interestingly, change on coral reefs from complex habitat-forming organisms (e.g. hard corals) to low-lying cover (e.g. low-lying algae), is also representative of a major pathway of change that can occur in many other ecosystems. For example, on rocky kelp-dominated reefs anthropogenic heating and other stressors have driven similar shifts from complex canopy-dominated kelp forests to low complexity sediment-laden algal turfs (Wernberg et al. 2016; Filbee-Dexter and Wernberg 2018; Pessarrodona et al. 2021). Furthermore, in terrestrial systems, the degraded state of complex forests is often open grassland savannahs (Hirota et al. 2011) with the potential for eventual transitions to desert states (Bestelmeyer et al. 2015). Indeed, changes in ecosystem state between complex and low-lying appear to be relatively common across multiple ecosystems (reviewed in Rocha et al. 2015). In the case of tropical reefs, such transitions may arise from the vulnerability of hard corals, soft corals and macroalgae to contemporary stressors. For example, climate change and associated heating is now the major stressor shaping reefs globally (Hughes et al. 2018a; Sully et al. 2019) and can significantly impact both hard and soft coral cover (Loya et al. 2001; Hughes et al. 2018b). Similarly, tropical macroalgae growth and survival is also impeded by heating (Straub et al. 2019; Graba-Landry et al. 2020) and it has been suggested that if heating continues, we may see a collapse of canopy-forming macroalgae in many tropical regions (Fulton et al. 2019), with further expansion of turfs (Straub et al. 2019). The loss of architecturally complex organisms, and expansion of low-lying cover, may therefore be a phenomenon that transcends multiple ecosystems in the Anthropocene.

A future outlook for reefs

These results imply that the dynamics of many future coral reefs will be intimately associated with a high coverage of low-lying algal communities. However, it is important to highlight that these low-lying algal communities are by no means homogenous, existing on a continuum from CCA, through sparse algal turfs + CCA, to long sediment-laden algal turfs (for a full discussion see Text A1 and Figs A3-A5 in Appendix A) (also see Chapters 4, 5 and 6). As such, where the state of low-lying algal communities falls on this continuum may be critical to the functioning of future reefs. Importantly, a benthic condition typified by low-lying algal communities composed of high CCA and/or short well-cropped algal turf cover is not resistant to the return of corals (Birrell et al. 2008; Diaz-Pulido et al. 2010; Gilmour et al. 2013; Speare et al. 2019) (also see Chapter 3). By contrast, if low-lying algal communities shift towards long sediment-laden algal turfs, as a result of stressors such as sedimentation or overfishing of herbivorous fishes (Goatley and Bellwood 2013; Fong et al. 2018), this can inhibit coral settlement and recovery (Birrell et al. 2008; Speare et al. 2019; Ricardo et al. 2021), as can reef states typified by high macroalgal cover (Birrell et al. 2008; Diaz-Pulido et al. 2010; Johns et al. 2018). As such, aiming to maintain low-lying benthic communities typified by CCA and short algal turfs may be beneficial, until climate change is addressed and/or corals adapt, to facilitate the return of corals to reefs.

In addition to being a more favourable benthic state for corals to return to compared to high macroalgal cover, if future coral reefs are typified by high coverage of low-lying algal communities there is also the possibility that the provision of many key services can be maintained under this benthic state. Indeed, fisheries catches in many reefal locations are already heavily composed of fishes that derive their nutrition from components of low-lying algal communities (Houk et al. 2012; Bejarano et al. 2013; Edwards et al. 2014). As such, maintaining the highly productive nature of short algal turf communities into the future may be important in maintaining fisheries catches in some areas (Tebbett et al. 2021) (Chapter 8). Moreover, a decrease in coral cover and coral derived calcification in the future (Cornwall et al. 2021), may mean that the role of CCA in calcification and reef building also becomes more important. In this respect the important roles of CCA in reef building are increasingly being recognised, with the suggestion that the substratum formed by CCA may be resistant to future climate change (Nash et al. 2013; Diaz-Pulido et al. 2014). Even if the outlook for reefs is typified by high coverage of low-lying algal communities it may, therefore, be possible to maintain some key ecosystem functions within this operating space if these algae can be maintained in states typified by CCA and short turfs. It appears, therefore, that an enhanced understanding of the condition of these low-lying algal communities may be a critical research endeavour if the goal is to sustain key ecosystem functions on future coral reefs.

Conclusions

Overall, the trajectories in this global survey carry substantial implications for the understanding of coral reef compositions at global spatial scales and the operating space in which coral reefs may occur in the future. It is clear that Western Atlantic reefs are typified by relatively high macroalgal cover, with the axes of change in this realm including one between hard corals and macroalgae. However, in the other realms, benthic composition rarely falls along this coral-macroalgae axis, nor does macroalgae appear to be a major benthic component. Instead, over more than two decades from 1997-2018 the low-lying algal community category has been consistently increasing on most reefs, with the vast majority of recent data falling along an axis of hard coral to low-lying algae. It appears likely that this axis will represent the critical operating space for most coral reefs in the future.

Chapter 3: Spatial patchiness in change, recruitment, and recovery on coral reefs at Lizard Island following consecutive bleaching events

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Abstract

The world's coral reef ecosystems are steadily being reconfigured by climate change. Lizard Island, on Australia's Great Barrier Reef, offers an opportunity to examine coral reef reassembly following disturbance, as this location has been impacted by consecutive tropical cyclones and consecutive coral bleaching events. Based on repeatedly monitoring the same 349 photoquadrats around Lizard Island over a 5-year period (2016–2021) I revealed that bleaching in 2016 drove a ~50% reduction in hard coral cover, and a concomitant increase in algal turf cover. From 2018 to 2021, significant increases (>600%) in coral cover were detected on two semi-exposed reefs and were associated with substantial *Acropora* recruitment. By contrast, fourteen lagoonal and back reefs exhibited virtually no recovery nor *Acropora* recruitment. Given that the timeframe between disturbances is set to decrease, my results suggest that some recovery is possible immediately after severe cumulative disturbances, although this recovery may be highly spatially heterogenous.

Introduction

Global warming now represents a substantial stressor for the world's ecosystems (Walther et al. 2002; Williams et al. 2003; Jiménez-Muñoz et al. 2016), with coral reefs providing a particularly clear example of how this stressor can disturb ecosystems (Stuart-Smith et al. 2018; Sully et al. 2019; Dietzel et al. 2021b). Indeed, the impacts of climate change manifest on reefs in the form of mass coral bleaching events (Hoegh-Guldberg 1999; Hughes et al. 2018a; Romero-Torres et al. 2020; Raj et al. 2021), as well as bringing the potential for more severe tropical cyclones/hurricanes (Cheal et al. 2017; Puotinen et al. 2020). As the future for coral reefs is set to be punctuated more frequently by such disturbances, understanding how reefs respond to, and recover/reassemble after, these disturbances is important (Graham et al. 2011; Bellwood et al. 2019a; Bruno et al. 2019). In this regard, examining the trajectories that coral reef benthic communities take immediately following disturbance events, especially in terms of their capacity to recover, may be particularly informative.

One location that may yield particularly interesting insights into the trajectories of coral reef communities post-disturbance is Lizard Island in the northern Great Barrier Reef (GBR), Australia. This is because, in recent years, Lizard Island has been impacted by numerous, cumulative, large-scale disturbances. These disturbances at Lizard Island include severe tropical cyclones in 2014 and 2015 and coral bleaching events in 2016 and 2017 that severely damaged coral cover across a 1400 km expanse of the GBR (Hughes et al. 2019b). While we have a relatively clear understanding of how such disturbances impact coral reef benthic communities, principally through the mass mortality of many coral species (Hoegh-Guldberg 1999; Marshall and Baird 2000; Loya et al. 2001; Hughes et al. 2018b), our understanding of the trajectories coral reefs take immediately after such significant cumulative disturbances, especially in terms of coral recovery, is less clear and may vary substantially (e.g. Gilmour et al. 2013; Pisapia et al. 2016; Gouezo et al. 2019; McWilliam et al. 2020; Cannon et al. 2021; Moritz et al. 2021).

Previous studies have suggested that factors such as high herbivory (Mumby and Steneck 2008; Chong-Seng et al. 2014; Viviani et al. 2019), coral larval supply and recruitment (Holbrook et al. 2018; Gouezo et al. 2021), and survival of settled corals (Chong-

Seng et al. 2014; Evans et al. 2020) may be important in the recovery trajectories of coral cover. However, our understanding of how these mechanisms operate and relate to the recovery of coral reefs following severe cumulative disturbances, such as those that have affected Lizard Island, remains limited. Indeed, the bleaching events in 2016 and 2017 were so severe that coral recruitment appeared to collapse along the GBR, with 89% fewer recruits than historical baselines (Hughes et al. 2019a). This led to the suggestion that the capacity for reefs to recovery around Lizard Island, at the centre of this recruitment failure, is highly uncertain (Hughes et al. 2019a). This uncertainty is further compounded by the fact that, in many cases, the data on coral reef benthic communities is not collected at a high spatial resolution (i.e. accurately at small scales with sampling across multiple sites) and often lacks adequate temporal replication, stymying our ability to assess 'patchiness' in post-disturbance benthic dynamics. We therefore have a surprisingly limited understanding of how and where benthic coral reef communities respond to, or recover/reassemble after, cumulative disturbances, especially when associated with collapses in coral recruitment across large spatial scales.

Understanding the capacity for corals to recover over short-term timeframes is becoming increasingly important as the expected 'recovery window' between disturbances on reefs is shrinking, principally because the effects of climate change are intensifying (Hughes et al. 2018a; Puotinen et al. 2020). However, given the extent of recent disturbances to Lizard Island, and the GBR in general, one may hypothesise that recruitment of corals and recovery of coral cover would be negligible over such short-term timeframes (i.e. 3-4 years post-disturbance). To explore this hypothesis the aims of this study were: a) to assess where and how coral reef benthic communities changed in response to large scale disturbances (consecutive coral bleaching), b) assess the spatial extent of coral cover recovery or regeneration over a short-term time frame, and c) assess the spatial extent of *Acropora* recruitment. To address these aims I tracked the benthic community composition dynamics of 349 spatially and temporally matched photo quadrats on shallow reefs around Lizard Island. In addressing these aims, this study will provide insights into how this location was disturbed by recent coral bleaching and then, specifically, it will allow me to explore the hypothesis of negligible coral recruitment and recovery at this location over the short-term.

Methods

Study site and disturbance history

Lizard Island is a granitic mid-shelf island located on the northern Great Barrier Reef (GBR), Australia, and is relatively remote in terms of direct human pressures (Fig. 3.1). Lizard Island was impacted by two severe cyclones (Ita in 2014 and Nathan in 2015) which passed close to the island as Category 4 systems and reduced coral cover on the reefs on the exposed and semi-exposed sides of the island (Madin et al. 2018) (Fig. 3.1b). Notably, these cyclones had little impact on the reefs on the sheltered leeward side of the island, or in the protected lagoon (Madin et al. 2018). Following these cyclones, this location was at the centre of the 2016 coral bleaching event that spanned the northern third of the GBR, and was, at the time, the most severe coral bleaching event recorded on the GBR (Hughes et al. 2019b). Subsequent coral beaching events that were less severe in the northern GBR also impacted this location in 2017 and 2020 (Hughes et al. 2021; Pratchett et al. 2021).

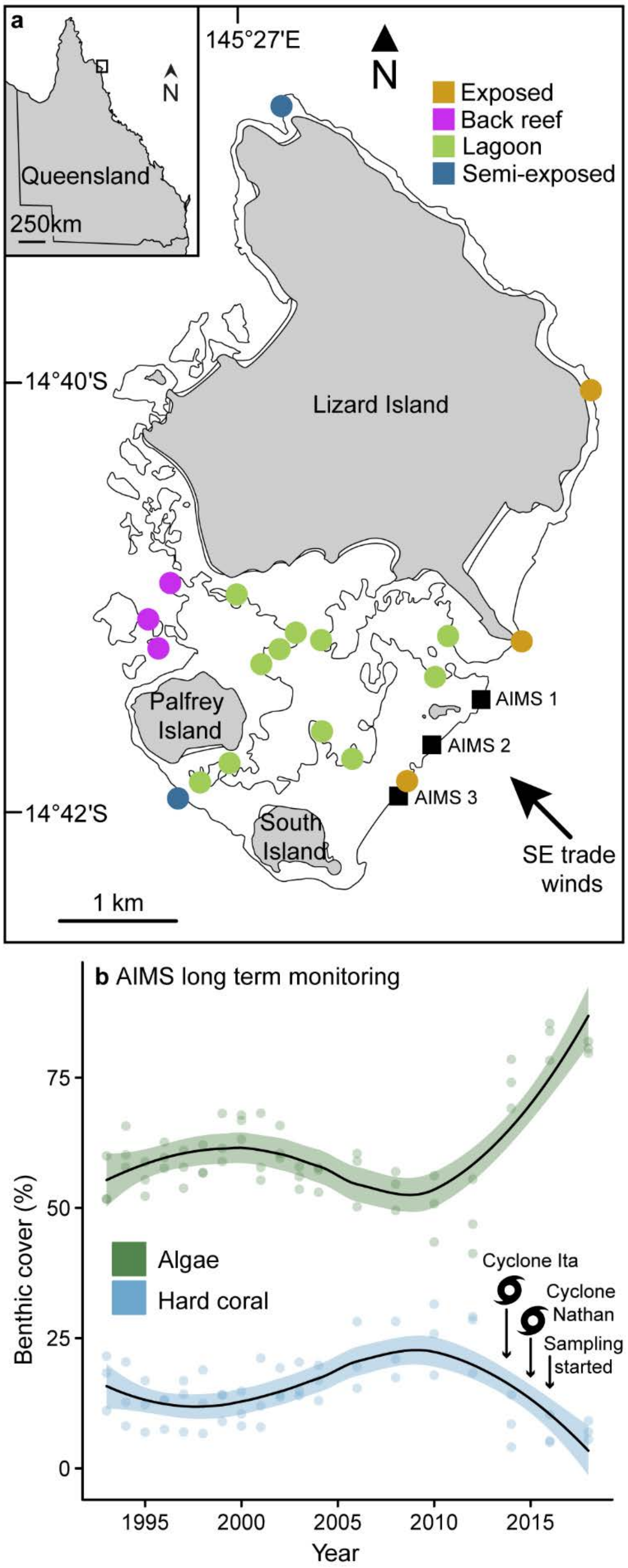

Figure 3.1 a) Map of Lizard Island showing the 19 sampling locations and their exposures, as well as the locations of the Australian Institute of Marine Science's (AIMS) long term

monitoring sites. The exposure categorisation was based on the position of locations relative to the prevailing south-east trade winds. The inset shows the location of Lizard Island relative to Queensland, Australia. b) The long-term trajectory of algae and hard coral cover at the AIMS long term monitoring sites. The coloured dots are the raw data points (sourced from Australian Institute of Marine Science [2015]), while a smoother and associated 95% confidence intervals were fitted based on a generalised additive model smoothing function to help visualise trends (Wickham 2016).

Sampling

In February 2016, immediately prior to the onset of major bleaching, 451 fixed quadrats (measuring 1 m^2) spread over 19 transects around Lizard Island were photographed. The quadrats were approximately 5 m apart along each transect, with transects varying in length from 12-38 quadrats depending on the nature of the reef. All quadrats were located on the reef crest/reef edge at a depth of 0 – 4 m below chart datum. Three transects were in exposed locations, two in semi-exposed locations, three in leeward back reef locations and eleven were spread across the protected lagoon (Fig. 3.1a). These exposure categories were based on the position of transect locations relative to the prevailing south-east trade winds (Fig. 3.1a) and follow the categories used in previous studies which have quantified water-flow speeds in some locations at Lizard Island (Fulton and Bellwood 2005; Johansen 2014). It should be noted that the first sampling period occurred after the two cyclones had impacted the island (Fig. 3.1b), and as such, I am unable to determine the spatial extent of their impacts on coral cover at my specific sites using these data (although see the section on ‘coral loss’ in the discussion for further details of how the cyclones in 2014/2015 impacted coral cover around Lizard Island).

For each quadrat location a photograph of the reef with the quadrat in place was taken from a 'birds-eye' view for benthic cover analysis. Photoquadrats were subsequently taken in October 2016, January 2018, January/February 2020 and January/February 2021 (Fig. 3.2). In all cases, photographs were taken with a Nikon Coolpix W300 camera. As the quadrats were not fixed in place, to minimise the impact on the location, the quadrats were relocated using a second Nikon Coolpix camera, loaded with the previous sampling periods photographs, to act as a guide. While most quadrats across the 5-year study period could be relocated, some could not be, or quadrat placement differed substantially from initial placement; these were excluded from the analyses. The final dataset, therefore, consisted of 349 quadrats in each of the five sampling periods. It should be noted that although there is a long-history of examining coral cover around Lizard Island (e.g. Done 1992a; Pratchett 2010; Madin et al. 2018) this photoquadrat method was initially designed to investigate fish-coral interactions (see Wismer et al. 2019a, 2019b). However, the first sampling trip (February 2016) coincided exactly with the 2016 coral bleaching event (April 2016) on the GBR. Given the high-resolution nature of my sampling method, and the potential for it to provide insights into the benthic trajectories of specific sites post-disturbance, the value in continuing sampling until January 2021 was immediately apparent.

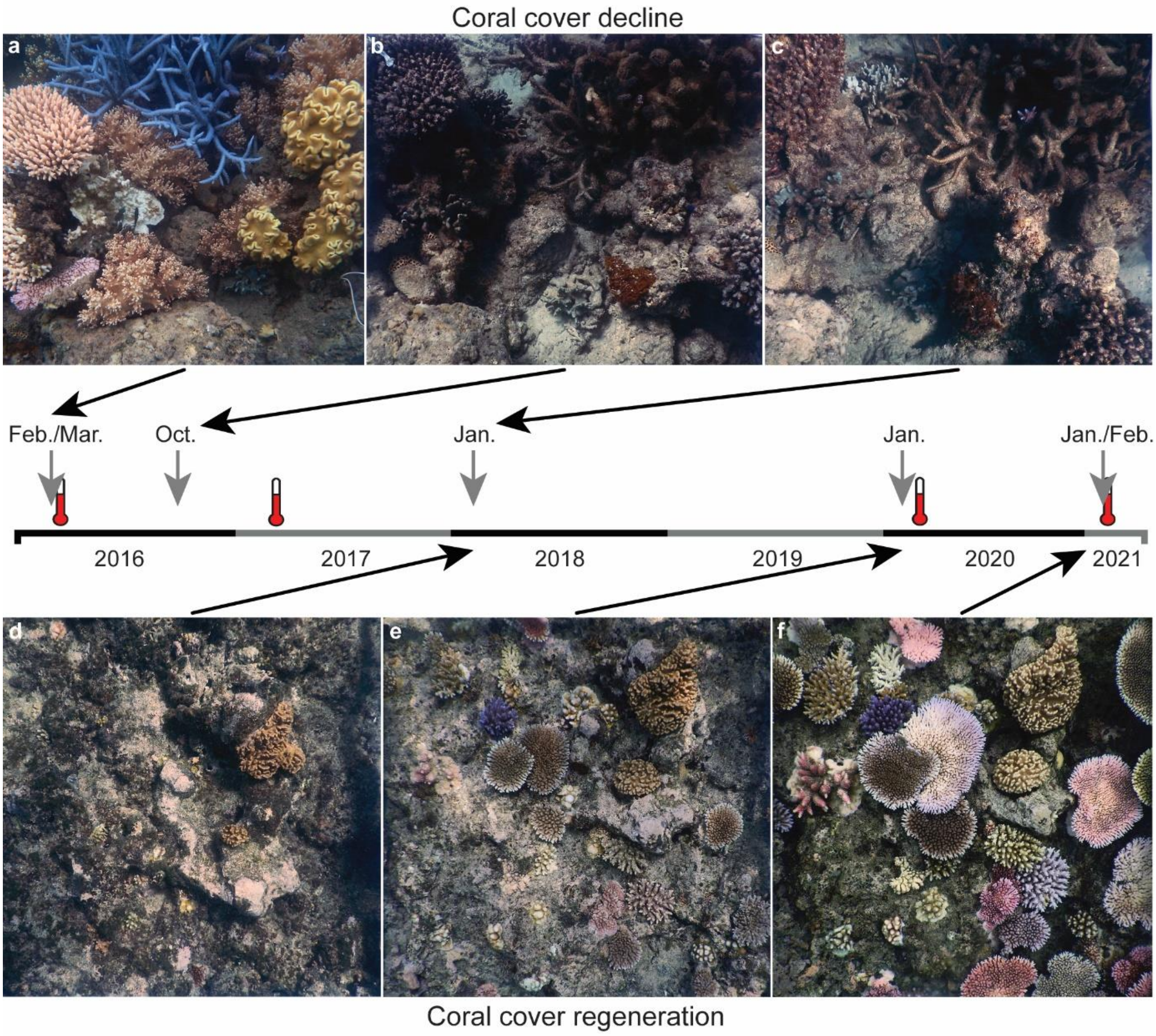

Figure 3.2 The loss of hard and soft corals between February 2016 and January 2018 at a reef site in the lagoon as a result of coral bleaching (a, b, c). The recovery of *Acropora* cover at a semi-exposed reef site from January 2018 to January 2021 (d, e, f). Note the onset of coral bleaching in (f) and the high cover of algal turfs in (b, c, d, e). Timeline of sampling (indicated by grey arrows) and coral bleaching events (thermometers).

Photograph analysis

From the photographs I quantified benthic cover under 40 randomly stratified placed dots in the software photoquad v_1_4 (Trygonis and Sini 2012). Under each dot I identified organisms to genera (where possible). Where taxonomy could not be applied, I used functional groupings based on the biotic covering and the substratum that category was on (e.g. algal turf on rubble, algal turf on dead coral). On the rare occasions where a dot fell on a benthic component that could not be identified, such as gaps in the reef, in holes or overhangs, these dots were excluded from the analyses. It is important to note that the use of random dot placement in each year factors out any effects of minor quadrat misplacement. This has previously been checked using a sensitivity analysis (see Wismer et al. 2019a). Furthermore, in the 2018, 2020 and 2021 photographs the numbers of new *Acropora* recruits in each quadrat were counted. A coral was considered a recruit if it was not visible in photographs of the previous sampling periods. Therefore, even small juvenile corals could be considered recruits because I could determine when they entered (i.e. recruited to) the population of interest (i.e. visible coral communities on the benthos). The minimum size of recruits detected in the photographs were 3 cm^2 (~2 cm in diameter), while the average size of recruits when they were first detected was 74.4 cm^2 with an average diameter of 9.7 cm (see Fig. B1 in Appendix B for an example). Given that *Acropora* recruits are ~1 cm in diameter at one year of age (Babcock 1985; Baria-Rodriguez et al. 2019) and can then grow (change in diameter) at up to ~5 mm per month to reach sizes of ~6-7 cm in diameter at two years of age (Trapon et al. 2013a; Baria-Rodriguez et al. 2019), the 'recruit' corals detected in the photographs were probably between one and two years of age. *Acropora* was chosen because this coral genus is numerically dominant on most GBR reefs and is critical in early-stage recovery (Johns et al. 2014; Hughes et al. 2019a; Roff 2021).

Statistical analyses

Initially, I visually explored variation in coral reef benthic community composition using multivariate ordination. Due to the high number of zeros in the data, I pooled benthic data into ten coarse categories based on biotic cover to facilitate analysis: *Acropora*, *Porites*, other hard scleractinian corals, soft corals, algal turfs, macroalgae, crustose coralline algae [CCA], cyanobacteria, sand and ‘other’ (please note that the other category was mainly composed of sessile invertebrates such as sponges and ascidians). Based on the percent cover of these categories in each quadrat I calculated a similarity matrix based on the Morisita-Horn index and fourth-root transformed data. The Morisita-Horn index was used as it is robust when sample sizes differ (Jost et al. 2011). To visualise variation in benthic composition, I used a CAP ordination, which was constrained by the factors year and exposure. 50% kernel density estimates were then calculated for each year and exposure combination to aid in the visualisation of the core areas of multivariate space occupied by the quadrats. Unlike convex hulls, which are traditionally used to visualise multivariate spaces, kernel density estimates show how multivariate space is occupied. They are less sensitive to outliers and, therefore, focus on key areas of multivariate space occupation, rather than how outlying data points influence the occupation of multivariate space (Blonder 2018). Kernel density estimates are becoming increasingly popular for examining space use with applications ranging from animal movement ecology (Worton 1989) to space use in multivariate analyses (Blonder 2018). In my case, I am examining the distribution of quadrats in multivariate space. It is important to note that the analysis was undertaken on the full dataset, however, only data from February 2016, January 2018 and January 2021 are shown on the plots for clarity.

Following the multivariate visualisations, I specifically examined the temporal dynamics in benthic cover of the two primary space holders on coral reefs in this location (hard scleractinian corals [all genera] and algal turfs). To do this I used generalised linear mixed effects models (GLMMs) fitted with a binomial distribution and logit-link function. I treated sampling trip and exposure as fixed categorical factors, while quadrat identity nested within transect identity were included as random effects, to account for the lack of independence due to the repeated sampling nature of this study. For both models, a full model was initially fitted which included an interaction term between the fixed factors. The models were then simplified, and the most parsimonious model was selected based on the corrected Akaike Information Criterion (AICc) (Table B1 in Appendix B). Model fit and assumptions were examined via residuals using simulation-based model-checking. Where overdispersion was detected, an observation-level random effect was added to the model to account for this. Post-hoc pairwise means comparisons were performed with a Tukey's adjustment to examine key within factor differences.

To explore spatial patterns in *Acropora* recruitment I used a GLMM to compare the total number of new recruits (summed across 2018, 2020 and 2021 due to the nature of the data) in each quadrat among exposure regimes (categorical fixed effect). In this case transect identity was fitted as a random effect to account for the lack of spatial independence. Due to the high number of zeroes in the data (even when summed together) I fitted a zero-inflated model with a tweedie distribution and log-link function. Model fit and assumptions, as well as post-hoc pairwise tests, were performed as above. A detailed examination of how *Acropora* recruitment related to key explanatory variables was also performed and these details are provided in Appendix B (Text B1 in Appendix B). All statistical analyses were conducted in the software R (R Core Team 2020), using the *glmmTMB* (Brooks et al. 2017a), *vegan* (Oksanen et al. 2019), *emmeans* (Lenth 2020), *tidyverse* (Wickham et al. 2019), *adehabitatHR* (Calenge 2006) and *DHARMa* (Hartig 2020) packages.

Results

Benthic change and coral loss

The composition of the coral reef benthic community changed markedly across the study period, with clear differences in the trajectory of these changes among locations of differing exposures (Fig. 3.3 and Figs B2, B3 in Appendix B). Notably, following the coral bleaching events, the lagoonal sites lost a substantial amount of soft coral cover as the area of multivariate space typified by soft corals was completely lost, and this had not recovered by January 2021 (Fig. 3.3d). Since January 2018, lagoonal sites were typified by high relative cover of *Porites*, sand, macroalgae and 'other' sessile benthic organisms (Fig. 3.3d). By contrast, back reef sites were consistently typified by soft coral cover throughout the study period (Fig. 3.3c). However, as for the lagoonal sites, the back reef sites also had relatively higher coverage of sand and *Porites* when compared to exposed and semi-exposed sites (Fig. 3.3c and Fig. B3 in Appendix B).

The dynamics of exposed and semi-exposed sites differ from those of lagoonal and back reef sites. Specifically, while exposed sites also lost soft corals during the bleaching event (Fig. 3.3a), they subsequently occupied an area of space typified by crustose coralline algae (CCA) and to a lesser extent cover of algal turfs and 'other' hard corals (Fig. 3.3a and Fig. B2 in Appendix B). Semi-exposed sites also occupied the area of multivariate space typified by high CCA cover (especially in January 2018) (Fig. 3.3b), although, from January 2018 to January 2021, there was a marked shift in semi-exposed sites towards the area of multivariate space typified by *Acropora* cover and to a lesser extent the cover of algal turfs and 'other' hard corals (Fig. 3.3b). In this respect, the shift in position of semi-exposed locations in multivariate space from January 2018 to January 2021 (towards an area typified by higher *Acropora* cover) was particularly notable as all other exposure regimes have largely occupied the same area of multivariate space between January 2018 to January 2021 (Fig. 3.3). This, therefore, suggested that the benthic community composition of semi-exposed reefs may have changed since the disturbance events, while benthic dynamics at other reef locations may have remained constant.

Interestingly, algal turf cover was not a strong driver of separation in any exposure regime (as indicated by the length of the corresponding vector loading in Fig. 3.3). However, bar plots of percent cover by the ten major benthic coverings showed that algal turfs consistently covered >50% of the benthos across all sampling periods (Fig. B2 in Appendix B). Indeed, together with all hard corals (i.e. *Acropora*, *Porites* and other hard corals), these two benthic coverings, algal turfs and hard corals, have consistently dominated benthic dynamics at Lizard Island, invariably covering >75% of the total benthos (Fig. B2 in Appendix B). It is also notable that hard coral cover at Lizard Island is principally composed of *Acropora* and *Porites* corals, with fluctuations in *Acropora* cover being particularly notable (Fig. B3 in Appendix B). Indeed, bar plots of the percent cover of the fifteen most abundant hard coral genera revealed that the other genera made minimal contributions to total benthic cover at Lizard Island during the study period. Although the almost complete loss of some genera such as *Seriatopora* from this location is notable (Fig. B3 in Appendix B).

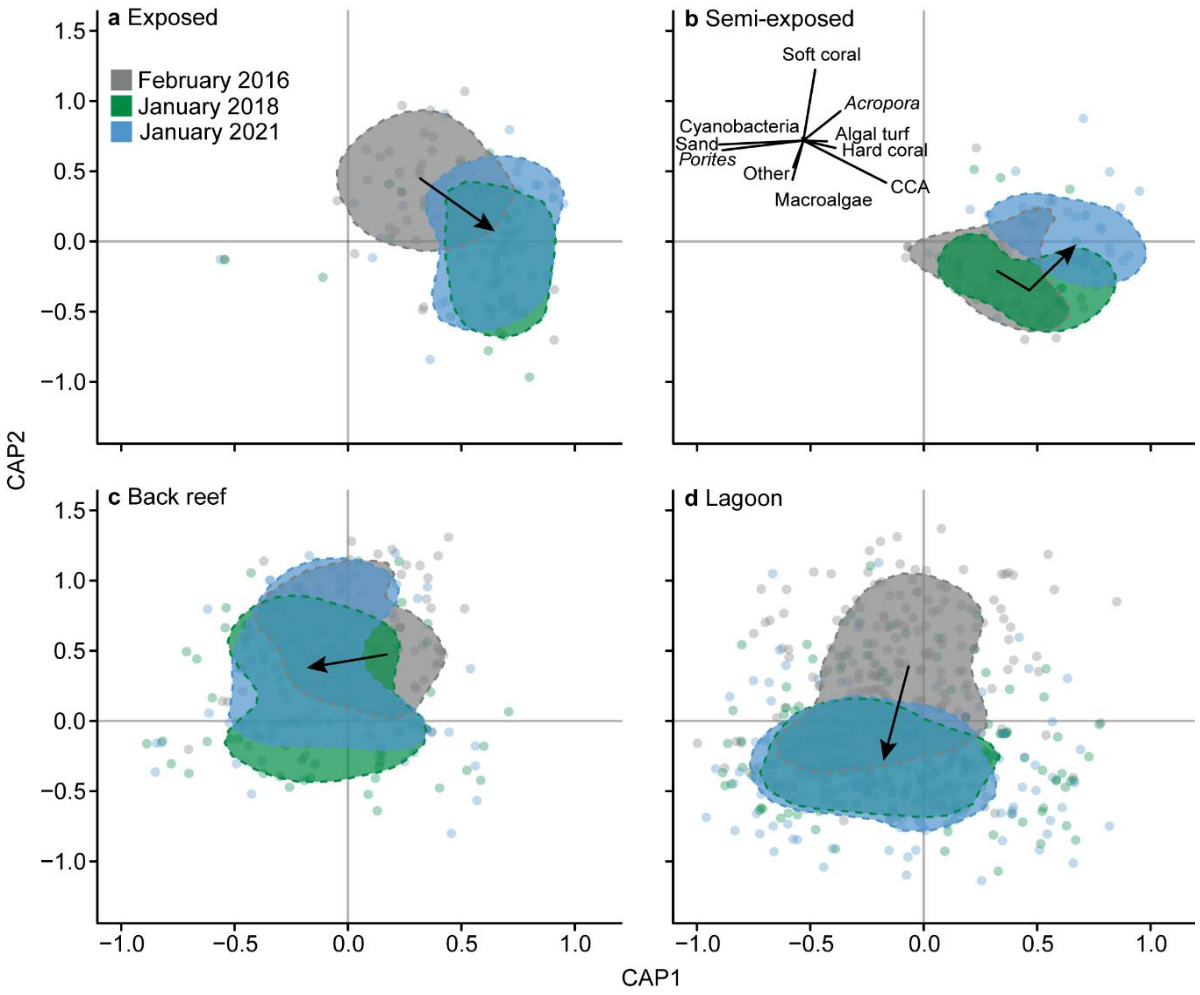

Figure 3.3 Constrained multivariate ordination plots of coral reef benthic composition based on the Morisita-Horn index in a) exposed, b) semi-exposed, c) back reef, and d) lagoonal habitats. The coloured dots are the positions of individual quadrats, while the coloured polygons denote 50% kernel density estimates which show where the quadrats are concentrated in multivariate space. The vectors (black lines) in b) show the relationship between the benthic categories and their contribution to the position of quadrats in multivariate space (indicated by their length). For clarity, only the benthic composition of quadrats in February 2016, January 2018 and January 2021 are shown. The black arrows in each panel highlight the direction of major shifts in benthic composition across years. CCA = crustose coralline algae, hard coral = hard corals other than *Acropora* and *Porites*. See Figs B2 and B3 in Appendix B for bar plots of benthic cover.

Due to the substantial contribution of algal turfs and hard corals (all genera) to the benthic composition at Lizard Island, a specific examination of how their respective cover varied among locations through time was warranted. In all habitats, the coral bleaching event in April 2016 resulted in a significant decrease in hard coral cover between February and October 2016 (Figs 3.2a, b, c, 3.4 and Fig. B4, Tables B2, B3 in Appendix B). Specifically, mean coral cover decreased by 50.2%, 52.6%, 50.3% and 41.8% across back reef, exposed, lagoonal, and semi-exposed habitats, respectively. However, as coral cover was initially higher in back reef and lagoonal sites, this correlated to an absolute decrease of 6.4%, 5.8%, 12.7%, and 2.8% across back reef, exposed, lagoonal, and semi-exposed habitats (to a mean cover of 6.4%, 5.2%, 12.6% and 3.9%), respectively. Importantly, the 2017 coral bleaching event did not appear to have any substantial effects on hard coral cover, as there was no significant change in hard coral cover between October 2016 and January 2018 in any habitat (Fig. 3.4; Tables B2, B3 in Appendix B). As coral was lost from February 2016 to October 2016, algal turf cover significantly increased in all habitats, apart from semi-exposed habitats (Fig. 3.4; Tables B2, B3 in Appendix B).

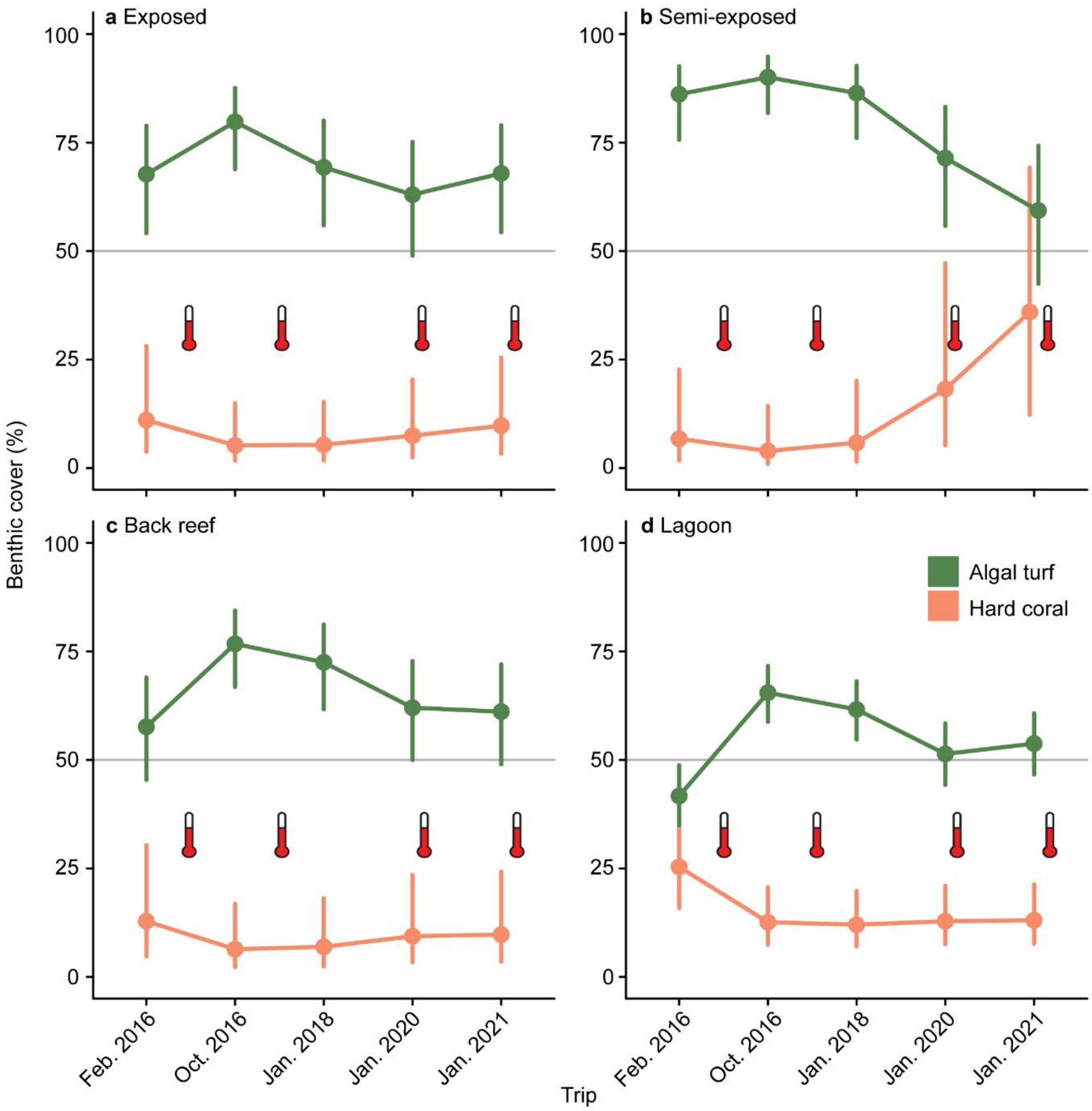

Figure 3.4 The temporal dynamics of algal turf cover and hard coral cover at a) exposed, b) semi-exposed, c) back reef and d) lagoonal reef sites. The coloured dots and ranges denote the mean predicted fit (± 95% confidence intervals) from generalised linear mixed effects models. Note the increase of algal turf cover from February 2016 to October 2016 associated with coral bleaching and subsequent mortality, as well as the marked increase in coral cover from January 2018 to January 2021 at semi-exposed reef sites. The thermometer symbols denote coral bleaching. See Fig. B4 in Appendix B for coral cover dynamics at the transect and quadrat scale.

Recruitment and coral recovery

My examination of *Acropora* recruitment around Lizard Island from January 2018 to January 2021 revealed marked spatial patchiness in this process with distinct differences among locations of different exposures (Fig. 3.5; Table B4 in Appendix B). Specifically, *Acropora* recruitment was significantly higher in semi-exposed locations compared to all other locations (Table B5 in Appendix B) and, on average, was 88-fold, 18-fold, and 9-fold higher on semi-exposed reefs than lagoonal, back reef or exposed locations, respectively (Fig. 3.5). Indeed, there was virtually no recruitment in lagoonal and back reef areas (zero recruits were recorded in 83.9% of lagoon and back reef quadrats) (Fig. B5 in Appendix B). By comparison, the GLMM suggested there was an average of 9.8 ± 5.78 (± SE) *Acropora* recruits m^{-2}, with up to 29 new *Acropora* recruits recorded in a single m^2 quadrat, on semi-exposed reefs over the 3-year period (Fig. 3.5a).

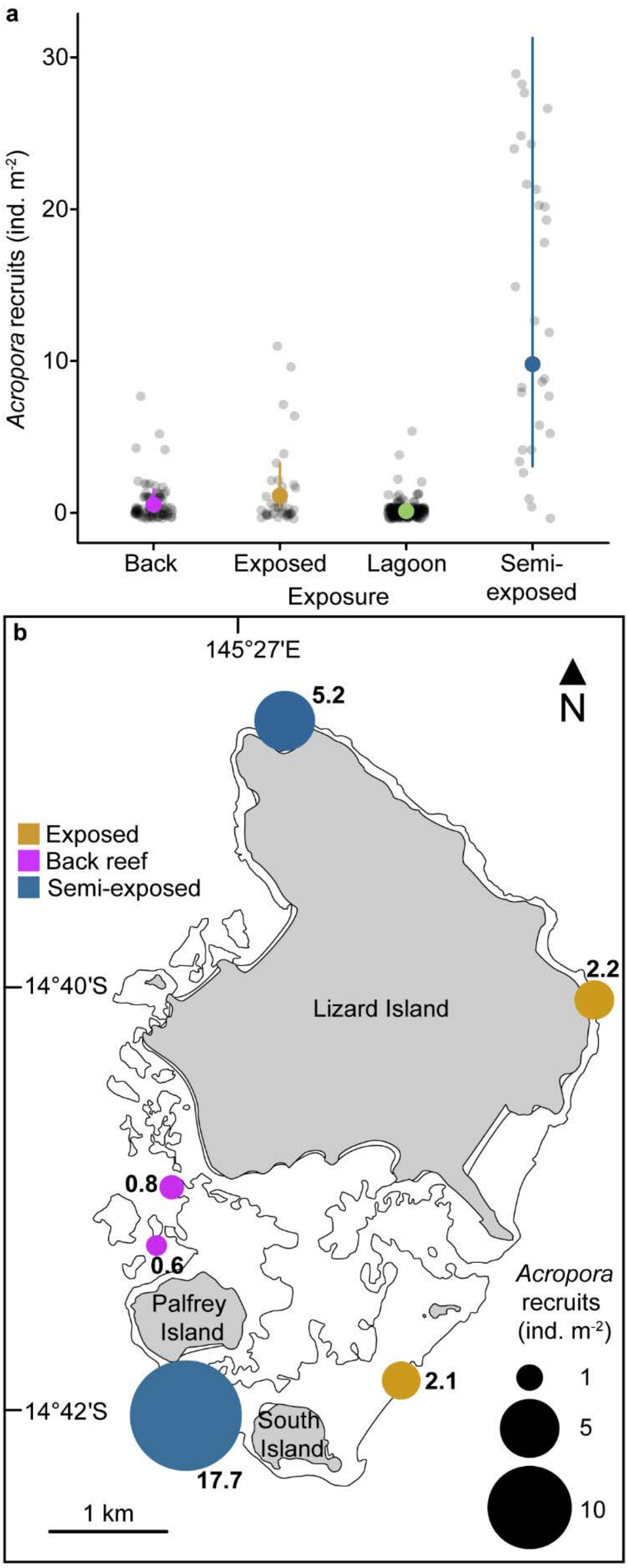

Figure 3.5 The spatial dynamics of *Acropora* recruitment around Lizard Island. a) The differences in *Acropora* recruitment among exposures revealed by a generalised linear mixed

effects model. The coloured dots and ranges denote the mean predicted fit (± 95% confidence intervals), while the grey dots denote the raw data points. b) Map of Lizard Island showing the distribution of *Acropora* recruits (the circles and adjacent numbers denote the mean density of recruits [individuals m^{-2}]). Only locations with mean recruit densities of >0.5 m^{-2} are shown. For the abundance of *Acropora* recruits in individual quadrats on each transect see Fig. B5 in Appendix B.

As for *Acropora* recruitment, the recovery of hard coral cover from January 2018 to January 2021 also diverged markedly among locations with different exposure regimes (Fig. 3.4), as initially indicated by the multivariate ordinations (Fig. 3.3). Specifically, there were significant increases in hard coral cover in back reef and exposed sites in the order of 40.6% and 82.4%, respectively (Fig. 3.4; Tables B2, B3 in Appendix B). However, this was negligible compared to hard coral cover dynamics on semi-exposed reefs, which increased by 616% from January 2018 to January 2021 (Figs 3.2d, e, f, 3.4; Tables B2, B3 in Appendix B). By contrast, there was no significant change in hard coral cover in lagoonal sites (Fig. 3.4; Tables B2, B3 in Appendix B). These increases in coral cover from January 2018 to January 2021 equate to an annual change in absolute cover of 0.9%, 1.5%, 0.3%, and 10% (to a total hard coral cover of 9.7%, 9.8%, 13.1% and 36% in January 2021) for back reef, exposed, lagoonal, and semi-exposed sites, respectively. It is important to note that the trajectories of coral cover described were the same at the individual transect scale and, generally, at the quadrat scales (see Fig. B4 in Appendix B), with increases predominantly being driven by increasing *Acropora* cover (Figs B2, B3 in Appendix B). Clearly, high *Acropora* recruitment occurred in the same exposure regime (semi-exposed reefs) where hard coral cover also increased the most from January 2018-January 2021 (Figs 3.4, 3.5).

Discussion

Coral reefs are facing a growing number and increasing intensity of disturbances, with stressors associated with climate change acting over the largest spatial scales (Bruno et al. 2019; Sully et al. 2019; McManus et al. 2020; Dietzel et al. 2021b). Indeed, the extent to which coral bleaching has affected coral communities (Berkelmans et al. 2004; Frade et al. 2018; Stuart-Smith et al. 2018; Hughes et al. 2019b, 2021) and recruitment (Hughes et al. 2019a) along the GBR are particularly well-documented. By tracking benthic dynamics in 349 quadrats around Lizard Island, I documented the local impact of coral bleaching in 2016. My findings on the effects of bleaching support previous studies from the GBR (e.g. Hughes et al. 2018b; Madin et al. 2018; Richardson et al. 2018; Stuart-Smith et al. 2018) and on many other coral reefs globally (e.g. Robinson et al. 2019a; Contreras-Silva et al. 2020; Babcock et al. 2021; Raj et al. 2021). Importantly, given the cumulative nature of recent disturbances to the northern GBR this led to the hypothesis that coral cover recovery and recruitment would be negligible at Lizard Island in the years immediately following these recent disturbances. Contrary to these expectations, I revealed significant levels of *Acropora* recruitment, and increases in hard coral cover, on some semi-exposed reefs at Lizard Island since January 2018. However, this finding must be set in the context of limited levels of *Acropora* recruitment and hard coral cover recovery across the lagoon and back reef sites and low total coral cover across these sites. In most locations where coral cover has remained static, benthic dynamics have been typified by consistently high cover of algal turfs.

Coral loss

In 2016 the northern third of the GBR was impacted by the most severe coral bleaching event recorded to-date on the GBR (Hughes et al. 2021). In 2017 the area was impacted by an even more severe heating event, resulting in the first record of mass bleaching events in consecutive years on the GBR (Hughes et al. 2019b). My results support previous studies in highlighting: a) the significant decline of live hard coral cover (an ~50% decrease) immediately post bleaching (Hughes et al. 2018b; Richardson et al. 2018; Stuart-Smith et al. 2018), and b) the minimal impacts of the 2017 bleaching event in the northern GBR despite more severe heating (Hughes et al. 2019b, 2021). It appears, the 2016 bleaching event was sufficiently severe to kill the majority of susceptible coral species, with negligible impacts of the second event on the few corals that remained. Notably, there was also bleaching at this location in 2020, however, the impacts again appear to have been minimal, potentially due to the fact that heating was more severe in the central and southern regions, rather than the northern region, of the GBR during 2020 (Hughes et al. 2021; Pratchett et al. 2021).

In terms of the spatial footprint of bleaching-mediated coral loss at my study locations, hard coral (and soft coral) loss was clearly highest, in absolute terms, in the lagoonal sites (Figs 3.3, 3.4 and Fig. B2 in Appendix B). This is probably a result of two principal factors. Firstly, reef morphology means that lagoons and other sheltered locations have restricted water circulation and longer water residency times (Lowe et al. 2009; Green et al. 2019). This morphology can afford a level of protection against disturbances such as tropical cyclones (depending on their trajectory) (Harmelin-Vivien 1994; Cuttler et al. 2018), but also it means that hot water can pool in these locations, potentially leading to more severe heating and coral bleaching (Jokiel and Brown 2004; Cowburn et al. 2019; Green et al. 2019; but see McClanahan et al. 2005; Safaie et al. 2018). As such, reef morphology and its interaction with hydrodynamics can underpin spatial heterogeneity in disturbance impacts on reefs.

Secondly, previous disturbances, especially tropical cyclones Ita and Nathan, that impacted my study location immediately prior to the onset of the sampling regime need to be considered. A previous study showed that these cyclones drove declines in coral cover of up to 90% on the exposed/semi-exposed reefs around Lizard Island (Madin et al. 2018). This was supported by the Australian Institute of Marine Sciences long term monitoring data which showed a clear decline in coral cover in exposed locations following the cyclone events (Fig. 3.1b). As such, there were few corals in these exposed and semi-exposed areas left to bleach by 2016 and this could explain why absolute coral loss in these locations was relatively low (although the bleaching event still reduced coral cover by a further 50% at these locations). By contrast, coral cover in the lagoon generally escaped the worst of the cyclone impacts (Madin et al. 2018), potentially leading to the higher absolute loss of coral cover in these locations in 2016.

It is important to note that these previous cyclone impacts could also explain why the extent to which bleaching in 2016 reduced coral cover at Lizard Island is relatively low (Fig. 3.4) compared to the wider northern region of the GBR during the same period (see Hughes et al. 2018b). Cyclones generally have a far smaller spatial disturbance footprint compared to bleaching events, with cyclone disturbances also impacting reefs in a more heterogenous manner compared to bleaching events (Dietzel et al. 2021b). This means that while coral cover at Lizard Island may already have been reduced by cyclones Ita and Nathan prior to the 2016 coral bleaching event, this situation was not the same across the entire northern GBR region, leading to the severe loss of coral at the regional level in 2016 due to coral bleaching (as documented in Hughes et al. 2018b). Overall, however, the cumulative nature of these disturbances clearly highlights the need to consider previous disturbance events when assessing the extent of coral loss on reefs (*sensu* Hughes et al. 2019b), and the widespread extent to which coral cover was reduced at Lizard Island from 2014 – 2017.

Coral recovery and recruitment dynamics

As for the loss of corals, there was a clear spatial footprint in short-term recovery of coral cover around Lizard Island, with a clear divergence in recovery capacity depending on the exposure of the reef locations. The substantial increase in absolute coral cover on semi-exposed reefs (10% year^{-1}), and negligible increase in the lagoon (0.3% year^{-1}) and back reefs (0.9% year^{-1}), is particularly notable as these values represent some of the highest and lowest rates, respectively, reported in the literature (Graham et al. 2011; Koester et al. 2020). Indeed, Graham et al. (2011) found that across 48 reef sites the global mean annual rate of change in absolute coral cover was 3.56% with a range of 0.13 - 12.49%. Similarly, the recruitment of *Acropora*, the genus of corals principally responsible for underpinning early coral recovery on Indo-Pacific reefs (Golbuu et al. 2007; Emslie et al. 2008; Linares et al. 2011; Johns et al. 2014; Roff 2021), also varied substantially, with individual 1 m^2 quadrats yielding from 0 up to 29 new *Acropora* colonies (Fig. B5 in Appendix B). Again, this recruitment was largely limited to semi-exposed locations with negligible *Acropora* recruitment in lagoons and back reefs (0 recruits in 83.9% of quadrats) despite surveying in January 2018, 2020 and 2021.

This divergence in recovery trajectories between locations in relatively close proximity (<100 m in some cases), is remarkable. While such habitat-dependent recovery has been documented previously (e.g. Connell et al. 1997; Golbuu et al. 2007; Gouezo et al. 2019; Moritz et al. 2021), other studies have found limited among-habitat differences in recovery (e.g. Morri et al. 2015; Koester et al. 2020), including the meta-analysis conducted by Graham et al. (2011). This variability in short-term recovery at Lizard Island, as well as in the existing literature, clearly highlights the context-dependent nature of coral recovery and has important implications for our understanding of the capacity for coral reefs to reassemble following cumulative disturbances.

From the patterns documented herein, it is clear that the greatest increases in coral cover occurred where the recruitment of *Acropora* was also highest (i.e. semi-exposed reefs). As in previous studies, this suggests that new coral recruits in this location are responsible for driving early recovery dynamics (Holbrook et al. 2018; Gouezo et al. 2019; Evans et al. 2020), rather than via regeneration and growth of existing corals (see Connell et al. 1997; Diaz-Pulido et al. 2009). A parsimonious explanation for these patterns, therefore, is that factors related to the supply of coral larvae, and subsequent settlement and survival of these larvae, probably underpinned the spatial patchiness in coral recovery dynamics (see Text B1 in Appendix B for further details). In this regard, the interaction between reef geomorphology and currents may be a key factor driving this among-exposure coral recovery heterogeneity. This is because currents bring new coral propagules to reefs (Wood et al. 2014; Gouezo et al. 2021) and as the currents predominantly interact with reefs around their windward perimeter at Lizard Island (Johansen 2014), this may maximise delivery of larvae to these areas. Furthermore, as currents frequently form eddies as they pass islands (Heywood et al. 1996; Wolanski et al. 2003), which concentrate coral larvae (Sammarco and Andrews 1988; Willis and Oliver 1990), it may be concluded that the semi-exposed sites are interacting with such eddies in a manner that facilitated high *Acropora* recruitment rates, as demonstrated in previous experiments on the GBR (Sammarco and Andrews 1988, 1989).

In addition to currents, other factors (beyond those considered in the supplemental examination see Text B1, Fig. B6 in Appendix B) may also have contributed to heterogenous *Acropora* recruitment around Lizard Island. For example, if corals settle soon after finding a suitable settlement area, and as semi-exposed/exposed reefs often have favourable settlement conditions (high CCA cover and low algal turf sediment loads [Harrington et al. 2004; Birrell et al. 2008; Speare et al. 2019; Ricardo et al. 2021]), it may be that the vast majority of corals settled in semi-exposed and exposed reef areas before the coral propagules ever filtered through to the more sheltered reef habitats. This factor may be particularly important in driving heterogeneity in this context considering that the number of *Acropora* propagules around Lizard Island was likely to be relatively low (Hughes et al. 2019a). It could also be that the numbers of coral propagules that make it through to lagoonal and back reef areas were further depleted by predation. Planktivorous fishes have been documented to feed on coral propagules (Pratchett et al. 2001), with prior evidence that such fishes can form a 'wall-of-mouths' that significantly depletes planktonic resources around reefs (Hamner et al. 1988). Even after the significant coral loss, many planktivorous fishes remained relatively abundant in the lagoons and back reef habitats around Lizard Island (Wismer et al. 2019a, 2019b), as well as on off-reef slopes (Morais and Bellwood 2019; Valenzuela et al. 2021). This may have been due to a greater propensity for behavioural flexibility than expected, as well as the fact that structures remained largely intact over short-term temporal scales (for details see Wismer et al. 2019a, 2019b). However, regardless of the exact mechanisms, although heterogenous, there has been a marked recovery of coral cover as well as relatively high *Acropora* recruitment at some locations around Lizard Island following cumulative disturbance by cyclones and bleaching events.

The fact that there has been a notable degree of coral recovery and *Acropora* recruitment at any location at all around Lizard Island is interesting given that coral recruitment following bleaching was previously reported to have collapsed along the GBR, especially around Lizard Island (Hughes et al. 2019a). Indeed, in 2017 and 2018 coral recruitment onto recruitment tiles at Lizard Island was reported to be just 1% and 3.2%, respectively, relative to pre-2016 bleaching recruitment rates (Hughes et al. 2019a). However, there are two primary reasons why my results differ from, and extend, those of Hughes et al. (2019a). Firstly, it is important to consider the temporal timing of the two studies. The most recent recruitment event quantified by Hughes et al. (2019a) was that which occurred across 2017/2018 (i.e. recruitment tiles were deployed in November 2017 and retrieved in January 2018). This aligns with the first year that I started recording *Acropora* recruits in my quadrats (i.e. January 2018). In this year I only documented 26 recruits across the entire 349 m^2 area censused. This supports the conclusions of Hughes et al. (2019a) as coral recruitment appeared to be extremely low at this location from 2016 to 2018. However, I also recorded recruits in January/February 2020 (466 new recruits documented) and 2021 (64 new recruits documented). As such, it appears that the major *Acropora* recruitment event at Lizard Island, in my dataset, occurred after the study by Hughes et al. (2019a) ended. Probably in the austral summer months of 2018/2019 given the size of recruits when they could be detected in my study. This lack of temporal overlap between studies may therefore be a major factor explaining any differences in the findings between the two studies.

The second factor that could have contributed to any differences in conclusions between my study and that of Hughes et al. (2019a) is how ‘recruits’ were quantified. Hughes et al. (2019a) used artificial recruitment tiles to quantify the abundance of settling coral larvae. By contrast, I counted the number of new *Acropora* colonies that ‘recruited’ to my specific censused areas. My recruits had successfully settled onto the reef substratum and survived the various immediate post-settlement bottlenecks, which can hinder coral survival at this life stage (Jones et al. 2015; Doropoulos et al. 2016). Importantly, a recent study by Evans et al. (2020), on reefs off Western Australia, revealed that there is little concordance between coral recruitment to tiles and juvenile coral densities on the substratum (i.e. my ‘recruits’). Indeed, Evans et al. (2020) found that coral recruitment to settlement tiles was not a good predictor of coral recovery. However, juvenile acroporid densities were found to be a good indicator of coral cover recovery in future years (Evans et al. 2020). This finding aligns remarkably well with my results from Lizard Island. This lack of a relationship between coral recruitment to tiles and recruitment to, and survival on, natural reef substrata may, therefore, have resulted in differences in the results of my study and those of Hughes et al. (2019a). This highlights the value, and complementary nature, of large scale macroecological studies and high-resolution examinations of individual reef systems.

It is also important to note that despite documenting some recovery and recruitment at specific locations around Lizard Island my results should be considered within the context of future disturbance regimes. Given that the frequency and severity of disturbances to coral reefs is set to increase in the future (Cheal et al. 2017; Hughes et al. 2018a; Sully et al. 2019) with the median return time between severe coral bleaching events on reefs now being just 6 years (Hughes et al. 2018a) then this is far shorter than the decade-long timeframe that previous studies have suggested is needed for the fastest growing coral assemblages to recover (Connell et al. 1997; Johns et al. 2014; Osborne et al. 2017; Romero-Torres et al. 2020). This point was highlighted by the fact that the 'recovering' corals in my quadrats were already exhibiting early stages of bleaching again in January 2021 during the last sampling period (Fig. 3.2f). This means that in semi-exposed reef habitats at Lizard Island where I documented significant levels of recovery over very short timeframes there was also the potential for rapid repeat bleaching. This is likely to facilitate boom and bust coral cover dynamics in this habitat (cf. Wilson et al. 2019; Pratchett et al. 2020; Morais et al. 2021a). By contrast, the lack of recovery and recruitment across the lagoon and back reefs may mean that these areas at Lizard Island have a limited capacity for regeneration before the next major disturbance and could remain dominated by the alternative benthic space holders that have succeeded following coral mortality. Boom and bust coral dynamics vs coverage by alternative space holders may represent spatially separated alternative conditions on future reefs (cf. Morais et al. 2021a).

The constancy of algal turfs

Despite the different dynamics of coral loss and recovery between locations in the current study, there was one overwhelming constant across all locations: the abundance of algal turfs. At all sampling time points, coverage generally exceeded 50% (Fig. 3.4). Importantly, this phenomenon is not just limited to Lizard Island, with similarly high levels of algal turf cover (>40-50%) reported from many other reef areas globally (Chapter 2) (Smith et al. 2016; Jouffray et al. 2019; Kennedy et al. 2020; Cannon et al. 2021), especially after coral bleaching events (Gilmour et al. 2013; Emslie et al. 2019; Koester et al. 2020). Moreover, this is not just a recent phenomenon, as the AIMS data highlighted that algal cover (principally composed of algal turfs in this area) already covered >50% of the benthos back to 1993 (Fig. 3.1b). This notion is supported by previous studies on other reefs during the latter half of the 20th century (e.g. Marsh 1976; Adey and Steneck 1985; Klumpp and McKinnon 1989; Adey 1998). The data herein, and previous literature, therefore, suggest that algal turfs can be the most abundant benthic covering on reefs, with this dominance potentially set to increase further as the loss of coral cover on reefs continues.

Conclusions

Lizard Island has endured consecutive cyclones and consecutive coral bleaching events in recent years. The latter resulted in widespread coral mortality and a collapse in coral recruitment across 1400 km of the GBR (Hughes et al. 2019a, 2019b). Yet Lizard Island, located at the centre of these disturbances, demonstrated that some recovery in hard corals was still possible over short time frames, even in the years immediately following disturbance. Indeed, I found that significant increases (>600%) in early successional coral cover occurred on semi-exposed reefs, driven primarily by recruitment of *Acropora*.

However, while I document that high rates of recovery are possible on a reef that has experienced consecutive severe cyclones and consecutive coral bleaching, it is important to note that this recovery was far from spatially homogenous. No detectable recovery in hard coral cover occurred across large expanses of reef area (in this case the entire lagoon at Lizard Island) reflecting an apparent failure of a chief recovery mechanism: *Acropora* recruitment. Recovery in these lagoonal areas may only occur on temporal scales exceeding those of the current study, or once local stock-recruitment dynamics recover. As such, the future of these lagoonal reefs is likely to be highly dependent on future disturbance regimes. Given that algal turfs already cover >50% of the benthos around Lizard Island, it appears likely that the future of these reefs could be one typified by high algal turf cover. In a world where the impacts of global climate change continue to operate, we may increasingly be working with algal turf-covered reefs with spatially patchy recovery of corals between disturbances.

Chapter 4: Algal turf sediments on coral reefs: what's known and what's next

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Abstract

Algal turfs are likely to rise in prominence on coral reefs in the Anthropocene. In these ecosystems the sediments bound within algal turfs will shape ecosystem functions and the services humanity can obtain from reefs. However, while interest is growing in the role of algal turf sediments, studies remain limited. In this review I provide an overview of our knowledge to-date concerning algal turf sediments on coral reefs. Specifically, I highlight what algal turf sediments are, their role in key ecosystem processes, the potential importance of algal turf sediments on Anthropocene reefs, and key knowledge gaps for future research. The evidence suggests that the management of algal turf sediments will be critically important if we are to sustain key functions and services on highly-altered, Anthropocene coral reef configurations.

Introduction

In the wake of increasing anthropogenic disturbances, marine ecosystems have changed profoundly (Wernberg et al. 2016; Hughes et al. 2017a; Vergés et al. 2019). In many cases these disturbances have driven a loss of canopy forming foundation organisms (Airoldi and Beck 2007; Wernberg et al. 2016; Hughes et al. 2018b; O'Brien and Scheibling 2018; Wismer et al. 2019a), and a rise in the coverage of algal turfs (Chapters 2 and 3) (Goatley and Bellwood 2011; Jouffray et al. 2015; Filbee-Dexter and Wernberg 2018; Feehan et al. 2019)

(Fig. 4.1). This has been epitomised on the world's coral reefs which have now undergone three global-scale coral bleaching events (Hughes et al. 2018a; Bruno et al. 2019). Indeed, the effects of climate change are now interacting with a myriad of other stressors, including terrestrial sediment inputs (Fabricius 2005; Ban et al. 2014; Bainbridge et al. 2018) and overfishing (Jackson et al. 2001; Graham et al. 2017), on coral reef ecosystems. Many coral reefs now exist in a coral depauperate state (Fig. 4.1c-f) (Chapter 2), with some punctuated by periods of apparent recovery or by transitions to alternative states (Chapter 3) (Bruno et al. 2019; Gilmour et al. 2019; Mellin et al. 2019; Wilson et al. 2019).

Following the trajectory outlined above, herein I posit that 'Anthropocene' (i.e. human modified) coral reefs will be characterised by lower coral cover, lower topographic complexity, and an increasing abundance of algal turfs (following Bellwood et al. 2019b, 2019a) and based on results in Chapters 2 and 3) (Fig. 4.1c-f). On these Anthropocene coral reefs the relative importance of ecosystem processes are in a state of flux (Hughes et al. 2017a; Bellwood et al. 2019b). In particular, the increasing prevalence of algal turfs has brought to the fore the capacity of sediments, when interacting with algal turfs, to shape reef processes such as herbivory and coral settlement (Birrell et al. 2005; Goatley et al. 2016; Duran et al. 2018; Fong et al. 2018; Tebbett et al. 2018a). This is because, after climate change, increasing sediment inputs/declining water quality is one of the most pervasive stressors faced by coral reefs (McCulloch et al. 2003; Bainbridge et al. 2012; Erftemeijer et al. 2012; Jones et al. 2019), with more than 50% of the world's reefs at risk (Burke et al. 2011). Importantly, algal turfs readily trap and accumulate these sediments (Gordon et al. 2016a; Tebbett et al. 2020c), and can represent the major reservoir of sediments on coral reefs (the off-reef sediment apron notwithstanding) (Latrille et al. 2019). As such, algal turfs represent a critical interface where sediments can impact reef organisms and reef processes.

However, while sediment impacts on coral reefs have been the focus of a substantial body of literature (reviewed in Rogers 1990; Fabricius 2005; Erftemeijer et al. 2012; Jones et al. 2015; Wenger et al. 2017; Bainbridge et al. 2018), this has largely focused on turbidity and water quality. By contrast, our understanding of algal turf sediments on coral reefs is still in its infancy but it appears to be a burgeoning research field. To engender further growth, this review will focus on providing an overview of our knowledge concerning algal turf sediments on coral reefs to-date. In doing so, I will highlight what algal turf sediments are, their roles in ecosystem processes, their importance on Anthropocene coral reefs, and key knowledge gaps for further research.

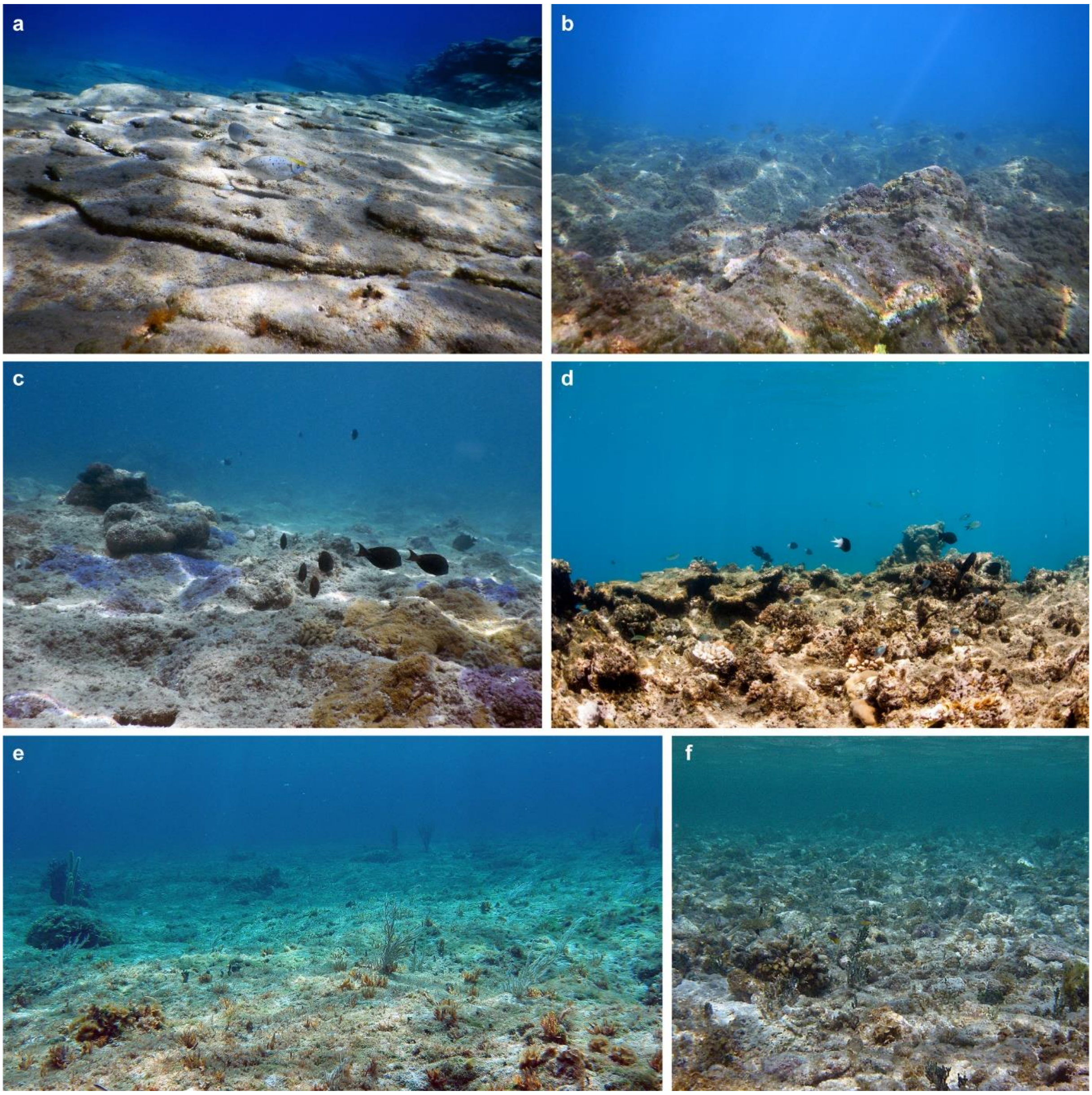

Figure 4.1 Low-complexity algal turf-covered a), b) subtropical rocky reefs off Crete in the Mediterranean, c), d) coral reefs around Lizard Island on the Great Barrier Reef, and e), f) coral reefs in the Caribbean off e) Little Cayman Island, and f) Carrie Bow Cay. Photographs were taken in a-d) 2018, e), 2005, and f) 2004. Photographs by a), e), f) D.R. Bellwood, b), c) S.B. Tebbett, d) V. Huertas.

Defining algal turf sediments

What are algal turfs?

Herein, I consider algal turfs to be the short (<2 cm), multispecies assemblage of generally filamentous macroscopic algae that cover the hard substratum on coral reefs (for further detail see Steneck and Dethier 1994; Fong and Paul 2011; Connell et al. 2014). It should be noted that past studies have included non-algal taxa (i.e. cyanobacteria) in their definition of algal turfs (e.g. Borowitzka et al. 1978; Larkum et al. 1988), however, for clarity cyanobacteria are considered separately. Algal turfs are often the most abundant benthic covering on coral reefs (Chapters 2 and 3) (Vroom et al. 2006; Wismer et al. 2009; Jouffray et al. 2015; Smith et al. 2016; Arias-González et al. 2017), especially following disturbances when their coverage under coral canopies is revealed (Goatley and Bellwood 2011) and early successional forms readily colonise dead coral skeletons following primary colonisation by cyanobacteria (which colonise within days) (Diaz-Pulido and McCook 2002; Arthur et al. 2005; Houk et al. 2010). Furthermore, algal turfs are remarkably productive (Wanders 1977; Carpenter 1985; Hatcher 1988; Klumpp and McKinnon 1992; Steneck 1997) and can support key trophic pathways on reefs, e.g. energy flows up the food chain through herbivorous fishes (Russ 2003; Kelly et al. 2017; Bellwood et al. 2018). However, they are also heterogeneous across multiple spatial (Scott and Russ 1987; Harris et al. 2015) and temporal scales (Diaz-Pulido and McCook 2002), and have been referred to under a number of different terms in the coral reef literature (see Connell et al. 2014).

During the 1980s-90s the term 'epilithic algal community' (EAC) was frequently used when describing algal turfs on coral reefs, to recognise that these were far more than a homogenous benthic covering and were a diverse community (e.g. Hatcher and Larkum 1983; Russ 1987; Klumpp and McKinnon 1989; Purcell 1996). This term morphed into the 'eplithic algal matrix' (EAM) in the late 90s (Wilson and Bellwood 1997) and has been used frequently in the literature since (e.g. Wilson et al. 2003; Rasher et al. 2013; Heenan et al. 2016; Tebbett et al. 2017c; McAndrews et al. 2019). The term EAM was coined to recognise the importance of other non-algal turf constituents within the matrix including organic detritus, inorganic sediments, microalgae and microbes [inc. cyanobacteria] (Wilson and Bellwood 1997). Similarly, the term 'turf algal sediment mats' (TAS mats) has been used in reference to reefs in the Atlantic to recognise the condition of algal turfs when they become laden with sediments (e.g. Roy 2004; Rodríguez-Martínez et al. 2011; Lacey et al. 2013; Shantz et al. 2015). Also in the Caribbean, the term 'hardpan' has been used to describe a coral reef state typified by a covering of sediment-laden algal turfs (Bellwood and Fulton 2008). More recently, the terms 'short productive algal turfs' (SPATs: ~ <5 mm and relatively sediment-free algal turfs) and 'long sediment-laden algal turfs' (LSATs: ~ >5 mm algal turfs that are laden with sediments) were coined to explicitly recognise a fundamental division in the nature of algal turfs, separating those with low sediment loads from those with high sediment loads (Goatley et al. 2016) (Fig. 4.2). The evolution of these definitions highlights the increasing importance placed on sediments contained within the algal turfs.

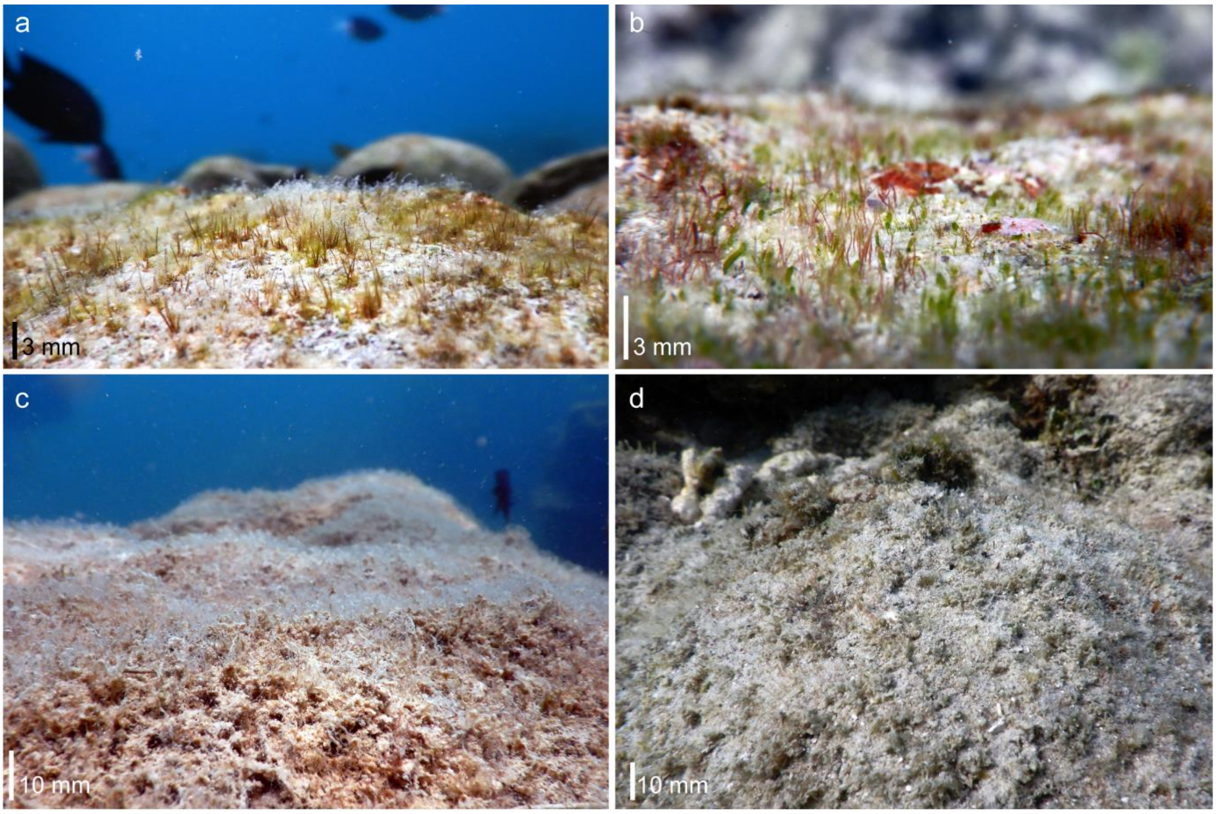

Figure 4.2 a, b) Short productive algal turfs (SPATs), note the lack of sediment (photographs R.P. Streit). c, d) Long sediment-laden algal turfs (LSATs) (S.B. Tebbett). Scale bars are approximate.

What are algal turf sediments?

Algal turf sediments are inorganic particulate material <2 mm (sands, silts and clays; ISO 14688-1:2017) bound within algal turfs on coral reefs (Goatley 2013; Tebbett et al. 2017c). However, the term 'sediments', when used in reference to algal turfs, has also been applied to all inorganic material in algal turfs including pieces >2 mm (e.g. Purcell 2000; Bellwood and Fulton 2008; Goatley and Bellwood 2012; Goatley et al. 2012), as well as both inorganic and organic particulate material combined, especially when only sediment depth is recorded (e.g. Goatley and Bellwood 2013; Clausing et al. 2014; Duran et al. 2018; Eurich et al. 2018; Fong et al. 2018). It should also be noted that the working definition of 'inorganic sediments' includes living organisms such as endolithic, microboring organisms that can be contained within inorganic calcareous sediments (e.g. Perry 1998). The organic particulate component of the benthic particulate mix within the EAM is defined more broadly as 'detritus', with a commonly used working definition of detritus being: non-living organic particulate material that is also likely to contain life in the form of microbes (for a comprehensive review of coral reef detritus see Wilson et al. 2003). The term 'benthic particulates' has been applied to both the organic and inorganic components when summed together, recognising this amalgamation (Tebbett et al. 2017b, 2018b). Clarity of terms and distinction amongst inorganic sediments and organic components of the particulate mixture is necessary to assess: a) the different effects of each component on ecosystem processes (Birrell et al. 2005; Gordon et al. 2016b; Tebbett et al. 2017b), and b) how organisms can utilise components. For example, the organic detrital and microbial component can represent a critical nutritional resource that is specifically targeted by a wide range of fishes (Robertson and Gaines 1986; Crossman et al. 2001; Choat et al. 2002; Wilson et al. 2003; Max et al. 2013).

Furthermore, algal turf sediments *sensu stricto* can be composed of both carbonates and silicates (Gordon et al. 2016a; Tebbett et al. 2018b; Latrille et al. 2019). The carbonate component is largely derived from the on-reef production of sediments via mechanisms such as bioerosion (Hutchings 1986; Bellwood 1996; Yarlett et al. 2018) and the physical breakdown of skeletal remains of calcifying organisms (Scoffin 1992; Fujita et al. 2009). By contrast, the siliceous component is largely derived from terrestrial sources (Goatley et al. 2016; Gordon et al. 2016a), and can be composed of 'new' sediments (i.e. recently deposited sediments from terrestrial runoff and river plumes) or 'old' sediment (i.e. settled sediments that have been resuspended and transported to reefs) (Wolanski et al. 2008; Orpin and Ridd 2012; Fabricius et al. 2014; Lewis et al. 2014; Bainbridge et al. 2018). In general, the different types of sediment have different characteristics including their density, association with organic material, size and ability to adsorb nutrients (Lutgens and Tarbuck 2006; Gordon et al. 2016a; Bainbridge et al. 2018). With the composition and amount of sediments being trapped in algal turfs depending on a range of factors including local sediment inputs (Browne et al. 2013; Tebbett et al. 2018b), reef geomorphology (Hopley et al. 2007; Tebbett et al. 2017c), hydrodynamics (Carpenter and Williams 1993; Purcell 2000; Bodde et al. 2014) and the feeding activity of fishes (Hoey and Bellwood 2008; Goatley and Bellwood 2010; Krone et al. 2011). While algal turf sediments can be disparate in terms of their composition, they can all generally be defined as inorganic particulate material <2 mm that reside within algal turfs.

How do sediments become algal turf sediments?

The diffusive boundary layer formed by the complex structure of algal turfs can slow water movement and is the predominant mechanism that facilitates the deposition and accumulation of sediments in algal turfs (Carpenter and Williams 1993; Latrille et al. 2019). In addition, this process is likely to be supplemented by other factors, such as the secretion of mucilaginous sheaths by filamentous cyanobacteria within the EAM which can bind sand particles together (Stal 2003). As such the EAM as a whole, and algal turfs in particular, appear to have a particularly remarkable propensity to accumulate and retain sediments. For example, algal turf sediments can accumulate to reach ambient levels following clearing in a matter of days (Tebbett et al. 2018a), and once trapped these levels can remain remarkably stable over 6 month-long temporal scales (Gordon et al. 2016a). Moreover, Latrille et al. (2019) highlighted that over a week-long period, algal turfs accumulated far more sediment than artificial sediment traps, which have previously been criticised for their excessive trapping abilities (Storlazzi et al. 2011). Unfortunately, while we know algal turfs can readily accumulate sediments and are likely to play a key role in sediment dynamics, our understanding of the links between suspended sediments, sediment input rates and algal turf sediment accumulation are relatively limited.

Recently, Latrille et al. (2019) began to place algal turf sediments into the context of suspended sediments and sedimentation. Latrille et al. (2019) highlighted that lateral accumulation of sediments was limited, and accumulation appeared to be driven primarily by direct deposition by parrotfishes and deposition of suspended sediments (including local resuspension from nearby 'sediment-saturated' algal turfs). Furthermore, Whinney et al. (2017) revealed that sedimentation rates were higher following turbidity peaks, however, the nature of the relationship was complex and varied across temporal scales due to factors such as wind speed and tidal phase. However, apart from these two studies, our understanding of links between algal turf sediments, sedimentation, and suspended sediments remains limited.

Quantification and distribution of algal turf sediments

How do we quantify algal turf sediment characteristics?

Algal turf sediments can be quantified directly in several ways including by depth (Goatley and Bellwood 2013; Clausing et al. 2014; Adam et al. 2018), coverage (Ceccarelli et al. 2005; Duran et al. 2018; Eurich et al. 2018) and mass (Purcell 2000; Rasher et al. 2012; Gordon et al. 2016a; Tebbett et al. 2017c). The exact method employed depends on the nature of the question being addressed and the level of detail required. As the properties of algal turf sediments can differ markedly depending on their composition and size (Gordon et al. 2016a; Latrille et al. 2019), the different methods vary in their ability to quantify different aspects.

The two most frequently used methods in the literature are depth measurements and underwater vacuum sampling for collection and mass analysis. Sediment traps are not included as they have a limited capacity to quantify algal turf sediments (Latrille et al. 2019). Each is outlined in detail below.

In-situ sediment depth and algal turf length measurements are non-destructive, fast and inexpensive to perform. Such measurements can indicate the nature of the algal turfs and the quantity of sediments they contain (i.e. SPATs vs LSATs; *sensu* Goatley et al. 2016), and can be readily employed in experimental scenarios to monitor changes in algal turf length (Goatley and Bellwood 2013; Tebbett et al. 2017d; Fong et al. 2018). For example, sediment depth and/or algal turf length can be measured using the depth probe of vernier callipers, which yields the same distance as between the tips of the callipers (Fig. 4.3a, b, e). This distance is then recorded by pressing the tips of the callipers into saltwater-resistant pressure-sensitive poster adhesive (blu tack) (Fig. 4.3c, f), which can then be measured more accurately in the laboratory using digital callipers. However, while fast and non-destructive, depth measurements only provide limited information on the sediments with no detail on the composition or size. Furthermore, as sediments can have different depths depending on their size and density (e.g. Gordon et al. 2016a; Latrille et al. 2019), depth and mass estimates are not necessarily comparable. If more detailed measures are required, depth measurements can be combined with sediment collection.

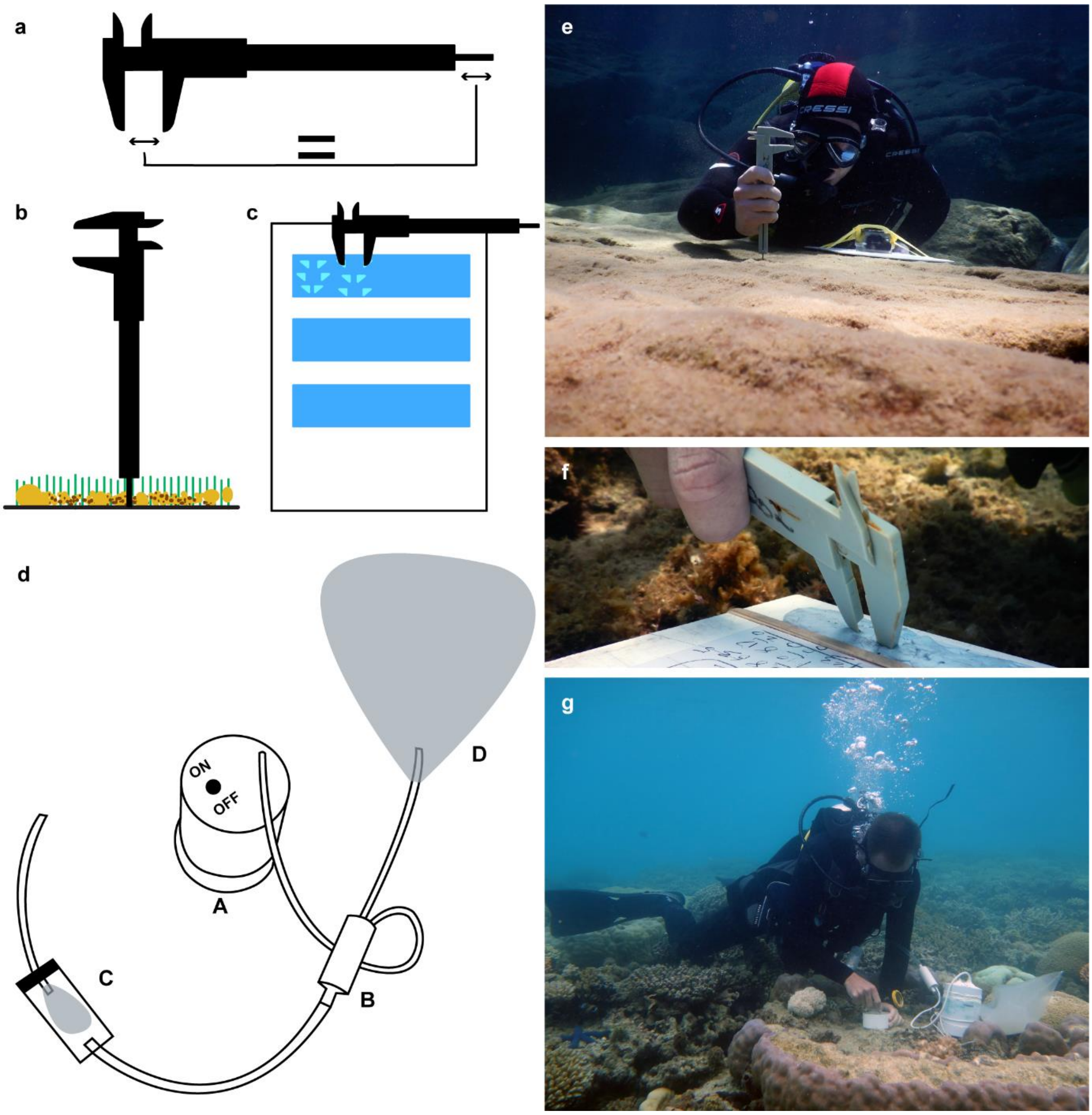

Figure 4.3 A schematic diagram showing the tools that can be used to quantify algal turf sediments. a) The depth probe of callipers is the same as the length between the tips, b) this depth probe can be used to examine algal turf filament length and/or sediment depth, and c) these measurements can be quickly recorded underwater in 'blu tack' for later quantification in the lab. d) a small handheld underwater vacuum sampler is composed of: A – a waterproof housing containing the battery, controlled by a toggle switch to provide power to B – a small inline water pump. The impellor in the water pump is protected by C – a container that holds a filter (~250 µm plankton mesh) that traps coarse sediments which are retained. Finer

sediments pass through the filter and are retained in D – a plastic bag (~5 L). B, C and D are all connected with clear vinyl tubing. e), f) S.B. Tebbett measuring algal turf length using the methods described above, and g) sampling algal turf sediments using an electronic vacuum sampler (photographs e], f]: D.R. Bellwood, g]: R.P. Streit).

Small underwater vacuum samplers (Fig. 4.3d, g), are frequently used for collecting sediments, organic detritus, and algal material from the substratum on coral reefs (e.g. Purcell 1996; Crossman et al. 2001; Kramer et al. 2012; Max et al. 2013; Kelly et al. 2017; Tebbett et al. 2017c). These samplers can remove all particulate material from the algal turfs for more detailed processing and scraping tools can be fitted to remove the algal turfs themselves (for detailed methods see Purcell 1996). The collected particulates can then be processed to yield information including depth, mass, inorganic vs organic ratios, silicate vs carbonate content, grain size distributions (using sieves or laser diffraction analysis) and nitrogen fractionation (Purcell 2000; Weber et al. 2006; Gordon et al. 2016a; Judy et al. 2018; Latrille et al. 2019). These indices can then be related to other properties of algal turfs such as length and biomass (Purcell 2000; Purcell and Bellwood 2001), yielding insights into local algal turf sediment dynamics (Goatley et al. 2016; Gordon et al. 2016a; Latrille et al. 2019).

It should be noted that attempts have been made to quantify algal turf sediments through more indirect methods such as sediment traps (for an overview see Storlazzi et al. 2011), SedPods (for an overview see Field et al. 2013), and TurfPods (for an overview see Latrille et al. 2019). However, preliminary evidence suggests that such methods provide only a partial, and in some cases, unrepresentative insight into the nature of algal turf sediments (for a detailed comparison of all methods see Latrille et al. 2019). Such methods are designed to quantify other aspects of sediment dynamics on coral reef, rather than algal turf sediments.

If working on algal turf sediments, the most accurate method is probably to quantify them directly.

Quantities and distribution of algal turf sediments

Algal turfs can represent the major reservoir of sediments on coral reefs (not including the off-reef sediment aprons) (Latrille et al. 2019). This is because algal turfs can contain far higher sediment levels than those accumulated on corals or suspended in the water column (Latrille et al. 2019). However, algal turf sediment loads can vary markedly, ranging from 10s of g m^{-2} to 1000s of g m^{-2} and from <1 mm to ~20 mm depth (Purcell 2000; Bellwood and Fulton 2008; Clausing et al. 2014; Tebbett et al. 2018b) (Fig. 4.4). This variability is exemplified across the continental shelf of Australia's Great Barrier Reef (GBR) with coastal reef crests containing average sediment loads up to 3681.8 ± 713.7 g m^{-2}, while sediment-depauperate mid-shelf reef crests can maintain average loads as low as 63.8 ± 19.4 g m^{-2} (Fig. 4.4a). The composition of sediments also varies across large scales. Reefs closer to shore generally have higher levels of siliceous sediments and, as expected, levels decrease with distance from the coast (Gordon et al. 2016a; Tebbett et al. 2018b).

At smaller, within-reef scales, algal turf sediment loads vary consistently among habitats (Fig. 4.4b). Low sediment loads occur on high-energy reef crests, while higher sediment loads accumulate in lower-energy reef slope and flat habitats (Purcell 2000; Gordon et al. 2016a) (Fig. 4.4b). Indeed, average sediment levels over 8000 g m^{-2} have been reported from the reef flat at Lizard Island, Australia (Goatley and Bellwood 2012). In addition to the amount of sediment, other metrics such as the grain size distribution (finer sediments occur in lower-energy habitats) and relative detrital levels (higher proportions of detritus are found on the reef crest) differ markedly among habitats (Purcell and Bellwood 2001; Gordon et al.

2016a; Tebbett et al. 2017c). Within reef habitats algal turf sediment loads can also be heterogenous due to fine scale factors such as fish feeding patterns (Goatley and Bellwood 2010) or structural complexity (Duran et al. 2018; Tebbett et al. 2020c). Clearly algal turf sediments vary at multiple spatial scales, but often in a predictable manner (i.e. regardless of the reef they generally decrease with distance from shore and are lowest on high-energy reef crests [Fig. 4.4]).

The predictable gradients in algal turf sediment loads may underpin other important ecological gradients on coral reefs especially in organisms that associate closely with algal turfs, e.g. herbivorous fishes and scleractinian corals. In the case of herbivorous fishes for example, species abundance, biomass and richness are frequently correlated with water quality gradients (e.g. Cheal et al. 2013; Moustaka et al. 2018). However, these correlations are more likely to be explained by gradients in algal turf sediment loads, which have a marked propensity to alter herbivorous fish feeding behaviour and potentially, therefore, their long-term persistence (outlined below) (also see Chapter 9). As such, while water quality gradients might be correlative, algal turf sediment gradients might offer a more plausible mechanistic basis for some observed ecological gradients.

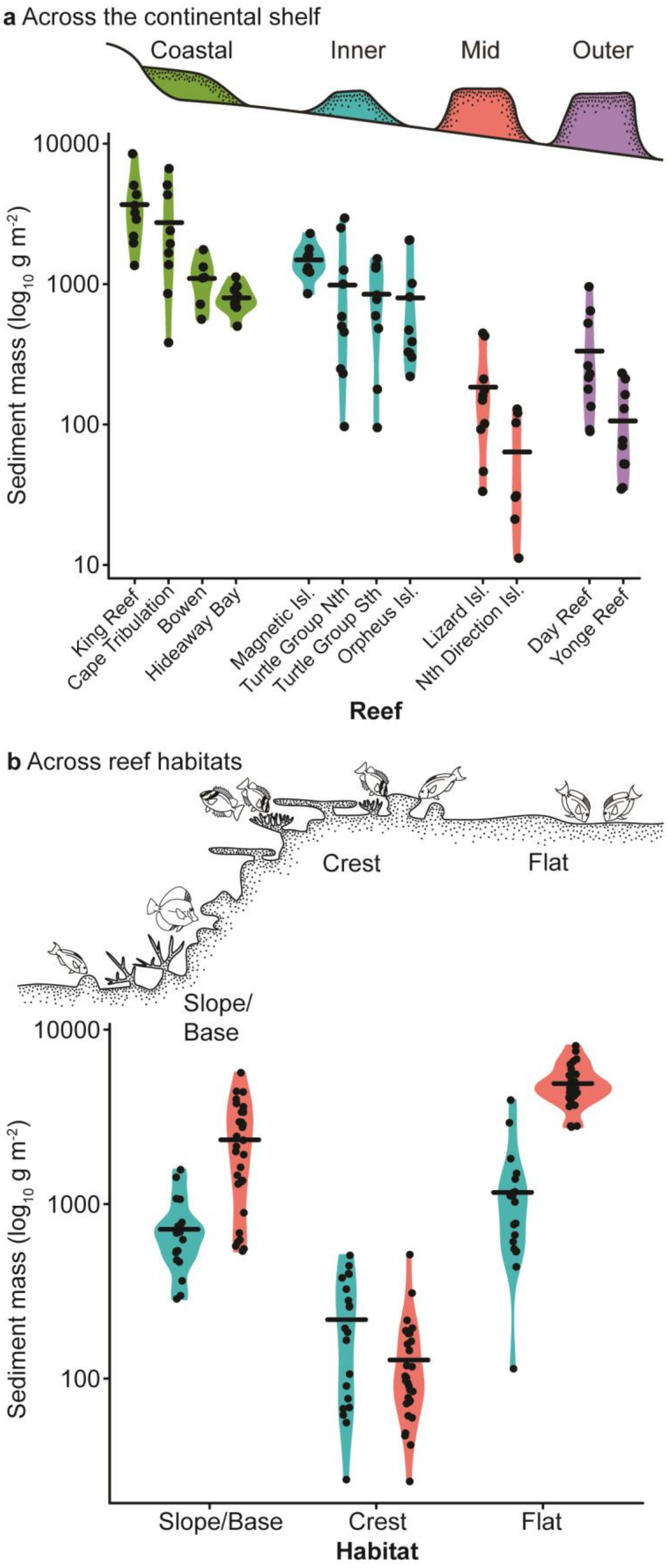

Figure 4.4 Sediment loads in algal turfs at different spatial scales a) on reef crests across the continental shelf of the Great Barrier Reef, Australia, and b) across different reef habitats on

an inner-shelf (Orpheus Island [turquoise]) and a mid-shelf (Lizard Island [orange]) reef, from the Great Barrier Reef. Note the consistent patterns of algal turf sediment loads among a) different reefs in the same shelf positions, or b) habitats between different reefs. Also note that the y-axis is logged in both cases. Cross-bars indicate the means. Data were sourced from Purcell (2000), Goatley et al. (2016), Gordon et al. (2016a) and Tebbett et al. (2017c, 2018b). Isl. = Island.

Sediment effects on coral reef organisms

Overview

Intuitively, algal turf sediments appear to primarily affect coral reef taxa that closely associate with the benthos, e.g. algae, nominally herbivorous fishes, and corals. Indeed, these three broad taxonomic groups have been the basis of most research to-date concerning algal turf sediments on coral reefs and will be the focus of this section. However, preliminary results have highlighted that algal turf sediments can influence the distribution patterns, and/or feeding behaviour of a suite of reef taxa including crytofauna (Logan et al. 2008; Kramer et al. 2012), invertebrate grazers (Sangil and Guzman 2016; Tebbett et al. 2018a), turtles (Goatley et al. 2012), and probably even microbes within algal turfs (Bourne et al. 2016; Zaneveld et al. 2016; Meirelles et al. 2018).

The primary mechanism underpinning the effects of algal turf sediments on coral reef organisms appears to be the positive association between algal turfs and algal turf sediments (Fig. 4.5). Algal turf sediments can release algal turfs from intense grazing pressure, with a positive relationship occurring between algal turf length and algal turf sediment load on coral reefs (Purcell 2000; Purcell and Bellwood 2001; Bonaldo and Bellwood 2011; Gordon et al.

2016a) (Fig. 4.5b). This correlation is due to either a) longer algal turfs developing first and trapping more sediment (Latrille et al. 2019), or b) algal turf sediments initially accumulating more sediments leading to less herbivory resulting in longer algal turfs and further sediment trapping (Goatley and Bellwood 2013; Goatley et al. 2016), or both. LSATs therefore develop as a result of a positive feedback as the increase in sediments leads to a decrease in herbivory, with resulting increases in algal turf length further increasing sediment trapping and decreasing herbivory. It is these long sediment-laden algal turfs (LSATs) that appear to have the largest effect on coral reef taxa (see below).

How do algal turf sediments affect algae?

Coral reef algae are frequently grouped together in three broad functional groups (crustose coralline algae [CCA], macroalgae and algal turfs) (see Steneck and Dethier 1994). As these functional groups are united based on morphological similarities, they are affected by algal turf sediments to various extents and in different ways. This was initially conceptualised by Steneck (1997) who highlighted the success of algal turfs, over other algal functional groups, when algal turf sediments are abundant (Fig. 4.5a). By contrast, CCA and macroalgae are more prolific in conditions where algal turf sediments are not as high (Steneck 1997) (Fig. 4.5a). This functional group approach is maintained herein to highlight the key effects of algal turf sediments on each group separately.

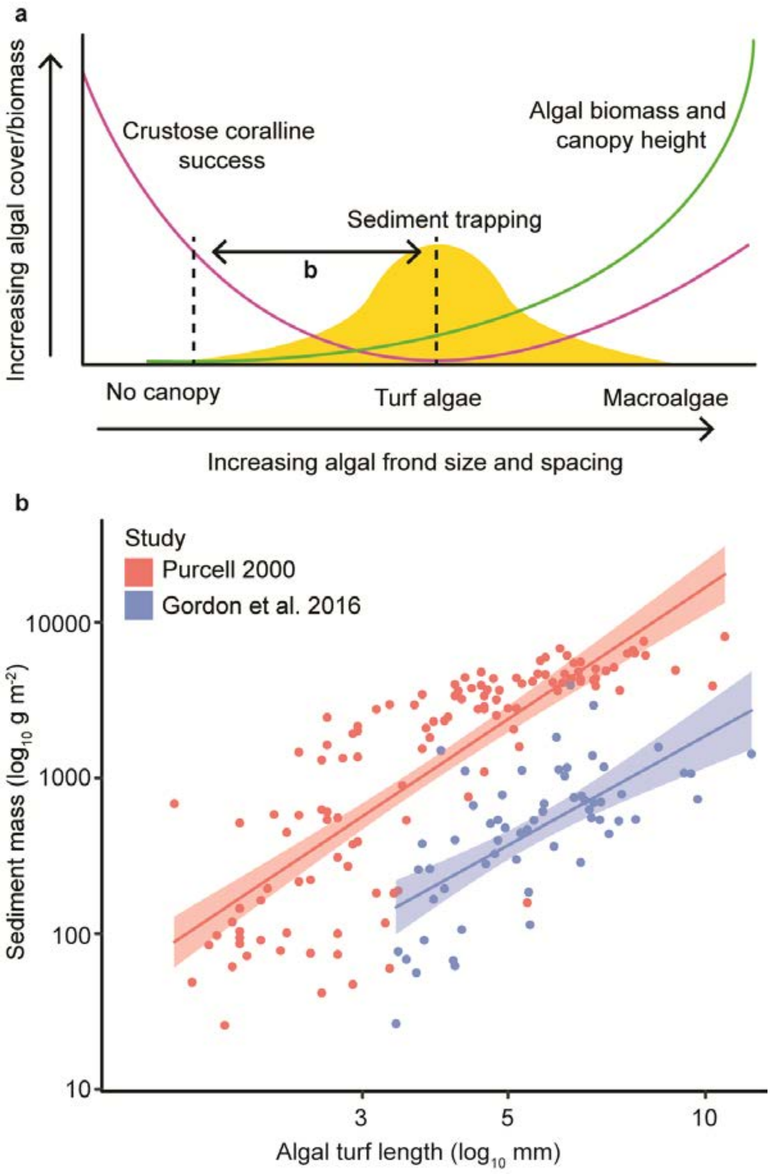

Figure 4.5 a) A conceptual model (modified after Steneck 1997) for the coexistence of three algal functional groups (crustose coralline algae, turf algae, and macroalgae) and the propensity for the assemblage to trap sediments. Note that when sediment trapping is maximised algal turfs dominate. The box delineated by dashed black vertical lines and arrows indicate the relationship described in further detail in panel b) i.e. the relationship between algal turf length and algal turf sediment mass at Orpheus Island (blue) (Gordon et al. 2016a) and Lizard Island (orange) (Purcell 2000), on the Great Barrier Reef, Australia. The coloured lines and grey shaded areas show the predicted fit of linear models and their 95% confidence intervals.

Algal turfs

While algal turf length is generally positively associated with increasing algal turf sediment load (Fig. 4.5), it is certain that a threshold exists, whereby, once too much sediment is trapped, conditions can become unfavourable even for algal turfs. For example, Tebbett et al. (2018a) experimentally demonstrated that higher algal turf sediment loads reduced algal turf biomass accrual, supported by similar results from subtropical rocky reef algal turfs (Airoldi and Virgilio 1998). One of the main factors underpinning such results may be the development of unsuitable conditions in deeper layers of algal turf sediments. Indeed, Clausing et al. (2014) found that at depths of 4 mm algal turf sediments can suppress the growth of algal turfs through the formation of hydrogen sulphide (H_2S). This formation of anoxic conditions is likely to be particularly prevalent if high loads of fine algal turf sediments get trapped in habitats with limited hydrodynamic activity. Although algal turfs appear to be a particularly stress-tolerant functional group of algae (Hay 1981), extreme accumulation of algal turf sediments appears to influence even these resistant algae.

Crustose coralline algae

CCA play a major role in reef building through calcification and cementation of the reef substratum, as well as promoting coral settlement (Adey 1998; Harrington et al. 2004). CCA are well suited to shallow, high-energy coral reef environments and are particularly resistant to the grazing pressure of herbivores, unlike other algal functional forms (Steneck 1983a). Indeed, for CCA to persist, it appears that high herbivory rates are crucial to control the growth and expansion of algal turfs (Steneck 1983a, 1997). However, while experimental evidence assessing the impacts of algal turf sediments on CCA is limited, evidence examining the influence of sediments alone suggests that CCA are likely to be highly susceptible to algal turf sediment impacts (McClanahan 1997; Steneck 1997; Fabricius 2005). For example, the cover of CCA is frequently negatively correlated with sedimentation rates (Fabricius and De'ath 2001; Fabricius and McCorry 2006; Albert et al. 2008) and burial of CCA by fine sediments has been experimentally demonstrated to decrease photosynthesis and compromise survival (Fabricius 2005; Harrington et al. 2005). Therefore, under such conditions, accumulated sediments are likely to foster the competitive ability of algal turfs, which can successfully compete with and overgrow CCA (Steneck 1997) (Fig. 4.5).

Macroalgae

Steneck (1997) suggested that macroalgae, like CCA, are sensitive to increased sediment loads. This notion was supported by Umar et al. (1998), who demonstrated that increased algal turf sediment loads can significantly reduce recruitment, growth, survival and vegetative regeneration in one species of tropical *Sargassum.* Unfortunately, beyond the study of Umar et al. (1998) our understanding of the effects of algal turf sediments on coral reef macroalgae is limited. However, these effects have been studied in far more detail in subtropical and temperate rocky reef macroalgae assemblages (reviewed in Airoldi 2003; O'Brien and Scheibling 2018). Indeed, several subtropical/temperate studies have found similar results to Umar et al. (1998) in that algal turf sediments significantly impede the settlement and survival of canopy forming macroalgae (e.g. Airoldi 1998; Isæus et al. 2007; Gorman and Connell 2009; Alestra et al. 2014). The evidence gleaned to-date from other systems suggests that the ability of algal turf sediments to impair the settlement abilities and survival of macroalgae may be widespread. As such, coral reef systems that have transitioned to LSAT-covered states may resist further transitions to macroalgae covered states, as suggested in Goatley et al. (2016).

How do algal turf sediments affect fishes?

There are two primary mechanisms by which algal turf sediments can affect fishes: a) by directly mediating feeding rates and behaviour (Bellwood and Fulton 2008; Goatley and Bellwood 2012; Gordon et al. 2016b), and b) by reducing the quality and productivity of nutritional resources in the epilithic algal matrix with the potential for bottom-up effects on fish productivity (Purcell and Bellwood 2001; Gordon et al. 2016a; Tebbett et al. 2018a) (also see Chapter 8). These two mechanisms are discussed in more detail below.

Feeding rates and behaviour

Based on observations, Randall (1955) suggested that surgeonfish feeding behaviour was mediated by algal turf sediments, as sediments controlled how fishes removed algal material and when sediments were removed by fishes they were often rejected. Initial experimental studies supported these observations, as removal of algal turf sediments on coral reefs led to marked increases in herbivorous fish feeding rates (Bellwood and Fulton 2008; Goatley and Bellwood 2012). Furthermore, Duran et al. (2019) highlighted that in the Caribbean, surgeonfishes, especially smaller size classes, selectively fed on SPATs compared to LSATs. Interestingly, these results are supported by findings from freshwater systems including the African Rift Lakes and South American streams that found: a) many grazing fishes avoided feeding on algae laden with sediments (Genner et al. 1999), b) feeding rates increased when algal sediments were removed (Rusuwa et al. 2006) and c) size-dependent selectivity for sediment-cleared grazing areas (Power 1984). Taken together, these studies highlight the pervasive nature of algal turf sediments in controlling herbivorous fish feeding rates and behaviour in aquatic systems.

Studies on nominally herbivorous coral reef fishes have now also begun to tease apart the mechanisms underpinning the interaction between fish feeding behaviour and algal turf sediments. This was achieved by exploring the effects of sediment size, source, mass and particulate organic content on the feeding behaviour of morphologically and functionally different fishes (Gordon et al. 2016b; Tebbett et al. 2017a, 2017b). For example, the 'brushing' surgeonfish *Ctenochaetus striatus*, must interact closely with algal turf sediments when targeting detritus using its long brush-like teeth (Tebbett et al. 2017d, 2018c), and appears to be highly sensitive to small increases in algal turf sediment mass (as little as 75 g m^{-2}) (Tebbett et al. 2017b) (Fig. 4.6a) (also see Chapter 9). By contrast, 'croppers' such as the surgeonfish *Acanthurus nigrofuscus*, appear to be more resilient to sediment increases as they can use their multidenticulate teeth to 'crop' off the tips of algal filaments protruding through the algal turf sediment layer (Tebbett et al. 2017b) (Fig. 4.6b). Finally, coarser algal turf sediments deter feeding by the scraping parrotfish *Scarus rivulatus* more than finer sediments (Gordon et al. 2016b). This appears to be a result of their morphology, specifically their beak-like teeth, which mean that scraping parrotfish must remove the entire EAM when feeding on the substratum (Bellwood and Choat 1990) (Fig. 4.6c). As such, scraping parrotfishes must either sort and reject, or ingest the algal turf sediments within the EAM. In this case coarser sediments are likely to represent a less nutritional resource (fine sediments are likely to contain more organic particulates) and are likely to be more energetically costly to process (Gordon et al. 2016a). These distinctions highlight how functionally different fishes interact with algal turf sediments in markedly different ways and offer insights into the mechanisms underpinning the effects of sediments on feeding behaviour. However, ultimately, in all cases, algal turf sediments appear to drive increased algal turf length by either a) reducing feeding rates (Goatley et al. 2016; Gordon et al. 2016b; Tebbett et al. 2017a) or b) limiting feeding to the 'above-sediment' portion of algal filaments (Tebbett et al. 2017b; Adam et al. 2018).

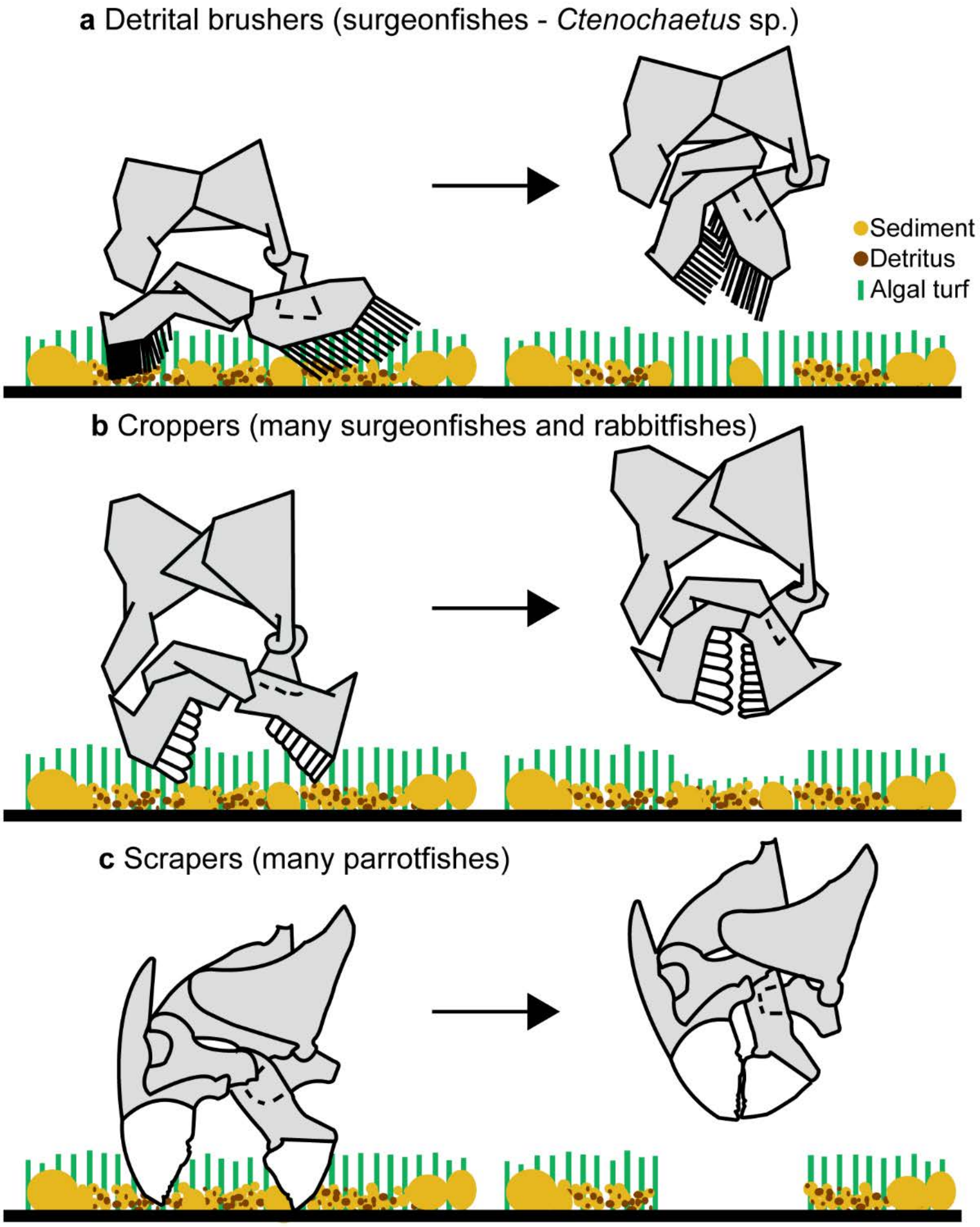

Figure 4.6 A schematic diagram showing how three functionally distinct herbivorous/detritivorous fishes interact with algal turfs, detritus and sediment. a) the lined bristletooth surgeonfish, *Ctenochaetus striatus*, selectively feeds on detritus (particulates) removing fine organic and inorganic particulates, b) the brown surgeonfish, *Acanthurus*

nigrofuscus, crops algal turfs above the layer of particulates and c) the surf parrotfish, *Scarus rivulatus*, scrapes the substratum removing the entire algal turf, sediment and detritus mixture (i.e. the complete epilithic algal matrix (EAM) including cyanobacteria, other microbes and microalgae etc). These functional differences may underpin the effect of sediments on fishes. *C. striatus* and *A. nigrofuscus* jaws redrawn from (Purcell and Bellwood 1993; Tebbett et al. 2017b). It should be noted that this diagram does not necessarily highlight the nutritional resources targeted, or assimilated by these fishes, as biomarker data suggests there are further differences between these fishes after assimilation (see Clements et al. 2017). My diagram highlights the different components of the EAM removed by fishes when feeding on coral reefs.

Nutritional consequences for fishes

In addition to directly mediating the feeding behaviour of fishes, algal turf sediments are likely to impact the ability of nominally herbivorous fishes to extract suitable nutritional resources from the EAM. Indeed, Choat (1991) suggested that sediments trapped in algal turfs could reduce the nutritional return per feeding event. This is because algal turf sediments on coral reefs can directly: a) reduce the productivity of the algal turfs (Tebbett et al. 2018a), b) 'water-down' the relative level of organic material within the algal turfs (Purcell and Bellwood 2001; Gordon et al. 2016b), and/or c) lead to the formation of LSATs which are likely to reduce the abundance of euendolithic cyanobacteria available for exploitation by parrotfishes (Hutchings et al. 2005; Clements et al. 2017). Indeed, a recent study revealed that sediment additions led to a 2000% and 3300% decrease in the potential yield of algal turf biomass and nitrogen to herbivorous fishes, respectively, relative to algal turfs containing ambient or reduced sediment loads (Tebbett et al. 2018a). Intuitively, such decreases in the productivity/nutritional value of the algal turfs could have significant bottom-up effects on the herbivorous fish community through reduced growth and/or altered distribution patterns (also see Chapters 8 and 9).

Support for bottom-up effects of algal turf sediments on the populations of herbivorous fishes can be gleaned from the freshwater literature (reviewed in Vadeboncoeur and Power 2017). For example, Munubi et al. (2018) found that sediment mass associated with benthic algae/biofilms was the strongest predictor of among-site variation in the density of a herbivorous cichlid in Lake Tanganyika. Furthermore, Takeuchi et al. (2010) posited that a decrease in the abundance of herbivorous cichlids in Lake Tanganyika over 20 years could be due to increased accumulation of sediments associated with algae/biofilms. While Power (1984) demonstrated that deposited benthic sediments imposed energetic costs on a South American armoured catfish. Taken together, these studies suggest sediments deposited on the benthos, particularly when associated with algae (i.e. algal turf sediments in the coral reef realm), may impose bottom-up effects on the fishes that interact with these sediments. In terms of coral reefs, it has been repeatedly suggested that the abundance of herbivorous and detritivorous fishes is heavily influenced by bottom-up forces (e.g. Purcell and Bellwood 2001; Russ 2003; Russ et al. 2015; Clements et al. 2017; Bellwood et al. 2018), suggesting that algal turf sediments may limit nutritional resources with direct consequences for herbivorous fish populations. Furthermore, as nominally herbivorous fishes can make up a large proportion of artisanal fisheries catches (Edwards et al. 2014; Russ et al. 2015; Robinson et al. 2019c) bottom-up effects may manifest themselves as less productive fisheries yields to humanity (Bellwood et al. 2018; Tebbett et al. 2018a; Morais and Bellwood 2019) (also see Chapter 8 where this is explored in more detail).

How do algal turf sediments affect corals?

There are two chief mechanisms by which algal turf sediments can impact corals: a) by reducing coral recruitment (Birrell et al. 2005; Speare et al. 2019) and b) by enhancing the competitive abilities of algal turfs when interacting with corals (reviewed in O'Brien and Scheibling 2018). Each is addressed separately below.

Coral recruitment

Coral recruitment is a critical ecosystem process on coral reefs that facilitates recovery after disturbances (Chapter 3) (Elmhirst et al. 2009; Ritson-Williams et al. 2010; Hughes et al. 2019a). However, corals require suitable surfaces and cues to settle, especially microtopographic refuges (Nozawa 2012; Brandl and Bellwood 2016) and crustose coralline algae (Harrington et al. 2004; Ritson-Williams et al. 2010). As such, the suppression of CCA development by algal turf sediments (see details above) may suppress key cues. Similarly, as the microbe community on the benthos can influence coral settlement (Sharp et al. 2015), if algal turf sediments influenced the microbiome within algal turfs (Bourne et al. 2016; Meirelles et al. 2018), this may also supress coral settlement rates.

When it comes to direct effects of algal turf sediments most studies have focused on the effects of sediments in isolation on coral recruitment. These studies have repeatedly highlighted that settlement on bare surfaces (e.g. glass, tiles, settlement plates) is heavily impacted by sediments (e.g. Hodgson 1990; Babcock and Smith 2000; Perez III et al. 2014; Moeller et al. 2017; Ricardo et al. 2017; but see Trapon et al. 2013b). By contrast, studies that have considered the effects of algal turfs in isolation on coral settlement have found more mixed results, revealing either limited changes (Diaz-Pulido et al. 2010; Speare et al. 2019) or significant decreases (Arnold et al. 2010) in settlement depending on the algal community (reviewed in Birrell et al. 2008). Surprisingly, studies directly considering both algal turfs and sediments together are limited to just three (Birrell et al. 2008; Leong et al. 2018; Speare et al. 2019). In these studies, algal turf sediments led to significant declines in coral settlement on reefs in both the Indo-Pacific (Birrell et al. 2005; Leong et al. 2018) and the Caribbean (Speare et al. 2019). Considering the paucity of studies examining the effects of algal turf sediments on coral settlement, and the clear potential for profound impacts, this research topic offers fertile grounds for further investigation.

Competitive interactions

Algal turf sediments also play a role in coral-algal turf competitive interactions. Coral-algal turf interactions have received a substantial degree of attention on coral reefs (e.g. McCook 2001; Nugues and Roberts 2003; Vermeij et al. 2010; Gowan et al. 2014; Wild et al. 2014; Liao et al. 2019). However, the findings are far from clear and appear to be highly context and taxon specific, with results ranging on a spectrum from competitive dominance by corals to competitive dominance by algal turfs (reviewed in McCook et al. 2001; O'Brien and Scheibling 2018). In certain contexts, algal turf sediments appear to enhance the competitive abilities of algal turfs, as they foster the growth and/or increased canopy height of algal turfs (Gowan et al. 2014; Liao et al. 2019) and probably alter the microbial community within algal turfs (Barott and Rohwer 2012; Roach et al. 2017; Brown et al. 2019). However, in other cases sediment accumulation on corals can lead to partial mortality, with subsequent expansions and development of algal turfs (Nugues and Roberts 2003). In the latter case, algal turfs are not directly competing with corals but instead are simply occupying new space, and as such, algal turf sediments are not involved in this interaction.

Unfortunately, it can be difficult to determine whether algal turf expansion is a result of the former or latter scenario (McCook et al. 2001), with other factors such as hydrodynamics (Gowan et al. 2014) and nutrients (Vermeij et al. 2010) likely to influence the nature of these interactions. Furthermore, studies examining competitive interactions rarely quantify the amount and nature of sediments trapped in the algal turfs (but see Liao et al. 2019). Without specifically investigating the nature of the algal turf sediments, our understanding of their role in competitive interactions, and the mechanistic basis underpinning competition, remains limited.

Algal turf sediments on Anthropocene coral reefs

Will algal turf sediments be important on Anthropocene coral reefs?

Yes. Following the global reconfiguring of coral reefs after repetitive bleaching events and other disturbances, algal turf sediments are poised to play an increasingly important role in structuring ecosystem processes such as coral settlement, herbivory, and benthic productivity (Hughes et al. 2018a; Bellwood et al. 2019a; Bruno et al. 2019). Indeed, it is becoming increasingly apparent that many, if not most, coral reefs, will simply emerge as lower-complexity systems covered in algal turfs (Chapters 2 and 3) (Bellwood and Fulton 2008; Jouffray et al. 2015; Smith et al. 2016; Brown et al. 2017; Bellwood et al. 2019a). Other configurations including an increased abundance of stress-tolerant coral taxa (e.g. *Porites*) (Marshall and Baird 2000; Loya et al. 2001), weedy fast-recovering coral taxa (e.g. *Acropora*, *Pocillopora*) (Berumen and Pratchett 2006; Johns et al. 2014; Torda et al. 2018), other sessile invertebrates (Norström et al. 2009; Tebbett et al. 2019), or fleshy macroalgae (Hughes 1994; Graham et al. 2006) are also possible in certain circumstances. However, even in such cases, algal turfs are likely to be abundant following disturbances and during regenerative phases. This is because algal turfs can be: a) 'uncovered' when coral canopies are lost (Goatley and Bellwood 2011), b) occupy recently dead coral skeletons rapidly following primary colonisation by cyanobacteria (Diaz-Pulido and McCook 2002; Arthur et al. 2005), c) are a particularly stress-tolerant functional group of algae (Hay 1981; Steneck and Dethier 1994) and d) even appear to benefit physiologically from future climate change conditions (Bender et al. 2015; Ober et al. 2016; Johnson et al. 2017b). This combination of traits sets the scene for a rise in algal turf cover on Anthropocene reefs.

Algal turf-covered reef configurations may continue to provide key services to humanity, such as fishable biomass production (Bellwood et al. 2018; Morais and Bellwood 2019; Robinson et al. 2019c). However, the functions provided by organisms in these systems, and in-turn the services reefs provide to humanity, are heavily dependent on the nature and amount of algal turf sediments (see above). Unfortunately, sediment-laden algal turfs are likely to proliferate on algal turf-covered reefs, especially close to shore, as sediment inputs are increasing from coastal development and dredging (Wolanski et al. 2009; Erftemeijer et al. 2012) and increased terrestrial runoff (McCulloch et al. 2003; Bainbridge et al. 2012). For example, even on the highly-regulated GBR, Hughes et al. (2015) noted that "in the past 10 years, more than 25 million cubic meters of dredge spoil from ports has been dumped at sea in the GBR WHA [World Heritage Area]…an amount that roughly equals the total volume of sediment historically delivered from all 35 rivers draining into the GBR each decade, prior to land-clearing".

The role of algal turf sediments on Anthropocene coral reefs is likely to be further increased through the loss of topographic complexity (Graham et al. 2006; Alvarez-Filip et al. 2009), which promotes sediment trapping in algal turfs (see Chapter 5) (Duran et al. 2018; Tebbett et al. 2020c), as well as through the overexploitation of nominally herbivorous fish communities which play a central role in algal turf sediment dynamics and potentially in the maintenance of SPATs (Goatley and Bellwood 2010; Krone et al. 2011; McAndrews et al. 2019). As such, algal turf sediments represent a multifaceted stressor that interacts with climate change, overfishing and human development (Bellwood et al. 2018; Tebbett et al. 2018a). The study of algal turf sediments, therefore, transcends marine/terrestrial boundaries and encompasses extensive social-ecological linkages. Unfortunately, like scraping parrotfish (*sensu* Steneck 1983b) – we are still just scratching the surface when it comes to understanding algal turf sediments on coral reefs.

What do we need to know about algal turf sediments?

Studies assessing the dynamics and ecological ramifications of algal turf sediments are still in their infancy. However, work on the GBR (Purcell 2000; Goatley and Bellwood 2012; Gordon et al. 2016a; Tebbett et al. 2018a), Pacific Islands (Clausing et al. 2014; Fong et al. 2018; McAndrews et al. 2019) and Caribbean (Steneck 1997; Adam et al. 2018; Duran et al. 2019; Speare et al. 2019), suggests that this is a burgeoning research field with clear opportunity for collaborations to enhance our understanding of algal turf sediments across biogeographic boundaries. Furthermore, advances are being made in understanding how algal turf sediments on coral reefs affect key ecosystem process (e.g. Duran et al. 2019; Speare et al. 2019) (also see Chapters 6, 8 and 9), are mediated by fishes (e.g. Fong et al. 2018; McAndrews et al. 2019), and accumulate in algal turfs (e.g. Latrille et al. 2019; Tebbett et al. 2020c) (also see Chapter 5). Yet, while considerable progress is being made, we still lack the answers to many basic questions.

In many coral reef regions we simply do not know how much sediment is in the algal turfs, or how these algal turf sediments are linked to suspended sediment levels and sedimentation. Furthermore, monitoring of coral reef algal turf sediment levels before, during and after exceptional sedimentation events, such as dredging activities, would provide valuable insights into how such events impact the deposition and accumulation of algal turf sediments. Indeed, there is remarkably little long-term data on sedimentation rates and algal turf sediment loads in coral reef systems. For example, examination of temporal dynamics in algal turf sediments loads (>6 months) is limited to just two studies (Goatley et al. 2016; Gordon et al. 2016a) from a single island on the GBR (also see Chapter 8). However, while it is often assumed sediment loads are increasing on other reefs globally, as a result of increasing inputs (Burke et al. 2011), there is little quantitative evidence to support this.

To achieve a comprehensive understanding of algal turf sediment dynamics this will require linking research on algal turf sediments with the vast and growing literature surrounding general sediment dynamics on coral reefs. For example, clear progress has been made in terms of understanding ridge-to-reef sediment transport (e.g. Bartley et al. 2014; Fabricius et al. 2014; Bainbridge et al. 2018; Comeros-Raynal et al. 2019), dredge plume dynamics and deposition (e.g. Fisher et al. 2015b; Jones et al. 2019), within reef sediment transport mechanisms (e.g. Ogston et al. 2004; Orpin and Ridd 2012; Pomeroy et al. 2017), and links between turbidity and sediment deposition (e.g. Whinney et al. 2017). However, apart from the study by Latrille et al. (2019) which began to place algal turf sediments into this context, our understanding of the links between algal turf sediments and other sediment dynamics remains exceedingly limited. Addressing these unknown links represents a critical knowledge gap on ecological time scales.

Furthermore, on geological time scales, there has been significant progress in our understanding of reef growth and development in sediment-rich habitats (e.g. Perry et al. 2012; Browne et al. 2013; Roff et al. 2015; Ryan et al. 2018). This is becoming increasingly topical as sea-level rise becomes an inevitability, along with the associated notion of 'drowned reefs' (van Woesik et al. 2015; Perry et al. 2018). However, while Bellwood and

Fulton (2008) posited that algal turf sediments may be a key factor underpinning reef drowning, algal turf sediments have received little attention within this context. As such, a multidisciplinary approach linking algal turf sediments with other reef processes and sediment dynamics may offer insights into the survival of coral reefs in both ecological and geological time scales.

In terms of furthering our understanding of the direct ecological effects of algal turf sediments there are several key research gaps across multiple spatial scales. For example, at small spatial scales, further examination of the interaction between algal turf sediments, 'crevice cleaning' fishes, and coral recruitment in microtopographic refuges is particularly important for understanding coral recruitment dynamics and potential recovery of reefs following disturbances (Brandl and Bellwood 2016; Ricardo et al. 2017). In conjunction with this line of research, furthering our understanding of the microbiome within algal turfs is necessary. As stressors such as overfishing and nutrient enrichment may affect the algal turf microbiome (e.g. Zaneveld et al. 2016; Meirelles et al. 2018), with potential effects on coral settlement (Bourne et al. 2016; Meirelles et al. 2018), examining the influence of algal turf sediments on these microbes could offer interesting insights into coral settlement dynamics.

Also, at small spatial scales, there have been calls for a more nuanced understanding of nutritional resources within the EAM, especially the role of cyanobacteria (Clements et al. 2017). Cyanobacteria are important early colonisers of dead coral reef substrata (Diaz-Pulido and McCook 2002) and are likely to play an important role in accumulating and binding algal turf sediments (Stal 2003). However, our understanding of the relationships between algal turf sediments and both epilithic and euendolithic cyanobacteria, is limited. These relationships warrant further investigation, especially considering that these cyanobacteria appear to be a key nutritional resource targeted by parrotfishes (Clements et al. 2017). Furthermore, as algal turf communities are composed of diverse algal taxa and morphological forms (Scott and Russ 1987; Harris et al. 2015), different algal turf communities are likely to: a) be influenced by algal turf sediments differently and/or b) trap and retain algal turf sediments at different rates. While there has been some attention paid to these factors in the subtropical/temperate rocky reef literature (Stewart 1983; Airoldi et al. 1995), our understanding of the relationships between algal turf taxonomy/form/composition and algal turf sediments is currently limited on coral reefs. Resolving these relationships with more precision will enhance our ability to predict the effects of sediments on algal turf communities, and the organisms that associate with, or use, algal turfs.

At larger reef-wide scales, understanding how SPATs are maintained is vital. For example, a comprehensive understanding of algal turf sediment removal, transport and maintenance by fishes, and the relative importance of different taxa is necessary (Bellwood 1995; Goatley and Bellwood 2010; Krone et al. 2011). At even larger regional spatial scales, understanding how to maintain key services such as fisheries productivity from algal turf-covered reefs is key. This is particularly important in 'telecoupled' (Liu et al. 2016) reef-land systems, where land-use and overfishing practices are linked (see Comeros-Raynal et al. 2019) which could potentially facilitate transitions to LSAT states in a synergistic nature (see Chapter 8 for more details). This represents a complex socio-ecological challenge, transcending ecosystem boundaries and requiring a multidisciplinary approach.

Clearly, there is a broad swath of questions to address in relation to algal turf sediments on coral reefs. These range from basic descriptive studies to more complex, multifaceted, socio-ecological investigations. Progress will require forward-looking studies that identify key functional interactions in algal turf-covered coral reef systems (see Chapters 5, 6, 8 and 9). This endeavour will help us to embrace change and address the major overarching goal of managing reefs in a manner that sustains the key functions and services coral reefs provide (Hughes et al. 2017a).

Conclusion

In many cases coral reef ecosystems now exist as highly altered configurations, and in this context the importance of once-critical ecosystem functions and functional groups are changing (Hughes et al. 2017a; Bellwood et al. 2019b). Specifically, the importance of algal turf sediments in mediating the functioning of these altered ecosystems is set to increase. However, despite evidence highlighting the importance of these sediments, our understanding remains limited. Herein, I have endeavoured to provide a brief overview of our knowledge to-date and hope that this will act as a 'spring-board' to encourage further scientific investigation within this field. On Anthropocene, low-coral cover reefs, there will be no shortage of algal turfs and the sediments they contain.

Chapter 5: A 3D perspective on sediment accumulation in algal turfs: implications of coral reef flattening

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Abstract

Globally, coral reefs are being transformed by a suite of stressors, the foremost being climate change. Increasingly, it is expected that these reconfigured reef systems will emerge with lower-complexity and will be dominated by algal turfs. Understanding this new operating space is vital if we are to maintain the services, such as fishable biomass production, that reefs provide. However, the functionality of these systems appears to depend on the nature of the algal turfs themselves, which is in-turn, intimately linked to the sediments they contain. As reefs are losing complexity, we need to understand if, and to what extent, algal turf condition and complex reef structure are connected. To address this issue, I took advantage of recent developments in 3D structure-from-motion technology to examine how complexity metrics (elevation and surface angle) related to the nature of algal turfs on a heavily climate-impacted coral reef. This represents a novel application of this technology in the context of coral reef ecosystems. I found that as both elevation and surface angle decreased, the nutritional value of the epilithic algal matrix also decreased while sediment accumulation increased. Furthermore, I showed that elevated surfaces were characterized by far shorter algal turfs, and are potentially herbivory hotspots, offering fertile grounds for further exploration of herbivory dynamics at sub-metre spatial scales. This study yields new insights into the operating-space of future reefs, and suggests that as reefs flatten, sediment accumulation is likely to increase even if sediment inputs remain unchanged, altering algal

turfs fundamentally. Maintaining key services provided by climate-transformed, low-complexity algal turf-dominated reefs of the future, will depend on managing the complex interactions between herbivory, sediments, algal turfs and reef structural complexity.

Introduction

Coral reefs are amongst the most rapidly changing, hyperdiverse ecosystems on Earth (Hughes et al. 2017a; Barlow et al. 2018). Repetitive, global coral bleaching events have challenged the status quo of these ecosystems (Hughes et al. 2018a; Wismer et al. 2019a). It is now critical to embrace these changes and understand how these transitioning ecosystems are functioning (Graham et al. 2014; Bellwood et al. 2019b). This understanding is vital if we wish to support the desired ecosystem services that reefs provide (Hughes et al. 2017a; Bellwood et al. 2019a). To understand future reef systems it will be critical to: a) identify the functional processes operating, and b) understand drivers of these processes.

The benthic configurations of future coral reefs is an area of ongoing uncertainty (Bruno et al. 2009; Norström et al. 2009; Smith et al. 2016; Bellwood et al. 2019a). Predictions range from dominance by fleshy macroalgae (Mumby et al. 2007; van de Leemput et al. 2016), through boom-and-bust cycles of weedy growing corals (Berumen and Pratchett 2006; Johns et al. 2014), to dominance by ‘stress tolerant’ coral taxa (Marshall and Baird 2000; Loya et al. 2001). However, increasing evidence suggests that many reefs will emerge as low-complexity systems, dominated by turf algae (Chapters 2 and 3) (Jouffray et al. 2015; Smith et al. 2016; Arias-González et al. 2017; Bellwood et al. 2018). Low-complexity algal turf-dominated reefs seem particularly likely because: a) complexity on reefs is influenced by the three-dimensional skeletons of scleractinian corals (Alvarez-Filip et al. 2009; Graham and Nash 2013), which are increasingly susceptible to death and erosion during bleaching events (Hughes et al. 2018b; Perry and Alvarez-Filip 2019), and b) algal turfs are often already the dominant benthic cover on many coral reefs (Chapter 2) (Wismer et al. 2009; Jouffray et al. 2015; Smith et al. 2016). Furthermore, this coverage is set to increase in the future because turf algae can rapidly colonise dead reef substrata (Diaz-Pulido and McCook 2002). This proliferation of algal turfs per se may not be detrimental to the ecological functioning of reef systems, but may offer interesting new ecological configurations on reefs as turf algae are particularly productive and already underpin key trophic pathways on reefs (Hatcher 1988; Russ 2003; Kelly et al. 2017). As such, productive, turf-dominated systems, may have the potential to sustain key services, such as exploitable biomass production of fishes (Bellwood et al. 2018; Robinson et al. 2019c).

However, the ability of algal turfs to sustain particular reef services appears to depend on the state of the algal turfs (Goatley et al. 2016; Tebbett et al. 2018a) (also see Chapters 6, 7 and 8). The state of algal turfs is, in-turn, intimately linked to the sediments they contain (Clausing et al. 2014; Goatley et al. 2016; Tebbett et al. 2018a) (also see Chapters 4 and 6). By mediating key processes such as herbivory (Goatley et al. 2016; Tebbett et al. 2017b), coral settlement (Birrell et al. 2005; Ricardo et al. 2017; Speare et al. 2019) and benthic productivity (Tebbett et al. 2018a) sediments can mediate many critical processes of reef systems (as outlined in Chapter 4). This recent recognition of the ecological importance of turf-bound sediments appears timely, given that more than 50% of reefs are forecast to be at risk of increased terrestrial sediment inputs (Burke et al. 2011). Indeed, declining water quality is considered one of the foremost stressors faced by coral reef systems, second only to climate change (Fabricius 2005; Jones et al. 2016; Harborne et al. 2017). We are therefore faced with low-complexity, algal turf-dominated reef configurations, whose critical process may be severely subdued by increased sediment inputs (Bainbridge et al. 2018; Tebbett et al. 2018a). Yet, we know relatively little about important benthic dynamics in these systems, especially how reduced three-dimensional (3D) complexity affects the condition of algal turfs.

In coral reef ecosystems, complexity has received considerable attention, especially regarding its role in structuring the communities of reef-associated organisms (e.g. Emslie et al. 2014; Darling et al. 2017; Richardson et al. 2017). In reef fishes, for example, the loss of structural complexity in particular, rather than the loss of coral cover per se, is expected to significantly alter the community composition (Wilson et al. 2006; Emslie et al. 2014). However, in terms of sediment dynamics, the effects of reduced structural complexity have received relatively little attention, especially regarding sediment dynamics related to algal turfs (but see Bodde et al. 2014; Pomeroy et al. 2015; Torres-Garcia et al. 2018). The effects of complexity loss on sediment dynamics have the potential to be just as striking as those seen in fishes. This is because feeding by nominally herbivorous fishes plays a key role in redistributing and maintaining low sediment loads in algal turfs (Goatley and Bellwood 2010; Bellwood et al. 2018) and this, in turn, appears to be mediated directly by structural complexity (Vergés et al. 2011; Catano et al. 2016). Complexity, furthermore, mediates hydrodynamic activity (Lowe et al. 2008; Rogers et al. 2018b), which in turn appears to impact algal turf sediment distributions on a range of spatial scales: from reef-wide distributions (Crossman et al. 2001; Purcell and Bellwood 2001; Tebbett et al. 2017c) down to the boundary layer created by algal turf filaments that enhances sedimentation rates (Carpenter and Williams 1993). Evidently, a loss of structural complexity could affect biological as well as physical drivers of the distribution and retention of algal turf sediments across the entire reef system.

Understanding this relationship between structural complexity and the condition of algal turfs appears important if we wish to comprehend the functioning of low-complexity coral reefs of the future. A first step is to examine how complexity and the condition of algal turfs are intertwined. To address this knowledge gap, I utilised recent developments in structure-from-motion (SfM) technology in combination with well-established algal turf sediment sampling on a heavily climate-impacted coral reef system. This represents the first application of SfM techniques to explore algal turf dynamics on reefs. This approach will allow new insights into the linking of sediments and complexity in a recently climate-reconfigured, algal turf-dominated system.

Methods

Study sites

This study was conducted in Mermaid Cove (14°38′49.21″S, 145°27′16.34″E) at Lizard Island in the northern Great Barrier Reef (Fig. C1 in Appendix C) in January 2018. Lizard Island offered an exceptional system to study because it had undergone multiple, recent, largescale disturbances including back-to-back cyclones in 2014 and 2015 (Brandl et al. 2016; Khan et al. 2017) and back-to-back coral bleaching in 2016 and 2017 (Wismer et al. 2019a) (Chapter 3). Thus, the condition of this reef appears on-track to resembling future reef configurations. Within Mermaid Cove, three study sites were examined along the reef edge in the northern side of the cove (Fig. C1 in Appendix C). Each site covered 36 m^2 (6 × 6 m) and was delineated using transect tapes.

Sediment sampling

Within each site, 13 – 15 sampling locations were randomly designated. The benthic particulates (inorganic sediments and associated organic material) contained within the turfs at each of these random points was then sampled from within a 58 cm^2 PVC ring using a submersible electronic vacuum sampler (modified after Purcell 1996). Suitable epilithic algal matrix (EAM)-covered areas for sampling were free of large sediment-retaining pits, macroalgae and encrusting organisms, and covered by turfing algae (following Tebbett et al. 2017c). Following particulate removal, within each sampling ring, 5 haphazardly selected algal turf filaments were measured using the depth probe of vernier callipers. To record this distance, the tips of the callipers were pushed into saltwater-resistant pressure-sensitive poster adhesive (blu tack) and measured using digital callipers (as outlined in Chapter 4). Algal turf length gives an indication of the ability of the turf to trap sediments, potential algal turf productivity and the intensity of grazing on algal turfs (Steneck et al. 2018; Tebbett et al. 2018a).

3D photogrammetry

Directly following the collection of particulate samples, the entire benthos at each site (36 m^2) was recorded using a Nikon Coolpix W300 camera by a diver swimming approximately 1.5 m above the reef following the methods described in Streit et al. (2019). This provided overlapping high-resolution imagery of the benthos, facilitating a photogrammetric reconstruction of the benthos using structure-from-motion software (Agisoft Photoscan Professional). This yielded orthorectified photomosaic maps, as well as 3D digital elevation models, of each site in sub-centimetre resolution (cf. Burns et al. 2015; Figueira et al. 2015; Raoult et al. 2017; Ferrari et al. 2018). The locations where particulates had been removed during the sediment sampling were clearly distinguishable on these photomosaic maps (see Fig. 5.1). Using the maps, the digital elevation models were overlayed and surface elevation (relative to the lowest point at each study site) and surface angle (angle degrees from horizontal orientation), in 10 cm diameter rings, for each sediment sampling location at each site, were calculated in the software-package *raster* in the R statistics software (Hijmans 2017; R Core Team 2020). These two complexity parameters were selected because they were: a) meaningful in relation to coral reef flattening, and b) readily measured and intuitive. Detailed methods of the photogrammetric technique are provided in Text C1 in Appendix C.

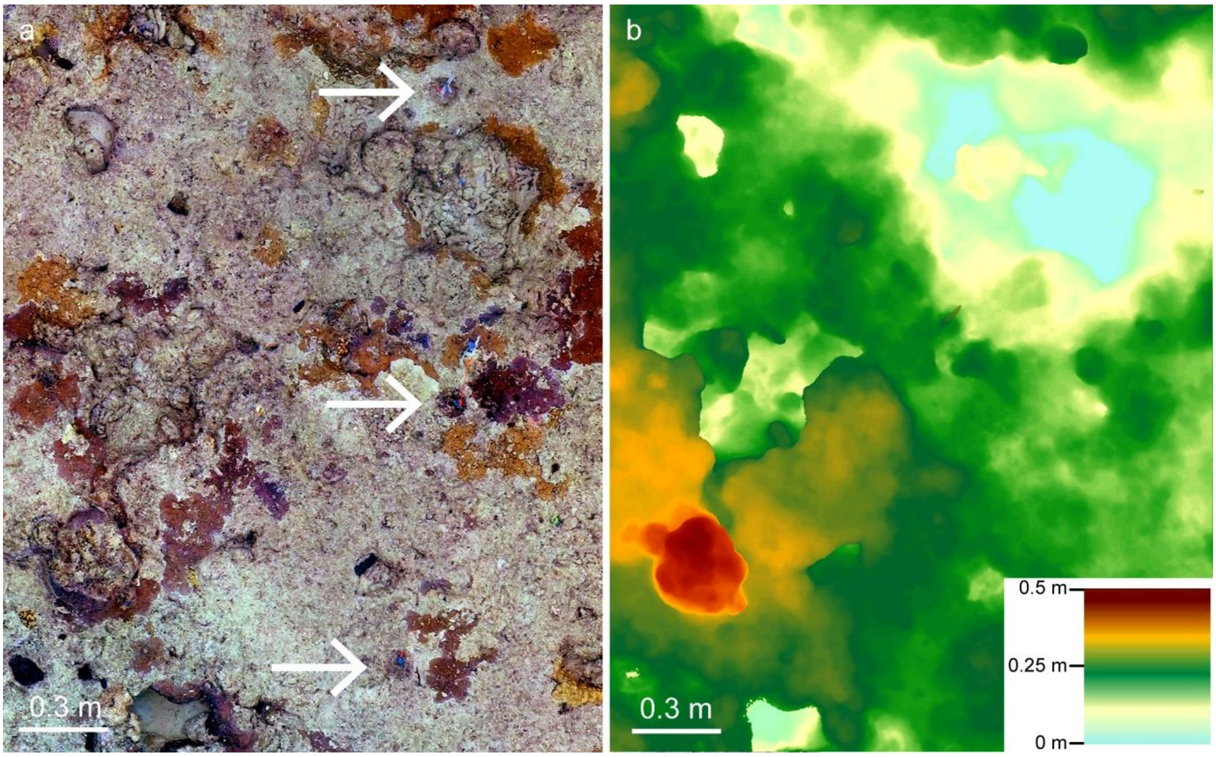

Figure 5.1 a) Section of an orthomosaic map of the benthic cover at one study site (note the high coverage of algal turfs and the arrows indicating three locations cleared of sediments). b) The same location represented as a digital elevation model that was used to extract complexity metrics (the colour gradient indicates the highest elevation = red, lowest elevation = blue).

Sediment sample processing

To fix organic material in each particulate sample, 16 ml of 4% buffered formaldehyde was initially added. Each sample was then transferred to an individual 9 l container and left for 3 hours to allow particulate material > 10 µm to settle before decanting the water (Purcell 1996). Samples were then transferred to individual 120 ml samples jars. Only particulate material < 2 mm (sands, silts and clays; ISO 14688-1:2017) in each sample was retained by wet sieving through a 2 mm stainless steel mesh. Each sample was then agitated and allowed to settle for 24 hours (to ensure a consistent settling period) before the depth of particulates in the sample jars was recorded at three haphazard locations around the jar. To give the relative depth of particulates in algal turfs on the reef, measurements were standardised by the sampling area.

Following depth measurements, salts were removed from each sample by rinsing with fresh water three times, leaving a minimum 3 hour settling period between rinses. The samples were then dried to a constant weight at 60˚C and weighed to yield total benthic particulate mass. To remove organic material, samples were bleached for at least two weeks using 30% hydrogen peroxide (H_2O_2) (following Gordon et al. 2016a). The samples were stirred and fresh H_2O_2 was added regularly. To yield inorganic sediment mass, organic mass, and proportion of organics in benthic particulates the samples were then re-dried and weighed, as above. Organic particulates (detritus) are a key trophic resource for nominal herbivorous fishes (Wilson et al. 2003) and their relative proportion to inorganic sediments is an indication of the nutritional quality of the EAM (Purcell and Bellwood 2001). Using a sieve stack (1000, 500, 250, 125, 63 µm) the bleached, dried samples were then fractioned by particle size and the size fractions were individually weighed.

Statistical analyses

A series of mixed effects models were used to examine how structural complexity influenced six different components of the turf: (1) average algal turf length (mm); (2) average benthic particulate depth in the algal turfs (mm); (3) benthic particulate mass (g m^{-2}), i.e. the total mass of particulates in algal turfs; (4) inorganic sediment mass (g m^{-2}), i.e. the non-nutritious component of particulates (Purcell and Bellwood 2001); (5) organic detrital particulate mass (g m^{-2}); and (6) proportion of organic detritus mass in the total particulate mass (i.e. the relative nutritional value of all particulates as a whole).

Two complexity metrics (surface elevation and surface angle) extracted from the 3D models were considered as mean-centred explanatory variables. Multi-collinearity of the two explanatory variables was examined using correlation plots. In each model the explanatory variables were initially fitted as interacting fixed continuous effects, with subsequent model simplification based on the corrected Akaike's Information Criterion (AICc) (Table C1 in Appendix C). All models also incorporated site as a random effect to account for the lack of spatial independence among samples. The model examining proportion of detritus in the particulates was based on a Beta distribution. In all other cases Gamma distributed, lognormal, and log-transformed models were considered, with final model selection based on residual plots and the fit of the model to the data (Table C1 in Appendix C). Model assumptions were assessed using residual plots, all of which were satisfactory. All statistical modelling was performed in the software R (R Core Team 2020) using the *lme4* (Bates et al. 2015), *nlme* (Pinheiro et al. 2017), *glmmTMB* (Brooks et al. 2017b), *AICcmodavg* (Mazerolle 2017) and *ggplot2* (Wickham 2009) packages.

The correlation between the complexity metrics and the accumulation of different sediment grain size fractions was also explicitly examined. To do this, a distance-based linear model (DISTLM), was formulated, based on a Euclidian distance matrix of standardised grain size data. DISTLMs use multiple regression to find the combination of explanatory models that best explains the variation in sediment grain size distributions (Anderson et al. 2008). Distance-based redundancy analysis (dbRDA) was then used to visualise the model. The DISTLM was performed in PRIMER 7.0 PERMANOVA+.

Results

Turf components and complexity

My results revealed strong relationships between topographic complexity and the different turf components of the EAM (Fig. 5.2). The depth of benthic particulates, mass of benthic particulates, sediment mass and organic mass all exhibited similar patterns, showing significant decreases as elevation of the sampled surface increased (LME; $p < 0.05$ in all cases; Fig. 5.2a, c; Table C2 and Fig. C2 in Appendix C). Similarly, all four metrics decreased significantly as the angle of the sampled surface increased (LME; $p < 0.001$ in all cases; Fig. 5.2b, d; Table C2 and Fig. C2 in Appendix C). In no cases did the interaction between elevation and surface angle result in the most parsimonious model (Table C1 in Appendix C), i.e. an interaction between elevation and surface angle was not better at explaining any variation in the different turf component measures compared to each factor alone.

By contrast, the proportion of organics in the benthic particulates, and algal turf length, were related to complexity in a different manner. Inverse to the previous measurements, the proportion of organics in particulates significantly increased with both increasing elevation (GLMM; $p < 0.01$; Fig. 5.2e; Table C2 in Appendix C) and increasing surface angle (GLMM; $p < 0.001$; Fig. 5.2f; Table C2 in Appendix C). Algal turf length was only influenced by the elevation of the sampled surface; surface angle had no effect (Fig. 5.2g, h; Table C1 in Appendix C). As elevation increased, algal turf length decreased significantly (GLMM; $p < 0.001$; Fig. 5.2g; Table C2 in Appendix C).

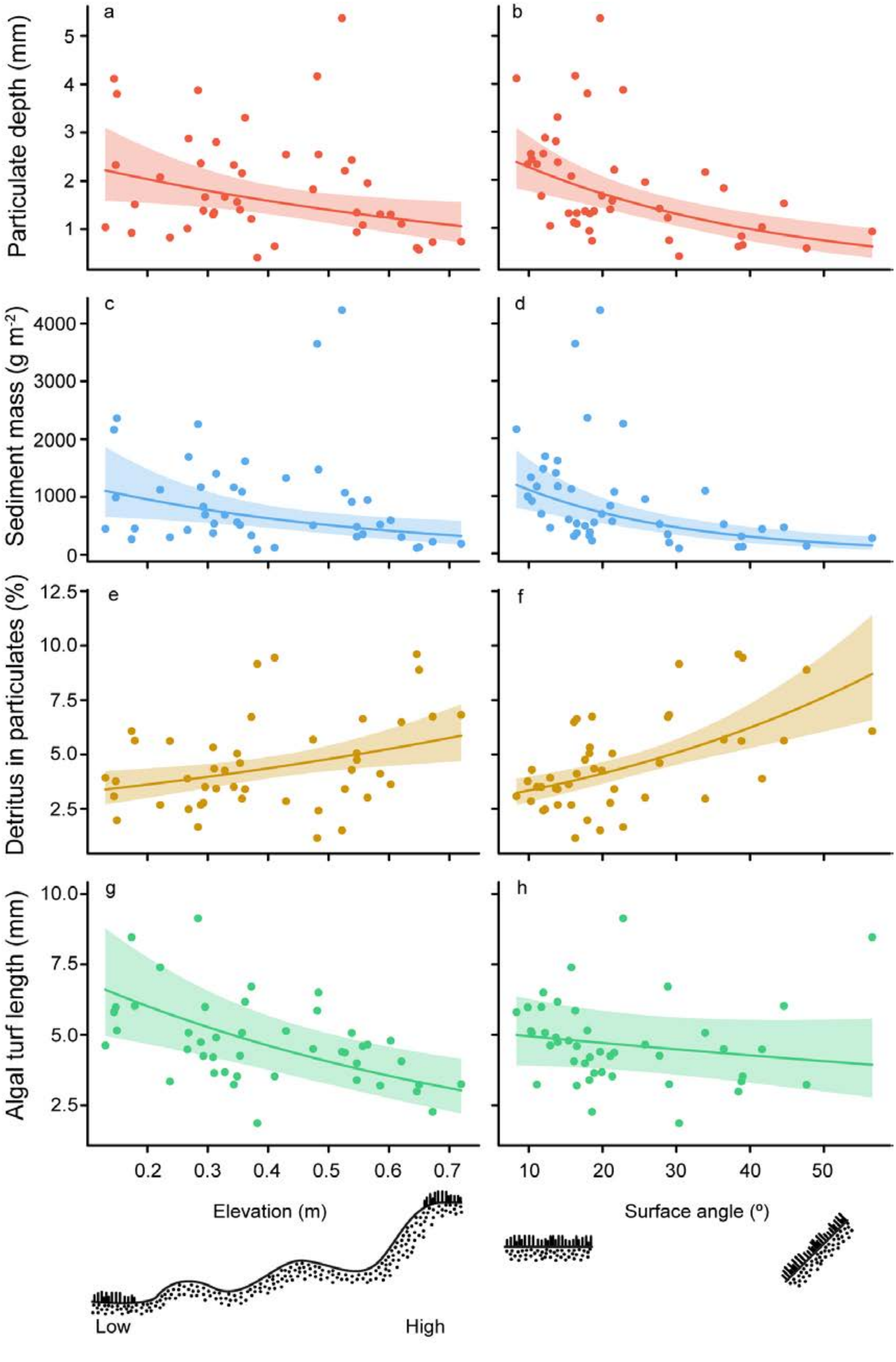

Figure 5.2 The relationship between the elevation (a, c, e, g) and angle (b, d, f, h) of the sampled surface and components of the algal turfs, (a, b) particulate depth, (c, d) inorganic

sediment mass, (e, f) the percentage of organic detritus (by mass) in benthic particulates, and (g, h) algal turf length. The lines denote the predicted fits from linear mixed effects models and their upper and lower 95% confidence interval, the points are the raw data points. For graphs of benthic particulate mass and organic particulate mass see Fig. C2 in Appendix C.

Grain size distributions

Elevation of the sampled surface was significantly correlated with the multivariate data cloud of sediment grain size distributions (DISTLM; pseudo $F = 11.79$, $p < 0.001$) which accounted for 21.9% of the total variation (Fig. 5.3). Silts and clays (sediment <63 µm), and, to a lesser extent, the intermediate 250 – 500 µm size class (medium sand), size fractions appeared to be positively associated with increasing elevation (Fig. 5.3). By contrast, coarse and very coarse sand (sediment 500 – 2000 µm) was negatively associated with increasing elevation (Fig. 5.3). In contrast to elevation, the angle of the surface was not significantly correlated with sediment grain size distributions (DISTLM; pseudo $F = 1.71$, $p = 0.17$), and only accounted for 3.9% of the variation.

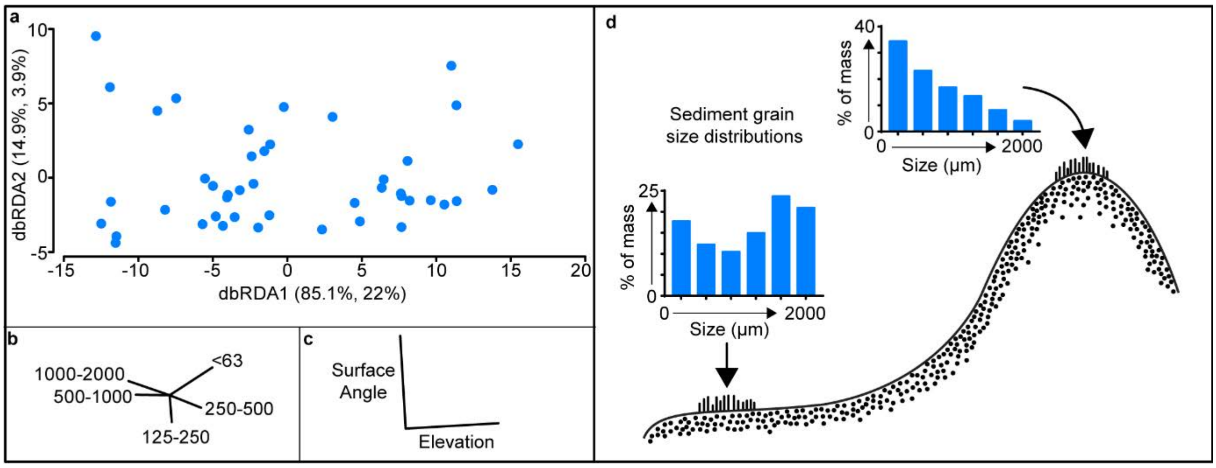

Figure 5.3 a) a distance-based redundancy analysis (dbRDA) plot of the relationship between algal turf sediment grain size distributions and complexity (surface angle and elevation)

based on a Euclidean distance matrix of standardised grain size distribution data (0 – 2000 µm). b) Vectors show the relationship among sediment grain size fractions (µm) and how they relate to c) the complexity metrics in the dbRDA plot. The 63 – 125 µm (very fine sand) vector did not contribute substantially to the observed patterns and is not shown. d) A conceptual diagram depicting the differences in grain size distribution at different elevations. Graphs of grain size distributions were based on the mean grain size distribution of 6 samples representative of low and high points, respectively (i.e. located to the extreme left and right of the dbRDA plot).

Discussion

Complexity in coral reef systems is expected to decline precipitously as corals, the architects of these ecosystems, are lost to repetitive largescale stressors (Graham et al. 2006; Alvarez-Filip et al. 2009). This loss of complexity is expected to have substantial ecological effects by restructuring the distribution, composition, abundance and interactions of reef organisms (Wilson et al. 2006; Graham and Nash 2013; Darling et al. 2017; Richardson et al. 2017). Here I show that loss of complexity may also result in a reconfiguration of algal turfs. Since turfs are a dominant reef substratum that underpins fundamental reef processes such as benthic primary productivity (Hatcher 1988; Klumpp and McKinnon 1989; Bellwood et al. 2018) (Chapter 7), coral settlement (Birrell et al. 2005; Arnold et al. 2010; Speare et al. 2019) and herbivory (Choat et al. 2002; Kelly et al. 2017), changing complexity could have far-reaching consequences for reefs.

While previous studies have suggested that microtopographic complexity is important in structuring the nature and photosynthetic abilities of algal turfs (Carpenter and Williams 1993; Brandl and Bellwood 2016), the role of topographic complexity at larger scales had remained relatively unexplored. The strong influence of complexity at the spatial scale assessed herein (cm – m) is likely to be a result of both hydrodynamic activity and the feeding activity of fishes. The effects of hydrodynamics are primarily revealed by the strong influence of elevation on sediment accumulation (Fig. 5.2). Elevated surfaces are more exposed to passing water currents, and wave activity, which limits the accumulation of sediments on such surfaces. Through mechanisms such as resuspension, or saltation, any sediments deposited on these elevated points are more likely to be dislodged and come to rest and accumulate in more protected, lower locations. This is particularly true for coarser sediments (Fig. 5.3). Similarly, in line with expectations, particulates also accumulated more on flat, low-angle surfaces where gravitational potential energy is minimised. Sediment accumulation on topographically-simple, flat locations appears intuitive and inevitable.

However, the accumulation of sediments is also likely to be driven by the feeding activities of nominally herbivorous fishes. These fishes interact with turf sediments in a number of ways. Fishes can maintain low sediment loads through direct removal (e.g. scraping by parrotfishes [Bellwood and Choat 1990], or brushing by surgeonfishes [Goatley and Bellwood 2010]), or by maintaining short, cropped algal turfs minimizing their propensity to trap sediments (Steneck 1997; Goatley et al. 2016). By contrast, if sediment loads get too high, sediments can directly reduce herbivory rates by mechanically protecting underlying algal filaments from removal or suppressing total fish feeding rates (Clausing et al. 2014; Goatley et al. 2016; Tebbett et al. 2017b; Eurich et al. 2018; Fong et al. 2018). Additionally, high sediment loads can indirectly reduce herbivory, by lowering the nutritional value of the turf, through reduced turf productivity (Tebbett et al. 2018a) or ‘watering-down’ relative levels of detritus in the particulate mixture (Purcell and Bellwood 2001) (also see Chapters 6 and 8). More directly, fishes can also increase sediment in low laying areas through ingestion, transport and defecation (Bellwood 1995), with parrotfishes defecating about 30 kg m^{-2} $year^{-1}$ of sediment in the study area (Tebbett et al. 2017c). Hence herbivory by fishes drives, and is driven by, sediment loads in the algal turfs.

Compared to the relationship between sediments and complexity, algal turf length differed in that it was only negatively related to increasing elevation, but not surface angle. This relationship again appears to be underpinned by the interaction between herbivory and sediments (see Brandl and Bellwood 2016; Tebbett et al. 2017b; Duran et al. 2018). Most nominally herbivorous fishes feed predominantly on horizontal surfaces (Goatley et al. 2016; Adam et al. 2018; Duran et al. 2018) (Chapter 9), presumably because algal turfs on these surfaces are most abundant especially on reef flats, where they can have high productivity through exposure to light (Carpenter 1985) (Chapter 7) or because this is where nutritionally important organic detritus accumulates (Crossman et al. 2001; Purcell and Bellwood 2001) (Fig. 5.2). However, this is also where inorganic sediments accumulate when surfaces are not elevated (Fig. 5.2). As high sediments can reduce herbivory rates on turfs (Clausing et al. 2014; Goatley et al. 2016; Tebbett et al. 2017b), this is likely to explain why I could not detect a relationship between surface angle and algal turf length. Essentially on horizontal surfaces, algal turf length appears to vary substantially based on the elevation. Specifically, on horizontal, but elevated, surfaces, where sediments do not accumulate readily, herbivory is likely to be high leading to short turfs (see below). By contrast, on lower horizontal surfaces, that accumulate high sediment loads, herbivory is likely to be reduced, facilitating the growth of longer turfs. In essence, different algal turf states (short productive algal turfs [SPATs] and long sediment-laden algal turfs [LSATs] *sensu* Goatley et al. 2016) are influenced heavily by reef topography (Fig. 5.4). This highlights the potentially complex interactions between herbivorous fishes, reef complexity and the nature of turfs. It also offers fertile grounds for exploration of the heterogeneity of herbivory, and its links with turf composition, at small scales (see Chapter 9).

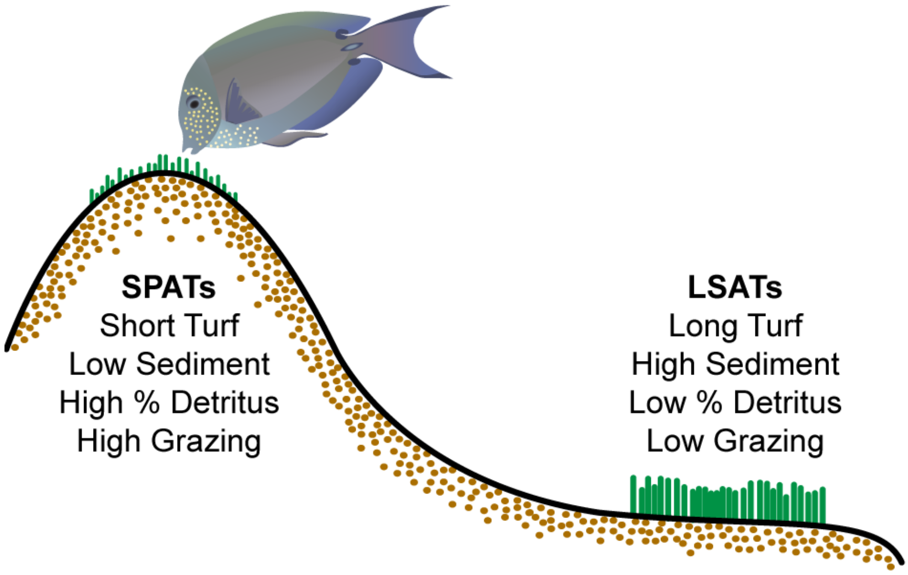

Figure 5.4 A conceptual diagram showing the different nature of algal turfs at different elevations and the potential implications of this for grazing herbivorous fishes on reefs. SPATs = short productive algal turfs, LSATs = long sediment-laden algal turfs.

It must be noted that Lizard Island, where this study was conducted, has been heavily impacted by repetitive stressors (Chapter 3) (Brandl et al. 2016; Khan et al. 2017; Wismer et al. 2019a) and appears to represent a potential future reef configuration. Indeed, there has been a substantial loss of coral cover, likely resulting in losses of complexity (Madin et al. 2018; Wismer et al. 2019a). While complexity had already been reduced at this location before my study, I still recorded up to 0.8 m of elevation between sampled surfaces; this level of elevation still had a clear effect on algal turfs and sediments. As heavily degraded reefs can approach 0 m of elevation (i.e. rugosity levels of 1) (Alvarez-Filip et al. 2009), there is likely to be further losses in complexity at Lizard Island, if reef recovery is delayed, promoting further sediment trapping in the algal turfs. Furthermore, as complexity was already reduced, the relationships between complexity and algal turf sediment dynamics described herein are likely to be conservative. On less impacted reefs, there is likely to be greater variation in complexity, and therefore, a larger magnitude of difference in algal turf sediments, potentially yielding stronger relationships. While the spatial scale of the current study was limited, my intuitive results support the results of other studies from other biogeographic locations (e.g. Duran et al. 2018), suggesting my general inferences would hold beyond Lizard Island.

Recently, evidence is emerging that fishes, particularly nominally herbivorous fishes, are far less dependent on complexity, especially that provided by corals, than often assumed (Russ et al. 2015; Tootell and Steele 2016). Indeed, it is becoming increasingly apparent that the nature and availability of nutritional resources may be far more important in structuring herbivorous fish communities than top-down factors (predation risk and shelter availability) (Russ et al. 2015; Tootell and Steele 2016) (also see Chapters 8 and 9). However, my data suggests that fish herbivory, nutritional resource quality and complexity, are tightly intertwined. Elevated points are likely to receive the highest herbivory rates because they are less likely to accumulate sediments, have relatively high detrital levels, and are likely to be zones of high algal turf productivity (Fig. 5.4) (Chapters 6 and 7). Furthermore, these elevated points allow a greater field of view over the landscape when fishes feed, lowering predation risk (Brandl and Bellwood 2015; González-Rivero et al. 2017; Bellwood et al. 2018). Therefore, elevated surfaces are likely to offer appealing feeding locations for herbivorous fishes, and this feeding activity could in-turn act to maintain low sediment loads in a positive feedback.

Essentially, the evidence suggests that turfs on flatter reefs can trap and retain more sediment, with LSATs prevailing. These LSATs are likely to be less productive with a lower nutritional value (Purcell and Bellwood 2001; Bellwood et al. 2018; Tebbett et al. 2018a). Such conditions have significant implications for the ability of these systems to sustain productive fisheries, especially in light of increasing sediment inputs onto coral reefs. Production of fishable biomass is one of the primary services provided by coral reefs to humanity, with many artisanal fisheries relying heavily on the herbivorous fish assemblage for this service (Edwards et al. 2014; Russ et al. 2015; Robinson et al. 2019c). Unfortunately, heavy exploitation of herbivorous fishes often goes hand in hand with increased sediment inputs from terrestrial sources, due to land-clearing and agricultural practices (Burke et al. 2011; Seemann et al. 2014; Hamilton et al. 2017). My findings highlight the importance of cumulative, anthropogenic burdens on reef systems: flatter reefs facilitate the trapping and retention of sediments in algal turfs, with potential flow-on effects on benthic productivity and harvestable fish productivity (Bellwood et al. 2018; Tebbett et al. 2018a) (Chapters 6 and 8). Sustaining productive reefs in the face of these multifaceted interactions appears to be a particularly complex problem. Maintaining key services from future, low-complexity turf-dominated reefs, appears to be intimately linked to herbivory, sediments, complexity and the condition of the algal turfs.

Chapter 6: 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. I 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 >450 km along Australia's Great Barrier Reef (GBR). Furthermore, to assess the capacity of sediments to shape productivity, I modelled algal turf productivity, as a function of sediment load, across multiple spatial scales. I 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 dense, less productive algae at high sediment loads. Importantly, these relationships provide a robust framework for estimating algal turf productivity on coral reefs. Indeed, when I applied my models to known sediment loads, I revealed that sediment loads alone can 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.

Introduction

Paradoxically, coral reefs exist as highly productive ecosystems within nutrient poor waters (Darwin 1842; Adey and Goertemiller 1986; Brandl et al. 2019b). A paradox that is highlighted by the algae that inhabit coral reefs, which maintain high productivity under such conditions (Hatcher 1988; Steneck 1997; Adey 1998). This productivity in turn supports core trophic pathways on coral reefs, including energy transfer up the food chain through herbivorous fishes (Russ 2003; Kelly et al. 2017). 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 (Hughes et al. 2017a; Bellwood et al. 2019a; Bruno et al. 2019). 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 (Hughes et al. 2017a; Bellwood et al. 2019b; Brandl et al. 2019a).

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 (Chapters 2 and 3) (Wismer et al. 2009; Smith et al. 2016; Donovan et al. 2018), 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. 2017b). As such, 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 (Fabricius 2005; Bainbridge et al. 2018; Magris and Ban 2019). 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 (Chapter 5) (Tebbett et al. 2020c). 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. 2018a). 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. 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. I 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.

Methods

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. D1 in Appendix D). 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 (Chapter 4) (Fabricius et al. 2014; Tebbett et al. 2017c) these two islands can provide differing insights into how sediment dynamics may influence algal turf productivity. Due to Orpheus Island's closer proximity to the mainland, it is also likely to have higher inputs of terrestrially derived nutrients and lower light levels on the benthos (due to higher turbidity levels), when compared to Lizard Island (Fabricius et al. 2014). Differences in these factors (nutrient and light availability) could be important in driving between island differences in algal turf productivity. Furthermore, each island has been subject to different stressors including coral bleaching, cyclone impacts, and sediment disturbances (Chapters 3 and 8) (Goatley et al. 2016; Gordon et al. 2016a; Wismer et al. 2019a). Therefore, as the context of these two islands differs markedly, comparing turf-sediment relationships between the two locations is important because it can provide an insight into the nature of such relationships in different contexts. Importantly, if relationships are found to be similar, then this suggests that variation in sediment loads is a key driver of algal turf condition regardless of the context in question.

At each island I had two sites, each within leeward facing bays (Fig. D1 in Appendix D), and at each site I 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) (also see Chapter 7). For details of the herbivorous fish community at each site see Text D1 and Table D1 in Appendix D.

Field sampling

At each site productivity was measured in terms of the change in turf length using a standard caging technique (following Russ 2003; Roff et al. 2019). 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. 2018a). 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 (Chapter 4) (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.

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 14688-1:2017). 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.

Statistical analyses

Initially I 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 D2 in Appendix D 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, I 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. 2018a), rather than turf length, I 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. I therefore built a model to predict initial sediment load as a function of initial algal turf length (see Text

D2 in Appendix D). I 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 analyses were performed in the software R (R Core Team 2020) using the *rstanarm* (Goodrich et al. 2018), *rstan* (Stan Development Team 2018), *brms* (Burkner 2017), *bayesplot* (Gabry and Mahr 2018), *tidybayes* (Kay 2019), *tidyverse* (Wickham et al. 2019) and *emmeans* (Lenth 2020) packages.

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 and McCook 1999; Russ 2003), while Tebbett et al. (2020c) 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. 2017c, 2020c). Therefore, to examine the potential impact of sediment loads on algal turf productivity across different spatial scales, I applied my 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 Chapter 5 (Tebbett et al. 2020c). 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-shelf (two islands in the Turtle Group), mid-shelf (Lizard Island and North Direction Island), and outer-shelf (Day Reef and Yonge Reef) reefs across the northern GBR were sourced from Tebbett et al. (2017c).

Results

Increasing algal turf sediments loads had a clear effect on the nature of the algal turfs (Fig. 6.1). There was a strong positive relationship between sediment load and algal turf length (Fig. 6.1a). 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 D3 in Appendix D). 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) (Fig. 6.1b; Table D3 in Appendix D). However, there was a marked effect of sediment load on the proportion of organic particulate material (detritus) in the total benthic particulate mass (Fig. 6.1c). The proportion of detritus in benthic particulates declined rapidly from 0 g m^{-2} of sediment until an inflexion point centred around a sediment load of ~68 g m^{-2} (Fig. 6.1c). 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 D3 in Appendix D). 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.

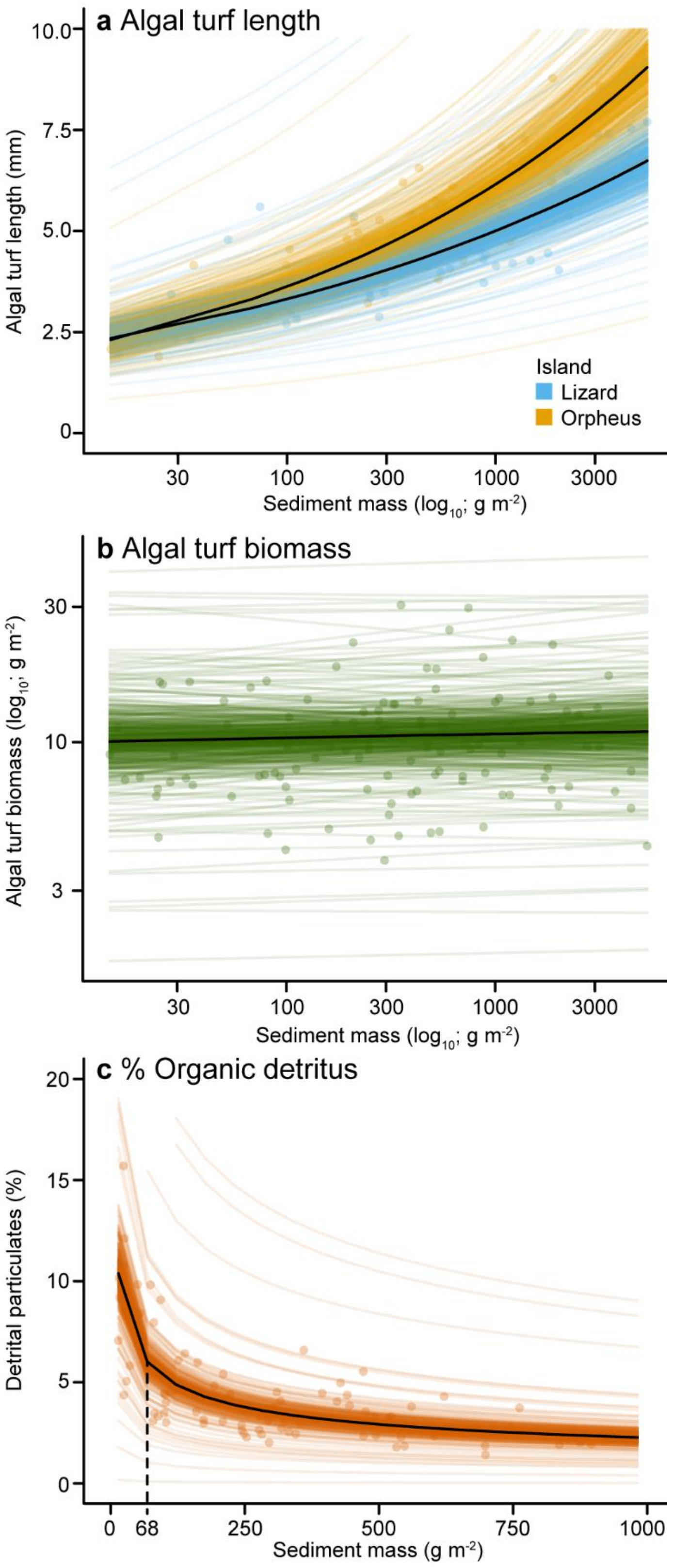

Figure 6.1 The relationship between algal turf sediment load and a) algal turf length, b) algal turf biomass, and c) percentage of organic detritus by mass in benthic particulates. The black lines indicate the mean predicted model fit, while the coloured lines are based on 500

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. D2b in Appendix D 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. 6.2). 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. 6.2). 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 D3 in Appendix D). 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 D3 in Appendix D). 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 D3 in Appendix D). 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.

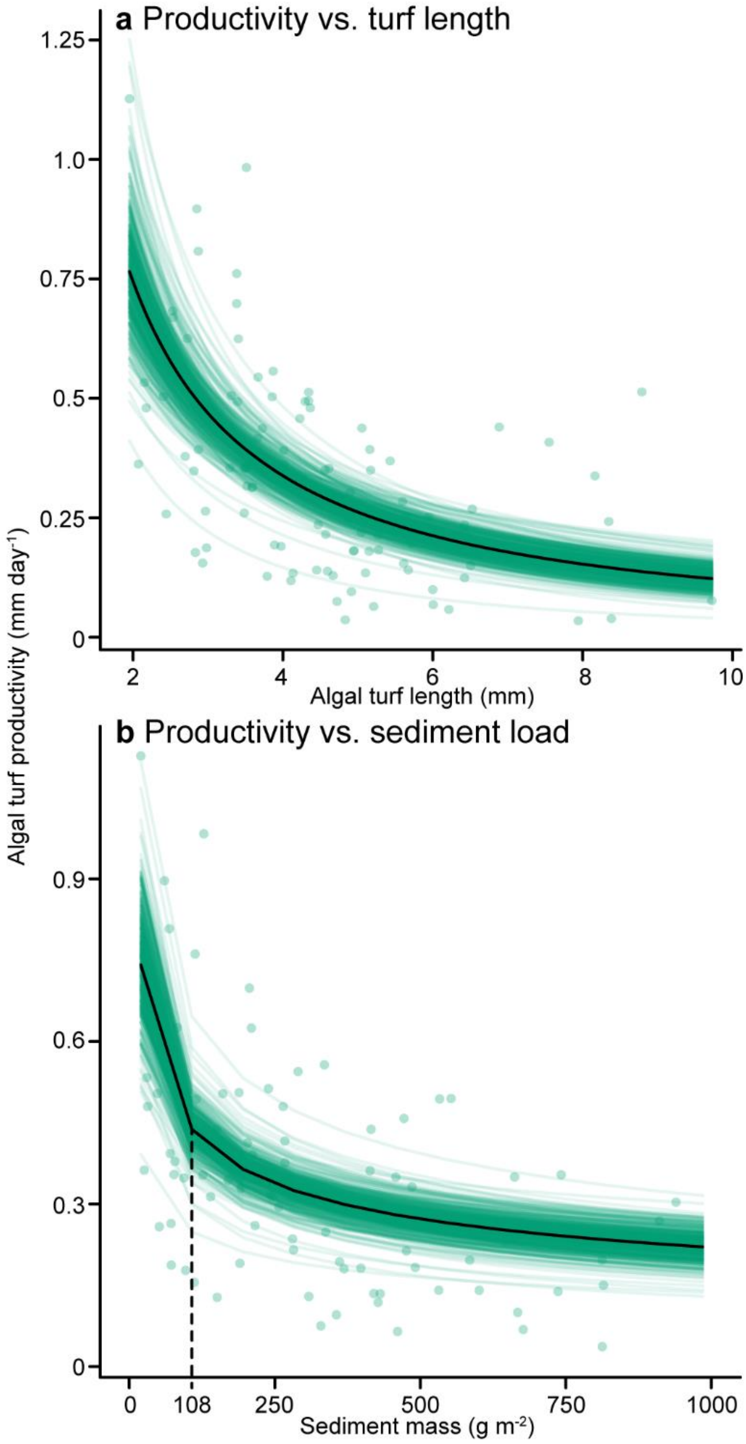

Figure 6.2 The relationship between algal turf productivity and a) initial algal turf length, and b) predicted initial algal turf sediment load. The black line indicates the mean predicted model fit, while the green lines are based on 500 randomly selected model fits sampled from the posterior distribution. 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. D2c in Appendix D 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. 6.3). 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. 6.3a). 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. 6.3b). 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. 6.3c). Taken together, these patterns highlight the potential of algal turf sediments to drive variation in algal turf productivity across multiple spatial scales.

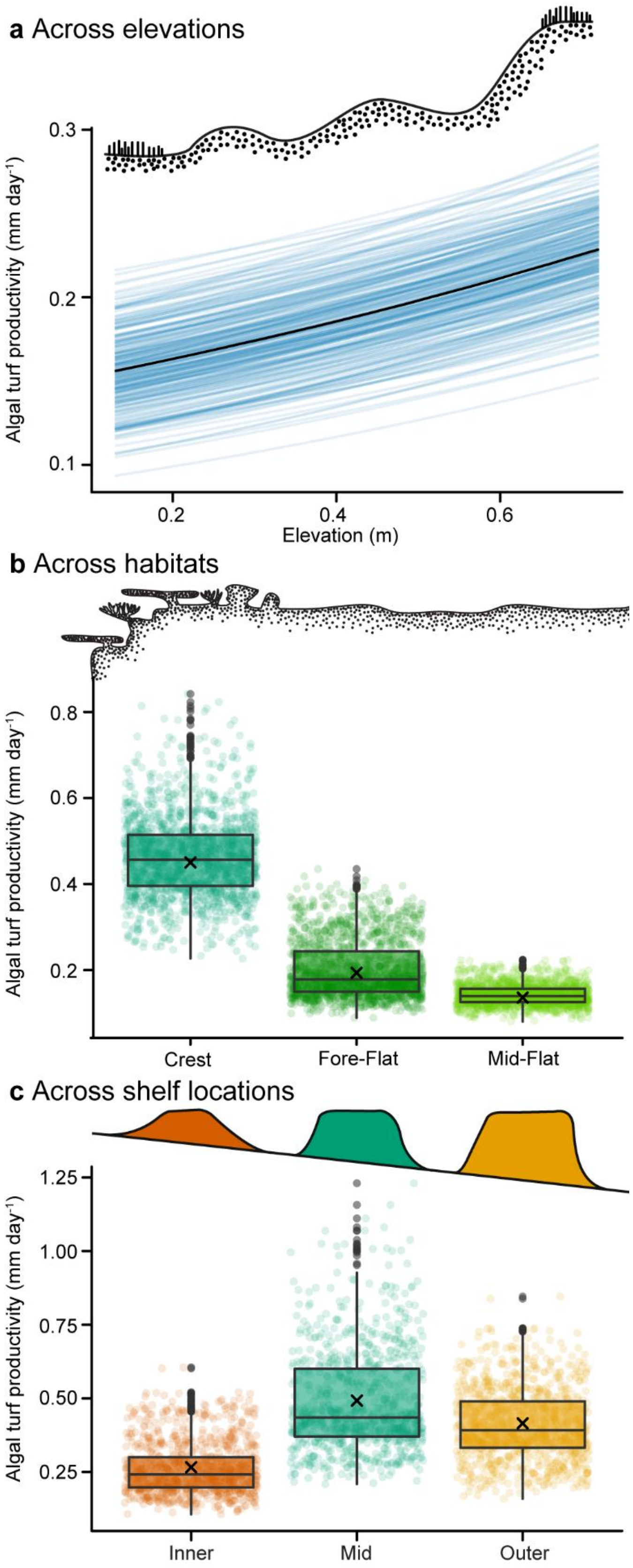

Figure 6.3 Predicted algal turf productivity across varying a) substratum elevations at Lizard Island, Australia, b) reef habitats at Lizard Island, and c) shelf positions across the Great

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.

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 (Chapter 2) (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; Ricardo et al. 2021), herbivory (Kelly et al. 2017; Duran et al. 2019; 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, I examined the relationship between sediments and the nature/functioning of algal turfs (Fig. 6.4). I 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 sediment loads increased. As such, even small shifts in the state of algal turfs towards LSATs, brought on by stressors such as enhanced sediment fluxes or overfishing (Goatley et al. 2016; Fong et al. 2018; Tebbett et al. 2018a), may have considerable bottom-up effects on coral reef ecosystem processes.

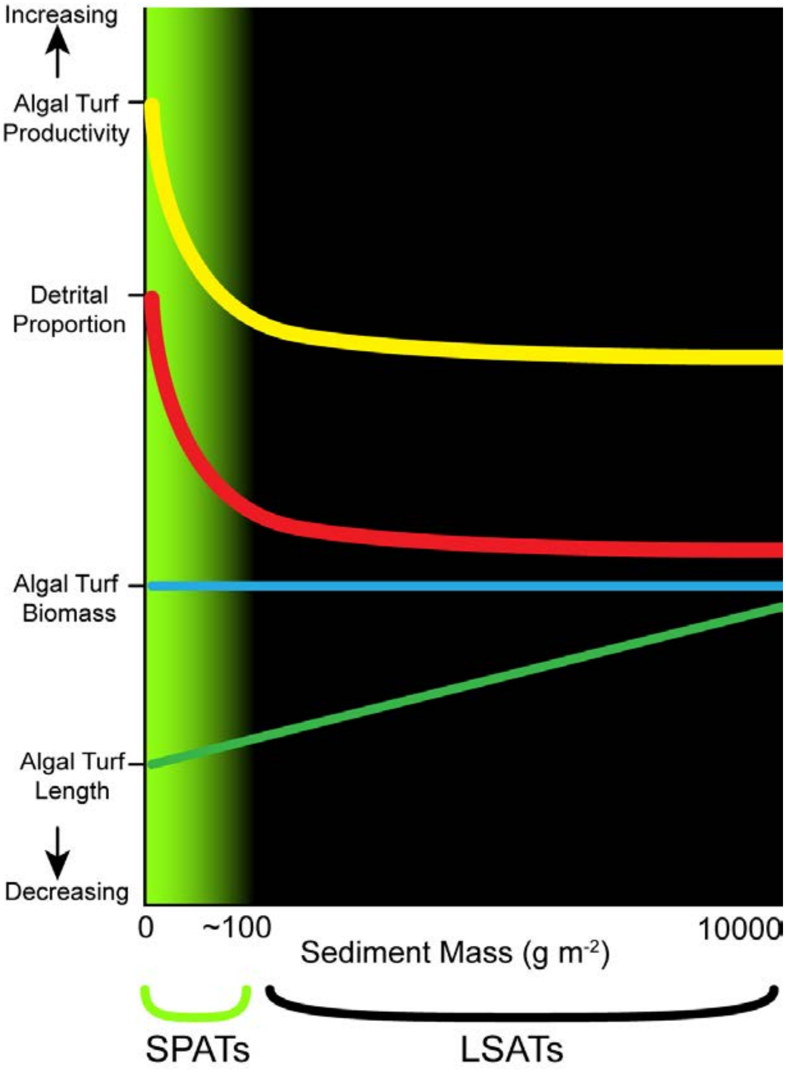

Figure 6.4 A conceptual diagram summarising the major changes in the nature of algal turfs on coral reefs across a spectrum from short productive algal turfs (SPATs) to long sediment-laden algal turfs (LSATs). Note that the nature of algal turfs in terms of productivity, and the relative nutritional value of particulates, decline rapidly from 0 to about 100 g m^{-2} of sediment (see Figs 6.1 and 6.2 for more details). The diagram therefore shows SPATs ending when algal turf length exceeds ~5 mm and sediment loads exceed ~100 g m^{-2}

My results support previous studies which have highlighted the positive relationship between algal turf length and sediment load on coral reefs (Purcell 2000; Gordon et al. 2016a;

Fong et al. 2018), 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, I highlight a fundamental shift in the productivity of algal turfs, with rapid changes at very low sediment levels <100 g m^{-2} (Fig. 6.4). Such low sediment levels can accumulate in algal turfs in less than three days (Tebbett et al. 2018a; Latrille et al. 2019). Importantly, I 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 dense, less productive algal taxa. Visually algal turfs appear to transition from a low dense complex algal turf community to sparse etiolated algal filaments. Such changes in algal turf community composition across sediment loads has been shown on subtropical rocky reefs (Stewart 1983; Airoldi et al. 1995), 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 my study is that it could provide 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 my case, algal turf length could be a similar 'universal trait' for benthic algal turfs (although confirmation of this will require replication of this study in other biogeographical regions). This one trait appears to be related to many facets of algal turf condition (Goatley et al. 2016; Flower et al. 2017; Steneck et al. 2018), including accumulated sediment mass (the underlying driver of most processes related to algal turfs [Clausing et al. 2014; Goatley et al. 2016; Fong et al. 2018]). Importantly, we can now estimate productivity as a function of algal turf length and/or sediment load, with this representing an important 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) (Chapter 4).

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 1989, 1992), caging techniques over extended temporal scales (e.g. Russ and McCook 1999; Russ 2003), 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. 2018a) (examined in more detail in Chapter 7). 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). My 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 I applied my models to estimate productivity at various spatial scales.

My estimated multi-scale patterns of algal turf productivity, as a function of sediment load (based on models derived from the 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), and generally far lower productivity on inner-shelf reefs relative to mid-, and outer-shelf reefs on the GBR (Williams et al. 1986; Russ and McCook 1999). Furthermore, my results support the suggestions of Tebbett et al. (2020c) (Chapter 5), that enhanced algal turf sediment accumulation on flatter, low-elevation, climate-modified coral reefs could reduce algal turf productivity. Based on the 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 (in the form of yield to herbivores) (Tebbett et al. 2018a). 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; Klumpp and McKinnon 1989; Hatcher 1990; Roff et al. 2019) (explored in more detail in Chapter 7), my results show that algal turf sediments could explain a substantial degree of productivity variation across natural and disturbed systems.

Remarkably, I 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 D1 in Appendix D]) (Cheal et al. 2012), physical (e.g. sediment resuspension, water visibility/light penetration and oceanic flushing) (Woolfe et al. 2000; Brodie et al. 2012b), and anthropogenically enhanced (e.g. terrestrial inputs of nutrients) (Kroon et al. 2012; Fabricius et al. 2014), drivers. Many of these drivers, especially nutrients, have been linked to algal productivity on coral reefs (Williams and Carpenter 1988; Hatcher 1990; Russ and McCook 1999; Smith et al. 2001; Graham et al. 2018). The variation in these drivers would have been captured in my 'island identity' factor. However, I found minimal between-island effects, 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.

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. 2020c). As such, my study carries particularly important 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. 2019c). 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 (see Chapter 8). 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 (Tebbett et al. 2018a; Morais and Bellwood 2019; Robinson et al. 2019c), this fishable biomass productivity may be intimately linked to the ability of the algae to provide nutritional resources to these fishes (Russ 2003; Kelly et al. 2017). However, I have highlighted that the capacity of algal turfs to provide these nutritional resources appears to be heavily dependent upon accumulated sediment loads. These findings come at a time when global climate change has driven widespread losses of coral cover on the world’s coral reefs, with many reefs now covered primarily by algal turfs (Hughes et al. 2017a; Bellwood et al. 2019a; Bruno et al. 2019). 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.

Chapter 7: Algal turf productivity on coral reefs: a meta-analysis

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Abstract

Algal turfs are an abundant and highly productive component of coral reef ecosystems. However, our understanding of the drivers that shape algal turf productivity across studies and among reefs is limited. Based on published studies I considered how different factors may shape turf productivity and turnover rates. Of the factors considered, depth was the primary driver of turf productivity rates, while turnover was predominantly related to turf biomass. I also highlight shortcomings in the available data collected on turf productivity to-date; most data were collected prior to global coral bleaching events, within a limited geographic range, and were largely from experimental substrata. Despite the fact turfs are a widespread benthic covering on most coral reefs, and one of the major sources of benthic productivity, our understanding of their productivity is constrained by both a paucity of data and methodological limitations. I offer a potential way forward to address these challenges.

Introduction

Globally, millions of people directly rely on highly productive, shallow-water coral reef ecosystems (Moberg and Folke 1999; Woodhead et al. 2019). This productivity is harnessed by people in the form of fishable biomass (Teh et al. 2013; Samoilys et al. 2017; Lau et al. 2019; Robinson et al. 2019c), with fishes acting as conduits that shunt primary productivity up the food chain (Russ and St. John 1988; Rogers et al. 2018a; Morais et al.

2020a). It is posited that primary productivity and its utilisation by herbivorous fishes are two of the eight core ecosystem processes that are fundamental to the functioning of coral reefs (Brandl et al. 2019a). If the goal of coral reef scientists and managers is to sustain the functioning of coral reef ecosystems into the future, especially in productive states that continue to provide key services to people (Hughes et al. 2017a; Bellwood et al. 2019a), then understanding the nature of primary productivity in these ecosystems is clearly important.

The highly productive nature of coral reefs is epitomised by the diminutive algal turfs, small <2 cm tall multispecies assemblages of algae (Fig. 7.1b), that cover the hard substratum in these ecosystems (Adey 1998; Connell et al. 2014; Tebbett and Bellwood 2019). Indeed, it has been widely suggested that these algal turfs are the major contributors to benthic productivity on coral reefs (e.g. Adey and Steneck 1985; Carpenter 1985; Hatcher 1988; Klumpp and McKinnon 1989). Productivity is considered herein as the biomass (g Carbon) produced by algal turfs in a given area over a given time (m^{-2} day^{-1}). This contribution of algal turfs to productivity is set to increase as global climate change, and a suite of other stressors, reduce coral cover on reefs, leading to an inevitable increase in algal turf cover (Chapters 2 and 3) (Holbrook et al. 2016; Brown et al. 2017; Ellis et al. 2019; Koester et al. 2020; Vercelloni et al. 2020). However, while the highly productive nature of algal turfs piqued the interest of formative reef scientists (e.g. Odum and Odum 1955; Wanders 1976; Hatcher 1981; Adey and Steneck 1985; Carpenter 1985; Russ 1987), we currently lack a full understanding of how algal turf productivity varies across previous studies and different coral reefs.

A broad suite of drivers have been linked to the productivity of algal turfs (Klumpp and McKinnon 1989; Hatcher 1990). These potential regulators of algal turf productivity are likely to include light availability (Carpenter 1985; Klumpp and McKinnon 1989), hydrodynamic activity (Roff et al. 2019), nutrients (Williams and Carpenter 1988; Sura et al.

2019) and sediment loads (Chapter 6) (Tebbett et al. 2018a). All such drivers vary among reefs. In addition to these drivers, the methods employed for quantifying algal turf productivity (e.g. the substratum algal turfs were grown on) may also shape our understanding of this process. However, to-date, the studies that have quantified algal turf productivity on coral reefs have not been considered together in a comparative framework, limiting our understanding of how and why algal turf productivity varies across studies and among coral reefs. This comes at a time when anthropogenic activity is altering the strength of many biophysical drivers on the world's reefs (Harborne et al. 2017; Hughes et al. 2017a; Williams et al. 2019a; França et al. 2020), with algal turfs set to play an ever more central role in the functioning of coral reef ecosystems into the future (Bellwood et al. 2019b; Tebbett and Bellwood 2019).

Considering the rapidly changing nature of reefs, it is surprising that we currently lack a clear understanding of how and why the productivity of a core group of benthic primary producers varies among reefs and across past studies. The aim of this study, therefore, is to gather available data on coral reef algal turf productivity and assess how it varies among coral reef locations. In doing so, I will explicitly consider how the available data in this research field, and the methods employed to quantify algal turf productivity to-date, may have shaped our understanding of algal turf productivity. To achieve these aims, this study will utilise a robust analytical framework to bring together data from disparate studies and provide an insight into the cross-study drivers of algal turf productivity on coral reefs.

Methods

Productivity database compilation

To assess how algal turf productivity varies across coral reefs I first had to compile a database of productivity measurements from previous studies. This was achieved by undertaking an extensive search of the literature. Initially, I undertook a formal search in Google Scholar using the search terms '("algal turf" OR "epilithic algal") AND (production OR productivity OR growth) AND "coral reef"'. This search yielded 4010 results in April 2020 (not including patents or citations). To check how comprehensive Google Scholar was I also ran this search through Scopus and Web of Science. These two search engines only yielded a total of 1945 and 78 results, respectively. I initially filtered the 4010 studies returned by Google Scholar for any potentially relevant studies based on the title and abstract, yielding a pool of 105 potentially relevant studies. To ensure that my search was comprehensive, and that I did not overlook any, more cryptic, studies, I also undertook two general searches of the literature in Google Scholar using the search terms 'algal turf productivity' and 'algal turf productivity coral reefs' and filtered the 1000 most relevant studies in each case. This process yielded an additional 26 potentially relevant studies. Based on my prior knowledge in this research field there were also 5 additional studies that I was aware of, and thought may contain relevant information on algal turf productivity. These 5 additional studies were added to the pool of potentially relevant studies for a total of 136 studies. It is important to note that these 5 additional studies were not found in the searches because they were relatively old and published in unusual journals, conference proceedings or in a PhD thesis. These studies would have been overlooked without extensively reading the relevant literature.

Each of the potentially relevant studies was then evaluated against a specific set of criteria to determine if it could be included in my analysis. These criteria were: a) that quantification of productivity was performed in-situ on the reef; b) details of the sampling month/depth/specific location were provided; c) the study quantified 'productivity' directly (N.B. data on 'yield to herbivores' [i.e. the amount of algal biomass removed by herbivores] was not included; see Russ [1987] for details of how productivity and yield to herbivores differ) in g Carbon m^{-2} day^{-1} (or in a form that could be converted into this unit of measure); d) the substratum that turfs were grown on had been conditioned to some extent on the reef; and e) the algal community examined fell within the general definition of small <2 cm tall multispecies assemblages of algae on a hard benthic substratum, i.e. algal turfs (Steneck and Dethier 1994; Connell et al. 2014; Tebbett and Bellwood 2019). Studies were deemed to have met this definition of algal turfs, and thereby warrant inclusion in my dataset, based on descriptions of the algal community examined, as well as photographs and diagrams, in each study. For example, the study by Hatcher and Larkum (1983) was not included in my dataset as algal turfs in their study included 'a 3- to 8-cm thick, fleshy algal turf'.

I applied the above criteria to ensure that: a) algal turf productivity was reflective of natural conditions on the reef and the relevant drivers at the study location (i.e. productivity was not measured under laboratory conditions where these drivers were altered); b) suitable information was available to assess potential drivers underpinning the productivity values recorded (especially depth and sampling month); c) I did not confuse 'yield to herbivore' measurements as 'productivity' measurements; d) I focused on the units most widely used for primary productivity on coral reefs (Hatcher 1988; Klumpp and McKinnon 1992; Russ and McCook 1999); e) values were not biased by initial algal turf settlement dynamics (Diaz-Pulido and McCook 2002; Fricke et al. 2011); and f) I only examined 'algal turfs' rather than macroalgae or productivity of entire reef communities. It should be noted that my definition of 'algal turfs' includes non-algal cyanobacteria (see Borowitzka et al. 1978; Diaz-Pulido and McCook 2002) and the methods commonly used to quantify algal turf productivity (e.g. scraping algal biomass from coral blocks) is likely to include contributions from endolithic algae and cyanobacteria in the surficial layers of the substratum matrix (e.g. (Odum and Odum 1955; Tribollet et al. 2002). After this filtering process I was left with a pool of just 17 studies (14 were derived from the initial formal search, 2 from the general search and 1 study that I was aware of). My search and filtering procedures were based on PRISMA protocols (Moher et al. 2009) with a flow-diagram provided (Fig. E1 in Appendix E).

From my pool of relevant studies, I then extracted data on algal turf net primary production (g Carbon m^{-2} day^{-1}). Where possible I also extracted data on turnover or calculated this based on standing biomass estimates provided in the studies. Here turnover was considered as the ratio of production (g C m^{-2} day^{-1}) to standing biomass (g C m^{-2}) measured in % day^{-1} (Odum and Odum 1955). From each study, data were sourced from tables or, where necessary, extracted from graphs using WebPlotDigitizer (Rohatgi 2019) (full details of data extraction procedures for each study are reported in Table E1 in Appendix E). In addition, all mean ± SE values used in the dataset are provided in Table E3 and the raw data extracted from each study is presented in Fig. E2 in Appendix E.

Explanatory variable compilation

In addition to extracting productivity and turnover data from each study, I also extracted information on available, relevant, variables to assess why and how productivity data vary. Firstly, I extracted information on the water depth in which each observation was quantified. Water depth was considered because it is a key environmental gradient that is strongly correlated with light availability (Roberts et al. 2019), hydrodynamic exposure

(Fulton and Bellwood 2005), sediment loads (Purcell 2000) and herbivory (Cooper et al. 2019), all of which have been linked to algal turf productivity levels (Carpenter 1985, 1986; Tebbett et al. 2018a; Roff et al. 2019).

Secondly, seasonal influences were considered by quantifying the sampling month for each observation reported in the study. Seasonal influences were standardised between northern and southern hemispheres as the month since first winter month (i.e. December = 1 in northern hemisphere locations, June = 1 in southern hemisphere locations). The yearly seasonal cycle has previously been related to algal turf productivity as both temperature and day length (light availability), vary during this cycle which influences productivity (Carpenter 1985) as well as herbivory (Van Rooij et al. 1998; Longo et al. 2019).

Thirdly, hydrodynamic exposure of the study location (windward, leeward or protected [lagoonal]) was noted based on information reported in each study. Again, hydrodynamic exposure has previously been linked to algal turf productivity (Roff et al. 2019), and it influences other factors such as algal turf sediment loads (Tebbett et al. 2017c), herbivory (Bejarano et al. 2017), turbidity/light availability (Whinney et al. 2017) and mass transfer to algal turfs (Carpenter and Williams 2007).

Fourthly, the reef identity was recorded. This reef identity factor accounted for the lack of spatial independence present in the dataset due to multiple measurements coming from the same reefs. This reef identity factor also concatenated the range of broader-scale drivers (e.g. sea surface temperature, water clarity, proximity to land, sediment loads, herbivore abundance, hydrodynamic exposure and light availability) that vary among reefs (e.g. Cheal et al. 2012; Fabricius et al. 2014; Assis et al. 2018; Tebbett et al. 2018b; Heenan et al. 2020) and could influence algal turf productivity levels over broader spatial scales. While concatenating these variables into a single categorical factor loses information on what specific variables may be important, it can effectively account for the lack of spatial independence in the database. In addition, limitations with the data (i.e. a spatial and temporal mismatch in the scale at which algal turf data were collected [i.e. cm scale] and data on explanatory factors at global scales is compiled [i.e. km scale]), and the high degree of co-linearity among explanatory variables, precluded the consideration of these broader scale factors in more detail.

Fifthly, the study identity was recorded. As above, this study identity factor accounted for the lack of independence present in the dataset due to multiple observations from the same studies. In addition, the study identity factor concatenated the potential effects of a range of 'study-level' factors (e.g. the quantification method, study substratum, and the conditioning time of substrata) that could influence productivity values. Notably, different methods have been used to quantify algal turf productivity including respirometry techniques and caging techniques, therefore, differences between these techniques, may have shaped productivity estimates. The surfaces algal turfs are grown on, as well as how long experimental surfaces are conditioned for, can also substantially influence their community composition (Harlin and Lindbergh 1977; Borowitzka et al. 1978; Hixon and Brostoff 1985) with potential impacts on the community's productivity. While noting this factor, I also specifically recorded the year each observation was taken, as well the substratum (natural coral reef benthos, block/tile cut from a dead coral skeleton, or artificial tile) from which algal turf productivity was quantified, to facilitate more nuanced insights into the algal turf productivity research conducted to-date.

Finally, standing biomass of the algal turfs in g C m^{-2} was extracted for each observation (details of how are provided in Table E1 in Appendix E). Unfortunately, this factor could only be quantified for turnover data because it was not available for all productivity observations. While standing biomass is inextricably linked to turnover estimates it represents an important explanatory variable because it provides information on the efficiency of algal turf productivity as biomass increases. Essentially, if turnover is related in some way to algal turf biomass this suggests that the factors associated with changes in algal turf biomass impact the productivity efficiency of turfs.

Boosted regression trees

To examine the relative importance of each explanatory factor in predicting algal turf productivity or turnover, as well as to examine the nature of the relationship between key explanatory variables and productivity/turnover, I used XGBoost (Chen and Guestrin 2016), an Extreme Gradient Boosted Regression Tree. I used this method because Gradient Boosted Regression Trees are a machine learning technique that can yield fast, accurate, predictions while efficiently modelling nonlinearity and multilevel interactions in data that may not be suitable for more traditional analysis (Elith et al. 2008). XGBoost in particular, utilises an algorithm that has been specifically designed to be efficient, flexible and robust, outperforming algorithms used by other Gradient Boosted Regression Trees (Chen and Guestrin 2016). For the XGBoost models I used Gamma distributions and treated algal turf productivity estimates (g C m^{-2} day^{-1}) or turnover (% day^{-1}) as the dependent variable and examined these against the potential explanatory variables.

Prior to running the XGBoost models to make predictions, two tuning steps were performed following Morais and Bellwood (2018). Firstly, the models were fitted repeatedly with combinations of model parameters (learning rate, maximum tree depth, gamma and subsampling rate) that were varied systematically. The combination of parameters that yielded the minimum root mean square error (rmse) was subsequently recorded (productivity model: learning rate = 0.4, maximum tree depth = 7, gamma = 0.1, and subsampling = 0.5;

turnover model: learning rate = 0.2, maximum tree depth = 7, gamma = 0, and subsampling = 0.5), while all other parameters were kept at their default values. During the second round of tuning, I fitted the models repeatedly with combinations of parameters drawn randomly from a uniform distribution bounded by the recorded parameters from the first tuning round ± 10%. Again, I recorded the parameters that resulted in the lowest rmse (productivity model: learning rate = 0.413, maximum tree depth = 8, gamma = 0.093, and subsampling = 0.543; turnover model: learning rate = 0.188, maximum tree depth = 6, gamma = 0.003, and subsampling = 0.493), however, the second tuning step did not improve rmse substantially in either case as it only changed from 0.329 to 0.333 and from 2.288 to 2.172 for the productivity and turnover models, respectively.

The accuracy and precision of my tuned XGBoost models were subsequently evaluated using a cross-validation procedure. To do this, the productivity and turnover datasets were randomly split into training and testing datasets. The training datasets were used to refit the models to generate coefficients for prediction and were based on 80% of the data. The testing datasets were used to contrast with predictions from the training dataset and were based on the remaining 20% of the data. I calculated a bias metric by subtracting each algal turf productivity/turnover value predicted by the respective XGBoost model from its actual value (an accurate model has a bias value at or close to zero). Precision of the models was assessed using prediction R^2 values which were calculated by fitting a linear regression model between the raw data values and the predicted values and recording the R^2 from this regression. These cross-validation steps were repeated 1000 times in each case.

Finally, predictions of algal turf productivity as well as turnover were calculated using my tuned and cross-validated XGBoost models across all explanatory variables. To generate a distribution of algal turf productivity and turnover predictions I bootstrapped the models for 1000 iterations and subsequently sampled the median predicted value ± 95% highest density intervals. The relative importance of different predictor variables, in accounting for variation of algal turf productivity and turnover estimates, were assessed against the expected importance of variables given chance alone (i.e. if all variables were equally involved in explaining variation within the dataset then each variable would account for 20% or 16.7% of the variability explained by the productivity or turnover XGBoost models, respectively). All XGBoost modelling was performed in the software R (R Core Team 2020) using the *XGBoost* (Chen et al. 2019) package.

Methodological considerations

In addition to assessing how and why algal turf productivity observations vary among coral reefs, I wanted to further consider how the methods used to quantify algal turf productivity could have shaped our understanding. Specifically, I wanted to consider the implications of quantifying algal turf productivity on experimental tiles/coral blocks, rather than natural reef substrata. Especially, considering recent research that has linked the accumulation of sediment in algal turfs to the growth of turfs (Clausing et al. 2014; Tebbett et al. 2018a; Tebbett and Bellwood 2020). I initially sourced data on sediment accumulation in natural algal turfs (n = 20) and in algal turfs on conditioned coral blocks (n = 43) from Tebbett et al. (2018a). Note the data contained within this previous study represented a direct comparison between natural reef substrata and coral blocks as all sediments were collected from the same location (Lizard Island), in the same habitats (the reef flat between Palfrey and South Island), at the same sites (two sites), during the same sampling period.

Initially, I specifically tested for differences in sediment loads in algal turfs on natural substrata versus coral blocks using a Bayesian generalised linear model (GLM) with a Gamma distribution and log link. Substratum identity (natural or block) and site identity were fitted as interacting fixed effects. The GLM was based on weakly informative priors, 3 chains, a warmup of 500 iterations, a thinning value of 3 and 3000 iterations. Model convergence, fit and assumptions were assessed using trace plots, autocorrelation plots, rhat plots, posterior predictive checks, effective sample sizes and residual plots. These tests suggested the chains were well mixed and had converged on a stable posterior, and that no patterns were present in the residuals. I then predicted potential algal turf productivity (mm growth day^{-1}), as a function of sediment load, on coral blocks and natural reef substrata. To do this I utilised a Bayesian model, relating potential algal turf productivity to sediment loads, formulated in Tebbett and Bellwood (2020) (Chapter 6), and fed each sampled sediment load to this model to estimate productivity (mm growth day^{-1}) for that specific sediment load. It should be noted that the term ‘productivity’ applies to increases in mass, however, in the case of this model the term ‘productivity’ is applied to increases in turf length. All statistical analyses were performed in the software R (R Core Team 2020) using the *rstan* (Stan Development Team 2018), *rstanarm* (Goodrich et al. 2018), *bayesplot* (Gabry and Mahr 2018), *tidybayes* (Kay 2019), *tidyverse* (Wickham et al. 2019) and *emmeans* (Lenth 2020) packages.

Results

Dataset

After examining the relevant literature on coral reef algal turf productivity my final dataset consisted of 214 productivity estimates and 155 turnover estimates from 17 and 11 studies, respectively. While I placed no spatial or temporal limitations on the inclusion of studies in this dataset there were some noticeable patterns. Firstly, despite observations being distributed around several of the world’s coral reef regions, the vast majority (54% and 63% of productivity and turnover observations, respectively) were from the Great Barrier Reef

(Fig. 7.1a). Secondly, the restricted temporal distribution of these observations was marked, with 80% and 94% of productivity and turnover data, respectively, collected prior to 1990 (Fig. 7.1c). Finally, most of the productivity and turnover observations (92% and 98%, respectively) were based on experimental substrata (coral blocks or artificial tiles), rather than studying natural reef substrata (Fig. 7.1d).

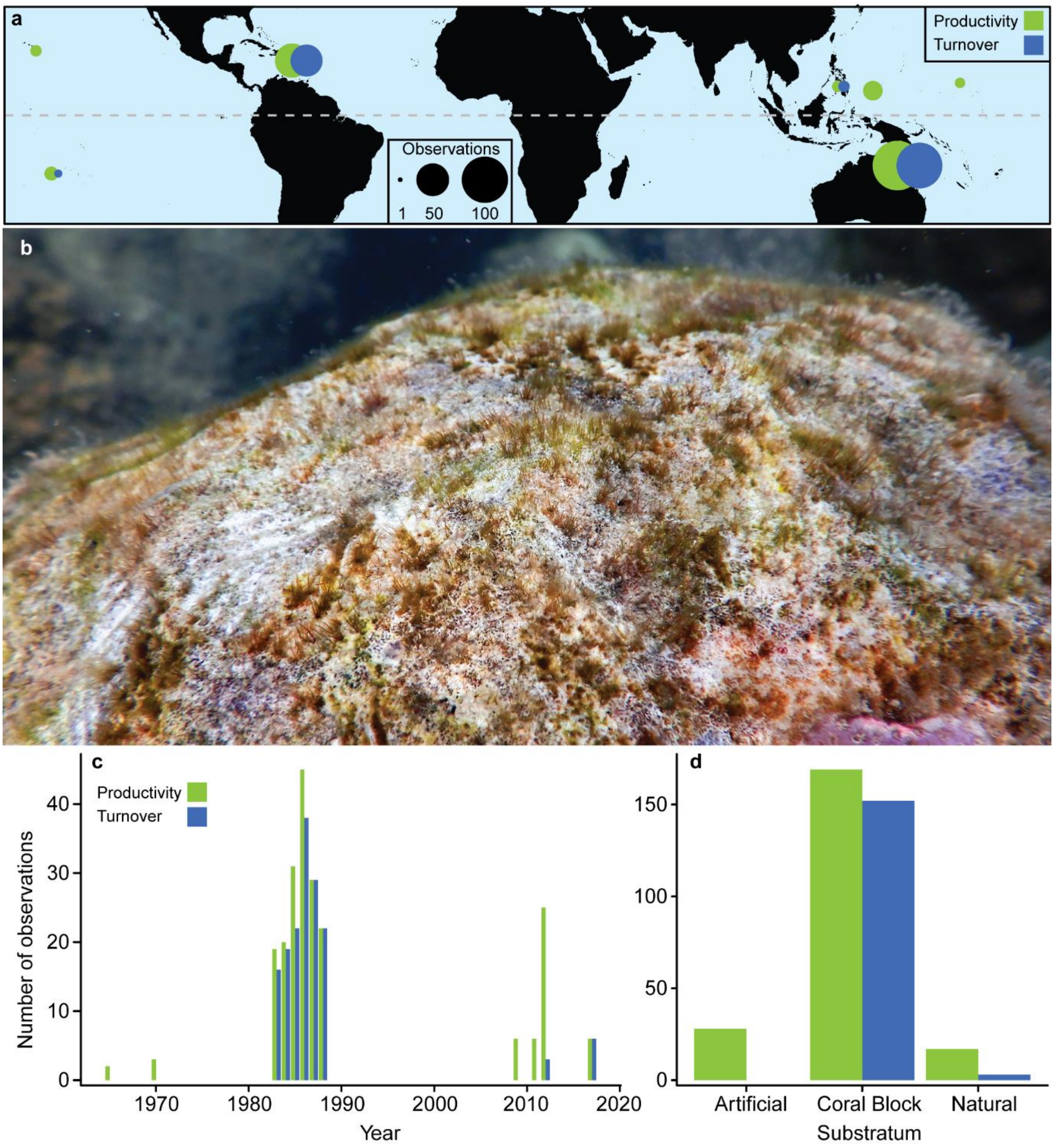

Figure 7.1 a) The distribution of algal turf productivity and turnover observations from coral reefs around the world in my dataset. b) A short productive algal turf community on a shallow-water coral reef at Orpheus Island on the Great Barrier Reef (photograph: CHR Goatley). c) The temporal distribution of algal turf productivity and turnover observations in my dataset. d) The frequency by which algal turf productivity and turnover were examined on different substrata in my dataset.

Drivers of algal turf productivity and turnover

The formulated XGBoost models resulted in a median bias that was close to zero (0.26 and 0.349 for the productivity and turnover models, respectively) suggesting that the models were relatively accurate. Furthermore, the median R^2 of the final models were 0.69 and 0.87 (for the productivity and turnover models, respectively), suggesting that the models were relatively precise. These XGBoost models revealed that some of the explanatory variables were far more important than others in accounting for patterns in algal turf productivity and turnover. In terms of productivity, depth was the single most important variable and explained 47.0% (median) (39.2% - 55.0%; upper and lower 95% highest density intervals) of the variation in productivity accounted for in the XGBoost model (Fig. 7.2a). In addition, study site (reef) explained more variation in algal turf productivity than expected by chance, accounting for 24.1% (19.3% - 30.3%) of the variation explained (although note that these intervals slightly overlapped the relative importance threshold at 20% suggesting the evidence for this effect is only moderate). Standing algal turf biomass was the single most important variable for explaining turnover patterns, with this variable accounting for 51.5% (46.3% - 58.1%) of the variation in turnover explained by the XGBoost model (Fig. 7.2b). The remaining explanatory variables all remained below the relative importance level expected by chance in both productivity and turnover models.

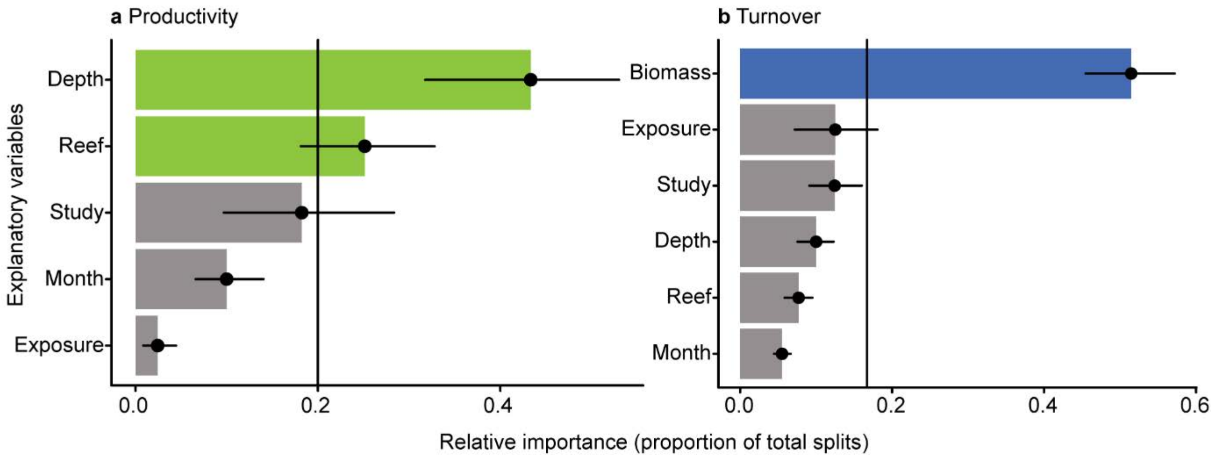

Figure 7.2 The relative importance of potential explanatory variables in accounting for a) algal turf productivity and b) turnover estimates from coral reefs. Black dots indicate the median relative importance value, while the range presented represents the 95% highest density intervals based on bootstrapping predictions 1000 times. The vertical black line indicates the relative importance expected for each variable by chance.

With the key explanatory variables identified, partial dependency plots provided an insight into how these variables related to algal turf productivity and turnover (Figs 7.3 and 7.4). In terms of the relationship between productivity and the key explanatory variables there was a clear decrease in algal turf productivity as depth increased. Notably, productivity remained relatively high down to 5 m, a depth which aligns well with the end of the reef crest habitat and the beginning of the reef slope habitat, before decreasing sharply and remaining relatively low down to 15 m (Fig. 7.3a). While the general nature of this relationship between depth and productivity appeared to be similar across sites (e.g. Fig. 7.3a), there was a distinct difference in the magnitude of productivity levels among sites (Fig. 7.3). Specifically, predicted productivity values from the reef in Tague Bay, St Croix (the only Caribbean site in this dataset) were approximately twice the productivity values from all other reef sites, which were generally very similar (Fig. 7.3b). Therefore, while decreases in algal turf productivity with depth appear to be a universal pattern, the magnitude of the productivity values may be dependent on the site in question.

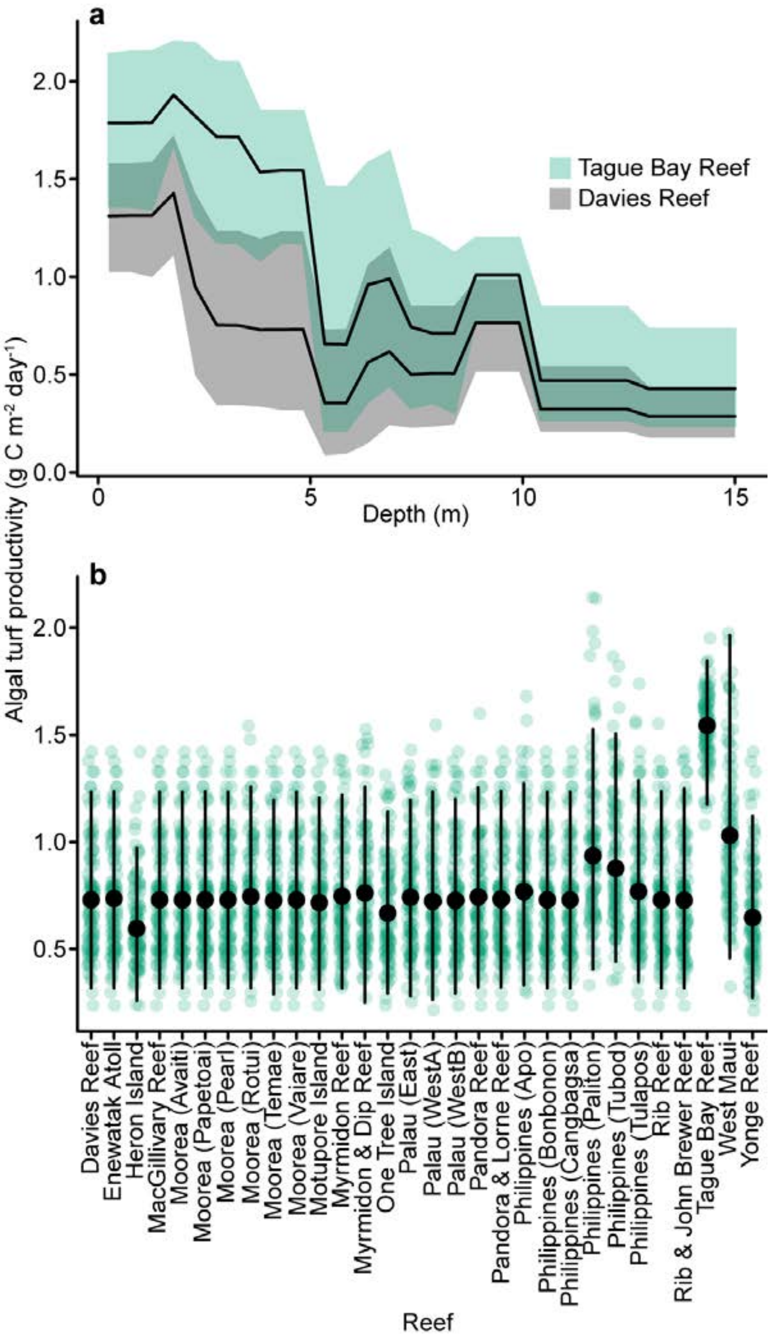

Figure 7.3 Partial dependency plots of the relationship between algal turf productivity and the key explanatory variables that accounted for more variability than expected: a) water depth and b) study site. All other variables were kept at their mean values and the most common category of categorical variables were used for plots (note in panel (a) that Davies

Reef and Tague Bay Reef were both equally common in the dataset [n = 55]). The black line (a) and the black points (b) represent the median predicted values, the coloured ribbons (a) and the point ranges (b) denote the 95% highest density intervals, and the green points (b) represent 100 randomly selected predicted values for each reef based on an extreme gradient boosted regression tree model (n = 1000 model iterations).

The relationship between algal turf turnover rates and standing biomass was inverse in nature. Turnover rates appear to be very high at low standing biomass levels but decreased markedly across the range of algal turf biomass levels examined (Fig. 7.4). However, the most precipitous decrease occurred at the lowest algal turf biomass levels (<10 g C m^{-2}), with turnover rates decreasing by more than half across this range alone (Fig. 7.4). This pattern suggests that algal turf productivity rates and standing biomass levels do not scale linearly, with a marked decrease in the ability of turfs to replace existing biomass as standing biomass increases.

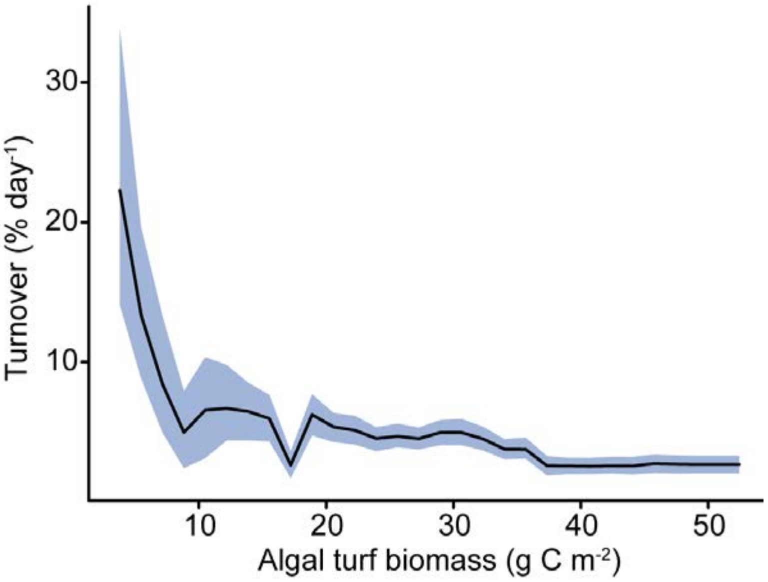

Figure 7.4 Partial dependency plot of the relationship between algal turf turnover and the key explanatory variable (standing algal turf biomass). All other variables were kept at their mean

values and the most common category of categorical variables were used for the plot. The black line denotes the median predicted values, while the coloured ribbon denotes the 95% highest density intervals, based on an extreme gradient boosted regression tree model (n = 1000 model iterations).

Methodological considerations

There were marked differences in the sediment loads accumulated in algal turfs on natural substrata compared to conditioned algal turf-covered coral blocks (Fig. 7.5a). Sediment loads were more than 10-fold higher in natural algal turfs (2031.1 [1292.9 – 3238.4] g m^{-2}; median ± 95% highest posterior density intervals) relative to algal turfs on coral blocks (188.9 [68.5 – 527.9] g m^{-2}) (Fig. 7.5a; Table E2 in Appendix E). The Bayesian model used to test these differences revealed that substratum type did influence sediment load as the 95% credibility intervals did not overlap one (as data were back-transformed from the log scale; Table E2 in Appendix E). There was no evidence that site had any effect on these sediment loads (Table E2 in Appendix E). The differences in accumulated sediment loads translated to clear differences in algal turf productivity when I used a second Bayesian model to predict potential algal turf productivity on each substratum (Fig. 7.5b). Predicted potential algal turf productivity was more than two-fold higher on conditioned coral blocks (0.44 ± 0.02 mm day^{-1}) relative to natural substrata (0.19 ± 0.01 mm day^{-1}). Together, these results suggest that algal turfs grown on coral blocks/tiles accumulate lower sediment loads, potentially yielding higher algal turf productivity rates.

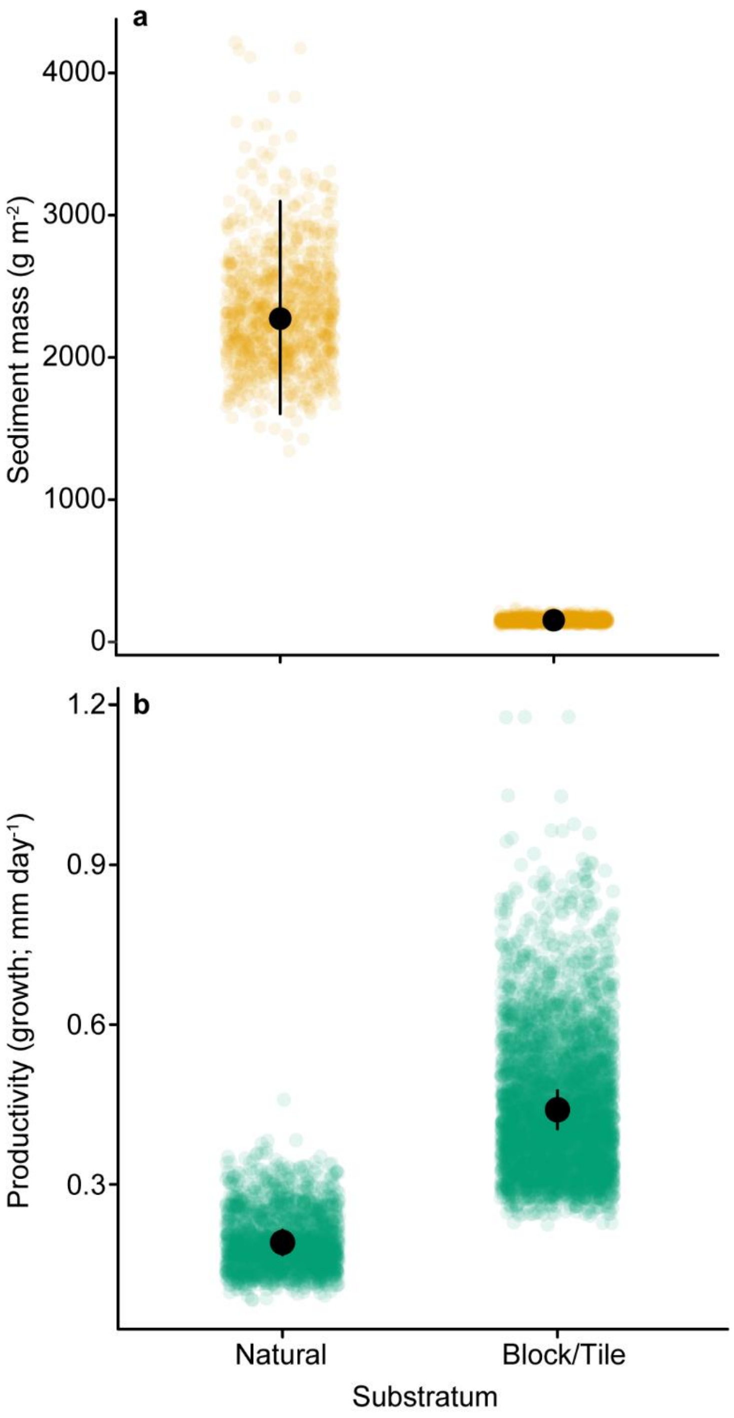

Figure 7.5 Differences in a) sediment loads, and b) estimated productivity, of algal turfs growing on natural substrata and coral blocks. Black points and range represent the mean predicted values and 95% credibility intervals; coloured dots represent 1000 random draws from the posterior distribution of Bayesian models to show the uncertainty around the estimates. The sediment data were sourced from Tebbett et al. (2018a).

Discussion

Algal turfs are a key component of coral reef ecosystems and can underpin their high productivity (Adey and Goertemiller 1986; Hatcher 1988; Steneck 1997) and fuel herbivorous trophic pathways (Russ and St. John 1988; Kelly et al. 2017; Morillo-Velarde et al. 2018). While algal turf productivity may be shaped by a range of factors (e.g. Carpenter 1985; Klumpp and McKinnon 1989; Roff et al. 2019), of the factors I considered, water depth was by far the most important in structuring this productivity on coral reefs. Moreover, my consideration of algal turf turnover revealed that algal turf productivity and standing biomass do not scale linearly together in a one-to-one relationship. This suggests that the efficiency of algal turf productivity decreases as standing biomass increases, i.e. higher biomass reduces the capacity of algal turfs to replace existing biomass. However, it is important to note that in undertaking this meta-analysis I also revealed a distinct paucity of data on algal turf productivity rates from many coral reef regions around the world. Furthermore, I highlighted that the methods employed to assess algal turf productivity on reefs may have shaped our understanding of this process. The implications of these methodological limitations need to be carefully considered when quantifying algal turf productivity on coral reefs in the future.

Productivity

Depth

The depth at which algal turfs exist on coral reefs clearly has a marked influence on their productivity. In this respect, my meta-analysis strongly supports the conclusion of previous studies that have highlighted a decrease in turf productivity with depth (e.g. Klumpp and McKinnon 1989; Carpenter 1990; Russ 2003), as well as variation in other qualities of algal turf communities such as turf yield-to-herbivores, cover and community composition

(Brokovich et al. 2010; Fricke et al. 2011; Magalhães et al. 2015). The clear decline in algal turf productivity as water depth increases is likely to be driven by a variety of key factors including light availability (Brokovich et al. 2010; Fricke et al. 2014; Roberts et al. 2019), wave-driven hydrodynamic activity (Fulton and Bellwood 2005), herbivory rates (Cooper et al. 2019) and algal turf sediment loads (Purcell 2000), that all correlate with water depth on coral reefs to varying extents. Of these factors, light availability is likely to be one of the most important. This is because, the rate of algal turf productivity is constrained as light levels decrease because algal turf photosynthesis rates are closely tied to irradiance levels (Carpenter 1985; Klumpp and McKinnon 1989). Interestingly, previous studies have highlighted that algal turfs are well adapted to high light intensity as rates of photosynthesis increase steadily with irradiance levels, showing few signs of photo-inhibition (Carpenter 1985; Klumpp and McKinnon 1989). This lack of photo-inhibition may underpin how algal turf communities maintain their highest productivity levels at the shallowest water depths.

While depth mediated light availability appears to shape algal turf productivity rates directly (Carpenter 1985; Klumpp and McKinnon 1989), it may also influence productivity rates indirectly by shaping the community composition of algal turfs. Specifically, different algal species make up the algal turf community across depth gradients, potentially due to different tolerances for light levels (Anderson et al. 2005; Fricke et al. 2014; Magalhães et al. 2015). In addition, herbivory is known to decrease substantially as depth increases (Brokovich et al. 2010; Cooper et al. 2019), and this factor can also shape the community composition of algal turfs (Scott and Russ 1987; Hixon and Brostoff 1996; McClanahan 1997). This is important because the nature of algal turf communities, in terms of the species that inhabit them, as well their structure and diversity, is likely to influence biomass and productivity levels, as per-unit biomass and productivity differs between algal species and functional groups (Rogers and Salesky 1981; Steneck and Dethier 1994; Bruno et al. 2006;

but see Williams and Carpenter 1990). As such, variation in algal turf community composition across depth/light gradients could also influence net productivity rates.

Site effects

Apart from factors associated with the depth at which algal turfs exist, there was some variability in productivity among sites. There are two notable points that can be drawn from these results. Firstly, there appeared to be remarkably little variation in algal turf productivity among the vast majority of reef sites. This suggests that the broader scale factors that vary among reefs such as temperature, light intensity and nutrient inputs may not have a substantial influence on algal turf productivity for many reefs. However, secondly, algal turf productivity from the Tague Bay Reef site was approximately two-fold higher than all other sites. These data suggest that a factor, or factors, operating at Tague Bay Reef led to far higher productivity levels at this site. Tague Bay, is located on Saint Croix in the Caribbean, and it has been suggested that Caribbean reefs function quite differently from other reef systems due to factors such as lower species and functional diversity, geographic isolation, and more severe anthropogenic impacts (Bellwood et al. 2004; Roff and Mumby 2012; Bruno et al. 2019; Siqueira et al. 2019). Unfortunately, determining which factors may be accounting for these higher productivity levels is difficult, as Tague Bay is the only site from the Caribbean in my dataset, and all productivity values at this location were quantified on the same experimental substrata, using the same methods. Therefore, it is unclear if these productivity estimates were driven by a methodological difference between the studies at this site vs other studies, a factor associated with the reef in Tague Bay, or a broader Caribbean phenomenon. In the future, quantifying algal turf productivity, as well as potential explanatory factors (e.g. light levels, nutrient concentrations, temperature etc), over matching temporal and spatial scales at a variety of locations, may help disentangle the key drivers of productivity further.

Turnover

Turnover was clearly related to algal turf biomass, highlighting a loss of productivity efficiency as biomass increased. Importantly, variation in algal turf biomass is likely to be associated with variation in the length and density of turf filaments (i.e. an alteration of the algal turf canopy structure) (Purcell 2000; Tebbett and Bellwood 2020), as well as the community composition of algal turfs (Scott and Russ 1987; Hixon and Brostoff 1996; Harris et al. 2015). Essentially, algal turfs exist on a gradient from short productive algal turfs (SPATs) to long sediment-laden algal turfs (LSATs) (Goatley et al. 2016; Tebbett and Bellwood 2020). SPATs are maintained by the constant grazing pressure of herbivorous fishes, as well as other herbivorous organisms, which remove algae, reduce sediment loads (Carpenter 1986; Steneck 1997; Goatley et al. 2016; Steneck et al. 2018; Humphries et al. 2020), and constrain the community of algal species to ones that tolerate high grazing (Sammarco 1983; Scott and Russ 1987; Hixon and Brostoff 1996; McClanahan 1997). However, when the strength of herbivory is reduced, through factors such as herbivore removal (Heenan et al. 2016; Steneck et al. 2018), or the accumulation of sediments that weaken herbivore feeding pressure (Tebbett et al. 2017b; McAndrews et al. 2019), this can result in an increase in algal turf length (Goatley and Bellwood 2013; Fong et al. 2018; Humphries et al. 2020) and/or changes in algal taxonomic composition (Scott and Russ 1987; Hixon and Brostoff 1996), resulting in LSATs.

Across this gradient in algal turf condition from SPATs to LSATs, a number of aboitic factors within the turf canopy varies, including flow speeds and mass transfer

(Carpenter and Williams 1993, 2007), light levels available for photosynthesis via self-shading (Williams and Carpenter 1990) and sediment loads (Purcell 2000; Latrille et al. 2019) (Chapter 6). As turf biomass increases this suite of factors may act together to reduce productivity in the basal portion of the turf community because these factors limit light and the exchange of nutrients. This could result in a turf community that is reliant on the apical portion of filaments for most of the production, i.e. the filament sections that are above the sediment layer and exposed to high water flow and light. As such, reductions in algal turf turnover rates may be driven by changes in the conditions within the turf community as biomass increases.

In addition to the abiotic factors described above, the community composition of the algal turf may be related to the productivity efficiency of the entire turf community as per-unit productivity rates can differ between algal species (Rogers and Salesky 1981; Steneck and Dethier 1994; Bruno et al. 2006; but see Williams and Carpenter 1990). However, unfortunately, our understanding of the specific nature of the relationships between sediment accumulation, canopy structure, productivity and algal turf community composition are currently limited (reviewed in Tebbett and Bellwood 2019), making it difficult to determine the relative importance of community composition changes, compared to abiotic conditions within the turf canopy, in driving variation in turnover. However, exploring these relationships in more detail offers fertile ground for further future research.

Methodological considerations and future studies

Despite evidence that algal turf coverage has increased on coral reefs in recent decades (Chapter 2) (Toth et al. 2014; Holbrook et al. 2016; Ellis et al. 2019; Kennedy et al. 2020; Koester et al. 2020), and algal turfs are likely to be an abundant benthic covering on coral reefs in the future (Bellwood et al. 2019a; Tebbett and Bellwood 2019), the paucity of available data on their productivity is concerning. Unfortunately, beyond the foundations laid by the pioneering research of formative reef scientists (e.g. Carpenter 1986; Klumpp and McKinnon 1992; Steneck 1997; Russ and McCook 1999) there appears to have been remarkably little quantification of algal turf productivity in-situ on coral reefs within the last three decades, within the scope of my meta-analysis. It is important to note that this result is not because of my search parameters and paper filtering methods, as the same units of measure (g C m^{-2} day^{-1}) are just as applicable to studies of productivity today as they were historically. Unfortunately, the exact reason behind the limited quantification of algal turf productivity in-situ on coral reefs in recent decades is unclear. It may be due to logistics (limited access to respirometery chambers or field time/access). However, it probably reflects a shift in emphasis, with attention focussed on documenting declines rather than understanding the system.

Regardless of the reasons behind the limited quantification of algal turf productivity, the amount of available data is sobering. Especially, considering the extent to which coral reef research has grown recently, the technological advances that have assisted this research, the strength and frequency of environmental disturbances (e.g. global coral bleaching events) that are now shaping this ecosystem (Cheal et al. 2017; Hughes et al. 2018a; Williams et al. 2019a), and the inevitable increase in algal turf area on reefs (Chapter 2) (Bellwood et al. 2019a; Tebbett and Bellwood 2019; Vercelloni et al. 2020). If we are to understand the functioning of coral reef systems into the future, it appears to be a logical imperative to enhance our knowledge about the productivity of one of the most widespread primary producers; algal turfs. To stimulate further research into the quantification of algal turf productivity on coral reefs, this may require the development of new technologies that are both relatively cheap and easy to use in the field (see below for further discussion), as well as greater collaboration between research groups with access to such technologies, or with access to areas where turf productivity has not been quantified. In addition, exploring potential links between algal turf productivity and other reef processes, that are viewed as inherently valuable (e.g. fishable biomass [Lau et al. 2019; Woodhead et al. 2019]), may help highlight the importance of turfs on coral reefs, and in-turn, encourage the study of turfs in other research fields.

Furthermore, it must be noted that our understanding of algal turf productivity to-date appears to have been shaped substantially by the methods used, especially the use of experimental substrata, and their interactions with sediments. Overwhelmingly, artificial tiles or coral blocks have been used to quantify in-situ algal turf productivity (>92% of observations in my dataset used these methods). Such tiles or blocks can be readily deployed, removed and quantified, and offer exact replicate units. However, these surfaces only represent ‘potential productivity’ at a location as they are not natural. Indeed, experimental surfaces such as coral blocks accumulate far lower sediment loads than the natural surrounding reef substratum (Fig. 7.5). This may be due to: 1) the elevation of tiles/blocks above the substratum making them more exposed to hydrodynamic activity (also see Chapter 5), 2) ‘edge effects’ and/or 3) enhanced fish grazing (Duran et al. 2018; Latrille et al. 2019; Tebbett et al. 2020c). The influence of these factors is likely to be relatively consistent across tiles, meaning that the patterns of algal turf productivity reported in prior studies are valid in relative terms. However, in terms of absolute productivity levels, we may have systematically overestimated productivity values for coral reef algal turfs. There is a clear need to estimate algal turf productivity on natural reef substrata more widely.

In terms of estimating algal turf productivity in-situ on natural reef substrata this may involve the use of specially designed incubation chambers (e.g. Miller et al. 2009; Tait and Schiel 2010; Murphy et al. 2012; Dellisanti et al. 2020), boundary layer approaches (McGillis et al. 2011; Takeshita et al. 2016), or pulse amplitude modulated fluorometers (PAMs) (Silveira et al. 2015). Indeed, the use of the Community In Situ Metabolism 'CISME' units appears to offer a particularly promising avenue for future research (Murphy et al. 2012; Dellisanti et al. 2020). However, it must be noted that the methods outlined above can be limited by constraints associated with expense, technical difficulties, and time. All would hamper our ability to quantify productivity efficiently across broader spatial scales. To address this issue, and expand this research field further, such methods may be used to establish relationships between easily measured universal traits (*sensu* Bellwood et al. 2019b), such as algal turf length/density or accumulated sediment load, and algal turf productivity rates (also see Chapter 6). Essentially, mechanistic relationships could be established between these traits and algal turf productivity, allowing for the estimation of productivity from more-easily, and cheaply, measured universal traits (as for the length and biomass production relationships established in reef fishes [e.g. Morais and Bellwood 2020]). If such relationships were established, this would allow productivity on natural reef substrata to be widely estimated and studied, allowing more nuanced insights into the functioning of coral reefs going forward.

Conclusions

In this study I identified water depth and standing algal turf biomass as important drivers that shape algal turf productivity and turnover on coral reefs, respectively. This strongly supports the conclusions of past studies (e.g. Klumpp and McKinnon 1989; Carpenter 1990; Russ 2003). However, I also uncovered potential limitations in our understanding of these ecosystem processes, and our approaches to measuring them. This comes at a time when climate change is changing the status-quo for coral reefs (Hughes et al.

2017a; Williams et al. 2019a), and when more people than ever before are depending directly on the productivity that coral reefs provide (Newton et al. 2007; Teh et al. 2013; Hicks et al. 2019). Into the future it appears likely that people will have to inceasingly depend on algal turf-covered reefs (Bellwood et al. 2018; Tebbett and Bellwood 2019), particularly as many reefs already support algal turf cover of >50% (Chapter 2) (Vroom 2011; Harris 2015; Aued et al. 2018; Bierwagen et al. 2018; Emslie et al. 2019). As such, renewed research into the quantification of algal turf productivity, particularly on natural reef substratum, will be important. This research will help us to understand how coral reefs will function in the future and the extent to which they can continue to provide the services that people require.

Chapter 8: 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. I 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. My 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.

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. 2017a; 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 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 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. 2017a; Williams et al. 2019a). 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 analyses 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 I apply these approaches to examine the impacts of environmental disturbances in a model inshore coral reef system. I 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/detritivorous 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, I 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). My goal is to determine if, and to what extent, coral reef ecosystem processes change when the reef is exposed to cumulative disturbance events, especially those related to sediments.

Methods

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, I collected data in 2018 and 2019 to match data from previous studies at this location (Fox and Bellwood 2007; Bonaldo and Bellwood 2011; 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 (Goatley et al. 2016; Gordon et al. 2016a; Torda et al. 2018) (Fig. 8.1).

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 (Chapter 2) (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. 2019b), and c) nominally herbivorous fishes support many fisheries around the world (Edwards et al. 2014; Bellwood et al. 2018; Robinson et al. 2019c).

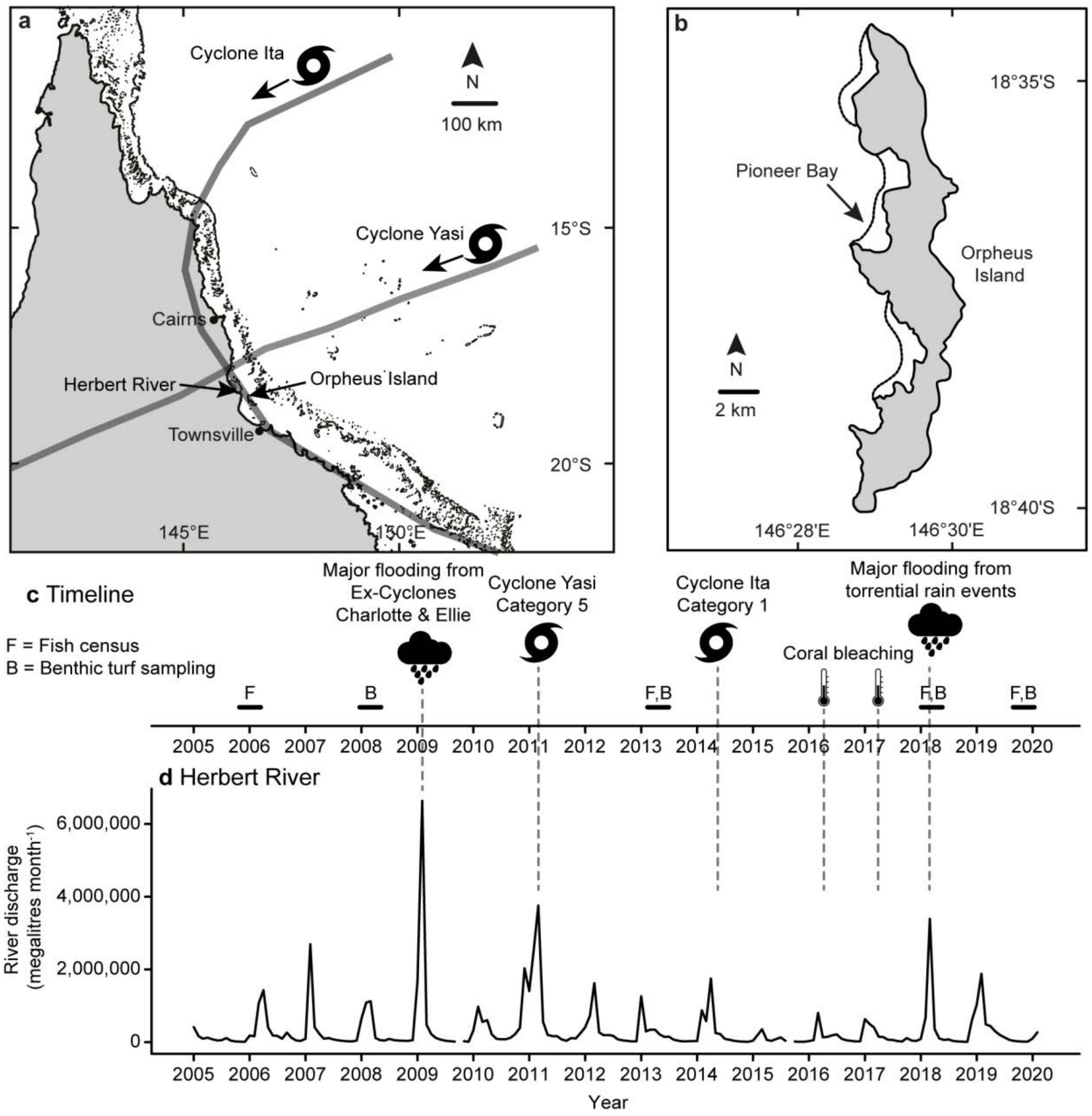

Figure 8.1 Overview of study location and sampling timeline. a) Map of North Queensland, Australia, showing the location of Orpheus Island relative to the Herbert River as well as the tracks of two relevant cyclones. b) Map of Orpheus Island showing the location of Pioneer Bay where sampling occurred. 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).

Benthic data: algal turfs and benthic production

Sample collection and processing

I 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. 2018a), these sampling time periods are likely to be representative of the years in which sampling was conducted. To sample the algal turf communities I 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. 2017c). Sampling areas were delineated using a 58 cm^2 PVC ring. Within the sampling area, I 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) (Chapter 4). 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 Chapter 6. Full particulate processing methods are provided in Text F1 and F2 in Appendix F.

Benthic data statistical analyses

I 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 Text F3 in Appendix F). 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 Table F1 in Appendix F 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, my 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 2020), using the *rstan* (Stan Development Team 2018), *rstanarm* (Goodrich et al. 2018), *bayesplot* (Gabry and Mahr 2018), *tidybayes* (Kay 2019), *tidyverse* (Wickham et al. 2019) and *emmeans* (Lenth 2020) packages.

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 community traits, during each sampling period (details of these calculations are provided in Text F3 in Appendix F). After all of the functions were calculated and compiled into a data matrix, I 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 I wanted to examine how the individual replicate sample units were positioned in multidimensional function-space I formulated a principal co-ordinate analysis from my 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 are located in multidimensional space rather than focusing on the outliers that are used to delineate polygons. To compute the heatmaps, I 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 my 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) (Table F2 in Appendix F). The benthic function-space was computed in the software R (R

Core Team 2020), 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 Text F4 in Appendix F.

Herbivorous fish assemblage: consumption of benthic production

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. 8.1). In April 2018 and December 2019, I repeated the same methods to match this existing data by performing 12 non-overlapping censuses across the bay (in each year). To minimise diver effects on fishes (Emslie et al. 2018) I used 5-minute timed swims (GPS calibrated length = 46.1 ± 1.1 m [mean ± 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).

Herbivorous fish data statistical analyses

Initially, I analysed more traditional monitoring data and a key function (biomass productivity; calculation details are provided in Text F5 in Appendix F) related to the herbivorous fish community. Specifically, I 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 Table F1 in Appendix F 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, I used a multivariate approach. Specifically, I computed a Bray Curtis similarity matrix for both species abundance and species biomass 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 were assessed as above (i.e. using a PERMDISP [Table F2 in Appendix F]). The statistical analyses were performed in the software R (R Core Team 2020), using the *rstan* (Stan Development Team 2018), *rstanarm* (Goodrich et al. 2018) and *vegan* (Oksanen et al. 2019) packages.

Herbivorous fish function-space

To understand how changes in the herbivorous fish community may have influenced its functioning, I 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 (g m^{-2} day^{-1}), consumed biomass (g m^{-2} day^{-1}), carbon respired (g m^{-2} 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 Text F4 in Appendix F 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 Text F5 in Appendix F).

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 I calculated bivariate KUDs and heatmaps). The herbivorous fish function-space was likewise analysed as above, i.e. using a PERMANOVA and PERMDISP (see Table F2 in Appendix F) and the same software packages.

Results

By examining the nature of the algal turfs (i.e. sediment loads and algal turf length) I revealed a fundamental change in the condition of the algal turf community at Orpheus Island (Fig. 8.2a, 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. 8.2a; Table F3 in Appendix F). Concomitantly, algal turf length increased by 38% (9% - 224%) from 2008 to 2019 (Fig. 8.2b; Table F3 in Appendix F). 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. 8.2c; Table F3 in Appendix F). 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. 8.2d; Table F3 in Appendix F) and a similar decline in herbivorous fish standing biomass (Fig. 8.2e; Table F3 in Appendix F). However, unlike abundance which declined steadily (Fig. 8.2d), biomass remained 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. 8.2e; Table F3 in Appendix F). 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 - 2019 (Fig. 8.2f; Table F3 in Appendix F). 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 (Fig. F1 and Table F4 in Appendix F).

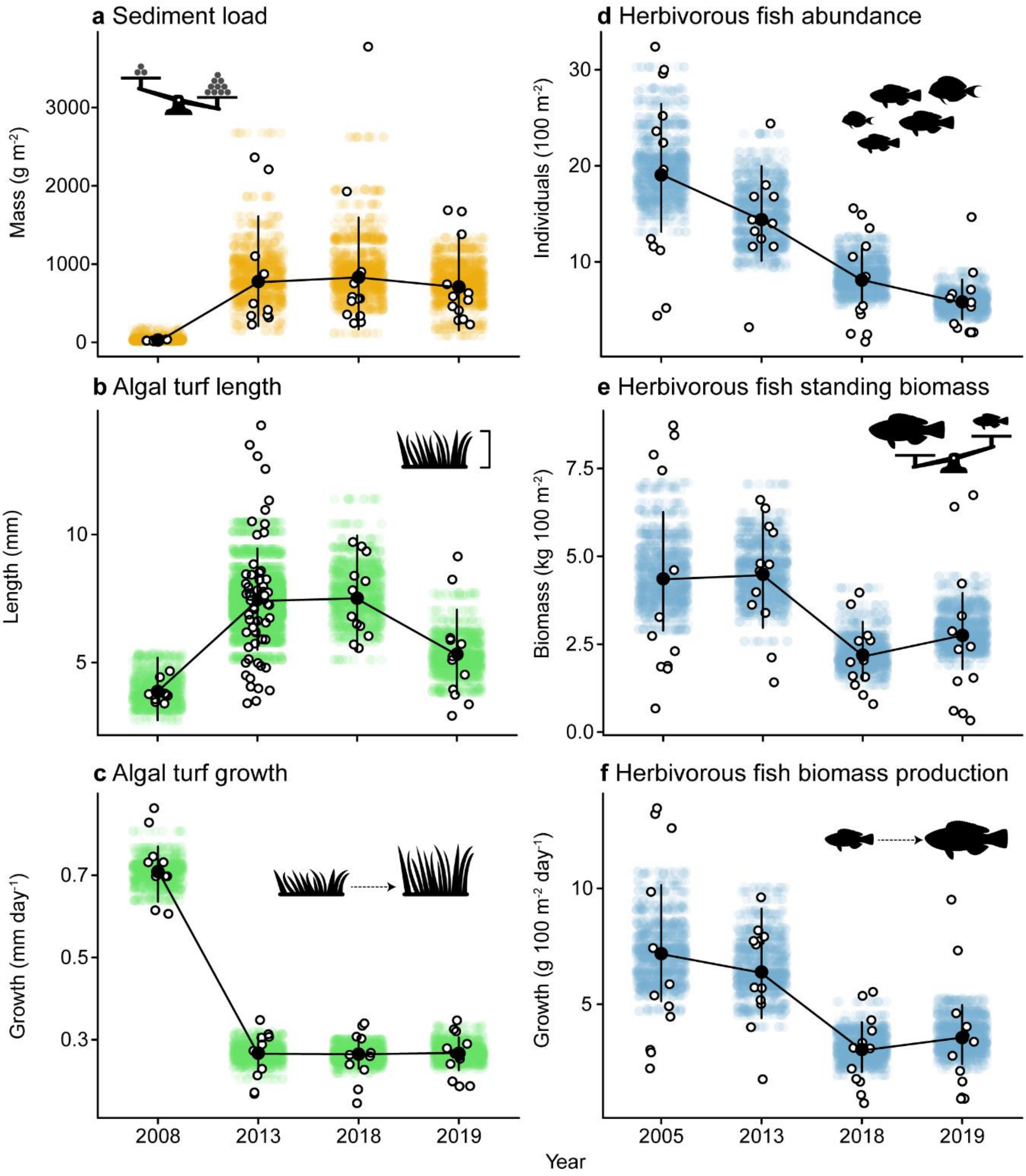

Figure 8.2 Changes in the algal turf and herbivorous fish communities on the reef crest in Pioneer Bay, Orpheus Island. There was a marked shift in the algal turf community in terms

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 abundance d), standing biomass e) and growth rate f). 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.

It is clear that the algal turf and herbivorous fish communities changed substantially across the study period with flow-on effects on ecosystem functions. My 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. 8.3; Fig. F2 and Table F4 in Appendix F). 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. 8.3). However, by 2013 the growth of algal turfs had reduced, while the relative levels of standing biomass of algal turfs, copepods and detritus had increased, leading to an alternative functional configuration in 2018/2019. This new functional 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. 8.3), eventually occupying a significantly different area of function-space in 2019 compared to 2005 (Table F4 in Appendix F). 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. 8.3). 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. 8.3). 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.

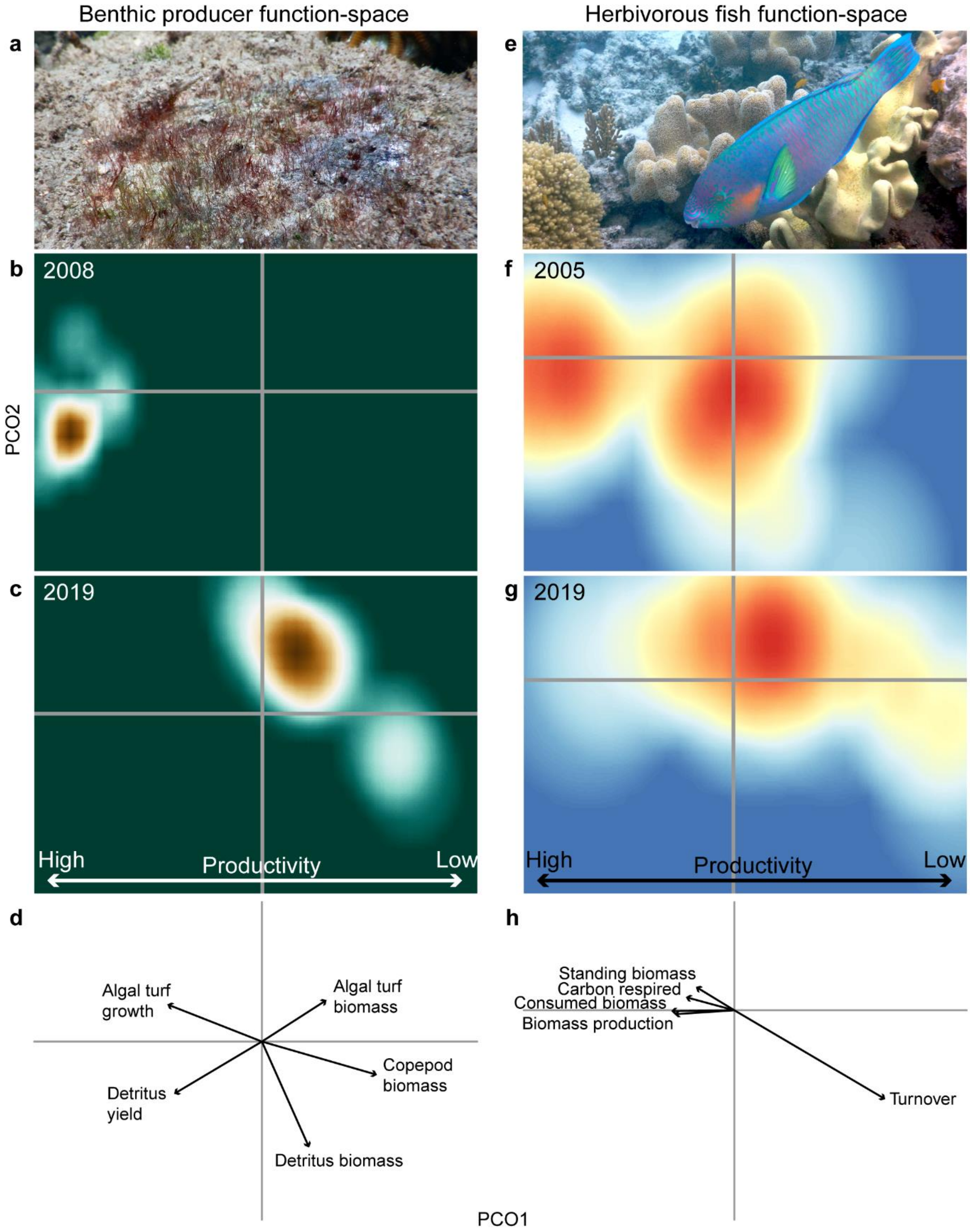

Figure 8.3 Function-spaces of the benthic algal turf community and the herbivorous fish community. The benthic function-space is a multivariate space that provides an overview of the ability of the algal turf community to provide nutritional resources to herbivorous fishes from 2008-2019 (b, c) based 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 2005-2019 (f, g) based on 5 specific functions h). The occupation of the function-space is represented as a heat map based on kernel utilisation 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 Fig. F2 for function-spaces from 2013 and 2018 and see Fig. F3 for specific levels of each individual function in Appendix F. Photographs of a benthic algal turf community a) and the herbivorous parrotfish *Scarus rivulatus* g) (Photographs: SB Tebbett).

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. 2017a; Bruno et al. 2019; Williams et al. 2019a; 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, I 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, I was able to examine and track ecosystem functions (i.e. the relative composition and strength of multiple functions). In doing so, I 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 I documented almost certainly occurred independent of fishing effects (see Morais et al. 2020a). My 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. 2014a; 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 (Fig. F1 in Appendix F), 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 this system, the most parsimonious explanation for the changes I 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. 8.1; see Text F6 in Appendix F 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. 2018a), 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 (Ricardo et al. 2017; Speare et al. 2019), reductions in algal removal rates (Goatley et al. 2016) and shifts in bioerosion patterns (Hutchings et al. 2005). Consistent with this prior evidence, I revealed the extent to which increasing sediment accumulation also correlates with declines in algal turf growth (Fig. 8.2c) and shifts in the functional configuration of the algal turf community (Fig. 8.3). Top-down control of turfs by herbivorous fishes is also possible (Smith et al. 2010; Tebbett et al. 2017d; Fong et al. 2018; McAndrews et al. 2019), however, as fish abundances were slow to change and biomass changes were delayed, in this case, it appears changes were driven from the 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 hysteris (Goatley et al. 2016; Hughes et al. 2017a).

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). My 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. 2019c; 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. 8.2f). 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.

A clear discrepancy between herbivorous fish abundance and biomass declines appeared to exist in this system (Fig. 8.2d, 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 (Fig. F4 in Appendix F). 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. 2019b, 2019c). 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. 2019c; Morais et al. 2020a). However, in my study system, despite a general increase in algal turf cover over the last 15 years (Text F7 and Fig. F5 in Appendix F), there has been a prolonged decline in herbivorous fishes (Fig. 8.2d) and a marked shift in the trophodynamic functioning of the herbivorous fish community (Fig. 8.3). 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. 2019b; Morais et al. 2020b). By contrast, I 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) (Text F7 and Fig. F5 in Appendix F). My results, therefore, pertain to changing algal turfs, not coral loss.

My 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. 2012a; Bartley et al. 2014; Oleson et al. 2017; Comeros-Raynal et al. 2019; Wenger et al. 2020) (also see Chapter 9).

Although based on just one reef system on the Great Barrier Reef, my 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 paramaters 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, my 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) (Chapter 6) and the feeding activities of some nominally herbivorous fishes are impacted (Tebbett et al. 2017b) (also see Chapter 9). In addition, sediment loads of approximately 250-500 g m^{-2} can correlate strongly with the absence of key fish species (Chapter 9) (Tebbett et al. 2020a). 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. Similarly, future work is required to link variation in algal turf sediment loads to coastal sediment loading. Deriving such a link would be important because it would allow the inclusion of coastal sediment loading in models to assess how increased sediment inputs could shape coral reef structure and function. 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. 2017a).

Overall, my study emphasises the importance of functional evaluations in understanding how disturbances shape ecosystems. I highlight how turf-bound sediments potentially disrupt the functioning of coral reefs through core trophic interactions. My 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. 2020a), 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. My 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.

Chapter 9: 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 I 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, I 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 gm^{-2} were associated with a marked decrease in fish abundance or feeding activity, suggesting that a common ecological threshold lies within this range. My 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), is needed.

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; Hughes et al. 2010; Graham et al. 2013; Strain et al. 2019). 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 (Mumby and Steneck 2008; Steneck et al. 2018; Mcleod et al. 2019). Such resilience-based management approaches are often implemented via national parks or marine protected areas (MPAs) (Roberts et al. 2017; Chung et al. 2019; Steneck et al. 2019; Williams et al. 2019b). 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. 2019b). 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 (McCook et al. 2010; Roberts et al. 2017; Chung et al. 2019; Williams et al. 2019b). However, the most pervasive stressors of coral reef ecosystems often transcend MPA boundaries (Jones et al. 2004; Suchley and Alvarez-filip 2018; Graham et al. 2020). At the forefront of these stressors is global climate change, which indiscriminately degrades coral reefs through mass coral bleaching and subsequent habitat degradation (Jones et al. 2004; Hughes et al. 2017b; Bruno et al. 2019; Graham et al. 2020). After climate-change, a major stressor faced by reefs is increased sediment inputs via terrestrial runoff, coastal development, and related dredging activities (Fabricius 2005; Erftemeijer et al. 2012; Bainbridge et al. 2018; Suchley and Alvarez-filip 2018). These sediment inputs often have widespread impacts inside and outside of MPAs (Bégin et al. 2016; Wenger et al. 2016; Suchley and Alvarez-filip 2018).

Increasing sediment inputs on coral reefs can have major implications for ecosystem functions (Fabricius 2005; Wenger et al. 2017; Bainbridge et al. 2018). 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 (Chapters 2 and 3) (Jouffray et al. 2015; Smith et al. 2016; Bellwood et al. 2019b), 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 (Kelly et al. 2016; Tebbett et al. 2017b; Eurich et al. 2018) 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) (also see Chapter 8). Despite the superficial appearance of resilience (a diverse and abundant herbivorous fish assemblage see Ford et al. [2018]) over the short-term (2005-2013), fish feeding appears to have been impacted over this timeframe (Goatley et al. 2016), with subsequent impacts on herbivorous fish population dynamics only manifesting in later years (2018 and 2019) (Chapter 8) (Tebbett et al. 2021). 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 (1983b): "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, I 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, I 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, I provide a mechanistic understanding of cross-scale links between algal turf sediments and ecosystem function on coral reefs, allowing me to predict the potential ramifications of degrading environmental conditions from increasing algal turf sediment accumulation.

Methods

Study species

The focal fish species, the bristletooth surgeonfish, *Ctenochaetus striatus* (Fig. 9.1a), 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 (Friedlander et al. 2010; Cheal et al. 2012; 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 (Robertson and Gaines 1986; Choat et al. 2002; Crossman et al. 2005; Tebbett et al. 2017d).

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. 9.1b), 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. 2018c). 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. 2017b). This distinct reduction in feeding appears to be driven primarily by increasing total sediment load (Tebbett et al. 2017b), rather than by a decrease in the relative levels of the targeted detritus (Tebbett et al. 2017b) or by the source of the sediment (river vs. reef) (Tebbett et al. 2017a). With this clear mechanistic understanding (sediment increases cause reduced feeding rates) at hand, I am therefore able to explore the relationship between total sediment loads and feeding by this abundant and broadly distributed surgeonfish species, ultimately allowing me to assess the potential delivery of functions across multiple spatial scales.

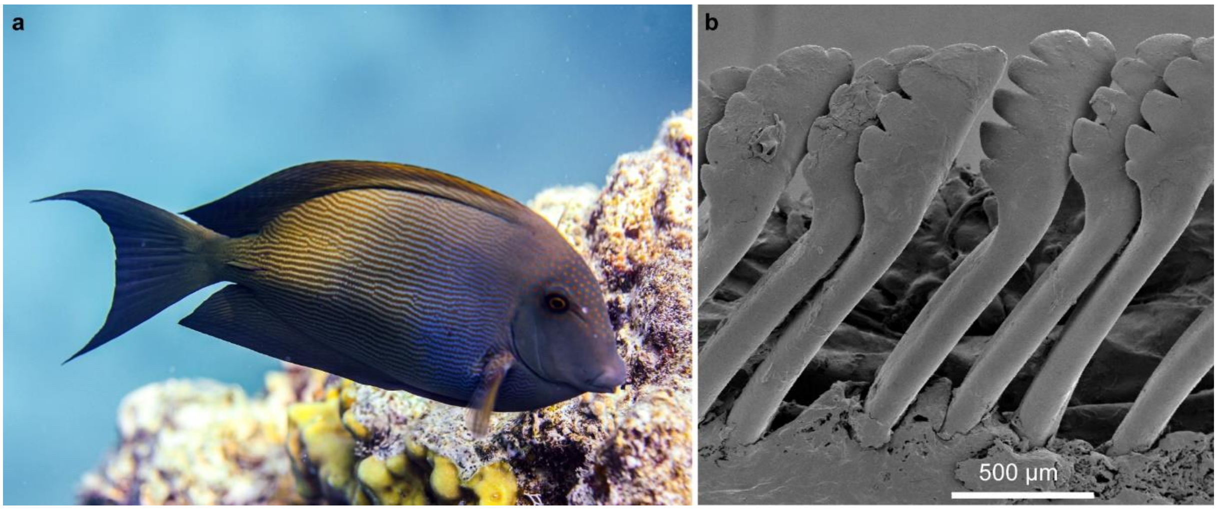

Figure 9.1 a) The study species *Ctenochaetus striatus* at Lizard Island, Australia (photograph V. Huertas). b) A scanning electron micrograph of the elongated comb-like teeth of *C. striatus* (anterior view of pre-maxilla).

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 9.1; Fig. 9.2). First, I 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, I 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 I 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, I 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).

Table 9.1 Overview of the five spatially stratified components involved in the study.

Part A - *C. striatus* vs. sediment distributions across (i) the GBR and (ii) reef habitats	
Goal	Assess the relationship between *C. striatus* abundance and sediment loads across (i) the Great Barrier Reef (GBR) and (ii) habitats, to establish potential threshold levels of sediment.
Scale	(i) inner-, mid- and outer-shelf reef crests across the GBR (Fig. 9.2a) (ii) flat, crest, and slope habitats across a mid-shelf reef (Fig. 9.2b)
Data used	Fish abundance data (Wismer et al. 2009) Sediment data (cross-shelf) (Tebbett et al. 2017c) Sediment data (cross-habitat) (Purcell 2000)
Approach	Iteratively sample and match fish data to sediment data, then use regression trees to determine a threshold sediment value that explains the largest difference in *C. striatus* abundance.
Part B - Preferred feeding surfaces of *C. striatus*	
Goal	Determine the potential spatial concentration of *C. striatus* feeding on preferred feeding surfaces relative to reef area.
Scale	Reef crest habitats at Lizard Island (Fig. 9.2b)
Data used	Bite data of 106 *C. striatus*, benthic cover data
Approach	Use Ivlev's electivity indices to determine the benthic cover, and angle of substratum, that *C. striatus* selectively feed on. Calculate the relative number of bites on these preferred surfaces, and the relative extent of this preferred feeding surface.
Part C - Spatial constraints of sediments on *C. striatus* feeding	
Goal	Ground-truth aquarium-based experiments by determining if *C. striatus* feed in areas of low sediment on the reef in unmanipulated conditions.
Scale	Reef crest habitats at Lizard Island (Fig. 9.2b)
Data used	Video footage of *C. striatus* feeding, photomosaic maps, sediment load data.
Approach	Map feeding area 'hot-spots' of *C. striatus* based on video footage onto photomosaic maps. Sample sediments from inside hot-spots and compare to randomly collected sediment samples from outside hot-spots.

Part D - Increasing sediment loads and *C. striatus* feeding	
Goal	Examine how the spatial configuration of *C. striatus* feeding could respond to increasing sediment loads.
Scale	Reef crest habitats at Lizard Island (Fig. 9.2b)
Data used	Sediment data on preferred feeding surfaces (established in part B) Simulated sediment load data (increasing accumulation) *C. striatus* bite rate vs. sediment model (Tebbett et al., 2017a).
Approach	Estimate *C. striatus* bite rate on sediment loads from an observed sediment load frequency distribution, and under scenarios of increasing sediment load accumulation.
Part E - Relationships between sediment loads and the EAM	
Goal	Examine how the condition of the epilithic algal matrix (EAM) changes with increasing sediment loads.
Scale	Reef crest habitats at Lizard Island (Fig. 9.2b)
Data used	Sediment data from part D, organic detritus and algal turf length data from the same samples used in part D.
Approach	Use statistical models to assess the nature of relationships between sediment loads and organic detrital load, relative levels of organic detritus and algal turf length.

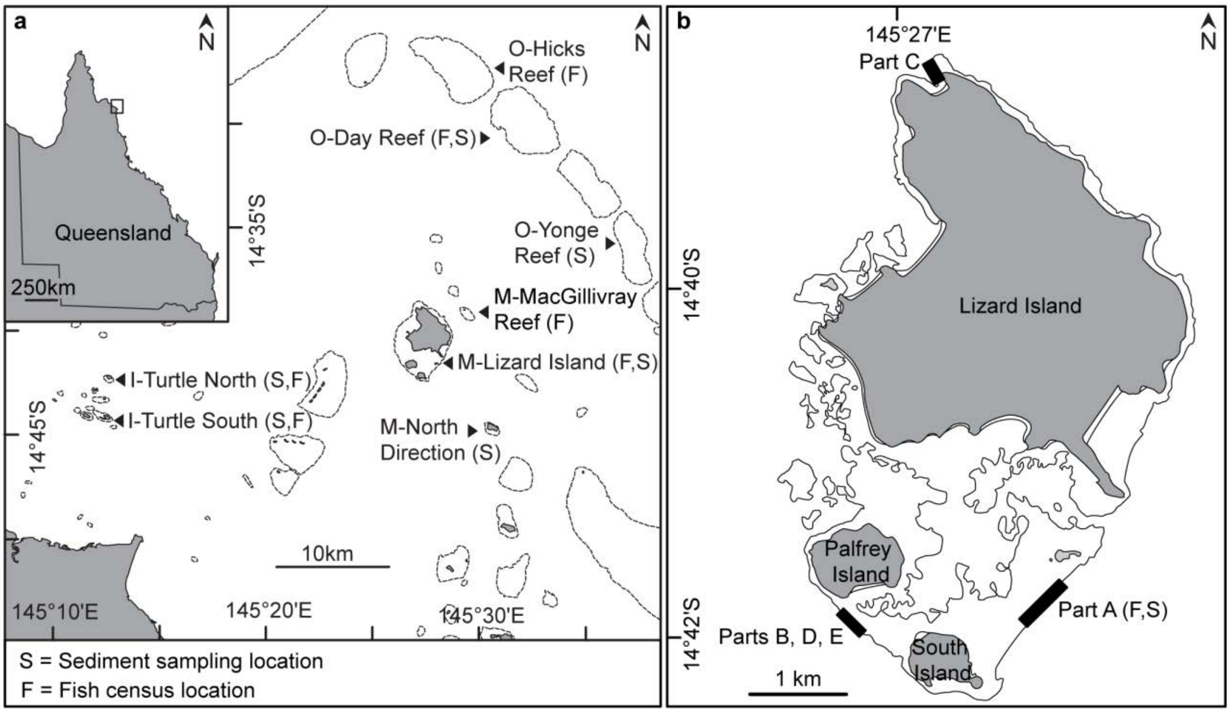

Figure 9.2 a) Map of the reefs around Lizard Island, Australia, showing the reefs at which the cross-shelf sediment sampling and fish censuses (part A) occurred. b) Map of Lizard Island showing the locations where different parts (A, B, C, D, E) of the study were conducted. Note that in panel (a) the letter preceding each reef label (i.e. I, M, O) corresponds to the shelf position (i.e. Inner, Mid, Outer) to which that reef belongs. Also note (S) denote locations where sediments were sampled while (F) denotes fish census locations.

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

I 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 me 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 9.1). 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. 9.2). 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 were sourced from Tebbett et al. (2017c) (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, I 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, I 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. I 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 I repeated the above procedures 10,000 times for both across-shelf and across-habitat analyses. I 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 2020) 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. 9.2), 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) (also see Chapter 4). 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. 2015, 2018) I 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.

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. 9.2b). 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. 2020c). 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.

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. 2017b). 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, three sites were established on the leeward reef crest in Mermaid Cove, Lizard Island (Fig. 9.2b). 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; Tebbett et al. 2020c and Chapter 5). 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, sediment loads and the surface angle of the location were quantified (see Text G1 in Appendix G for full details of sediment sampling and processing).

I 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 G1 in Appendix G). 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 2020) using the *glmmTMB* (Brooks et al. 2017a), *MuMIn* (Barton 2018) and *tidyverse* (Wickham et al. 2019) packages.

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. 9.2b). 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 Text G1 in Appendix G. 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; Chapter 4) 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 Text G2 in Appendix G). 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. 2017b). 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.

I 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) and Chapter 8. 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 G2 in Appendix G]), to account for natural limitations in the amount of sediment that algal turfs can accumulate (Gordon et al. 2016a; Tebbett et al. 2018a; Latrille et al. 2019). 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 (also see Chapter 8 and Tebbett et al. 2021). Therefore, the two increases I 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 five-year period. All modelling was performed in the software R (R Core Team 2020).

It should be noted that my 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. 2017b). 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 and Bellwood 2017) and as adults many nominally herbivorous fishes, including *C. striatus*, are highly site attached with restricted home ranges (e.g. Krone et al. 2008; Welsh and Bellwood 2012; Davis et al. 2017b). 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. 2019a).

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. I 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 were 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 2020), using the *tidyverse* (Wickham et al. 2019), *glmmTMB* (Brooks et al. 2017a), *patchwork* (Pedersen 2020) and *emmeans* (Lenth 2020) packages.

Results

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. 9.3a, 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. 9.4a]). 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. 9.3b, 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. 9.4b). 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. 9.3), 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. 9.3). 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*.

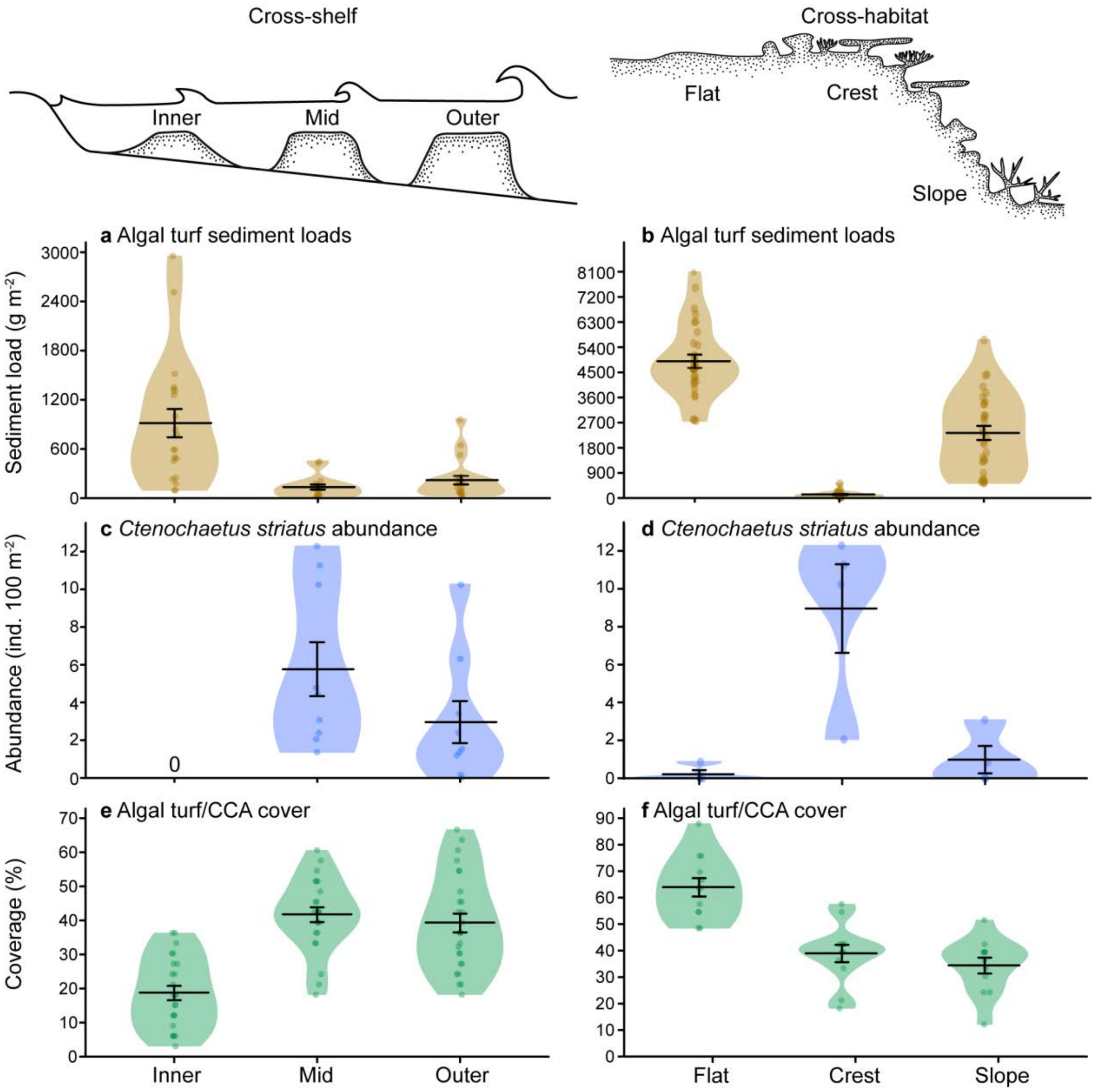

Figure 9.3 Sediment loads (a, b) and the abundance (c, d) of the surgeonfish *Ctenochaetus striatus* across the continental shelf of the Northern Great Barrier Reef, Australia (a, c) and reef habitats at Lizard Island, Australia (b, d). The coverage of algal turfs and crustose coralline algae (CCA) were 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.

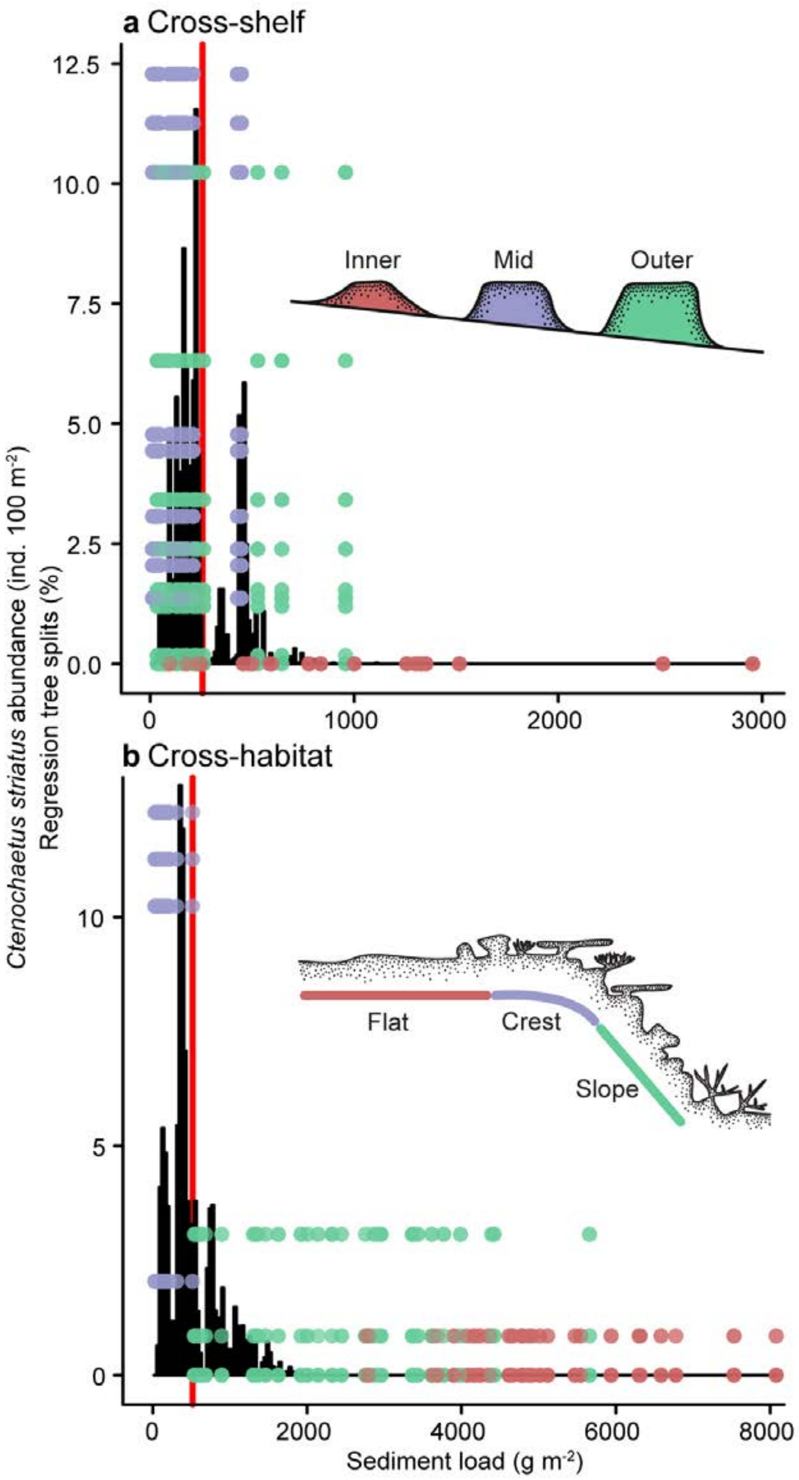

Figure 9.4 The relationship between the abundance of *Ctenochaetus striatus* and sediment loads across a) the continental shelf of the Great Barrier Reef, Australia and b) habitats at Lizard Island, Australia. Coloured dots were based on an iterative process whereby observed sediment load data were randomly matched to each census of *C. striatus* abundance (see Fig.

9.3) (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).

Preferred feeding surfaces of C. striatus – Part B

On the upper reef crest at my 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. 9.5a, 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. 9.5b, d) (for details of how percentages were calculated see Text G3 and Fig. G1 in Appendix G). This indicates that function is delivered by *C. striatus* in a concentrated manner, focussing on a restricted range of preferred surfaces.

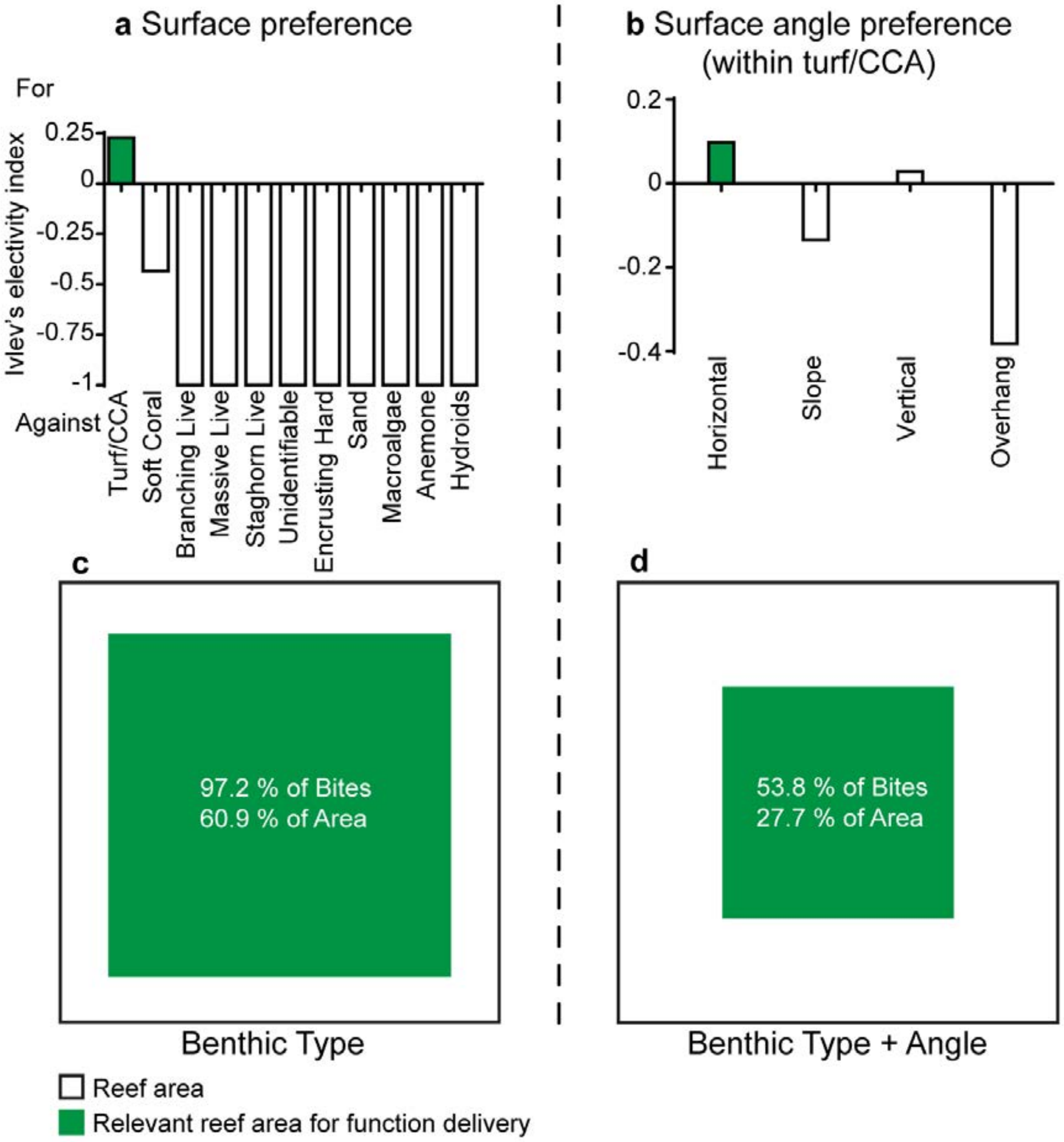

Figure 9.5 Ivlev's electivity indices of *Ctenochaetus striatus* feeding in response to: a) benthic cover type, and b) preferred benthic cover and the angle of the surface with that cover. The percent of reef area relevant for *C. striatus's* function delivery considering its different levels of feeding selectivity is represented as green squares (c, d). For details on percentage calculations see Text G3 and Fig. G1 in Appendix G.

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. 9.6). Note that the sediment loads of feeding hot-spots closely reflects the sediment load abundance thresholds found at larger spatial scales (Fig. 9.4). The model revealed that there was a significant interaction between surface angle and hot-spot vs. random locations (GLMM; $p < 0.05$, Table G2 in Appendix G). 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. 9.6). 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.

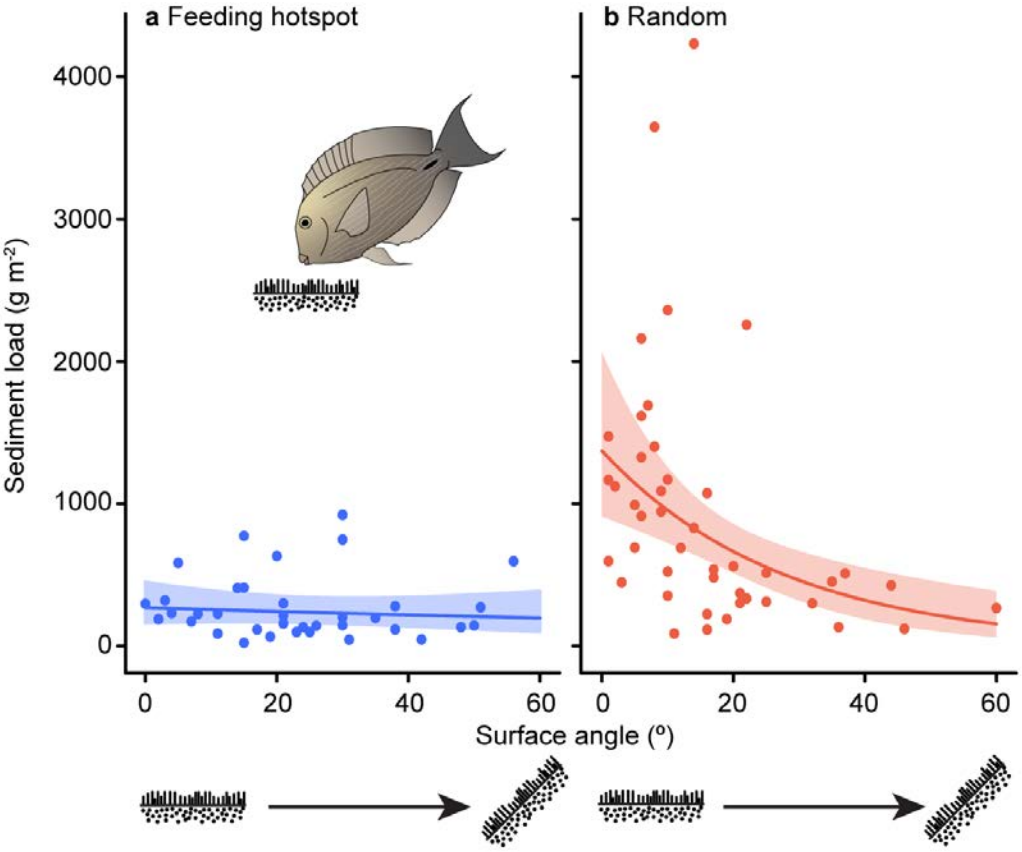

Figure 9.6 The relationship between sediment loads and the angle of the sampled surfaces in areas that were: a**)** *Ctenochaetus striatus* feeding hot-spots and b) randomly sampled areas from the same sites. Coloured lines are the mean predicted fit of a generalised linear mixed-effects model, shaded areas are the upper and lower 95% confidence intervals, and coloured dots are the observed data points.

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 substrata and substrata angle (Fig. 9.4c, 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. 9.7a, 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 Text G3 and Fig. G1 in Appendix G).

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. 9.5a, b), resulted in a 44.3% reduction in total *C. striatus* feeding, relative to observed levels (Fig. 9.7). 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. 9.7c, f). This highlights the potential of sediments to impair *C. striatus* feeding, limiting function delivery to specific locations on the reef.

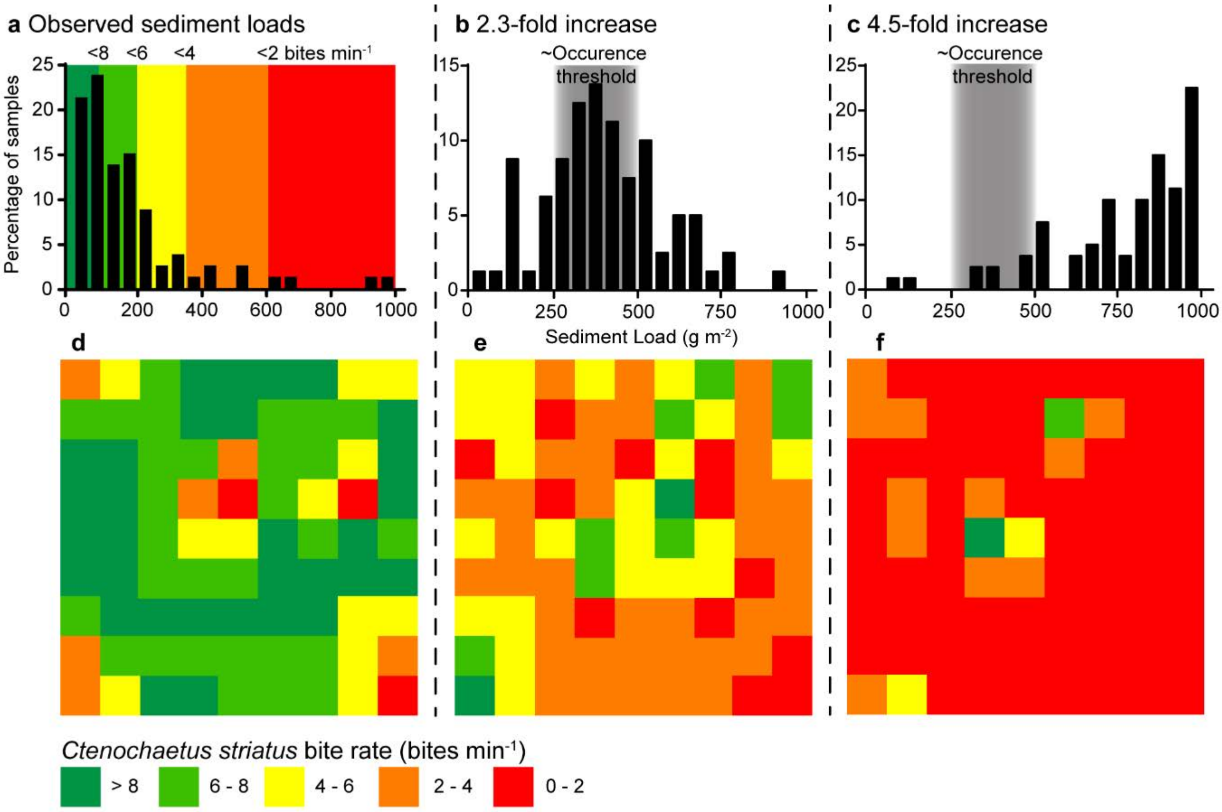

Figure 9.7 Frequency distributions of sediment loads on horizontal algal turf/crustose coralline algae covered surfaces. a) shows the observed frequency distribution of sediment loads on a mid-shelf reef crest on the Great Barrier Reef, b) represents a projected 2.3-fold increase in mean sediment load 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. 9.4). 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.

Relationships between sediment loads and the EAM – Part E

Clear relationships existed between sediment loads and the nature of the EAM (Fig. 9.8). Specifically, as sediment loads increased in the EAM so did the standing mass of organic detritus, with a significant ($p < 0.001$) positive relationship between these two variables (Fig. 9.8a; Table G3 in Appendix G). 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 ($p < 0.001$; Fig. 9.8b; Table G3 in Appendix G). 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 ($p < 0.001$; Fig. 9.8c; Table G3 in Appendix G), 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*.

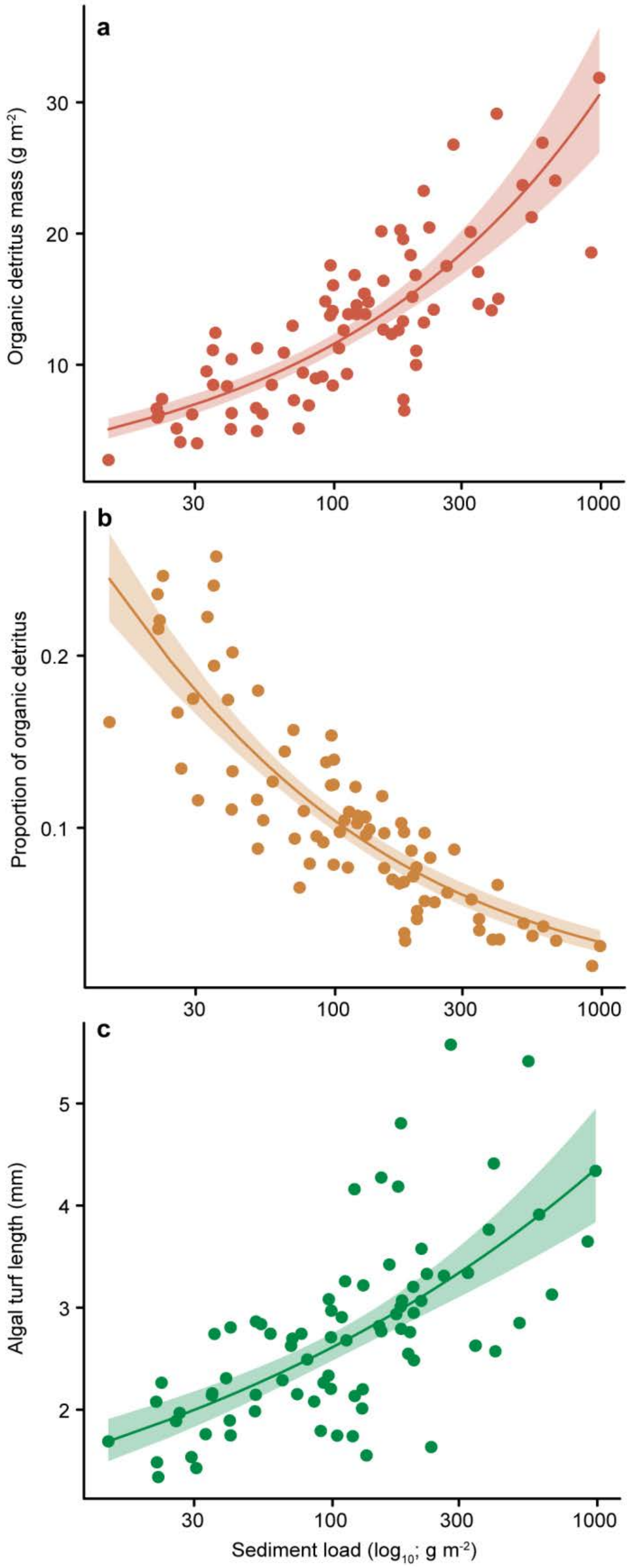

Figure 9.8 The relationship between inorganic sediment loads and a) organic detrital loads, b) the relative level of organic detritus in benthic particulates by mass and c) algal turf length.

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.

Discussion

Using a hierarchical multi-scale approach, ranging from patterns across a continental shelf down to centimetres within a single reef habitat, I 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.

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. 2017b; 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 my study I 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. 9.5). 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; Welsh and Bellwood 2012; Carlson et al. 2017; Clements et al. 2017; Streit et al. 2019). 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. 2020b)]), 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. 9.7). In a management context, therefore, trying to conserve function, by solely managing the abundance of *C. striatus*, could fail (see Williams et al. 2019b). 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?

Functional interpretations: the influence of scale

I examined relationships between *C. striatus* and sediments across multiple spatial scales spanning several orders of magnitude. At every spatial scale, I 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. Russ 1984; Cheal et al. 2012, 2013; McClure et al. 2019), with previous suggestions that sediment may influence such distribution patterns (Cheal et al. 2012, 2013; Samoilys et al. 2019). My 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. My 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. 2017b) and on the reef (Bellwood and Fulton 2008).

In combination, the previous experimental evidence with my 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 my modelled *C. striatus* feeding patterns (Fig. 9.7). 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. 9.7). 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. 9.8b) preventing the long-term persistence of *C. striatus* in these areas (also see Chapter 8).

Algal turf sediments and consideration of other explanatory drivers

My 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 (Graham and Nash 2013; Emslie et al. 2014), hydrodynamic exposure (Fulton et al. 2005; Bejarano et al. 2017; Bellwood et al. 2018) and turbidity (Mallela et al. 2007; Moustaka et al. 2018) and social drivers such as competition (Francini-Filho et al. 2010; Davis et al. 2017a) and predation (Rizzari et al. 2014b; Catano et al. 2016; Rasher et al. 2017).

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 Bellwood and Fulton 2008; Tebbett et al. 2017b). Specifically, a) algal turf sediments directly mediate the length (Fig. 9.8c), productivity, and composition of algal turfs (Chapter 6) (Airoldi et al. 1995; Purcell 2000; Goatley and Bellwood 2013; Clausing et al. 2014; Tebbett and Bellwood 2020) and b) the rate and extent of sediment accumulation in algal turfs is mediated by topographic complexity (Chapter 5) (Tebbett et al. 2020c), hydrodynamic activity (Purcell 2000; Bodde et al. 2014; Tebbett et al. 2017c), and sediment deposition (from suspended sediments that cause turbidity) (Whinney et al. 2017; Latrille et al. 2019). 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. 9.8b). However, in two prior experiments conducted in Tebbett et al. (2017b) 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. 9.8a) and the relative amount of detritus in particulates (Fig.

9.8b). 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. 2017a). 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 (Wolanski et al. 2008; Cunning et al. 2019; Jones et al. 2019; Latrille et al. 2019). 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) (Russ et al. 2015, 2018; Robinson et al. 2019b). However, *C. striatus* abundance, again, appeared to be largely independent of this in the current study (Fig. 9.3), 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 (Russ 2003; Tootell and Steele 2016; Bellwood et al. 2018) (also see Chapter 8).

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 9.1), I 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 (Francini-Filho et al. 2010; Davis et al. 2017a), 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 (Randall 1965; Rizzari et al. 2014b; Catano et al. 2016; Rasher et al. 2017; Atwood et al. 2018). 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 (Chapter 5) (Tebbett et al. 2020c), 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.

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 three of my model [Fig. 9.7]), 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 (Goatley and Bellwood 2010; Krone et al. 2011; Tebbett et al. 2017b; Fong et al. 2018; McAndrews et al. 2019). Where nominally herbivorous fishes feed, they can maintain low sediment loads, and keep algal turfs cropped close to the substratum (Tebbett et al. 2017b; Fong et al. 2018). However, as sediments can constrain the spatial extent of feeding, this increases the spatial concentration of these functions being delivered to the reef (Fig. 9.7). In areas where algal turf sediments accumulate, and feeding is reduced, previous studies would predict: a) the development of longer algal turfs (Fig. 9.8c) (Goatley et al. 2016; Fong et al.

2018), 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 (Chapter 8) (Bellwood et al. 2019b).

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; Chapter 4). 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; Wenger et al. 2016; Hamilton et al. 2017; Jones et al. 2019), 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.

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. 2019b), by managing their abundance, biomass or biodiversity. However, using a multi-scale approach, I 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 (Hughes et al. 2018a; Bruno et al. 2019), managing ecosystem functions has been proposed as a particularly important endeavour (Hughes et al. 2017a; Bellwood et al. 2019a). 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).

Chapter 10: General discussion

Since beginning the research for this thesis, the entire world was nudged into a new status-quo by the Covid-19 pandemic. This disease has taken a devastating toll on people and livelihoods, however, the global scale effort by humanity to overcome this problem provides a glimmer of hope that when faced with global-scale problems, people have the capacity to address them. In this respect, several similarities are shared between the Covid-19 pandemic and global climate change (Fuentes et al. 2020; Manzanedo and Manning 2020), with climate change representing a significant global problem, that must be addressed. Indeed, the sixth assessment report released by the Intergovernmental Panel on Climate Change (IPCC) in August 2021 was particularly sobering as it highlighted that time is rapidly running out if we are to constrain warming to just 1.5°C above pre-industrial baselines (IPCC 2021). While there remains hope that humanity will successfully tackle and overcome this global climate problem (Obama 2017; Fuso Nerini et al. 2019; Folke et al. 2021), the ramifications of the warming that has already occurred are set to reverberate around the world for decades or centuries (Hoegh-Guldberg et al. 2019; IPCC 2021). This represents the context, or operating space, in which the world's ecosystems will exist for the foreseeable future. Throughout this thesis I have explored how one such ecosystem, coral reefs, may be configured within this context.

Importantly, despite three global scale coral bleaching events over the last two decades (Skirving et al. 2019), the expectations that fleshy macroalgae would typify most coral reef ecosystems as they degrade (e.g. Hughes et al. 2003, 2017a; Bellwood et al. 2004) has largely failed to eventuate. Instead, in **Chapter 2** I revealed that for the majority of reefs, their futures are likely to be closely tied to higher coverage of low-lying algal categories such as algal turfs. Interestingly, such states appear to be more amenable to coral recovery than macroalgae dominated states (Birrell et al. 2008; Diaz-Pulido et al. 2010), providing hope that if climate change is addressed, recovery of coral assemblages is a possibility (also see Dietzel et al. 2021a). Indeed, this notion was supported by the findings of **Chapter 3** which highlighted that even after cumulative large-scale disturbances, coral communities can have a marked propensity to start recovering in algal turf-dominated reef states. Although, this must be tempered by the fact that such recovery appears to be spatially patchy initially, with recovery across larger spatial scales likely to be dependent on the time before the next disturbance (**Chapter 3**). A window of time which appears set to continually decrease if warming continues (Hughes et al. 2018a; Puotinen et al. 2020).

Unfortunately, over recent decades science concerned with coral reef degradation, resilience and management has largely centred around the notion that reefs often degrade from coral dominated to macroalgae dominated systems (reviewed in Bruno et al. 2019). As this does not appear to reflect most realities, especially on reefs outside the Western Atlantic, it means that we may lack the necessary understanding to comprehensively manage these future coral reef systems (Bellwood et al. 2019b). In this respect, the functional groups of organisms once viewed as critical may not actually be as important as first thought, while our understanding of the groups that are likely to be critical, in the context of future reefs, may be far from complete (Bellwood et al. 2019b). A clear example of this issue was provided in **Chapter 7**. This chapter revealed that while algal turfs are frequently considered to be one of, if not the, most productive benthic primary producers on reefs (Odum and Odum 1955; Carpenter 1985; Adey and Goertemiller 1986; Hatcher 1988), the quantification of their productivity is remarkably limited, especially in recent years. Indeed, virtually no data exists on algal turf productivity in-situ on natural substrata, while our understanding of productivity measurements derived from other experimental surfaces may have been shaped by the effects of sediments (**Chapter 7**). Considering that the productivity of these turfs is utilised by a variety of herbivorous organisms on reefs (Choat et al. 2002; Altman-Kurosaki et al. 2018; Humphries et al. 2020) that people, in-turn, exploit (Russ and St. John 1988; Morais et al. 2020a; Purcell et al. 2020), then this lack of knowledge is concerning and provides a clear opportunity for future research. A similar point was made by Marsh (1976), in reference to algae on coral reefs, when they stated that "*it seems obvious that workers studying reef productivity should focus more attention on small filamentous forms and the reef zones dominated by them.*" It appears that this notion is still applicable over four decades later.

Beyond the productivity of algal turfs, the present thesis (**Chapters 4, 6, 8, 9**) as well as other lines of evidence (e.g. Fong et al. 2018; Duran et al. 2019; McAndrews et al. 2019; Speare et al. 2019; Harvey et al. 2021) have begun to reveal that the condition of algal turfs, especially in terms of how much sediment they contain, can be critical to how they function and influence other processes on reefs. Indeed, such sediments appear to have the capacity to affect herbivorous food chains from the bottom-up (**Chapter 8**; Tebbett et al. 2018a, 2021), potentially explaining decreases in fisheries yields on sediment-impacted coral reefs (Orlando and Yee 2017; Delevaux et al. 2018; Wenger et al. 2020). Unfortunately, the results of **Chapter 5**, also suggest that on offshore reefs, even without increased sediment inputs, the flatter low-complexity reefs that are expected in the future (Graham and Nash 2013; Perry and Alvarez-Filip 2019), are likely to be associated with algal turfs that contain relatively high sediment loads. The results of this thesis, therefore, paint a picture that near-future coral reefs will be typified by high algal turf cover (or other low-lying algal forms), and these algal turfs will inevitably be associated with sediments that influence numerous critical ecosystem processes.

These results hold a variety of implications for the monitoring and management of coral reefs. This is principally because algal turf sediments remain unquantified and unmonitored on virtually all coral reefs globally (**Chapter 4**). Moreover, the results of

Chapter 9 highlight that classic ecosystem-based monitoring/management approaches, which hinge on the assumption that fish presence is equal to ecosystem function delivery, may not be applicable in the wake of increasing sediments (also see Halpern et al. 2013; Arias-González et al. 2017). For example, monitoring populations of critical functional groups of fishes (e.g. Green and Bellwood 2009) may not be sensitive enough to detect ecosystem changes until it is too late (e.g. Goatley et al. 2016). Detecting such changes in the condition of algal turfs represents a challenge as these changes occur on the scale of millimetres (**Chapters 6** and **8**; Goatley et al. 2016; Fong et al. 2018) and can, therefore, be easily overlooked. However, if not detected, such changes can result in sustained shifts in ecosystem processes that manifest over decades (**Chapter 8**).

Unfortunately, the management of sediments onto coral reefs does not represent an easy task as it is a multifaceted social-ecological problem that can transcend terrestrial and marine interfaces (Blanchard et al. 2017). For example, increased sediment inputs onto coral reefs can arise from land-clearing for agriculture, and other destructive land-use practices (Cortes and Risk 1985; Bégin et al. 2014; Tulloch et al. 2016; Carlson et al. 2019). If these sediments accumulate on reefs, the evidence suggests that the productivity of these systems could ratchet-down, resulting in lower fisheries catches (**Chapter 8**; Delevaux et al. 2018; Tebbett et al. 2018a; Wenger et al. 2020). As such, a positive feedback may be developed whereby reduced fisheries catches can result in social problems such as malnutrition and hunger (Kent 1997; Hatcher and Hatcher 2004; Cruz-Trinidad et al. 2014), potentially fuelling further land clearing for agriculture (Hatcher and Hatcher 2004; Hafezi et al. 2020), in-turn leading to more sediment release and less productive reefs. To address such linked problems this will require close collaboration between stakeholders and multiple management groups to develop appropriate strategies to address underlying social problems (Fidelman et al. 2012; Foale et al. 2013; Blanchard et al. 2017). Furthermore, it is in cases such as these where appropriate terrestrial restoration strategies may prove particularly cost-effective, with approaches such as reforestation having the potential for ecological benefits across multiple ecosystems (Klein et al. 2012; Maina et al. 2013; Shelton and Richmond 2016; Suárez-Castro et al. 2021). Evidently, this offers the opportunity for further research to explore how social problems are linked to algal turf sediments on coral reefs, as well as explore the potential efficacy of remediation or management interventions.

Interestingly, this linked terrestrial-marine problem of sediment accumulation in algae and decreased fisheries production is not exclusive to coral reefs. For example, the freshwater lakes in the African Rift Valley are home to a diversity of fishes, many of which feed on epilithic algal communities (much like the algal turf communities on coral reefs) (Fryer 1959; Yamaoka 1983; Reinthal 1990; Hata et al. 2015). Sediments can also become trapped in these freshwater algal communities where they shape the feeding behaviour and populations of these fishes (Cohen et al. 1993; Genner et al. 1999; Rusuwa et al. 2006; Takeuchi et al. 2010; Munubi et al. 2018), with previous studies also suggesting increased sedimentation from land clearing for agriculture has resulted in decreased fisheries productivity in these lakes (Britton et al. 2017; McGlue et al. 2021). In addition to freshwater lakes, many temperate systems, that were previously dominated by kelp, have undergone transitions to sediment-laden algal turf states (Filbee-Dexter and Wernberg 2018; Pessarrodona et al. 2021). This is again suggested to have negative consequences for fisheries production (Krumhansl et al. 2016; Filbee-Dexter and Wernberg 2018). These changes have often been linked to the effects of climate change (Bennett et al. 2015; Filbee-Dexter et al. 2016, 2020; Wernberg et al. 2016), as well as terrestrial pollution and increased sediment inputs (Connell et al. 2008; Gorman et al. 2009; Moy and Christie 2012). Clearly, sediment-laden epilithic algal communities are common to many aquatic ecosystems around the world. In the future, directly exploring the similarities and differences in the rise of sediment-laden algal communities across aquatic ecosystems may, therefore, yield interesting insights into this pathway of change.

In the future, a sustained effort by scientists to quantify and understand the ramifications of sediments bound within algal communities more broadly on coral reefs, as well as other aquatic systems, appears necessary. This is because, while the effects of algal bound sediments appear to be a common problem in aquatic ecosystems, our understanding of how sediments get there, what effects these sediments can have, and even how much sediment there is in algal communities is still remarkably limited relative to other research fields (**Chapter 4**). In the case of coral reefs, the majority of our understanding comes from the Great Barrier Reef (GBR), particular on clearer-water offshore reefs. Indeed, there is just a single timeseries of algal turf sediment load data, from one inshore reef, currently in existence across all coral reefs globally (see **Chapter 8**). Moreover, it is interesting to note that sediments, when suspended in the water column, interact closely with light availability (Storlazzi et al. 2015; Morgan et al. 2020; Luter et al. 2021) and that the nature of algal turfs is closely dependent on light (Carpenter 1985; Klumpp and McKinnon 1989), yet our understanding of these interactions, and how they shape the propensity of algal turfs to trap sediments, is limited. As suspended sediments and light availability can vary substantially on reefs, especially across inshore to offshore gradients (Fabricius et al. 2014, 2016), disentangling these factors for algal turfs may be particularly interesting in future research. Clearly, there are many avenues for further work within this research field, especially in terms of assessing the generality of the findings contained within this thesis and how they could apply differently to offshore versus inshore reefs. Such work will be crucial in managing reefs to maintain short productive algal turfs (SPATs) and limit potential transitions to long sediment-laden algal turf (LSAT) states.

Importantly, while the future for many coral reefs appears to be coupled with high algal turf cover and lower-coral cover (**Chapter 2**), there remains hope that services, in this case fisheries productivity, can be sustained to a certain extent in these systems if they are managed correctly. This is because herbivorous fish abundance and/or biomass often scales with the availability of nutritional resources (Russ et al. 2015; Cheal et al. 2017; Pratchett et al. 2018; Robinson et al. 2019b), and if SPATs are maintained on such reefs, then herbivorous fishes could remain a productive component of fisheries yields. Indeed, over three decades ago Russ and St. John (1988) recognised the potential for herbivorous fishes, which utilise benthic productivity from algal turf communities, to support fisheries yields. With Robinson et al. (2019c), recently demonstrating that even following coral bleaching and associated regime shifts to algal dominated states in the Seychelles, larger population sizes of herbivorous rabbitfishes sustained, or increased, fishery catches. Moreover, recent work has highlighted the importance of pelagic subsidies in underpinning the productivity of reef fish assemblages (Brandl et al. 2019b; Morais and Bellwood 2019; Morais et al. 2021b), with this pathway of productivity showing a degree of resilience to coral loss and reef degradation (Morais and Bellwood 2019; Morais et al. 2020b). As these two trophic pathways, benthic and pelagic, represent the major drivers of fish productivity on reefs (Hatcher 1988; Brandl et al. 2019b; Morais and Bellwood 2019), sustaining fisheries catches on future reefs could represent an achievable goal (but see Bell et al. 2013; Capitani et al. 2021; Eddy et al. 2021).

Importantly, these insights into fish productivity were derived from focusing on ecosystem processes directly. A focus which I have endeavoured to maintain throughout this thesis. Indeed, in **Chapter 8** I developed the multivariate ‘function-space’ framework which focuses on ecosystem processes directly. This framework was modified after the more widespread trait-based analyses which have been used extensively in coral reef ecology (e.g. Mouillot et al. 2014; Madin et al. 2016; McWilliam et al. 2018; Denis et al. 2019), as well as ecology more generally (e.g. Violle et al. 2007; Dehling et al. 2014; Lamanna et al. 2014; Fountain-Jones et al. 2015), to provide insights into the functional composition of ecosystems. However, the clarity of insights into ecosystem processes from trait-based analyses has been hindered by our ability to relate traits directly to specific ecosystem functions (Mlambo 2014; Bellwood et al. 2019b; van der Plas et al. 2020). By utilising the rates of different functions directly, to parameterise function-space, this approach overcomes the problem of trait-function links and yields more direct insights into the composition and functional status of a given ecosystem (**Chapter 8**). As such, this function-space framework may prove to be a valuable approach for conducting functional assessments of ecosystems that could be considered complimentary to existing trait-based analyses. This may warrant further investigation in the future.

Overall, this thesis has challenged prevailing paradigms concerning coral reef degradation. In doing so, this thesis took a forward-looking approach to understanding coral reef composition and the functions which are likely to be critical in these systems. This assessment was facilitated by focusing on ecosystem functions directly, as well as considering the factors which shape them. From this assessment it is clear that humble algal turfs, and the sediments they contain, may be crucial to shaping how coral reefs operate into the future, especially in terms of potential reef productivity. While some transitions to long sediment-laden algal turf states on coral reefs now appear inevitable, there is room for some degree of optimism that, if managed correctly, low coral cover reefs of the future could still be a source of productive fisheries yields to people. There also remains some hope that if climate change is addressed, coral assemblages have the capacity to return and recolonise algal turf-covered coral reefs. Perhaps the reef assemblages of the recent past that are rapidly vanishing, will once again exist in my lifetime.

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Appendix A: Supporting information for chapter 2

Text A1 Further discussion on low-lying algal communities

When designing the data collation methods for this study I initially set out to have algal turf and crustose coralline algae (CCA) as separate benthic categories due to the different contributions of the two algal groups to ecosystem processes (e.g. Steneck and Dethier 1994; Steneck 1997; Adey 1998; Birrell et al. 2008; Tebbett and Bellwood 2019). However, it rapidly became clear that such data did not exist at the temporal and spatial resolution relevant for this study. There are two main problems. Firstly, it appears that over the last few decades of coral reef research and monitoring, these benthic groups have, for the most part, been systematically overlooked or quantified under categories such as ‘dead coral’, ‘rock’, ‘rubble’ or ‘hard substrate’ (Fig. A1). While such categories are frequently viewed as ‘abiotic’ it is widely acknowledged in the literature that they are almost invariably covered in one or more low-lying algal components (i.e. algal turfs, CCA or cyanobacteria) (e.g. Dahl 1973; Diaz-Pulido and McCook 2002; Fong and Paul 2011; Kelly et al. 2012; Harris et al. 2015; Smith et al. 2016; Perry and Morgan 2017; Fraser et al. 2021; Wolfe et al. 2021). Secondly, in many other cases all low-lying algal categories have been excluded, with many studies focusing solely on ‘coral vs algae’ (as discussed in Smith et al. 2016). Indeed, this point is highlighted by my dataset. If all data points are removed that include miscellaneous benthic categories such as ‘dead coral’ and ‘rubble’ (which have no indication of what was covering them but would have been either algal turf, CCA, cyanobacteria or a combination of the three), then of the initial 24,468 data points just 748 remain between 1997 and 2018. This represents just 3.1% of all data points in my study. Although even if this small subset of the data is examined (with CCA and algal turfs as separate categories) it is important to note that my results pertaining to benthic dominance of low-lying algal communities still hold (see Fig.

A2).

To compile a robust dataset of benthic compositions at a broad spatial and temporal resolution it was, therefore, necessary to pool algal turf and CCA, along with the data categories such as ‘dead coral’ and ‘rubble’, that are invariably covered in algal turf, CCA or cyanobacteria/biofilm, into a single low-lying algal community category. However, it is critical to note that the decision to use this single low-lying algal category is not unique to my study. It is based on a widespread precedent in the coral reef literature that has been used for decades (e.g. Aronson and Precht 2000; Edmunds 2002, 2014, 2019; Nugues and Bak 2008; Idjadi et al. 2010; Gilmour et al. 2013; Toth et al. 2014; Edmunds and Lasker 2016; Johnston et al. 2016; Tsounis and Edmunds 2017; Alemu I and Mallela 2021; Alves et al. 2022; Obura et al. 2022). Given the available data the only pragmatic solution that would enable me to use the bulk of the data currently in existence was to follow this precedent and use a single pooled low-lying algal category.

While unfortunate, this lack of clarity in delineating the low-lying algal community in the bulk of existing data is understandable because, unlike simple divisions such as hard corals vs. soft corals, there is not an easy dichotomous division between algal turfs and CCA. Rather, these low-lying algal communities exist on a continuum from CCA to long sediment-laden algal turfs up to 20 mm in length (Figs A3, A4, A5) (Steneck 1997; Goatley et al. 2016; Tebbett and Bellwood 2020). On this continuum, intermediate stages include various levels of cover by both CCA and algal turfs, with ‘sparse turf’ or ‘short productive algal turf’ states being a mix of algal turfs and CCA (Fig. A3). Importantly, the evidence suggests that the position of low-lying algal communities along this continuum is largely dependent on benthic sediment accumulation (Steneck 1997; Goatley et al. 2016; Fong et al. 2018; Tebbett and Bellwood 2020) (which in-turn is largely modified by hydrodynamic drivers [Carpenter and Williams 1993; Purcell 2000; Tebbett et al. 2017a; Latrille et al. 2019]) as well as herbivory/detritivory (Bellwood 1996; Goatley and Bellwood 2010; Krone et al. 2011; McAndrews et al. 2019).

To explore the nature of this continuum, I sourced existing empirical data on 3334 individual algal turf length measurements (quantified using callipers as outlined in Tebbett and Bellwood 2019), the mass of inorganic sediments contained on/within these low-lying algal communities from 442 samples (quantified using vacuum sampling modified after Purcell 1996), and matching algal turf length and sediment mass from 237 samples (all turf/sediment data were soured from Tebbett et al. 2017a, 2018b, 2020a, 2020b, 2021; Tebbett and Bellwood 2020). These data were then visualised using density plots and scatterplots to reveal the distribution of data points (Fig. A4). In doing so, the data suggests that: a) low-lying algal communities exist on a continuum from >0 mm to <20 mm (all algal turfs are <20 mm in length, with algae taller than this being macroalgae; therefore supporting the divisions made in past literature from a range of geographic locations [e.g. Borowitzka 1981; Carpenter 1988; Connell et al. 2014; Harris et al. 2015; Tebbett and Bellwood 2019]), b) sediment loads in low-lying algal communities span several orders of magnitude from 10s g m^{-2} to nearly 10,000 g m^{-2} across the continuum, and c) a distinct relationship exists between algal turf length and sediment loads. Consequently, the cover of CCA and sparse turfs relative to long sediment-laden algal turfs is likely to be inversely correlated (Fig. A2).

Importantly, while low-lying algal communities have previously been pooled in quite coarse categories (necessitating the same approach herein) (Fig. A1), going forward it will be increasingly important to recognise and quantify the status of low-lying algal communities along this continuum. This is because the position of low-lying algal communities on this continuum dictates their role in ecological processes. For example, CCA, whether alone or mixed in short productive algal turf communities (Fig. A3a-c), play a critical role in reef building via calcification and cementation of loose substrata (Adey 1998; Chisholm 2000;

Weiss and Martindale 2017; Teichert et al. 2020; Cornwall et al. 2021). In addition, many nominally herbivorous fishes readily feed on the biofilms and detritus that accumulate on CCA and in sparse algal turf communities (Wilson et al. 2003; Crossman et al. 2005; Clements et al. 2017; Mendes et al. 2018), while others target the highly productive turf forming algae directly (Choat et al. 2002; Miyake et al. 2015; Kelly et al. 2016; Humphries et al. 2020). Furthermore, coral settlement is also facilitated by many forms of CCA, and CCA are seen as a key benthic covering in promoting reef recovery (Harrington et al. 2004; Ritson-Williams et al. 2010; Tebben et al. 2015; Jorissen et al. 2021). Interestingly, despite often being viewed as an inhibitor of coral settlement, several experimental studies have revealed that algal turfs themselves (when free of sediment) do not inhibit coral settlement, with coral recruitment rates to well established algal turf covered substratum being comparable to CCA covered substratum or substratum cleared of algal turf and sediment (Birrell et al. 2005; Diaz-Pulido et al. 2010; Speare et al. 2019; but see Arnold et al. 2010). As such, coral reefs covered in CCA and sparse/short algal turf communities are likely to be relatively amenable to the recovery of coral and can support a variety of critical ecosystem functions such as reef building and nutritional resource provision to fishes.

The capacity of low-lying algal communities to deliver critical functions, however, appears to be directly related to the amount of sediment contained within the communities. For example, as sediment accumulation increases in low-lying algal communities, turf forming algae can become competitively dominant over CCA (McClanahan 1997; Steneck 1997; Albert et al. 2008) and underpin a shift towards long sediment-laden algal turfs (Goatley et al. 2016; Tebbett and Bellwood 2020). Furthermore, as sediments progressively accumulate in low-lying algal communities this dilutes the nutritional value and productivity of the resources that nominally herbivorous fishes exploit (Clausing et al. 2014; Tebbett et al. 2018a; Tebbett and Bellwood 2020), with marked impacts on herbivorous fish feeding behaviour (Bellwood and Fulton 2008; Goatley and Bellwood 2012; Gordon et al. 2016; Tebbett et al. 2017b, 2020a) and the potential for driving bottom-up collapses of herbivorous fish populations (Wenger et al. 2020; Tebbett et al. 2021). As herbivorous fishes are widely regarded as pivotal players in coral reef resilience (Bellwood et al. 2004; Burkepile and Hay 2008; Hughes et al. 2010; Steneck et al. 2019), such sediment-driven impacts may have substantial ecological consequences. Finally, sediments accumulated on the benthos and within low-lying algal communities can have substantial impacts on the capacity of coral reefs to recover, as they inhibit coral settlement (Hodgson 1990; Birrell et al. 2005; Ricardo et al. 2017; Speare et al. 2019; Wakwella et al. 2020). Therefore, as I note in the main text, the condition of this low-lying algal community is likely to be critical to how reefs function, and their capacity to recover.

To-date, the amount of sediment contained in low-lying algal communities remains largely unquantified and unmonitored on virtually all coral reefs globally (reviewed in Tebbett and Bellwood 2019). Indeed, virtually all published data on low-lying algal community sediment loads is limited to just a few reefs on Great Barrier Reef (reviewed in Tebbett and Bellwood 2019). However, the importance of quantifying algal turf length is gradually becoming more recognised and adopted in coral reef ecological research (e.g. Fong et al. 2018; Ford et al. 2018; Steneck et al. 2018; Duran et al. 2019). For example, the Atlantic and Gulf Rapid Reef Assessment (AGRRA) program now recognises three divisions in the state of low-lying algal communities (CCA, sparse turfs, and turf associated with sediment). Although of course, given the continuous nature of the transition from CCA-dominated to sediment-laden turfs, the use of such categorical divisions will inevitably lead to some inconsistencies in classification (see Fig. A3, A5). It should be noted that the AGRRA data could not be included in my current dataset, however, as soft corals (i.e. corals from the order Alcyonacea) are pooled with other sessile invertebrates, while 'rubble' (a component of the low-lying algal community) has been pooled with 'unknown' and 'other' categories in the AGRRA monitoring scheme. Due to the lack of these divisions the AGRRA data could not be reliably matched with the data in my dataset.

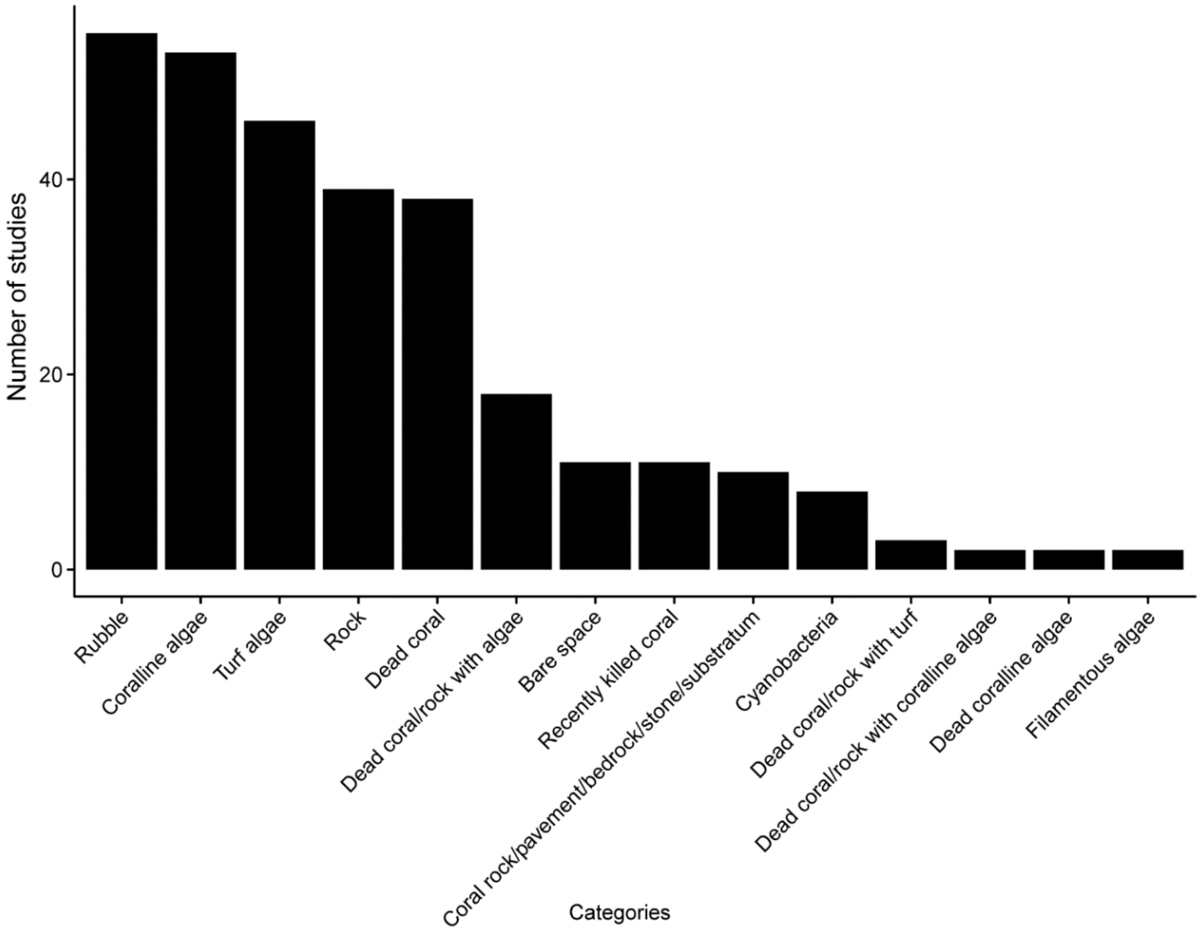


Figure A1 A frequency distribution showing the number of times different categories were used in studies that quantified the cover of low-lying algal communities on reefs. All benthic categories in this distribution are covered by algal turfs, crustose coralline algae and/or a biofilm/cyanobacteria on reefs. As such, this highlights the varied nature in which low-lying algal community cover is quantified on reefs. The frequency distribution was based on the terms used in the 83 studies incorporated into my benthic composition dataset.

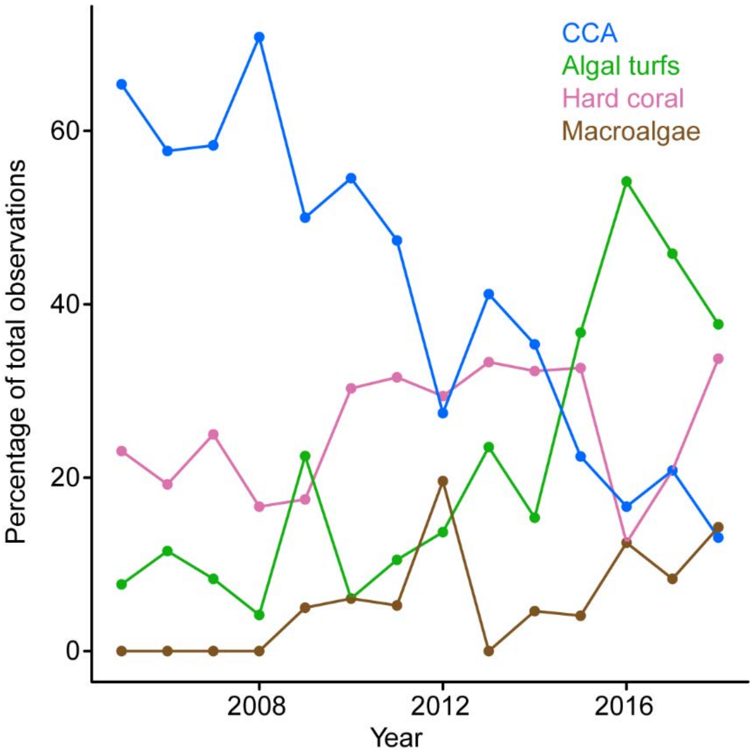
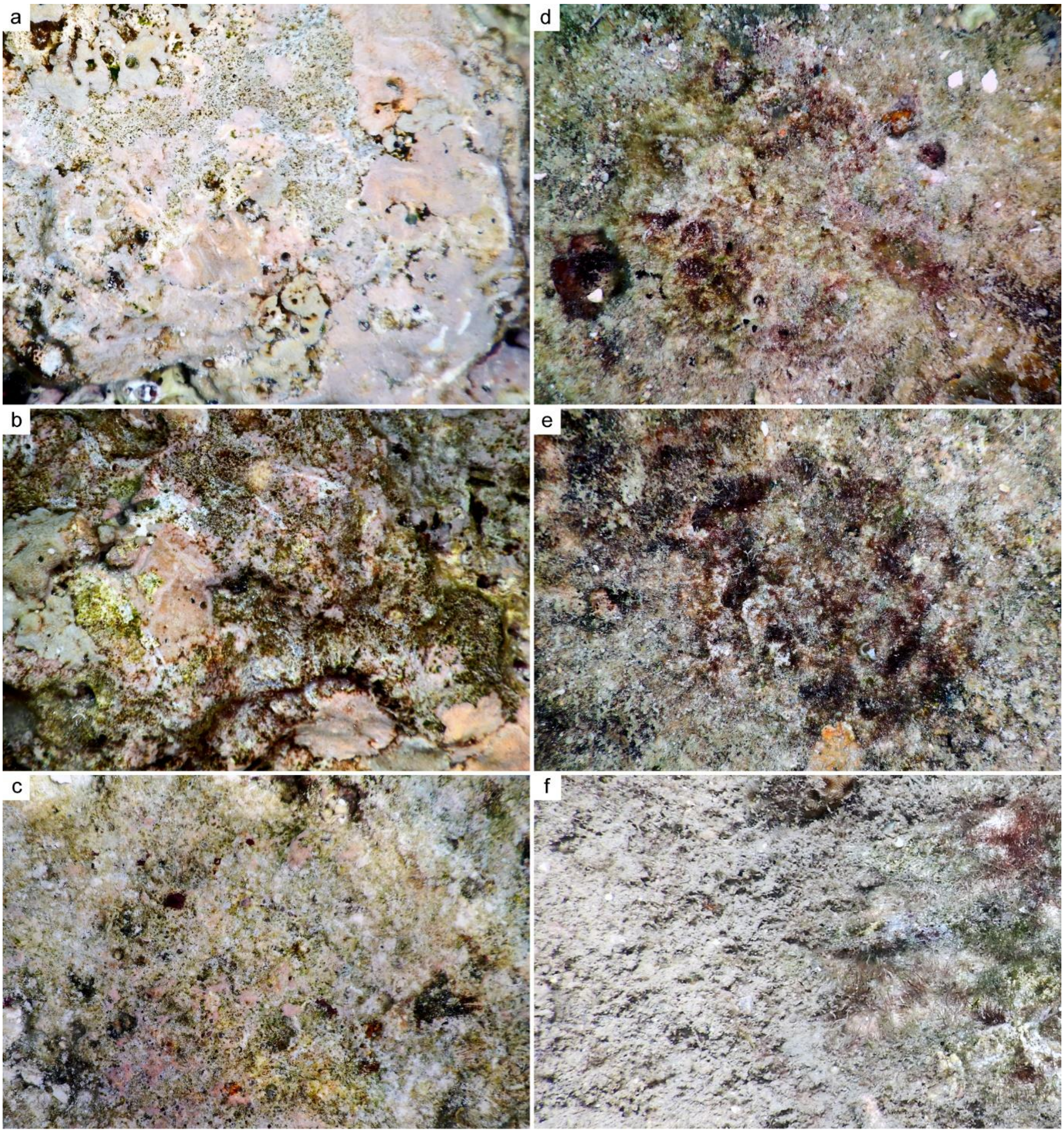


Figure A2 Benthic composition trends when the low-lying algal community is divided. The percentage of reef sites on which crustose coralline algae (CCA), algal turfs, hard corals or macroalgae were the most abundant benthic covering (i.e. the highest % covering of the benthos) in each year (only years with >20 replicate measurements are included; n = 722 in total). It is important to note that even when the low-lying algal community category is divided into CCA and algal turfs, then either CCA or algal turfs are still the most abundant benthic covering on reefs across most years (as per the results in the main text). Indeed, this plot suggests that the major change on reefs is in the state of the low-lying algal community, rather than between hard coral vs macroalgae cover.



Figures A3 The continuum of conditions in which the low-lying algal community on coral reefs can exist. This continuum ranges from a crustose coralline algae and sparse turf state (a) through to a long sediment-laden algal turf state (f). All photographs by SB Tebbett from the Great Barrier Reef, Australia.

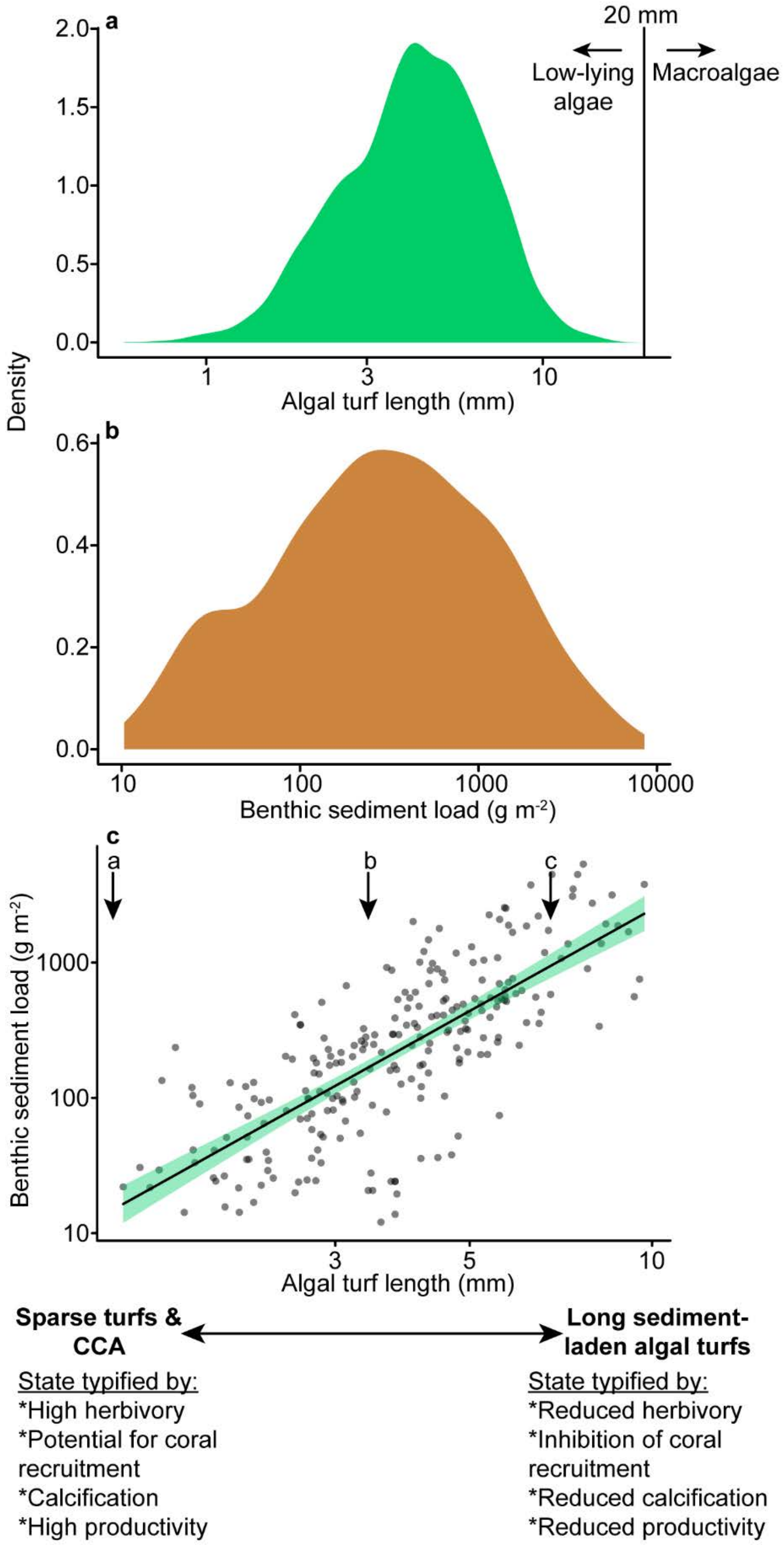


Figure A4 Plots of algal lengths and sediment loads across the continuum of low-lying algal community conditions on coral reefs. The distribution (density of data points) of (a) algal turf length (n = 3334 individual turf measurements) and (b) algal turf sediment load (n = 442 samples) as well (c) the relationship between matched algal turf length (the mean of individual turf filament measurements) and sediment load (n = 237 samples) data collected across various reefs on the Great Barrier Reef, Australia. Note the x-axis is on a log10 scale in (a) and (b), while both the x-axis and y-axis are on a log10 scale in (c). Also note in (a) how all algal length data is clearly contained below the 20 mm size threshold which is often used to define macroalgae vs low-lying algal communities. The letters and arrows in panel (c) denote the approximate locations of the algal turf communities in Fig. A5 below this continuum. The black line and shaded green area in (c) denote the fit and 95% confidence intervals, respectively, of a linear regression model fitted to help visualise the trend. All algal length and sediment mass data were sourced from Tebbett et al. 2017a, 2018b, 2020a, 2020b, 2021; Tebbett and Bellwood 2020.

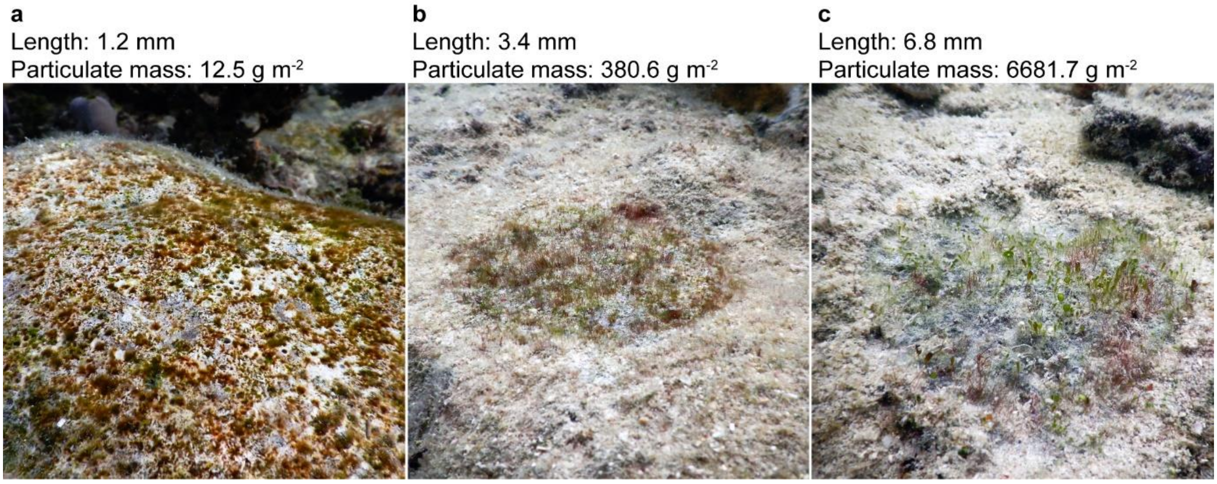


Figure A5 Low-lying algal communities across a continuum of lengths and particulate loads. The average length, accumulated particulate load and corresponding photograph of a) a community typified by sparse algal turfs and crustose coralline algae, b) a community typified by intermediate length algal turfs, and c) a community typified by long sediment-laden algal turfs. The cleared circular areas in (b) and (c) show the area of the low-lying algal community in which particulates were removed by vacuum sampling prior to photographs being taken. All photographs SB Tebbett from Lizard Island, Australia.

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Table A1 Summary of fixed effects terms from generalised additive mixed effects models used to examine the temporal variation in the dominance of key benthic components on coral reefs globally. All models used a binomial distribution with logit link. edf = estimated degrees of freedom, ref.df = reference degrees of freedom.

Response variable	**Predictor variable**	**edf**	**ref.df**	**Chi.sq**	***p* value**
Hard coral dominance	Year sampled	6.83	7.91	125.91	< 0.001
	Depth	4.75	5.83	21.24	< 0.01
Macroalgae dominance	Year sampled	6.82	7.86	83.63	< 0.001
	Depth	5.73	6.90	57.39	< 0.001
Low-lying algae dominance	Year sampled	7.75	8.58	160.52	< 0.001
	Depth	5.05	6.17	28.88	< 0.001

Table A2 Summary of fixed effects terms from generalised additive mixed effects models used to examine among realm differences in temporal trends of hard coral, macroalgae and low-lying algal community cover. Models used a tweedie distribution with log link. edf = estimated degrees of freedom, ref.df = reference degrees of freedom.

Response variable	**Predictor variable**	**edf**	**ref.df**	**F-value**	***p* value**
Hard coral cover	Year sampled:Central Pacific	9.59	9.95	56.68	< 0.001
	Year sampled:Indo-West Pacific	6.70	7.97	2.74	< 0.01
	Year sampled:Western Atlantic	8.13	9.21	41.05	< 0.001
	Depth:Central Pacific	6.28	7.24	17.40	< 0.001
	Depth:Indo-West Pacific	4.90	5.57	5.67	< 0.001
	Depth:Western Atlantic	2.92	3.65	2.33	< 0.05
Macroalgae cover	Year sampled:Central Pacific	11.52	12.87	27.49	< 0.001
	Year sampled:Indo-West Pacific	12.37	13.53	17.71	< 0.001
	Year sampled:Western Atlantic	8.84	10.53	13.65	< 0.001
	Depth:Central Pacific	5.68	6.71	5.04	< 0.001
	Depth:Indo-West Pacific	5.09	5.72	6.88	< 0.001
	Depth:Western Atlantic	1.00	1.00	43.06	< 0.001
Low-lying algae cover	Year sampled:Central Pacific	8.09	8.72	32.48	< 0.001
	Year sampled:Indo-West Pacific	8.47	8.92	15.78	< 0.001
	Year sampled:Western Atlantic	7.87	8.64	9.51	< 0.001
	Depth:Central Pacific	5.44	6.47	2.83	< 0.01
	Depth:Indo-West Pacific	4.42	5.17	4.29	< 0.01
	Depth:Western Atlantic	5.86	7.03	22.96	< 0.001

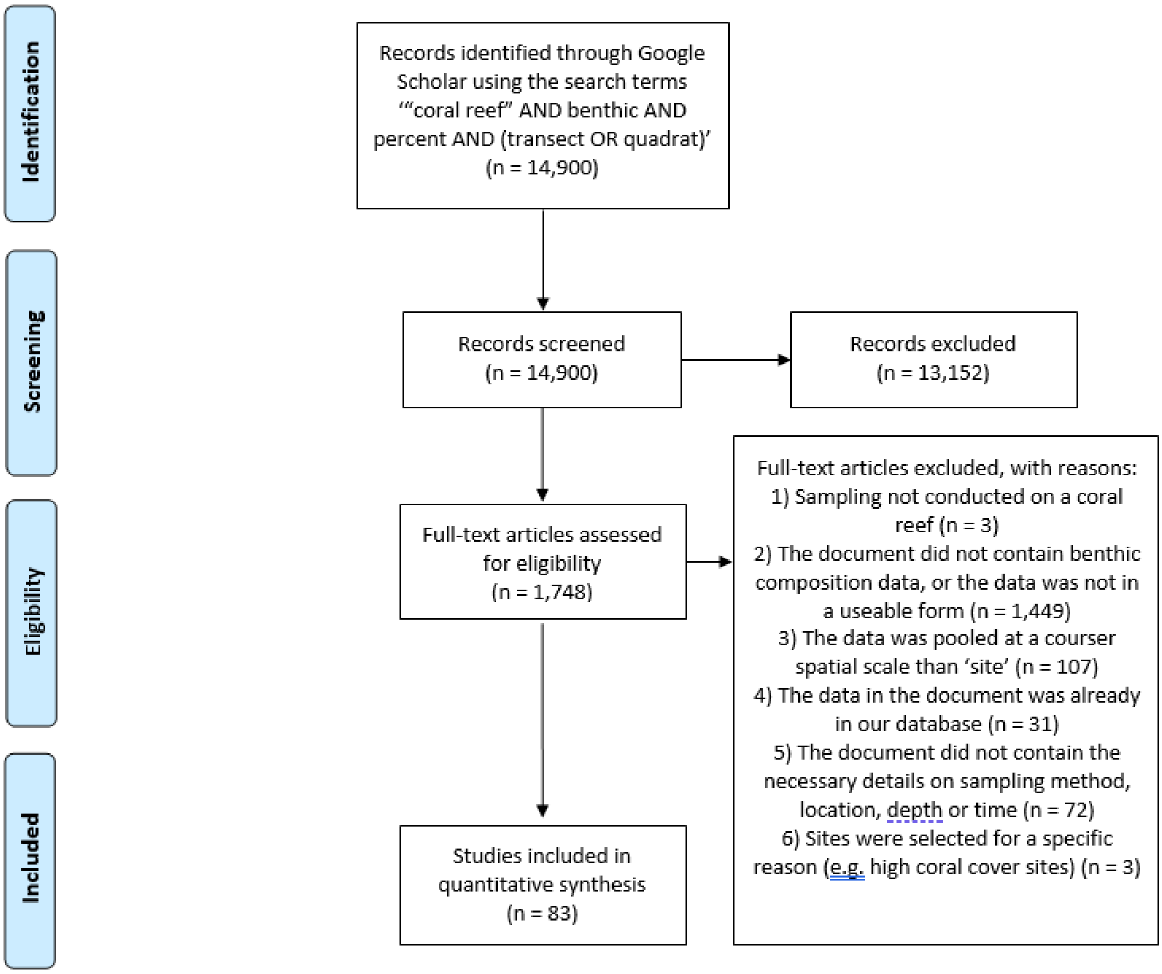

Figure A6 Flow diagram detailing the literature search and screening process used to compile the benthic composition dataset**.** The flow diagram was modified after Moher et al. (2009).

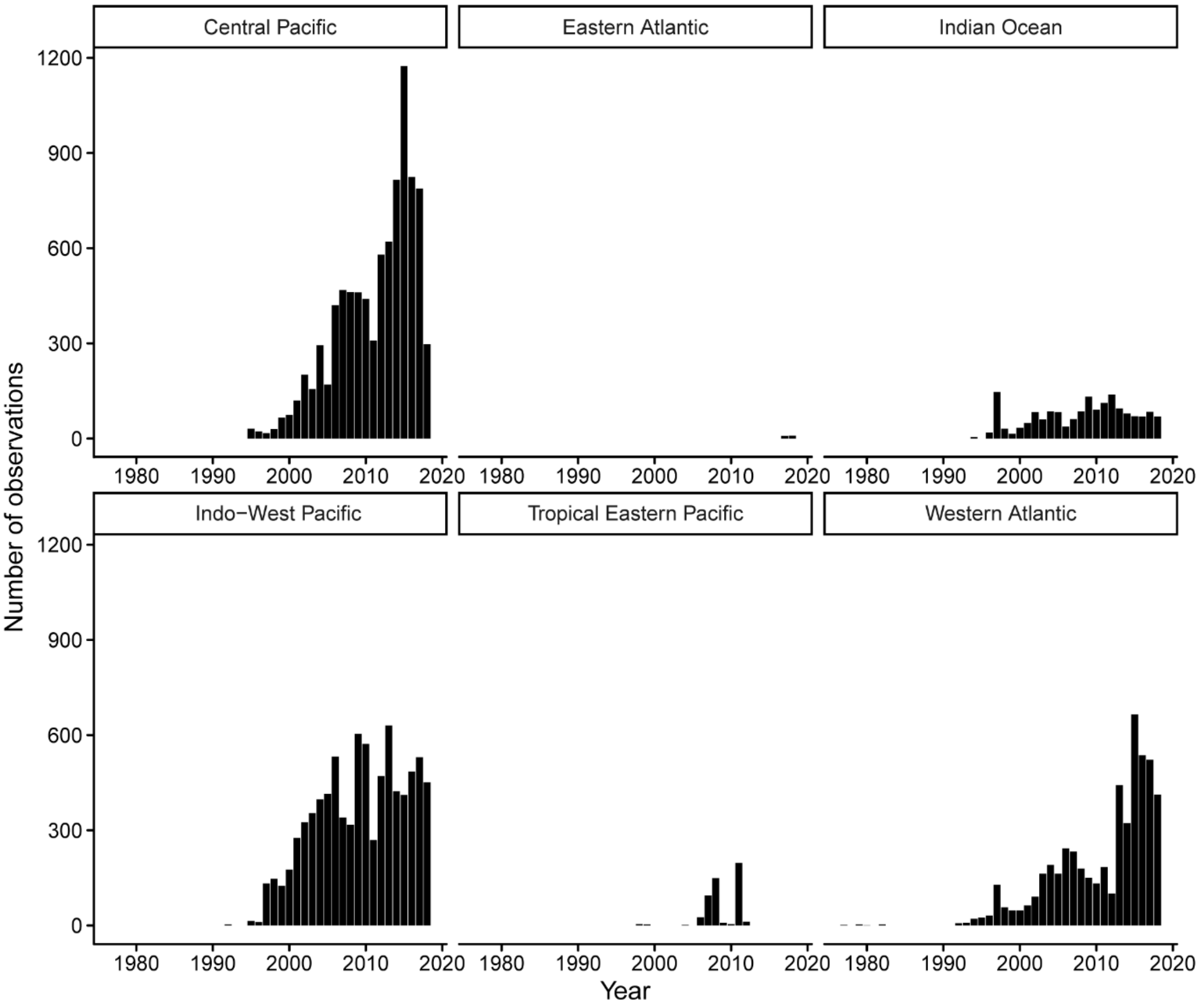

Figure A7 Frequency histogram of the benthic composition data among realms through time.

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Text A3 Note on Reef Check Australia Data

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Appendix B: Supporting information for chapter 3

Text B1 Examination of correlations between *Acropora* recruitment and explanatory variables

Overview and methods

As the recruitment of corals can be a key driver of recovery (Gouezo et al. 2019), it is important to understand major correlates of this process to provide an insight into the recovery potential of a given location. To do this I assessed how seven explanatory variables related to the *Acropora* recruitment data using XGBoost (Chen and Guestrin 2016), an Extreme Gradient Boosted Regression Tree. An XGBoost model was used because it can efficiently model nonlinearity and multilevel interactions in data that may not be suitable for more traditional analysis, while yielding accurate predictions (Elith et al. 2008).

The seven correlates considered in the regression tree were: CCA cover, macroalgae cover, rubble cover, biomass of scraping/excavating parrotfishes, biomass of other nominally herbivorous fishes, the depth of each quadrat and exposure level. The cover of CCA on hard substrata, macroalgae and rubble (covered in algal turfs, CCA or cyanobacteria) in each quadrat was based on the benthic cover data for January/February 2018 (i.e. near the beginning of the recovery period). The cover of these three benthic categories were considered as explanatory factors as previous experiments have demonstrated that they either facilitate coral settlement (CCA) (Harrington et al. 2004; Ritson-Williams et al. 2010) or inhibit coral settlement and survival (macroalgae and rubble) (Diaz-Pulido et al. 2010; Kenyon et al. 2020). Likewise, the biomass of nominally herbivorous fishes (parrotfishes, surgeonfishes, rabbitfishes and kyphosids) was included as this factor is frequently related to coral recovery and reef resilience (Mumby and Steneck 2008; Chong-Seng et al. 2014). However, I considered the biomass of scraping/excavating parrotfishes separately from the biomass of other herbivorous fishes, as it has also been suggested that the former may impede coral recruit survival as they scrape the substratum clean (Trapon et al. 2013). In each case the mean biomass of fishes at each sampling site was used. Details of how herbivorous fish biomass was quantified are provided in Text B2. The depth of each quadrat below chart datum was included as depth represents a major environmental gradient on coral reefs relating to both light availability and exposure to hydrodynamics which structure coral communities (Roberts et al. 2019) and even small-scale differences in reef elevation/depth can shape the nature of the benthos (Tebbett et al. 2020). Depth was measured during quadrat placement in January/February 2021 based on a Suunto D4i dive computer and adjusted to the tide height at the time of measurement. Habitat (exposed, semi-exposed, lagoon, back reef) was included to encapsulate among exposure differences in environmental parameters, such as hydrodynamic activity, which have been shown to relate to coral recruitment (Gouezo et al. 2021).

In terms of the XGBoost model, I used a poisson distribution for count data. The total number of new recruits (summed across 2018, 2020 and 2021) in each quadrat was treated as the dependent variable. Two tuning steps were performed prior to running the XGBoost model following Morais and Bellwood (2018). Firstly, I repeatedly fitted the model with combinations of model parameters (learning rate, maximum tree depth, gamma and subsampling rate) that were varied systematically. The combination of parameters that yielded the minimum root mean square error (rmse) was subsequently recorded (learning rate = 0.25, maximum tree depth = 7, gamma = 0.1, and subsampling = 0.6), while all other parameters were kept at their default values. During the second round of tuning, the models were repeatedly fitted with randomly drawn combinations of parameters from a uniform distribution bounded by the recorded parameters from the first tuning round ± 10%. The parameters that resulted in the lowest rmse were recorded (learning rate = 0.274, maximum tree depth = 6, gamma = 0.093, and subsampling = 0.632). The second tuning step only improved rmse marginally 2.45 to 2.36.

A cross-validation procedure was then used to assess the accuracy and precision of my tuned XGBoost model. This was achieved by randomly splitting the recruitment data into training and testing datasets. The training datasets were based on 80% of the data and were used to refit the models to generate coefficients for prediction. The testing datasets were based on the remaining 20% of the data and were used to contrast with predictions from the training dataset. A bias metric was calculated by subtracting each *Acropora* recruitment value predicted by the XGBoost model from its actual value (a bias value at or close to zero is apparent in accurate models). Prediction R^2 values were used to assess the precision of the models. The R^2 was calculated by fitting a linear regression model between the raw data values and the predicted values. The cross-validation steps were repeated 1000 times.

Predictions of *Acropora* recruit numbers were estimated using my tuned and cross-validated XGBoost model across all seven explanatory variables. To generate a distribution of predictions the model was bootstrapped for 1000 iterations. Subsequently, the median predicted value ± 95% highest density intervals were calculated from this distribution. The relative importance of different predictor variables was assessed against the expected importance of variables given chance alone (i.e. if all variables were equally involved in explaining variation in *Acropora* recruitment then each variable would account for 14.3% of the variability explained by the XGBoost model). All XGBoost modelling was performed in the software R (R Core Team 2020) using the *XGBoost* (Chen et al. 2019) and *tidybayes* (Kay 2019) packages.

Results

The boosted regression tree I used to examine the importance of different variables had a rmse of 0.23 and a R^2 of 0.65 suggesting that it was relatively precise and accurate, respectively. Based on this boosted regression tree, exposure emerged as the only variable that accounted for more variation in *Acropora* recruitment than expected (Fig. B6a). Indeed, exposure alone accounted for 52.4% of all variation in *Acropora* recruitment explained by the boosted regression tree (Fig. B6a). With all other variables held at their mean levels, *Acropora* recruitment appeared to be 3-4 times higher on semi-exposed reefs compared to any other exposure regime (Fig. B6b).

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Text B2 Herbivorous fish quantification

In January 2021 the abundance of nominally herbivorous fishes (parrotfishes [Labridae], surgeonfishes [Acanthuridae], rabbitfishes [Siganidae], chubs [Kyphosidae]) was quantified in the vicinity of each of the benthic transect locations. In all cases two fish censuses were performed at each transect location, and all censuses were composed of 50 m tape transects. All fishes >10 cm total length (TL) were counted as the tape was laid in a 5 m wide transect, then all fishes <10 cm TL were counted in a 1 m wide transect along the same tape. 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 and species identity data were subsequently converted to biomass using Bayesian length-weight regression parameters (Froese and Pauly 2018).

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Table B1 Comparison of models used to examine the variation in hard coral cover and algal turf cover at Lizard Island on Australia's Great Barrier Reef from 2016 - 2021. Models are compared using the corrected Akaike Information Criterion (AICc). Shown are number of parameters (k), model maximum log-likelihood (logLik), AICc, change in AICc (Δ) and AICc weight (wAICc).

Response variable	**Variables**	**k**	**logLik**	**AICc**	**Δ**	**wAICc**
Hard coral cover	Trip×Exposure	22	-5155.21	10355.02	0	1
	Trip	7	-5526.12	11066.31	711.29	0
	Trip+Exposure	10	-5524.93	11069.99	714.97	0
	Null	3	-5890.95	11787.92	1432.9	0
	Exposure	6	-5889.77	11791.58	1436.57	0
Algal turf cover	Trip×Exposure	23	-5622.27	11291.18	0	1
	Trip+Exposure	11	-5686.81	11395.77	104.59	0
	Trip	8	-5693.32	11402.72	111.53	0
	Exposure	7	-5842.03	11698.12	406.94	0
	Null	4	-5848.51	11705.03	413.85	0

Table B2 Summary of results from generalised linear mixed-effects models (GLMMs) used to examine variation in hard coral and algal turf cover at Lizard Island from 2016-2021. Model outputs are on the logit-scale.

Response variable	**Model used**	**Predictor variable**	**Estimate**	**SE**	***z* value**	***p* value**
Hard coral cover	Binomial GLMM	Intercept	-1.917	0.554	-3.461	<0.001
		Oct.2016	-0.768	0.077	-9.922	<0.001
		Jan.2018	-0.681	0.077	-8.894	<0.001
		Jan.2020	-0.352	0.074	-4.767	<0.001
		Jan.2021	-0.309	0.073	-4.213	<0.001
		Exposed	-0.169	0.806	-0.210	0.834
		Lagoon	0.836	0.630	1.328	0.184
		Semi-exposed	-0.709	0.903	-0.785	0.433
		Oct.2016:Exposed	-0.042	0.158	-0.266	0.790
		Jan.2018:Exposed	-0.105	0.157	-0.671	0.503
		Jan.2020:Exposed	-0.079	0.146	-0.538	0.590
		Jan.2021:Exposed	0.172	0.140	1.228	0.219
		Oct.2016:Lagoon	-0.088	0.089	-0.996	0.319
		Jan.2018:Lagoon	-0.229	0.088	-2.590	<0.05
		Jan.2020:Lagoon	-0.484	0.086	-5.652	<0.001
		Jan.2021:Lagoon	-0.507	0.085	-5.940	<0.001
		Oct.2016:Semi-exposed	0.197	0.190	1.038	0.299
		Jan.2018:Semi-exposed	0.526	0.176	2.983	<0.01
		Jan.2020:Semi-exposed	1.475	0.154	9.594	<0.001
		Jan.2021:Semi-exposed	2.358	0.149	15.836	<0.001
Algal turf cover	Binomial GLMM	Intercept	0.307	0.251	1.225	0.221
		Oct.2016	0.886	0.111	7.966	<0.001
		Jan.2018	0.661	0.110	6.004	<0.001
		Jan.2020	0.183	0.109	1.679	0.093
		Jan.2021	0.145	0.109	1.322	0.186
		Exposed	0.434	0.386	1.123	0.261
		Lagoon	-0.643	0.290	-2.219	<0.05
		Semi-exposed	1.520	0.433	3.507	<0.001
		Oct.2016:Exposed	-0.254	0.197	-1.288	0.198
		Jan.2018:Exposed	-0.588	0.194	-3.032	<0.01
		Jan.2020:Exposed	-0.392	0.193	-2.034	<0.05
		Jan.2021:Exposed	-0.136	0.193	-0.707	0.480
		Oct.2016:Lagoon	0.090	0.133	0.677	0.498
		Jan.2018:Lagoon	0.148	0.131	1.128	0.259
		Jan.2020:Lagoon	0.207	0.130	1.592	0.111
		Jan.2021:Lagoon	0.342	0.131	2.615	<0.01
		Oct.2016:Semi-exposed	-0.510	0.229	-2.222	<0.05
		Jan.2018:Semi-exposed	-0.640	0.224	-2.855	<0.01
		Jan.2020:Semi-exposed	-1.093	0.216	-5.050	<0.001
		Jan.2021:Semi-exposed	-1.594	0.215	-7.416	<0.001

Table B3 Results of key post-hoc means comparisons for hard coral cover and algal turf cover among years and exposures.

Response variable	**Model used**	**Comparison**	**Estimate**	**SE**	***t* ratio**	***p* value**
Hard coral cover	Binomial GLMM	**Back reefs**				
		Feb.2016 – Oct.2016	0.768	0.077	9.922	<0.001
		Feb.2016 – Jan.2018	0.681	0.077	8.894	<0.001
		Feb.2016 – Jan.2021	0.309	0.073	4.213	<0.001
		Oct.2016 – Jan.2018	-0.087	0.082	-1.066	0.71
		Oct.2016 – Jan.2021	-0.459	0.079	-5.800	<0.001
		Jan.2018 – Jan.2021	-0.372	0.078	-4.747	<0.001
		Exposed				
		Feb.2016 – Oct.2016	0.810	0.138	5.874	<0.001
		Feb.2016 – Jan.2018	0.786	0.137	5.736	<0.001
		Feb.2016 – Jan.2021	0.137	0.119	1.151	0.658
		Oct.2016 – Jan.2018	-0.024	0.155	-0.154	0.999
		Oct.2016 – Jan.2021	-0.673	0.140	-4.795	<0.001
		Jan.2018 – Jan.2021	-0.649	0.140	-4.652	<0.001
		Lagoon				
		Feb.2016 – Oct.2016	0.856	0.044	19.643	<0.001
		Feb.2016 – Jan.2018	0.910	0.044	20.735	<0.001
		Feb.2016 – Jan.2021	0.816	0.044	18.780	<0.001
		Oct.2016 – Jan.2018	0.053	0.046	1.157	0.654
		Oct.2016 – Jan.2021	-0.040	0.046	-0.887	0.812
		Jan.2018 – Jan.2021	-0.093	0.046	-2.042	0.173
		Semi-exposed				
		Feb.2016 – Oct.2016	0.571	0.173	3.292	<0.01
		Feb.2016 – Jan.2018	0.155	0.159	0.978	0.7619
		Feb.2016 – Jan.2021	-2.048	0.130	-15.816	<0.001
		Oct.2016 – Jan.2018	-0.416	0.177	-2.346	0.088
		Oct.2016 – Jan.2021	-2.619	0.153	-17.142	<0.001
		Jan.2018 – Jan.2021	-2.204	0.135	-16.320	<0.001
Algal turf cover	Binomial GLMM	**Back reefs**				
		Feb.2016 – Oct.2016	-0.886	0.111	-7.966	<0.001
		Feb.2016 – Jan.2021	-0.145	0.109	-1.322	0.383
		Oct.2016 – Jan.2021	0.742	0.112	6.643	<0.001
		Exposed				
		Feb.2016 – Oct.2016	-0.632	0.163	-3.874	<0.001
		Feb.2016 – Jan.2021	-0.008	0.159	-0.052	0.999
		Oct.2016 – Jan.2021	0.624	0.163	3.834	<0.001
		Lagoon				
		Feb.2016 – Oct.2016	-0.976	0.072	-13.547	<0.001
		Feb.2016 – Jan.2021	-0.487	0.072	-6.802	<0.001
		Oct.2016 – Jan.2021	0.490	0.072	6.801	<0.001
		Semi-exposed				
		Feb.2016 – Oct.2016	-0.377	0.201	-1.876	0.146
		Feb.2016 – Jan.2021	1.449	0.185	7.834	<0.001
		Oct.2016 – Jan.2021	1.826	0.191	9.547	<0.001

Table B4 Summary of results from a generalised linear mixed-effects model (GLMM) used to examine variation in *Acropora* recruitment around Lizard Island. Model outputs are on the log-scale.

Response variable	Model used	Predictor variable	Estimate	SE	*z* value	*p* value
***Acropora* recruits**	Zero-inflated tweedie GLMM	Intercept	-0.604	0.518	-1.166	0.244
		Exposed	0.726	0.746	0.973	0.331
		Lagoon	-1.587	0.646	-2.455	<0.05
		Semi-exposed	2.885	0.785	3.676	<0.001

Table B5 Results of post-hoc means comparisons for *Acropora* recruitment among exposures around Lizard Island.

Response variable	Model used	Comparison	Estimate	SE	*t* ratio	*p* value
***Acropora* recruits**	Zero-inflated tweedie GLMM	Back – Exposed	-0.726	0.746	-0.973	0.765
		Back – Lagoon	1.586	0.646	2.455	0.069
		Back – Semi-exposed	-2.885	0.785	-3.676	<0.01
		Exposed – Lagoon	2.312	0.651	3.554	<0.01
		Exposed – Semi-exposed	-2.159	0.798	-2.706	<0.05
		Lagoon – Semi-exposed	-4.472	0.706	-6.337	<0.001

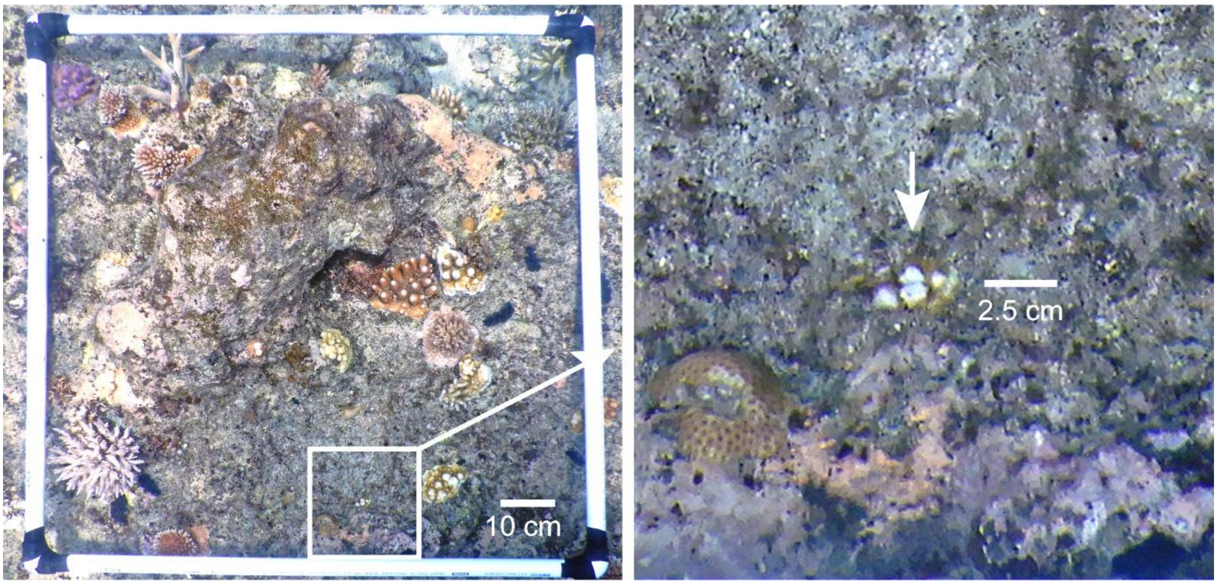

Figure B1 An example of a photograph used to count *Acropora* recruits with a close-up view of a small recruit.

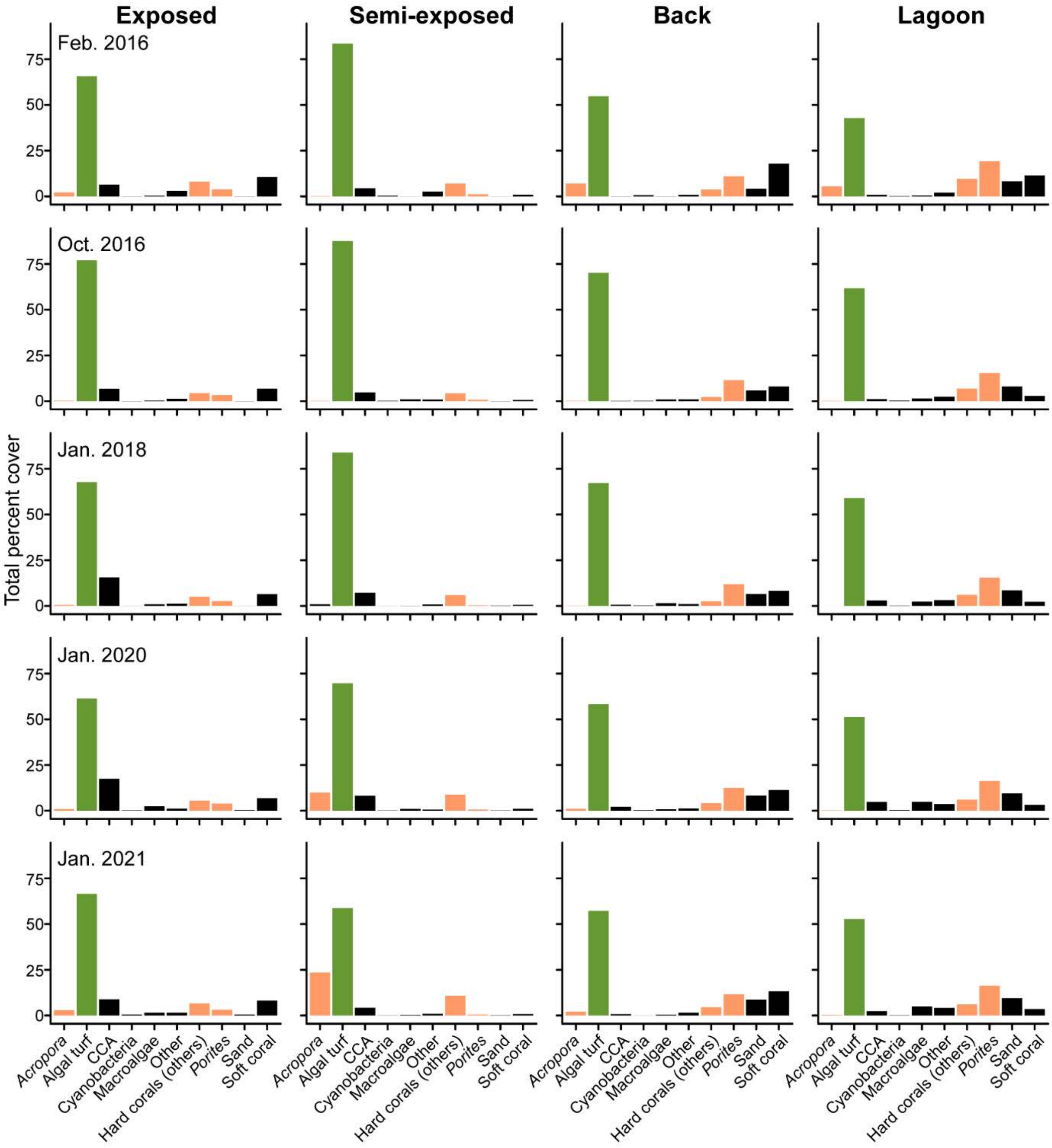

Figure B2 The total percentage cover of major benthic categories across all quadrats in each exposure regime in each sampling trip. The major benthic groups (algal turfs and hard corals [*Acropora* spp., *Porites* spp and other taxa], green and orange, respectively) used in analysis in the main text are highlighted.

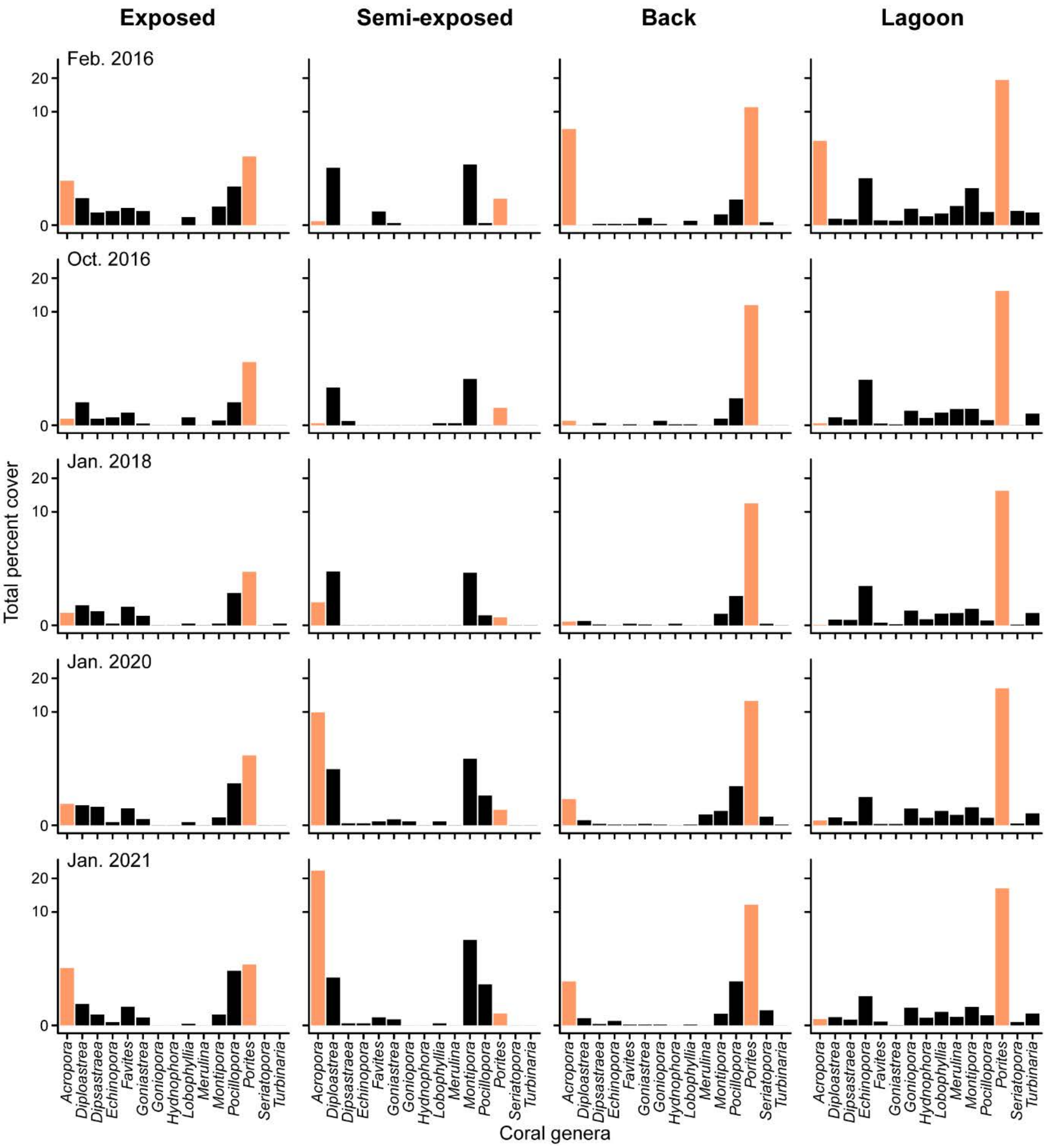

Figure B3 The total percentage cover of the 15 most abundant hard coral genera (i.e. those with a cover of >0.1%) across all quadrats in each exposure regime in each sampling trip. The two major genera (i.e. *Acropora* spp. and *Porites* spp.) are highlighted in orange to ease comparisons with Fig. B2. Please note the y-axis is on a log10 scale to ensure that changes in the cover of other coral genera can be seen.

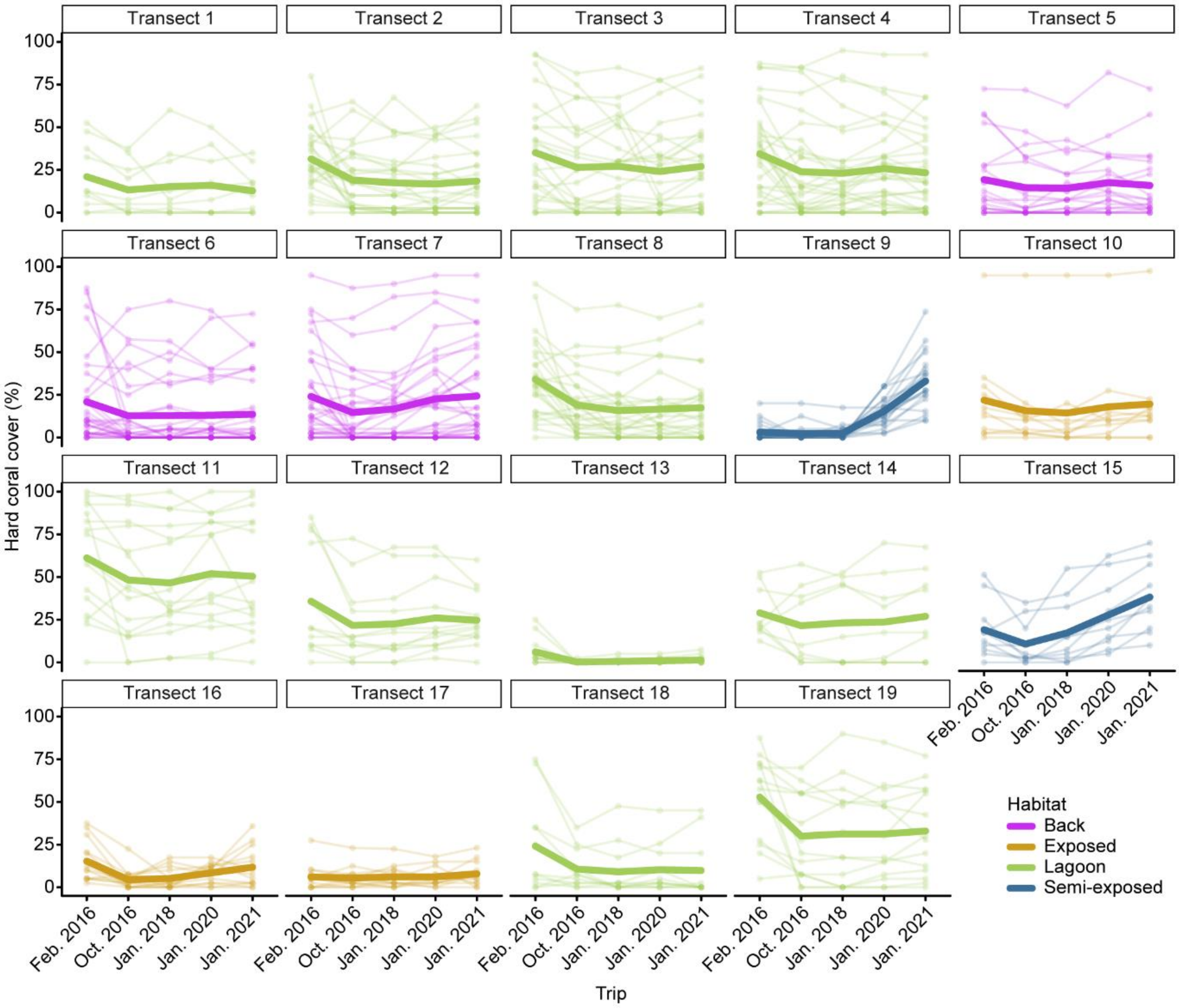

Figure B4 The cover of hard corals in each quadrat across all sampling trips. Pale points and lines denote the trajectory of individual quadrats while the thick lines denote the transect level mean. Note the similarity in trajectories across transects in the same habitats.

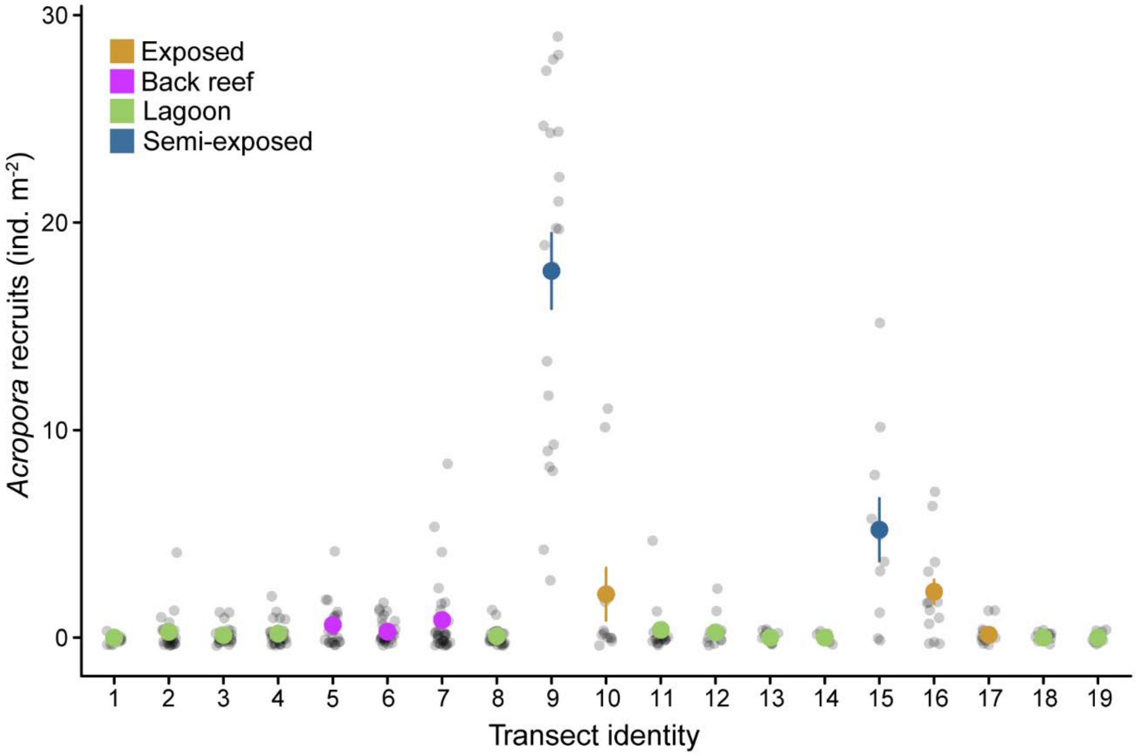

Figure B5 The abundance of *Acropora* recruits along each transect. The coloured point and range denote the mean and standard error, while the grey dots show the number of *Acropora* recruits in each quadrat on each transect.

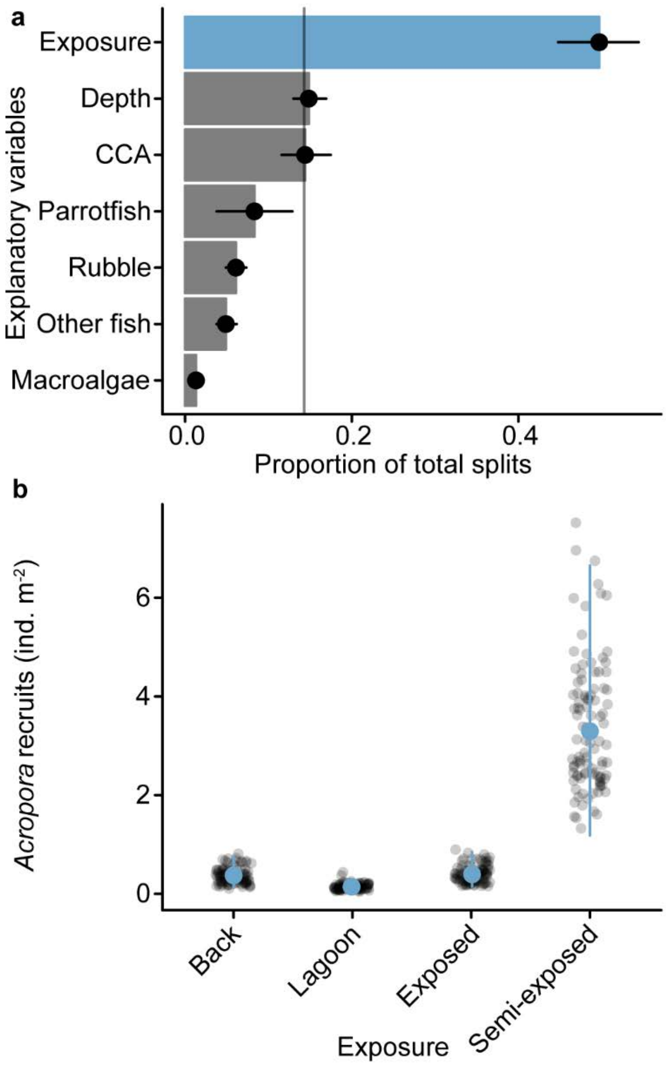

Figure B6 a) The relative importance of explanatory variables examined in an extreme gradient boosted regression tree in accounting for the total number of *Acropora* recruits detected in quadrats from January 2018-January 2021. The vertical grey line shows the relative importance expected for each variable by chance alone. Note 'other fish' refers to other nominally herbivorous fishes. b) Partial dependency plots from the regression tree showing the relationship between reef exposure and the number of *Acropora* recruits when all other variables were held at the mean values. The black circles and ranges in a), and blue circles and ranges in b), indicate the median relative importance value ±95% highest density intervals based on bootstrapping the predictions 1000 times. The black dots in b) denote 100 randomly selected predicted values for each exposure regime.

Appendix C: Supporting information for chapter 5

Text C1 Methods associated with photogrammetry

At each of the three sites, transect tapes were laid out on the reef benthos to delineate a quadratic 6×6 m (36 m^2) area. Within this delineated area the entire benthos at each site was recorded using a Nikon Coolpix W300 camera by a diver swimming slowly in an overlapping zig-zag pattern approximately 1.5 m above the reef, video-recording the reef from a birds-eye perspective. From the videos, every fifth video-frame was extracted, yielding approximately 3000 images per site as source data for photogrammetric reconstructions in structure-from-motion software (Agisoft Photoscan Professional). This software was chosen because it is readily available, cost-effective, widely used and can produce high-resolution 3-dimensional (3D) models, orthorectified photomosaic maps, as well as 3D digital elevation models, of each site in sub-centimetre resolution (cf. Burns et al. 2015; Figueira et al. 2015; Raoult et al. 2017; Ferrari et al. 2018). These methods followed Streit et al. (2019).

Agisoft Photoscan software reconstructs 3D surface information by utilising changing viewing angles in partially overlapping high-resolution imagery, similar to the principle of stereoscopic vision. In brief, the software identifies unique ‘tie points’ in supplied images, matches identical points in overlapping images, displays these points in relative distances to one-another and thus creates a ‘point cloud’ that represents the original 3D structure. The models of my experimental sites used approximately 3000 images as source data from which around 2 to 3 million points were identified and spatially matched. Subsequently, this point cloud is manually adjusted and scaled according to known, real-world measurements. Underwater transect tapes recorded in the original imagery were used as ground control points (i.e. ensuring that the same points were correctly matched in overlapping images) and to scale the model in the planar x-y-dimension using the millimetre-graduations visible on the transect tapes. After adjustments and scaling of the initial model the software is used to build a 'dense point cloud' (containing upwards of 50 million individual points for each of the study sites), which provides a quasi-continual surface model of the study site. This dense cloud was used in a final step to create a 3D digital elevation model (DEM) and orthorectified photomosaic (see e.g. Burns et al. [2015] for details on the software and workflow).

The photomosaic (see Fig. 5.1a) shows the entire study site in an orthogonal birds-eye-view, i.e. in an idealised flattened perspective as distortion arising from camera lenses and from surface shapes are accounted for. The DEM (see Fig. 5.1b) is a planar map containing the elevation value of each cell (or pixel). Minimum cell/pixel size is defined by the point count in the 'dense point cloud' model, which in turn is driven by substrate contrast, original image quality and is hence not consistent across models of different study sites. Across the models, resolution ranged from 0.09 to 0.18 cm^2 per pixel. To allow comparison across sites, I standardised the resolution to 1 cm^2 per pixel (using the function 'aggregate' in the R-package 'raster', Hijmans [2017]).

The lowest point in each study site was defined to have an elevation of zero, rather than using water-depth below chart-datum as a reference for elevation, since the latter could not be measured with sufficient accuracy on the centimetre-scale. All elevation values are thus not absolute, geographically informed measurements, but rather locally constrained, relative values. All were in 2-4 m of water at all times. These elevation values were ground-truthed in the produced DEMs by measuring the modelled height of bricks, which had been placed within the study sites prior to image capture. The elevation of four point pairs per brick were calculated. A pair of points included one point on top of the brick, and one point just adjacent to the brick on the surrounding substratum. Each side of the brick contained a pair of points to account for the potentially uneven nature of the substratum on which the bricks were sitting. The difference in elevation between each pair of points was then calculated (i.e. the brick height estimated by the model). This estimate of elevation was then subtracted from the known dimension of the brick to get an error value, separately for each point pair. On average (± SE), across all sites, the elevation estimates were accurate to within 2.8 ± 2.9 mm. Therefore, I am highly confident in the elevation estimates.

Both, the photomosaic map and DEM of each study site were subsequently georeferenced and precisely layered on top of one another using ArcGIS (ArcMap version 10.4.1, ESRI). Each sediment-sampling site was visually identified on the photomosaic map (see Fig. 5.1a) and the GPS-coordinates of its centre-point recorded. To extract surface information from the DEMs, further processing was done in R statistics software using the R-package 'raster' (Hijmans, 2017; R Core Team, 2020). For each individual sediment sampling location a circle of 10 cm diameter was created (using GPS coordinates), which was used as a 'cookie cutter' on the DEM of the respective study-site (function 'mask') to extract the elevation information of each sediment sampling location. Additionally, the function 'terrain' was used to calculate surface angles (in degrees from horizontal) from the elevation data contained in the DEM of each sediment sampling location.

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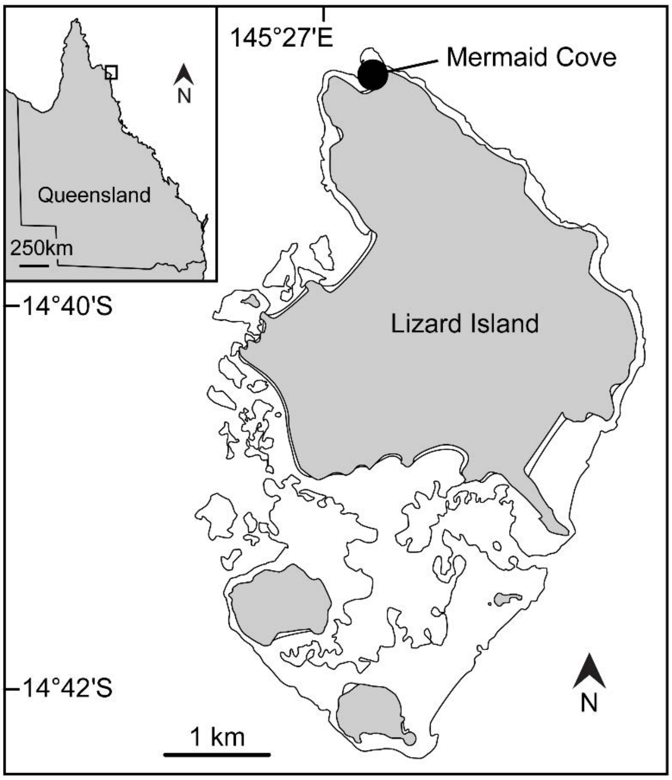

Figure C1 Map of Lizard Island showing the location of the study sites in Mermaid Cove.

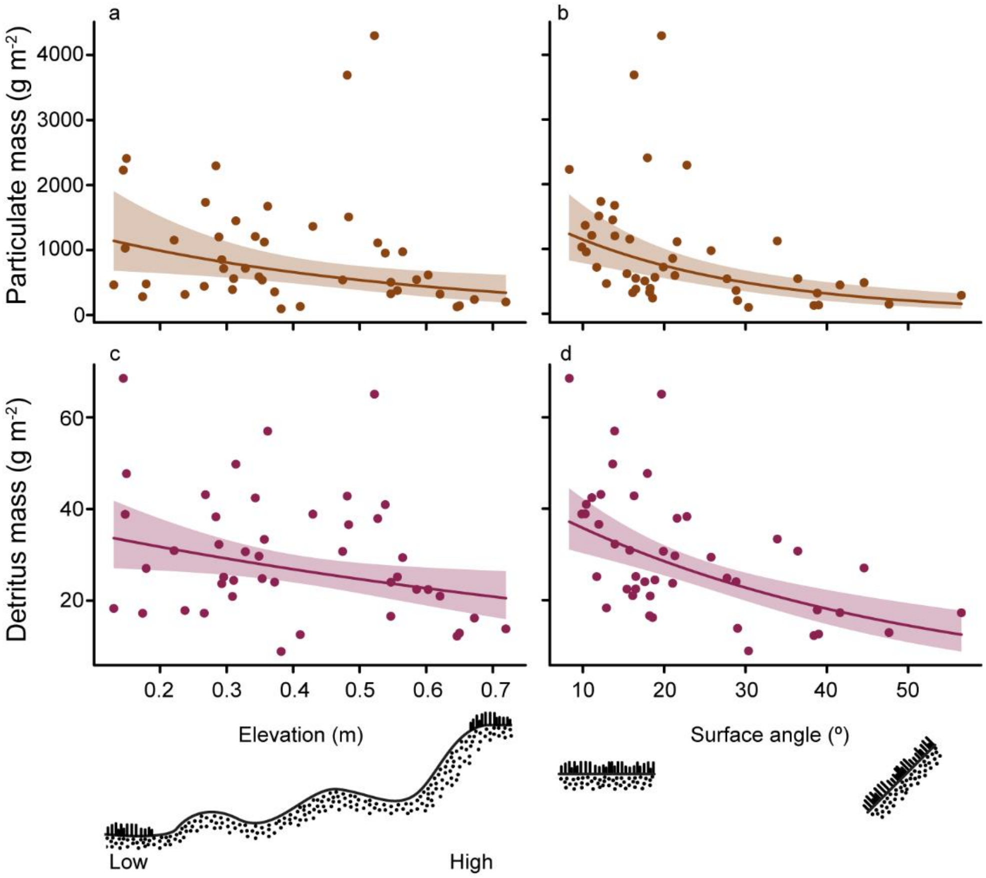

Figure C2 The relationship between the elevation (a, c) and angle (b, d) of the sampled surface and components of the algal turfs, (a, b) total particulate mass, (c, d) organic particulate mass. The lines mark the predicted fits from linear mixed effects models and their upper and lower 95% confidence interval. The points are the raw data points.

Table C1 Comparison of models used to examine the effect of complexity metrics (elevation and angle) on algal turf components. Models are compared using the corrected Akaike Criterion (AICc). Shown are numbers of parameters (k), model maximum log-likelihood (logLik), AICc, change in AICc (Δ) and AICc weight (wAICc).

Response variable	Variables	k	logLik	AICc	Δ	wAICc
Turf length	Elevation	4	-70.28	149.59	0.00	0.54
	Elevation×Angle	6	-68.50	151.26	1.67	0.24
	Elevation+Angle	5	-69.93	151.43	1.84	0.22
	Null	3	-76.74	160.08	10.48	0.00
	Angle	4	-75.98	160.98	11.38	0.00
Turf particulate depth	Elevation+Angle	5	-28.01	67.61	0.00	0.67
	Elevation×Angle	6	-27.80	69.86	2.26	0.22
	Angle	4	-31.01	71.05	3.44	0.12
	Elevation	4	-36.68	82.38	14.78	0.00
	Null	3	-38.93	84.45	16.85	0.00
Turf particulate mass	Elevation+Angle	5	-45.09	101.77	0.00	0.65
	Elevation×Angle	6	-44.67	103.61	1.84	0.26
	Angle	4	-48.36	105.74	3.97	0.09
	Elevation	4	-54.67	118.37	16.61	0.00
	Null	3	-57.04	120.68	18.92	0.00
Turf inorganic sediment mass	Elevation+Angle	5	-46.04	103.66	0.00	0.65
	Elevation×Angle	6	-45.59	105.45	1.80	0.26
	Angle	4	-49.34	107.70	4.05	0.09
	Elevation	4	-55.66	120.35	16.70	0.00
	Null	3	-58.06	122.72	19.06	0.00
Turf organic particulate mass	Elevation+Angle	5	-16.88	45.34	0.00	0.66
	Elevation×Angle	6	-16.66	47.60	2.26	0.21
	Angle	4	-19.83	48.69	3.35	0.12
	Elevation	4	-26.28	61.59	16.25	0.00
	Null	3	-28.44	63.48	18.14	0.00
Proportion of organics in particulates	Elevation+Angle	5	122.05	-232.52	0.00	0.65
	Elevation×Angle	6	122.57	-230.87	1.65	0.29
	Angle	4	118.38	-227.73	4.79	0.06
	Elevation	4	113.78	-218.54	13.98	0.00
	Null	3	111.35	-216.09	16.43	0.00

Table C2 Summary of model results used to examine the effect of complexity metrics (elevation and surface angle) on algal turf components.

Response variable	Model used	Predictor variable	Estimate	SE	*t/z* value	*p* value
Turf length	Gamma (GLMM)	Intercept	1.5356	0.1022	15.024	< 0.001
		Elevation	-1.3222	0.3634	-3.639	< 0.001
Turf particulate depth	Log (LME)	Intercept	0.4676	0.0932	5.02	< 0.001
		Elevation	-1.2435	0.509	-2.443	< 0.05
		Angle	-0.0280	0.0064	-4.399	< 0.001
Turf particulate mass	Log (LME)	Intercept	6.5001	0.1466	44.3291	< 0.001
		Elevation	-2.0315	0.7721	-2.631	< 0.05
		Angle	-0.0434	0.0094	-4.6033	< 0.001
Turf sediment mass	Log (LME)	Intercept	6.4537	0.1496	43.146	< 0.001
		Elevation	-2.0851	0.7883	-2.645	< 0.05
		Angle	-0.0445	0.0096	-4.618	< 0.001
Turf organic mass	Log (LME)	Intercept	3.2929	0.0555	59.376	< 0.001
		Elevation	-0.8383	0.3454	-2.427	< 0.05
		Angle	-0.0227	0.0049	-4.676	< 0.001
Proportion organics	Beta (GLMM)	Intercept	-3.091	0.0582	-53.11	< 0.001
		Elevation	0.9736	0.3406	2.86	< 0.01
		Angle	0.0218	0.0044	4.9	< 0.001

Appendix D: Supporting information for chapter 6

Text D1 Herbivorous fish surveys

The abundance and biomass of nominally herbivorous fishes (Acanthuridae, Labridae [Scarini], Kyphosidae and Siganidae) present at each site were quantified using visual census (two 50 m transects). Two divers performed the censuses. The first diver counted all nominal herbivores >10 cm total length (TL) in a 5 m wide belt transect while the second diver counted all nominal herbivores <10 cm TL in a 1 m wide belt transect while simultaneously laying the tape. All fishes were placed into TL size categories (5 cm intervals for fishes >10 cm TL and 2.5 cm intervals for fishes <10 cm TL). Fish biomass was estimated using Bayesian length-weight regression parameters (Froese and Pauly 2018). See Table D1 for an overview of the nominal herbivorous fish communities.

References

Froese R, Pauly D (2018) Fishbase. www.fishbase.org

Text D2 Predicting algal turf sediment loads

To be able to predict initial algal turf sediment loads in caged plots, as a function of initial algal turf length, I used a Bayesian generalised linear mixed effects model (GLMM) relating sediment load to algal turf length sampled from plots adjacent to the cages. In this model sediment load (g m^{-2}) was treated as the response variable, while algal turf length (mm; continuous factor, logged) and island identity 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 used a Gamma distribution with a log-link and weakly informative priors (see Table D2 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, I 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 model revealed a positive relationship between sediment load and algal turf length with a clear effect of the interaction between algal turf length and island identity as the 95% credibility intervals did not overlap zero (Fig. D2a; Table D3). In essence, the slope of the relationship was shallower for Orpheus Island compared to Lizard Island (Fig. D2a). I then fed the initial algal turf length of each caged plot to the model, thus predicting initial algal turf sediment load. These predicted algal turf sediment loads could then be related to algal turf productivity. All statistical analyses were performed in the software R (R Core Team 2020) using the *rstanarm* (Goodrich et al. 2018), *bayesplot* (Gabry and Mahr 2018), *tidybayes* (Kay 2019), *tidyverse* (Wickham 2017) and *emmeans* (Lenth 2019) packages.

References

Gabry J, Mahr T (2018) bayesplot: plotting for Bayesian models. R package version 1.6.0

Goodrich B, Gabry J, Ali I, Brilleman S (2018) rstanarm: Bayesian applied regression modeling via Stan. R package version 2.17.4

Kay M (2019) tidybayes: tidy data and geoms for Bayesian models. R package version 1.0.4

Lenth R (2019) emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.3.2

R Core Team (2020) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Wickham H (2017) tidyverse: Easily Install and Load the "Tidyverse". R package version 1.2.1.

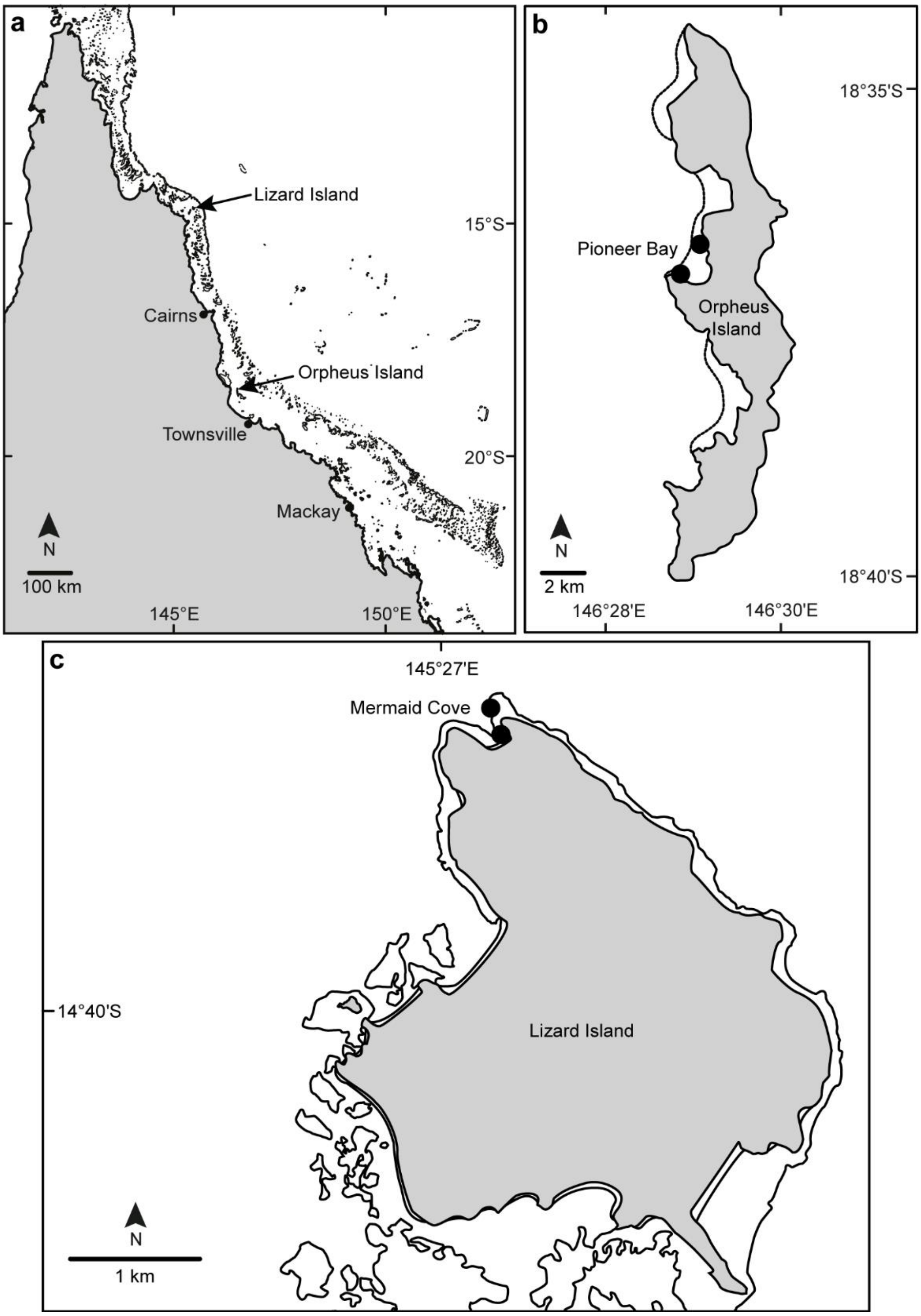

Figure D1 a) Map of Australia's north Queensland coast showing the positions of Orpheus Island and Lizard Island. The study sites within b) Pioneer Bay, Orpheus Island, and c) Mermaid Cove, Lizard Island.

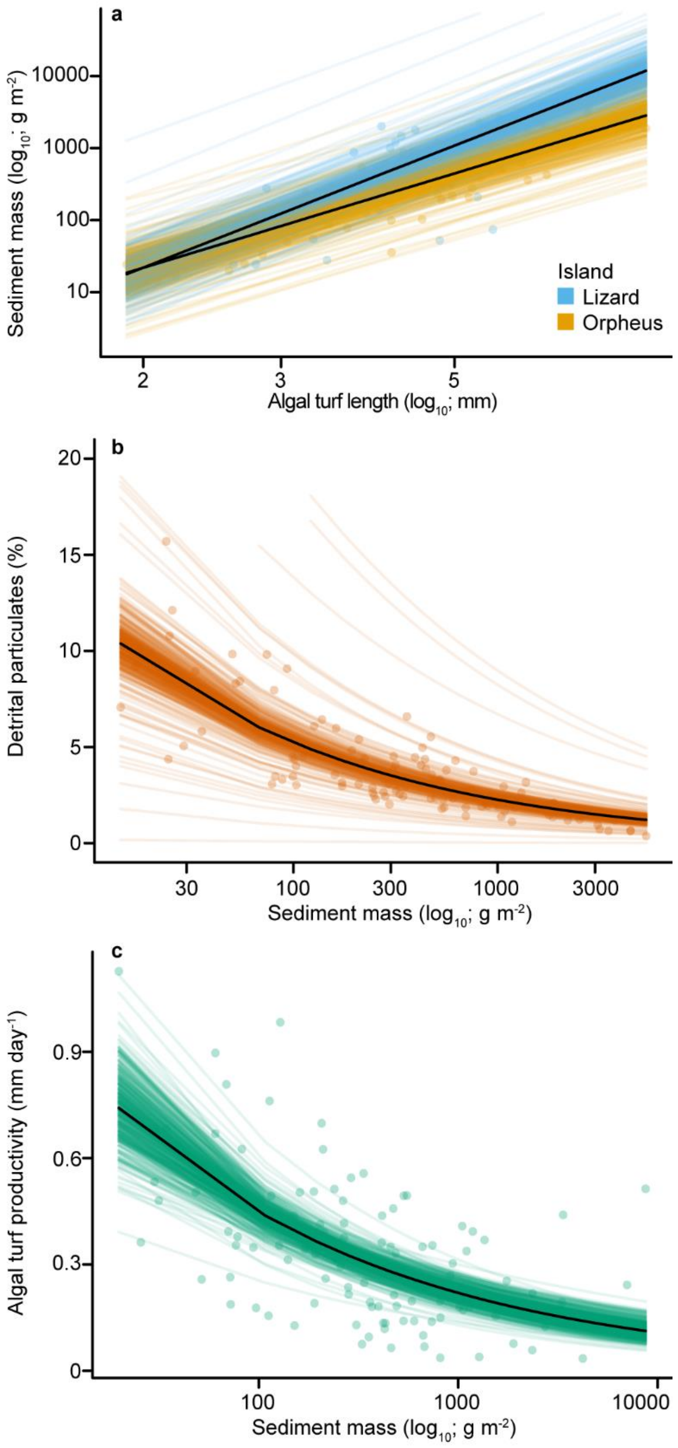

Figure D2 The relationship between a) algal turf sediment load and algal turf length, b) percentage of organic detritus by mass in benthic particulates and algal turf sediment load, and c) algal turf productivity and predicted algal turf sediment load. The black lines indicate the mean predicted model 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.

Table D1 The average (± SE) abundance and biomass per 250 m^{-2} of each nominally herbivorous fish species (Acanthuridae, Labridae [Scarini], Kyphosidae and Siganidae) present at the study locations.

Lizard Island			**Orpheus Island**		
Species	**Abundance (ind. 250 m^{-2})**	**Biomass (g 250 m^{-2})**	**Species**	**Abundance (ind. 250 m^{-2})**	**Biomass (g 250 m^{-2})**
Ctenochaetus striatus	35.75 ± 13.60	4697.89 ± 2253.26	*Scarus sp.*	31.25 ± 19.83	150.37 ± 106.74
Acanthurus nigrofuscus	25.75 ± 13.95	776.67 ± 349.65	*Scarus rivulatus*	18.5 ± 3.71	6575.31 ± 2001.71
Chlorurus spilurus	12.75 ± 11.43	628.91 ± 366.48	*Siganus doliatus*	11 ± 2.83	555.94 ± 189.07
Scarus sp.	11.25 ± 11.25	167.04 ± 167.04	*Chlorurus spilurus*	6.75 ± 2.95	93.41 ± 39.68
Acanthurus sp.	6.25 ± 3.75	13.1 ± 10.34	*Scarus schlegeli*	1 ± 0.58	201.00 ± 130.23
Scarus psittacus	3.75 ± 2.06	493 ± 342.87	*Siganus puellus*	0.75 ± 0.48	164.15 ± 104.77
Siganus argenteus	3.5 ± 3.5	327.63 ± 327.63	*Acanthurus nigricauda*	0.5 ± 0.50	135.67 ± 135.67
Siganus doliatus	2.25 ± 0.95	249.6 ± 119.74	*Scarus flavipectoralis*	0.5 ± 0.29	136.69 ± 78.92
Acanthurus nigricauda	2 ± 1.68	542.67 ± 456.72	*Siganus canaliculatus*	0.5 ± 0.50	51.32 ± 51.32
Zebrasoma scopas	1.75 ± 1.18	105.86 ± 71.47	*Acanthurus grammoptilus*	0.25 ± 0.25	12.79 ± 12.79
Scarus rivulatus	1.5 ± 1.50	561.82 ± 561.82	*Naso unicornis*	0.25 ± 0.25	672.50 ± 672.50
Ctenochaetus binotatus	1.25 ± 1.25	12.16 ± 12.16	*Chlorurus microrhinos*	0.25 ± 0.25	1055.82 ± 1055.82
Naso annulatus	1 ±1.00	239.33 ± 239.33	*Scarus dimidiatus*	0.25 ± 0.25	282.95 ± 282.95
Chlorurus microrhinos	0.5 ± 0.29	201.98 ± 126.18			
Scarus altipinnis	0.5 ± 0.29	219.28 ± 126.6			
Scarus frenatus	0.5 ± 0.50	448.26 ± 448.26			
Scarus schlegeli	0.5 ± 0.29	80.06 ± 65.38			
Siganus punctatus	0.5 ± 0.29	124.4 ± 111.64			
Zebrasoma velifer	0.25 ± 0.25	122.13 ± 122.13			
Scarus niger	0.25 ± 0.25	54.78 ± 54.78			
Kyphosus vaigiensis	0.25 ± 0.25	11.62 ± 11.62			

Table D2 Prior values and chain details for the Bayesian models used to compare relationships between the nature of algal turfs and sediments at Lizard Island and Orpheus Island on Australia's Great Barrier Reef. For Gaussian and Gamma distribution the prior value refers to the adjusted scale.

Response variable	Distribution	Prior information	Iterations	Thin	Chains	Warmup
Algal turf length	Gaussian (log-link)	Intercept (14.39) Coefficients (2.53, 3.60, 1.21) Auxiliary (1.44)	6000	6	3	1500
Proportion of detritus	Beta	Intercept (student_t[3, 0, 10]) Phi (gamma[0.01, 0.01])	13000	14	3	4000
Algal turf biomass	Gamma (log-link)	Coefficients (1.74, 2.50, 0.84)	5000	4	3	1500
Algal turf sediment load	Gamma (log-link)	Coefficients (7.74, 2.50, 3.13)	6000	4	3	2000
Change in algal turf length	Gaussian (log-link)	Intercept (2.06) Coefficients (1.46, 0.51, 0.64) Auxiliary (0.21)	6000	4	3	1500
Change in algal turf length (using predicted sediment)	Gaussian (log-link)	Intercept (2.06) Coefficients (0.42, 0.51, 0.18) Auxiliary (0.21)	5000	4	3	1500

Table D3 Summary outputs of Bayesian models used to compare relationships between the nature of algal turfs and sediments at Lizard and Orpheus Island on Australia's Great Barrier Reef. Values are on the link scale and therefore an effect is apparent if the upper and lower CIs do not overlap 0. SE = standard error, CI = credibility interval

Response variable	**Distribution**	**Term**	**Estimate**	**SE**	**CI Low**	**CI High**
Algal turf length	Gaussian (log-link)	Intercept	0.3795	0.1713	0.0518	0.6799
		Sediment	0.1779	0.0149	0.1492	0.2069
		Orpheus Island	-0.1521	0.2538	-0.6127	0.3224
		Sediment:Orpheus Island	0.0525	0.0245	0.0091	0.1039
Proportion of detritus	Beta (logit-link)	Intercept	-1.0244	0.3367	-1.5773	-0.5084
		Sediment	-0.4023	0.0277	-0.4555	-0.3468
		Orpheus Island	-0.2682	0.4592	-1.2495	0.4307
		Sediment:Orpheus Island	0.0485	0.0440	-0.0352	0.1349
Algal turf biomass	Gamma (log-link)	Intercept	2.1129	0.4804	1.2175	3.0357
		Sediment	0.0419	0.0379	-0.0339	0.1145
		Orpheus Island	0.3262	0.6358	-0.9435	1.5497
		Sediment:Orpheus Island	-0.0583	0.0619	-0.1779	0.0607
Algal turf sediment load	Gamma (log-link)	Intercept	0.1312	0.6266	-1.0725	1.3660
		Turf Length	4.2632	0.2824	3.6965	4.8027
		Orpheus Island	0.6608	0.8418	-0.9154	2.4487
		Turf Length:Orpheus Island	-0.9730	0.3901	-1.7115	-0.1926
Change in algal turf length	Gaussian (log-link)	Intercept	0.2890	0.2207	-0.1508	0.7215
		Turf Length	-1.0022	0.1709	-1.3331	-0.6524
		Orpheus Island	0.4158	0.3147	-0.1914	1.0215
		Turf Length:Orpheus Island	-0.2807	0.2364	-0.7394	0.1832
Change in algal turf length	Gaussian (log-link)	Intercept	0.3945	0.2329	-0.1254	0.8070
		Sediment	-0.2510	0.0424	-0.3376	-0.1715
		Orpheus Island	0.4572	0.3287	-0.1734	1.1206
		Sediment:Orpheus Island	-0.1181	0.0632	-0.2442	0.0039

Appendix E: Supporting information for chapter 7

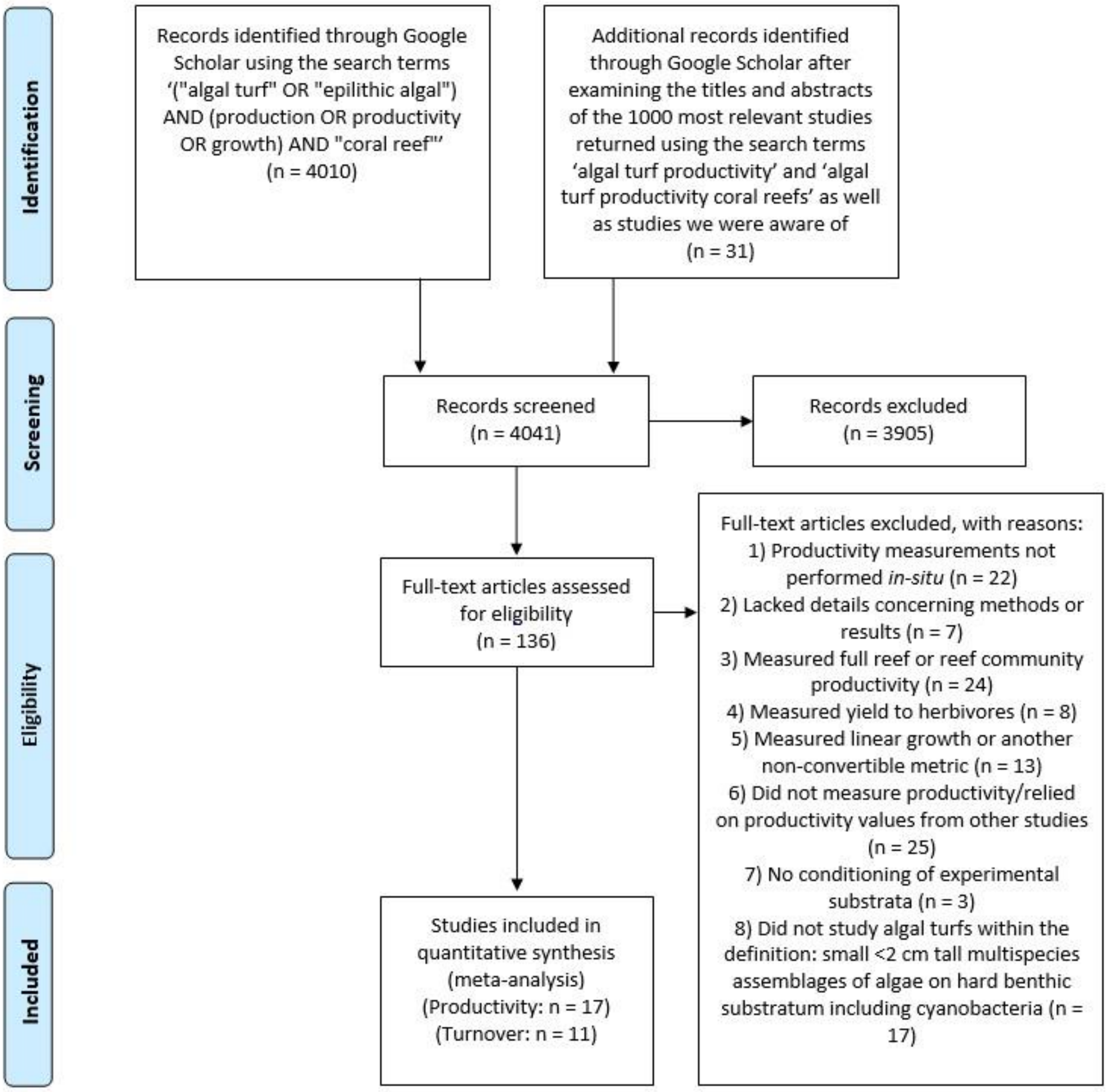

Figure E1 Flow diagram outlining the literature search and screening process used to compile the dataset of algal turf productivity and turnover estimates. The flow diagram was modified after Moher et al. (2009).

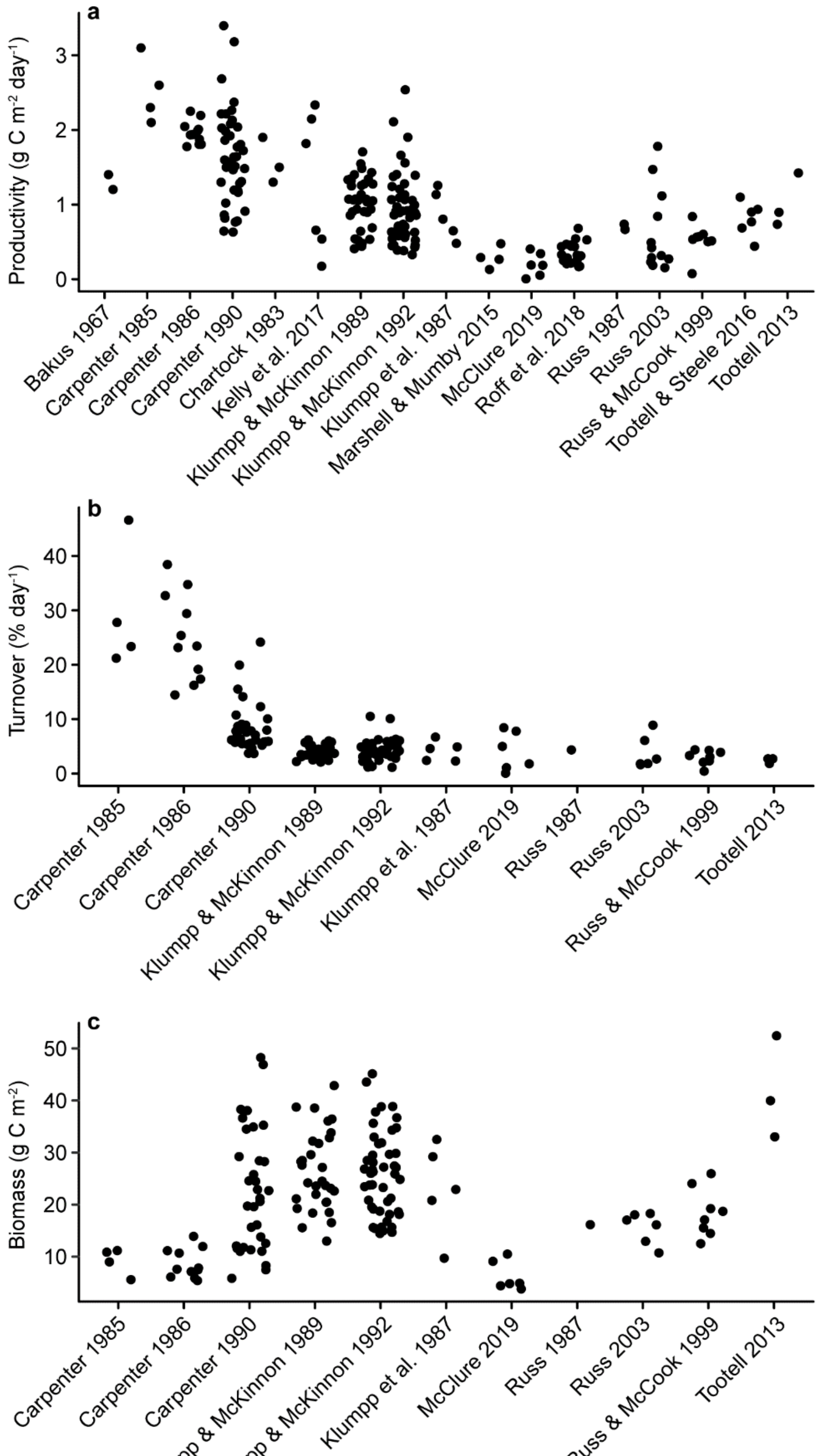

Figure E2 Raw a) productivity, b) turnover, and c) biomass data extracted from each study used in the meta-analysis.

Table E1 Details of the studies included in the algal turf productivity and turnover databases with notes on data extraction from each study.

Study	**Location**	**Dataset used for**	**Data extraction notes**
Bakus 1967	Enewetak Atoll	Productivity	Calculated the mean (± SE) net primary production (g C m^{-2} day^{-1}) for each site based on values provided in table 2.
Carpenter 1985	Caribbean	Productivity & Turnover	Sourced mean (± SD) net primary productivity (g C m^{-2} day^{-1}) values from table 4. Sourced mean (± SD) standing biomass (g dry mass) from table 3. Standing dry mass was converted to grams of Carbon using the conversion factor 0.31 following Carpenter (1985, 1986). Turnover was calculated based on the mean productivity as a percentage of mean biomass.
Carpenter 1986	Caribbean	Productivity & Turnover	Sourced mean (± SD) net algal turf biomass production (g dry mass) from table 6 and standing biomass (g dry mass) from Fig. 4 using WebPlotDigitiser. Only data from blocks open to all herbivores (i.e. unmanipulated control conditions) were used. Dry mass was converted to grams of Carbon using the conversion factor 0.31 following Carpenter (1985, 1986). Turnover was calculated based on the mean productivity as a percentage of mean biomass.
Carpenter 1990	Caribbean	Productivity & Turnover	Extracted data on mean (± SD) standing biomass (g dry mass) from Fig. 2 and net primary productivity in g O^2 m^{-2} hr^{-1} at the solar zenith from Fig. 5 using WebPlotDigitiser. Data were converted to net primary productivity in g C m^{-2} day^{-1} using methods modified after Carpenter (1985, 1986). Essentially, productivity was assumed to ascend and descend uniformly to and from the solar zenith following the path of a semi-ellipse. The area under the semi-ellipse (i.e. daily net productivity) was then estimated based on the day length of the 15th day in the respective month in the respective year and net productivity at the solar zenith. Data on daily net primary productivity in g O^2 m^{-2} day^{-1} and standing biomass were converted to carbon equivalents assuming a conversion factor of 0.31 following Carpenter (1985, 1986). Turnover was calculated based on the mean productivity as a percentage of mean biomass.
Chartock 1983	Enewetak Atoll	Productivity	Sourced mean (± SE) net primary productivity (g C m^{-2} day^{-1}) values from table 1.
Kelly et al. 2017	Hawaii	Productivity	Used WebPlotDigitiser to extract mean net algal turf biomass production (g dry mass) from supplemental Fig. S2. A separate mean (± SE) was calculated for each different caging timespan. Dry mass was converted to grams of Carbon using the conversion factor 0.31 following Carpenter (1985, 1986).
Klumpp and McKinnon 1989	Great Barrier Reef	Productivity & Turnover	Sourced mean (± SE) net primary productivity (g C m^{-2} day^{-1}), turnover and standing biomass (g C m^{-2}) values from tables 1 and 5.
Klumpp and McKinnon 1992	Great Barrier Reef	Productivity & Turnover	Used WebPlotDigitiser to extract mean (± SE) net algal turf productivity (g C m^{-2} day^{-1}), turnover and standing biomass (g C m^{-2}) values from Figs 4, 5, 6 and 7.
Klumpp et al. 1987	Great Barrier Reef &	Productivity & Turnover	Sourced mean (± SE) net primary productivity (g C m^{-2} day^{-1}), turnover and standing biomass (g C m^{-2}) values from tables 1 and 2. Only productivity values from

	Papua New Guinea		outside damselfish territories were used, as damselfishes were reported to increase algal turf productivity.
Marshell and Mumby 2015	Great Barrier Reef	Productivity	Used WebPlotDigitiser to extract mean (± SE) g net ash free dry weight production values from Fig. 2. Ash free dry weight was converted to grams of Carbon using the conversion factor 0.55 from Bakus (1967).
McClure 2019	Philippines	Productivity & Turnover	Used WebPlotDigitiser to extract mean (± 95% confidence intervals) net algal turf productivity (g dry mass) and standing biomass (g dry mass) values from Fig. 5.3. Dry mass was converted to grams of Carbon using the conversion factor 0.31 following Carpenter (1985, 1986). Turnover was calculated based on the mean productivity as a percentage of mean biomass.
Roff et al. 2019	Micronesia	Productivity	Sourced mean (± SE) net algal turf biomass production (g dry mass) from supplemental table S3. Dry mass was converted to grams of Carbon using the conversion factor 0.31 following Carpenter (1985, 1986).
Russ 1987	Great Barrier Reef	Productivity & Turnover	Used WebPlotDigitiser to extract mean (± 95% confidence intervals) net primary productivity (g C m^{-2} day^{-1}) and standing biomass (g C m^{-2}) values from Figs 2 and 3. Only productivity values from outside damselfish territories were used, as damselfishes were reported to increase algal turf productivity. As the standing biomass of algal turfs was pooled across both sites a single turnover estimate was calculated based on this mean standing biomass value and the mean value of net primary productivity across both sites.
Russ 2003	Great Barrier Reef	Productivity & Turnover	Used WebPlotDigitiser to extract mean net algal turf productivity (g C m^{-2} day^{-1}) and standing biomass (g C m^{-2}) values from Fig. 2. As the different sites could not be identified from the Figs turnover estimates were based on the mean standing biomass and mean productivity measure for each habitat in each sampling period.
Russ and McCook 1999	Great Barrier Reef	Productivity & Turnover	Used WebPlotDigitiser to extract mean net algal turf productivity (g C m^{-2} day^{-1}) and standing biomass (g C m^{-2}) values from Fig. 3. Where mean values were the mean of two reefs these sites were given a unique identity in the site factor in the XGBoost model. Turnover was calculated based on the mean productivity as a percentage of mean biomass.
Tootell and Steele 2016	French Polynesia	Productivity	Used WebPlotDigitiser to extract mean (± SE) g ash free dry weight net production values from Fig. 2. Ash free dry weight was converted to grams of Carbon using the conversion factor 0.55 from Bakus (1967).
Tootell 2013	French Polynesia	Productivity & Turnover	Used WebPlotDigitiser to extract mean (± SE) g ash free dry weight net production and standing biomass values from Figs 3.12 and 3.13. Ash free dry weight was converted to grams of Carbon using the conversion factor 0.55 from Bakus (1967).

Table E2 Summary output of a Bayesian model used to compare differences in algal turf sediment loads on natural substratum and coral blocks at Lizard Island on Australia's Great Barrier Reef. The model was based on weakly informative priors (Intercept: location = 0, scale = 2.5 using a normal distribution; coefficients: location = 0, scale = 2.5 using a normal distribution; Auxiliary: exponential [rate = 1]). Values are on the response scale and therefore an effect is apparent if the upper and lower CIs do not overlap 1. The estimate is based on the median. SE = standard error, CI = credibility interval based on highest posterior density.

Response variable	**Distribution**	**Term**	**Estimate**	**SE**	**CI Low**	**CI High**
Sediment load	Gamma (log-link)	Intercept	2031.119	1.269	1292.897	3238.382
		Coral Blocks	0.093	1.332	0.053	0.163
		Site B	1.237	1.404	0.650	2.455
		Coral Block*SiteB	0.530	1.506	0.241	1.204

Table E3 The mean ± SE algal turf productivity, turnover and standing biomass estimates that comprised the dataset used in the present study. Note that '-' indicates that the SE estimate was unavailable.

Productivity (g C m^{-2} day^{-1})	**Turnover (% day^{-1})**	**Standing Biomass (g C m^{-2})**	**Study**
1.4 ± 0.17			Bakus 1967
1.2 ± 0.29			
3.1 ± 0.14	27.78 ± -	11.16 ± 1.32	Carpenter 1985
2.6 ± 0.1	46.59 ± -	5.58 ± 1.24	
2.3 ± 0.05	21.2 ± -	10.85 ± 1.09	
2.1 ± 0.07	23.36 ± -	8.99 ± 1.97	
1.93 ± 0.04	17.37 ± -	11.14 ± 2.41	Carpenter 1986
1.78 ± 0.08	23.44 ± -	7.58 ± 1.95	
1.99 ± 0.17	32.71 ± -	6.09 ± 2.07	
1.81 ± 0.07	23.15 ± -	7.81 ± 2.76	
1.88 ± 0.12	34.76 ± -	5.4 ± 1.95	
1.81 ± 0.09	25.39 ± -	7.12 ± 1.84	
2.01 ± 0.05	14.46 ± -	13.89 ± 1.84	
2.25 ± 0.38	38.44 ± -	5.86 ± 1.03	
1.94 ± 0	16.23 ± -	11.94 ± 1.03	
2.19 ± 0.13	29.41 ± -	7.46 ± 2.07	
2.05 ± 0.19	19.16 ± -	10.68 ± 2.07	
1.81 ± 0.13	24.16 ± -	7.48 ± 1.17	Carpenter 1990
1.19 ± 0.11	10.76 ± -	11.03 ± 1.11	
1.77 ± 0.06	14.14 ± -	12.54 ± 1.33	
1.92 ± 0.09	12.3 ± -	15.63 ± 0.49	
2.04 ± 0.07	8.91 ± -	22.88 ± 0.96	
1.98 ± 0.15	5.21 ± -	38.06 ± 4.07	
2.37 ± 0.18	6.19 ± -	38.29 ± 3.42	
2.68 ± 0.28	5.72 ± -	46.9 ± 5.49	
3.18 ± 0.38	8.69 ± -	36.63 ± 2.68	
2.08 ± 0.21	7.12 ± -	29.23 ± 3.45	
3.4 ± 0.25			
1.29 ± 0.04	15.52 ± -	8.28 ± 2.48	
2.13 ± 0.23	10.05 ± -	21.2 ± 2.33	
2.22 ± 0.09	9.06 ± -	24.47 ± 2.33	
2.26 ± 0.17	8.01 ± -	28.26 ± 2.33	
2.03 ± 0.19	5.87 ± -	34.5 ± 2.39	
1.86 ± 0.23			
1.78 ± 0.17	3.68 ± -	48.25 ± 2.45	
1.64 ± 0.14	4.66 ± -	35.25 ± 2.36	
1.48 ± 0.11			

1.64 ± 0.17			
1.16 ± 0.06	19.94 ± -	5.84 ± 1.35	
1.31 ± 0.07	6.36 ± -	20.59 ± 2.11	
1.57 ± 0.06	7.99 ± -	19.71 ± 2.43	
1.47 ± 0.05			
1.72 ± 0.16	7.6 ± -	22.69 ± 3.06	
1.51 ± 0.11	6.17 ± -	24.56 ± 4.32	
2.22 ± 0.2	7.8 ± -	28.41 ± 3.64	
1.5 ± 0.09	5.82 ± -	25.77 ± 4.99	
1.3 ± 0.12	3.72 ± -	34.91 ± 6.43	
1.02 ± 0.13			
0.78 ± 0.08	7.07 ± -	11.04 ± 1.8	
0.86 ± 0.06	5.34 ± -	16.1 ± 3.04	
1.6 ± 0.18	8.16 ± -	19.59 ± 2.97	
0.64 ± 0.08	5.47 ± -	11.77 ± 1.69	
0.63 ± 0.04	5.58 ± -	11.31 ± 2.1	
0.82 ± 0.04	5.92 ± -	13.8 ± 2.33	
1.19 ± 0.17			
0.77 ± 0.1	6.35 ± -	12.05 ± 2.14	
0.91 ± 0.08	7.86 ± -	11.59 ± 1.43	
1.9 ± 0.19			Chartock 1983
1.5 ± 0.22			
1.3 ± 0.83			
2.15 ± 0.82			Kelly et al. 2017
2.33 ± 1.13			
1.82 ± 0.72			
0.54			
0.66 ± 0.22			
0.17			
0.52 ± 0.04	2.5 ± 0.2	21.96 ± 2.45	Klumpp and McKinnon, 1989
0.54 ± 0.04	3.4 ± 0.3	15.56 ± 0.81	
0.9 ± 0.05	5.1 ± 0.4	18.49 ± 1.19	
1.32 ± 0.21	2.8 ± 0.4	42.86 ± 3.41	
1.07 ± 0.13	3.1 ± 0.2	33.8 ± 2.42	
1.71 ± 0.11	6 ± 0.8	32.19 ± 2.87	
1.48 ± 0.09	5.5 ± 0.4	28.48 ± 1.89	
1.08 ± 0.15	4.5 ± 0.6	24.18 ± 1.48	
1.43 ± 0.18	5.2 ± 0.6	27.58 ± 2.1	
1.4 ± 0.05	6.2 ± 0.5	24.5 ± 2.34	
1.04 ± 0.06	4.7 ± 0.4	23.56 ± 1.32	
0.94 ± 0.04	4.1 ± 0.2	23.67 ± 0.89	
0.91 ± 0.09	3.5 ± 0.5	28.27 ± 2.15	
1.28 ± 0.1	4.2 ± 0.4	31.74 ± 2.29	
1.34 ± 0.09	5.2 ± 0.4	27.15 ± 2.67	
1.06 ± 0.11	2.9 ± 0.4	38.73 ± 2.65	

1.33 ± 0.11	3.7 ± 0.3	36.05 ± 1.4	
0.69 ± 0.05	3.6 ± 0.6	20.48 ± 1.43	
0.44 ± 0.03	2.2 ± 0.4	22.61 ± 3.63	
0.48 ± 0.03	2.1 ± 0.2	23.12 ± 1.34	
1.55 ± 0.11	5.7 ± 0.6	29.6 ± 3.48	
0.9 ± 0.08	2.4 ± 0.2	38.55 ± 3.44	
1.07 ± 0.05	3.1 ± 0.3	36.44 ± 3.63	
1.05 ± 0.07	3.2 ± 0.3	32.83 ± 1.49	
1.28 ± 0.11	5.8 ± 0.7	21.11 ± 3.03	
0.86 ± 0.06	4.8 ± 0.4	18.37 ± 1.6	
0.41 ± 0.1	3.3 ± 0.6	12.98 ± 1.52	
0.53 ± 0.01	3.4 ± 0.2	16.53 ± 1.18	
0.64 ± 0.03	3.4 ± 0.3	20.44 ± 1.76	
1.05 ± 0.1	5.6 ± 0.9	19.26 ± 1.59	
1.13 ± 0.06			
0.94 ± 0.06			
1.34 ± 0.09			
1.26 ± 0.12			
1.04 ± 0.07			
1.25 ± 0.08			
1.9 ± 0.09	5.62 ± 0.39	34.76 ± 2.21	Klumpp and McKinnon, 1992
1.24 ± 0.02	4.91 ± 0.39	27.2 ± 1.78	
0.71 ± 0.02	2.8 ± 0.23	26.69 ± 2.04	
1.66 ± 0.06	6.05 ± 0.37	29.49 ± 1.61	
1.4 ± 0.05	6.24 ± 0.5	24.83 ± 1.95	
0.97 ± 0.08	4.47 ± 0.61	23.81 ± 2.12	
0.91 ± 0.06	3.57 ± 0.46	28.47 ± 1.78	
1.28 ± 0.1	4.3 ± 0.38	31.86 ± 2.29	
1.56 ± 0.11	5.89 ± 0.44	29.83 ± 3.39	
0.91 ± 0.07	2.44 ± 0.15	38.81 ± 3.39	
1.07 ± 0.04	3.15 ± 0.29	36.69 ± 3.64	
1.07 ± 0.04	3.28 ± 0.25	32.97 ± 1.53	
0.86 ± 0.03	4.92 ± 0.38	18.73 ± 1.53	
0.64 ± 0.05	4.49 ± 0.48	15.59 ± 1.69	
0.54 ± 0.02	3.49 ± 0.15	16.78 ± 0.93	
0.63 ± 0.03	3.49 ± 0.23	20.59 ± 1.95	
2.54 ± 0.3	10.51 ± 1.25	25.9 ± 1.01	
0.89 ± 0.06	2.86 ± 0.37	34.3 ± 2.83	
1.39 ± 0.09	6 ± 2.64	35.62 ± 3.24	
2.11 ± 0.09	10.09 ± 0.58	23.27 ± 1.52	
1.09 ± 0.07	4.32 ± 0.6	27.42 ± 1.21	
0.94 ± 0.12	3.11 ± 0.96	45.13 ± 5.67	
0.86 ± 0.05	4.84 ± 0.48	20.84 ± 1.01	
0.6 ± 0.05	3.72 ± 0.66	19.12 ± 5.06	
0.43 ± 0.02	2.24 ± 0.27	19.53 ± 1.11	

0.66 ± 0	3.7 ± 0.08	18.62 ± 0.51	
1.38 ± 0.04	5.14 ± 0.24	28.11 ± 0.42	
0.63 ± 0.01	3.75 ± 0.31	18.11 ± 0.67	
0.63 ± 0.08	2.3 ± 0.19	26.29 ± 1.64	
0.89 ± 0.07	3.91 ± 0.21	23.45 ± 1.27	
0.56 ± 0.01	3.91 ± 0.14	15.41 ± 0.24	
0.46 ± 0.03	3.28 ± 0.14	14.67 ± 0.11	
0.68 ± 0.04	4.92 ± 0.31	31.69 ± 3.52	
1.13 ± 0.13	5.06 ± 0.48	27.12 ± 2.68	
0.45 ± 0	2.42 ± 0.2	19.53 ± 1.41	
0.71 ± 0	4.92 ± 0.26	15.67 ± 0.67	
0.39 ± 0.1	1.13 ± 0.17	37.79 ± 3.99	
1.06 ± 0.08	3.71 ± 0.19	29.66 ± 1.27	
0.38 ± 0.02	5.55 ± 0.31	14.94 ± 0.82	
0.74 ± 0	4.18 ± 0.21	18.11 ± 0.89	
0.58 ± 0.01	1.76 ± 0.02	38.85 ± 1.76	
1.21 ± 0.06	4.95 ± 0.33	25.99 ± 0.71	
0.52 ± 0.06	3.57 ± 0.05	15.65 ± 0.94	
0.92 ± 0.05	6.31 ± 0.36	14.44 ± 0.22	
0.46 ± 0.06	1.19 ± 0.2	43.54 ± 1.29	
0.99 ± 0.07	4.25 ± 0.57	26.84 ± 0.42	
0.33 ± 0.02	1.3 ± 0.28	23.76 ± 2.35	
0.83 ± 0.03	4.61 ± 0.34	21.22 ± 3.44	
1.26 ± 0.12	4.6 ± 0.67	29.2 ± 2.5	Klumpp et al. 1987
0.81 ± 0.08	2.4 ± 1.25	32.5 ± 1.5	
0.48 ± 0.07	2.3 ± 0.6	20.8 ± 3.4	
1.13 ± 0.18	4.9 ± 1.2	22.9 ± 3.5	
0.65 ± 0.01	6.7 ± 0.4	9.7 ± 0.4	
0.13 ± 0.02			Marshell and Mumby 2015
0.29 ± 0.06			
0.26 ± 0.04			
0.48 ± 0.12			
0.41 ± 0.06	8.42 ± -	4.81 ± 2.05	McClure 2019
0.19 ± 0.06	1.78 ± -	10.48 ± 1.9	
0.19 ± 0.06	4.99 ± -	3.8 ± 1.9	
0.05 ± 0.06	1.08 ± -	4.88 ± 2.05	
0 ± 0.07	0.05 ± -	9.09 ± 2.19	
0.34 ± 0.07	7.79 ± -	4.4 ± 1.94	
0.54 ± 0.09			Roff et al. 2018
0.68 ± 0.09			
0.32 ± 0.06			
0.25 ± 0.03			
0.46 ± 0.06			
0.33 ± 0.09			
0.31 ± 0.09			

0.44 ± 0.09			
0.53 ± 0.09			
0.44 ± 0.06			
0.17 ± 0.03			
0.47 ± 0.03			
0.21 ± 0.03			
0.44 ± 0.03			
0.17 ± 0.03			
0.26 ± 0.06			
0.29 ± 0.06			
0.21 ± 0.03			
0.67 ± 0.23			Russ 1987
0.74 ± 0.25			
	4.35 ± -	16.15 ± 9.47	
0.19 ± -			Russ 2003
0.29 ± -			
0.23 ± -			
0.15 ± -			
0.42 ± -			
0.49 ± -			
0.27 ± -			
0.32 ± -			
0.84 ± -			
1.12 ± -			
1.47 ± -			
1.78 ± -			
	1.83 ± -	12.94 ± -	
	1.79 ± -	10.73 ± -	
	2.68 ± -	17.02 ± -	
	1.63 ± -	18.03 ± -	
	6.08 ± -	16.11 ± -	
	8.89 ± -	18.28 ± -	
0.07 ± 0.05	0.43 ± -	17.07 ± 1.14	Russ and McCook 1999
0.57 ± 0.04	3.05 ± -	18.7 ± 1.01	
0.51 ± 0.1	3.31 ± -	15.53 ± 0.58	
0.84 ± 0.05	4.37 ± -	19.22 ± 0.88	
0.53 ± 0.06	4.27 ± -	12.49 ± 0.49	
0.5 ± 0.1	2.09 ± -	24.04 ± 1.43	
0.6 ± 0.14	2.32 ± -	25.94 ± 1.77	
0.56 ± 0.14	3.91 ± -	14.46 ± 1.77	
0.94 ± 0.06			Tootell and Steele 2016
1.1 ± 0.13			
0.9 ± 0.07			
0.77 ± 0.14			
0.69 ± 0.08			
0.44 ± 0.15			

0.74 ± 0.26	1.84 ± -	39.96 ± 3.05	Tootell 2013
1.42 ± 0.25	2.72 ± -	52.43 ± 3.14	
0.9 ± 0.14	2.72 ± -	33.02 ± 3.81	

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Appendix F: Supporting information for chapter 8

Text F1 Methods for particulate processing

To preserve organic material in the collected particulate samples, 15 ml of 4% buffered formaldehyde was added. Each sample was then transferred into a 9 l container and left for 3 h to settle, before decanting the water. All samples were then wet sieved through a 2 mm stainless steel mesh, retaining all material <2 mm (sands, silts and clays; ISO 14688-1:2017), and then transferred to 120 ml sample jars. Once in sample jars, each sample was agitated and left to settle for 24 hours before the depth of particulates in the sample jars was quantified using electronic callipers. Depth was measured in three haphazard locations around the jar, and the subsequent measurements were standardised by the sampling area to give the depth and volume of particulate loads within algal turfs on the reef (see Text F2 for how depth and volume were calculated for 2008 and 2013 data).

Following depth measurements, salts were removed by rinsing each sample with fresh water three times, leaving a minimum 3 h settling period between rinses. Total particulate mass was then quantified by drying each sample to a constant weight at 60˚C and weighing each sample to 0.0001 g. Organic material was then removed from the samples by bleaching the samples for two weeks using 30% hydrogen peroxide (H_2O_2). During this time, samples were stirred, and fresh peroxide was added regularly. Samples were then re-dried and weighed, as above, yielding a) total sediment mass and b) the mass of organic detrital particulate material. The methods for particulate processing follow Purcell (1996) and Tebbett and Bellwood (2020).

Text F2 Volume and depth calculations for 2008 and 2013 data

Unfortunately, data on particulate volume were not available for the 2008 and 2013 samples, therefore I formulated a Bayesian statistical model relating particulate mass and volume for the 2018 and 2019 sampling periods to predict particulate volume for the 2008 and 2013 samples. Specifically, a Bayesian generalised linear model (GLM) fitted with a Gamma distribution and log-link was used to find the relationship between particulate volume (response variable) and particulate depth (logged continuous fixed effect). The model was based on weakly informative priors (see Table F1 for prior details and chain specifications). Model convergence, fit and assumptions were assessed using trace plots, autocorrelation plots, rhat plots, posterior predictive checks, effective sample sizes and residual plots, as in the main chapter. Statistical analysis was performed in the software R (R Core Team 2020), using the *rstan* (Stan Development Team 2018) and *rstanarm* (Goodrich et al. 2018) packages.

A strong positive relationship clearly existed between benthic particulate mass and volume (Fig. F6, Table F2). With this formulated relationship at hand, I then predicted the particulate volumes of the 2008 and 2013 samples, based on the mass of particulates in these samples.

Text F3 Methods for the calculation of benthic functions

Algal turf biomass and potential algal turf growth were calculated from two Bayesian statistical models that relate sediment mass to algal turf biomass and algal turf growth (Chapter 6) (Tebbett and Bellwood 2020). These models were based on data collected at Orpheus Island and Lizard Island on Australia's Great Barrier Reef in April/May 2019. In both cases, no difference in the relationship between sediment mass and algal turf biomass, or sediment mass and algal turf growth, were documented between islands. Estimating these functions in this manner is based on similar principles to those used for estimating reef fish biomass; a widely accepted method in coral reef ecology (cf. Kulbicki et al. 2005; Froese et al. 2014). In addition to these derived metrics, the standing detrital mass was quantified directly from the benthic particulates (see sample processing Text F1), while the detrital mass return per feeding episode was calculated for each sample as the relative amount of organic detritus in the total particulate mixture, by mass.

To calculate harpacticoid copepod standing biomass, I sourced data on the relationship between copepod abundance and particulate volume in algal turfs on the reef crest in Pioneer Bay from Kramer et al. (2014). Abundance estimates of copepods were then converted to copepod biomass estimates (μg AFDW m^{-2}) following the steps outlined in Kramer et al. (2017). To calculate copepod biomass in each of my samples, as a function of particulate volume, I developed a Bayesian statistical model relating these two variables. Specifically, a Bayesian GLM based on copepod biomass (dependent variable) and particulate volume (continuous independent variable) with weakly informative priors and a Gamma distribution with log link was formulated. Full details of chain values and prior information can be found in Table F1. Model convergence, fit and assumptions were assessed using trace plots, autocorrelation plots, Rhat plots, posterior predictive checks, effective sample sizes, and residual plots, as in the main chapter. With this formulated model at hand, I calculated copepod biomass for each sample based on the particulate volume of each sample. It should be noted that estimating copepod biomass in this manner assumes that the relationship between copepods and particulates will hold under varying sediment conditions. This assumption is likely to be robust, considering that similar relationships have been documented on multiple reefs under varying environmental conditions (Kramer et al. 2012, 2014).

Text F4 Additional discussion on correlation, non-independence, uncertainty, and interpretation of benthic functions

It should be noted that the five benthic functions are non-independent and are likely to be correlated. Despite the lack of independence between the functions, each provides an insight into a different aspect of the algal turf community's ability to provide nutritional resources to fishes and paints a more detailed picture of its functional configuration compared to relying on one metric or trait (e.g. turf length). These functions do not capture the full extent of algal turf functioning; they just provide a more in-depth insight into the specific aspects examined (i.e. the ability of algal turfs to provide resources to fishes). The non-independence and correlation among the different functions are not an issue in terms of the analyses undertaken in this study as correlation among variables is essential for multivariate analyses to work properly. Indeed, multivariate analyses work by collapsing multiple variables (in this case five functions) into a lower-dimensional space by finding correlations between the different variables (Clarke 1993; Clarke and Gorley 2015). This approach facilitates the examination of how the community (in this case, a community of functions) is structured and how it changes through time. Furthermore, it should be recognised that where functions have been calculated these represent the mean estimated value, and they should be interpreted accordingly. As with any calculation, uncertainty around the estimates exist. As such, I have relied on methods that draw attention to the general areas of function-space that the communities are likely to occupy rather than individual data points.

Text F5 Methods for the calculation of herbivorous fish functions

Standing biomass is the cumulative weight of individuals estimated from the surveys and was calculated using Bayesian length-weight regression parameters (Froese and Pauly 2018). Von Bertalanffy Growth Model (VBGM) trajectories form the basis of individual-level estimates of somatic growth. Species-specific VBGM parameters were predicted from species traits and water temperature using an extreme gradient boosting technique that generates accurate and precise estimates (Morais and Bellwood 2018, 2019). These species-specific growth trajectories were used to calculate the expected growth per day, assuming each fish survives this period, with the cumulative growth representing the total biomass produced (Morais et al. 2020). Consumed biomass was calculated as the expected per-capita loss of biomass due to mortality. It was obtained by multiplying the daily mortality probability calculated for each individual fish by its body weight (Morais et al. 2020). Mortality probability was calculated as the reciprocal of the exponential functions of instant mortality rate parameters typically obtained for marine fishes in fisheries models (Hilborn and Walters 1992). Instant mortality rate parameters were calculated for each fish using the VBGM parameters as estimated above, mean water temperature, and individual lengths using the empirical equation in Gislason et al. (2010). Finally, turnover was calculated as the sum of two components: net turnover, which is the ratio between productivity and standing biomass; and consumption turnover, the ratio of consumed and standing biomass (Morais et al. 2020). Together, these functions indicate how fast new biomass is either stocked as standing biomass or subsequently transferred to a different trophic level.

The energy use function (Carbon respired) was calculated by deriving expected routine metabolic rates for individual fishes, assuming that average total carbon respiration follows routine metabolic rates (Barneche et al. 2014). This was done following equation 5 in

Barneche et al. (2014), based on the body size of individual fishes, water temperature, and critical parameters estimated from empirical data by those authors (e.g. alpha, E_r, T_{opt}).

Text F6 Source of algal turf sediments

While the composition of algal turf sediments in 2008 was not assessed, they were assessed in 2013 (when the >2100% increase in algal turf sediment loads was first apparent). Specifically, the inorganic sediment samples from 2013 were dry sieved through a sieve stack (1000, 500, 250, 125, 63 µm) to determine grain size distributions. They were then treated with a 5% hydrochloric acid solution to dissolve carbonates and rinsed with freshwater three times before being re-dried, re-weighed and re-sieved. Details of the original processing of these 2013 sediments as well as the subsequent data on the grain size distributions and siliceous terrestrially derived sediment content of algal turf samples was originally published in Goatley et al. (2016).

The processing of the 2013 sediment samples in this manner revealed that the smallest grain size fraction (<63 µm), which is the most likely to be transported to reefs from terrestrial sources, made up 49.4 ± 6.3 % (mean ± SE) of the samples by mass. This represents the largest contribution of this grain size class to algal turf sediment loads currently documented on the GBR (on other inner-shelf and coastal reefs this grain size class generally represents 5-25% of the total sample by mass [Tebbett et al. 2017, 2018]). In addition, it was found that terrestrially derived siliceous sediments made up 34.6 ± 4.2 % of the total sediment loads and accounted for 70.9 ± 2.2 % of the <63 µm sediments (Goatley et al. 2016). Subsequent studies conducted in 2014 and 2018 reported similar levels and suggested a relative stability in the composition of siliceous sediments in algal turf sediments in this location since 2013 (Gordon et al. 2016; Latrille et al. 2019). This role of terrestrial siliceous sediments in the structure of algal turf sediment loads could have originated from a substantial sedimentation event occurring between 2008 and 2013 at this location. Such an event would have facilitated the increase in the length of algal turfs, and subsequent trapping of more sediments (including on-reef produced carbonates that still account for a large proportion of the sediment samples). However, unfortunately, without more in-depth analysis of the age and original source of the sediments this hypothesis is merely speculative, and a definitive answer cannot be attained.

Text F7 Benthic cover through time

To explore how the coverage of key benthic space holders (hard corals, soft corals, algal turfs and macroalgae) varied across the duration of this study I sourced all relevant data from Reef Check Australia (2005, 2006, 2019 and 2020) and from Loffler et al. (2015) (2013). All data were from the reef crest in Pioneer Bay, Orpheus Island in 2-3 m of water and based on point intercept transects (n = 8, 20 m transects in 2005, 2006, 2019, 2020 and n = 6, 30 m transects in 2013). Changes in the mean (± SE) coverage of each key space holder at each time point was subsequently explored graphically (Fig. F5). As a condition of using data from Reef Check Australia it must be noted that: "This document contains information or data belonging to, and reproduced with the permission of Reef Check Foundation Limited ("Reef Check Australia"). Reef Check Australia has not evaluated the data or information contained in this document. Reef Check Australia gives no warranties and makes no representations in respect to the data. The data belonging to Reef Check Australia, shall not be copied or in other way made use of by any person without the express written consent of Reef Check Australia."

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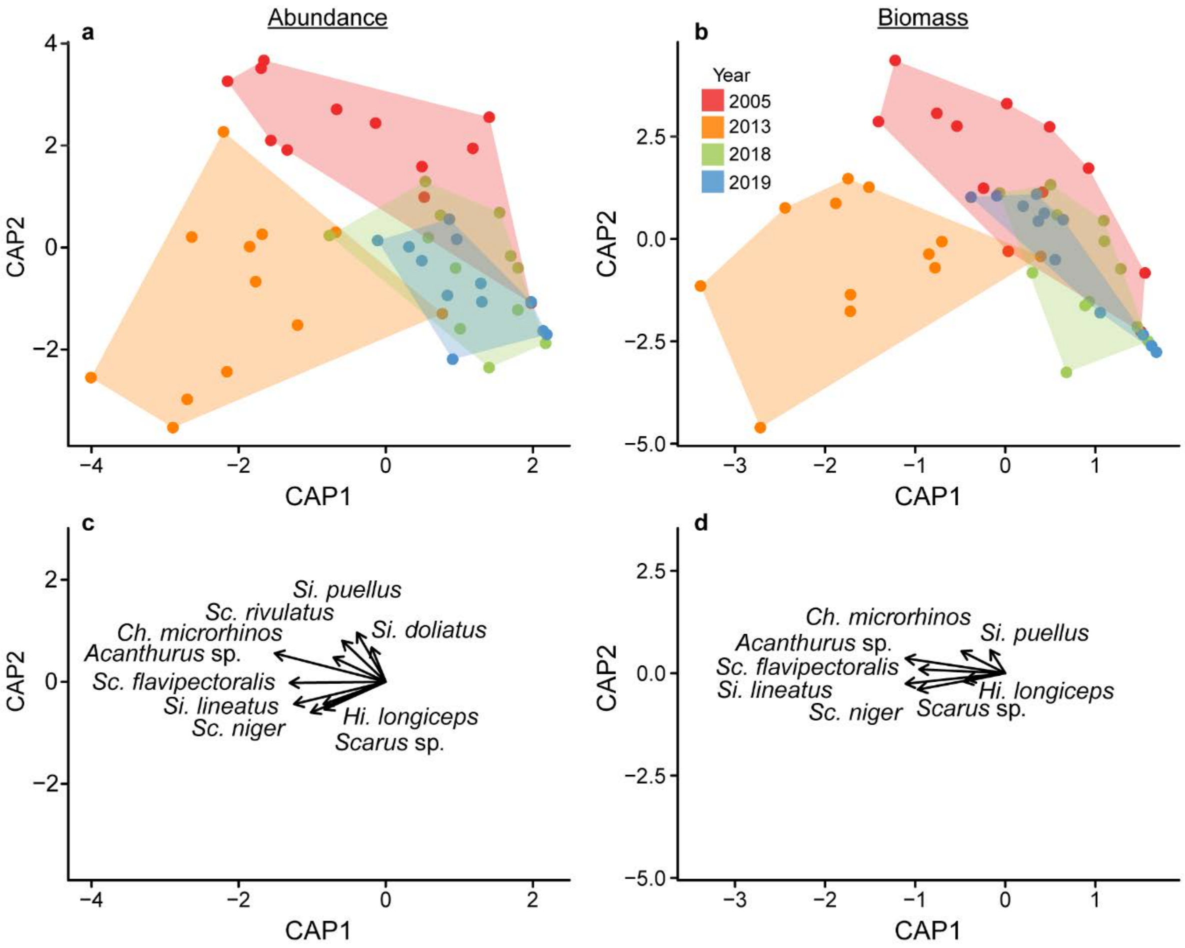

Figure F1 The community composition of herbivorous fishes in Pioneer Bay, Orpheus Island on Australia's Great Barrier Reef. Multivariate ordinations of the herbivorous fish assemblage based on species level a) abundance and b) biomass data and constrained by the census year (coloured polygons are to aid interpretation and do not represent significant groupings). Vectors showing the herbivorous fish species that contributed substantially to the patterns observed in the ordination plots for abundance and biomass (c and d respectively). Fish genus abbreviations: Ch. = *Chlorurus*, Hi. = *Hipposcarus*, Sc. = *Scarus*, Si. = *Siganus*.

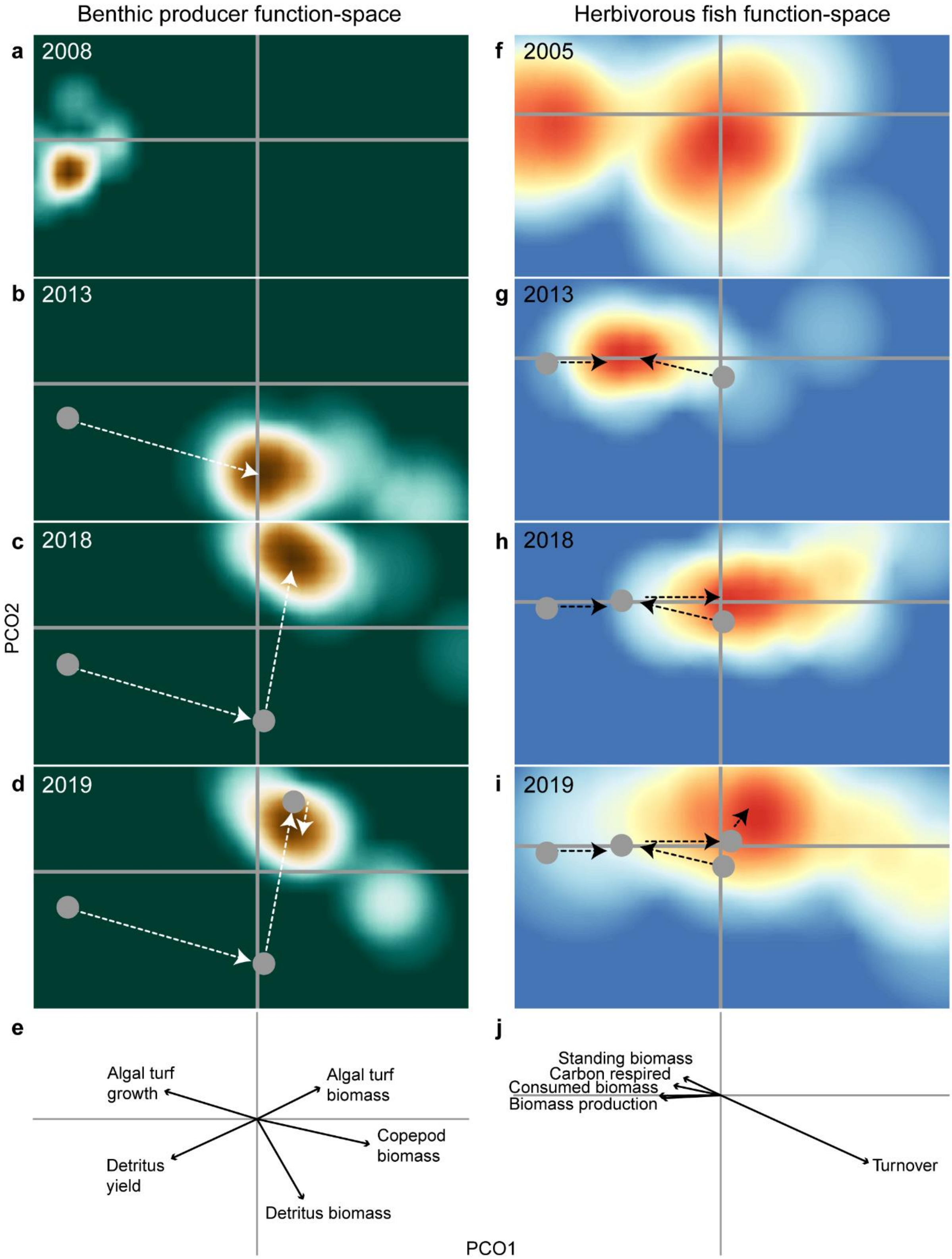

Figure F2 Function-spaces of the benthic algal turf community and the herbivorous fish community. The benthic function-space is a multivariate space that provides an overview of the ability of the algal turf community to provide nutritional resources to herbivorous fishes from 2008-2019 (a, b, c, d) based on 5 specific functions (e). The herbivorous fish function-space is a multivariate space that examines the trophodynamic functioning of the herbivorous fish assemblage from 2005-2019 (f, g, h, i) based on 5 specific functions (j). The occupation of the function-space is represented as a heat map based on kernel utilization densities (note brown areas [a, b, c, d] and red areas [f, g, h, i] indicate more samples with that particular combination of function levels, not necessarily more 'functions' per se). Arrows show trends in the community shift through time and grey circles represent the locations of past 'hotspots'.

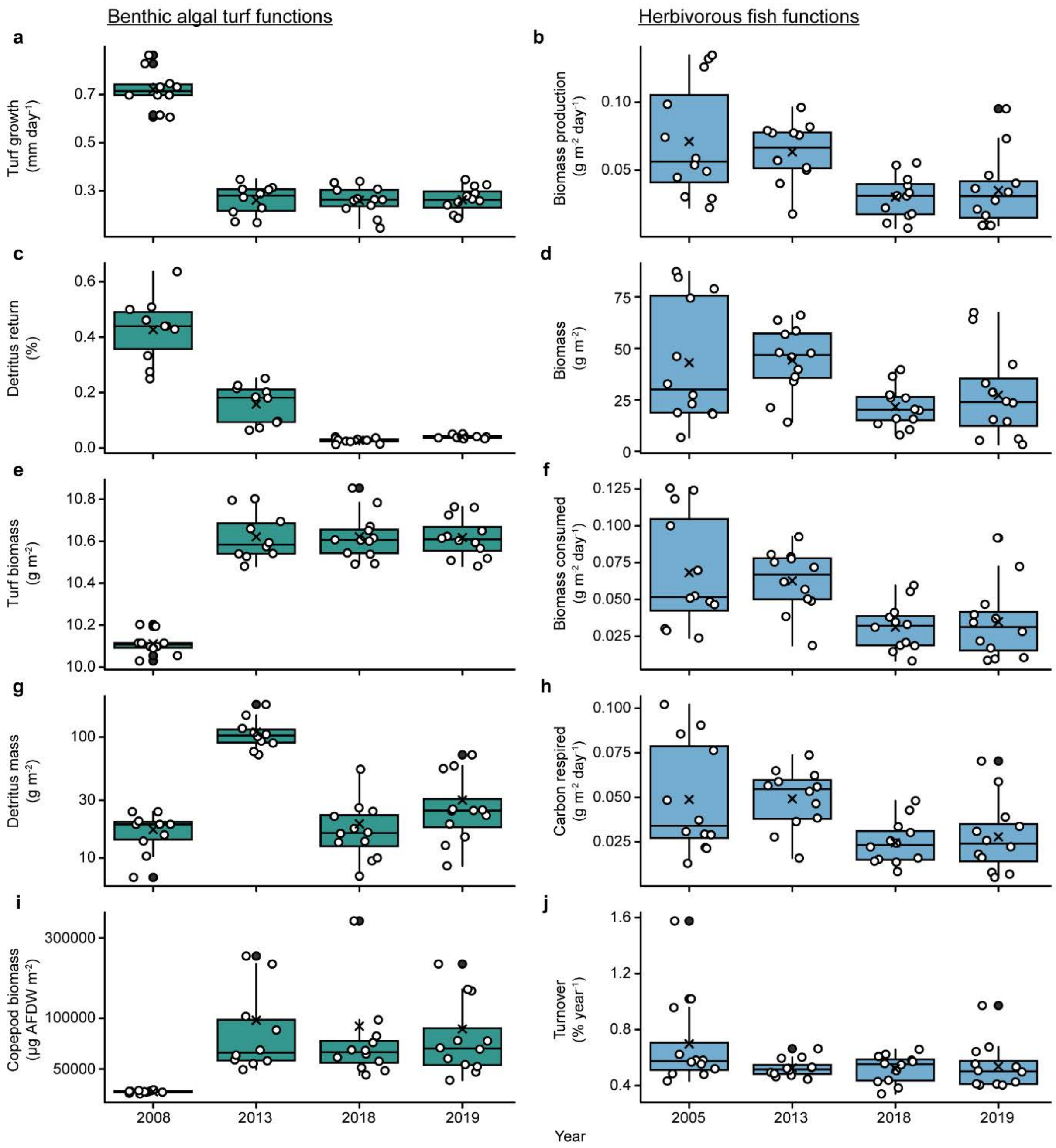

Figure F3 Levels of each individual function used to construct the function-spaces. The benthic functions (a, c, e, g, i) were based on properties of the algal turf communities while the fish functions (b, d, f, h, j) were based on the trophodynamics of the herbivorous fish community. All functions were based on the reef crest habitat in Pioneer Bay, Orpheus Island on Australia's Great Barrier Reef. Boxplots show the median, 25th percentiles and black dots are outliers, the crosses denote the mean value, and open circles are the raw data points.

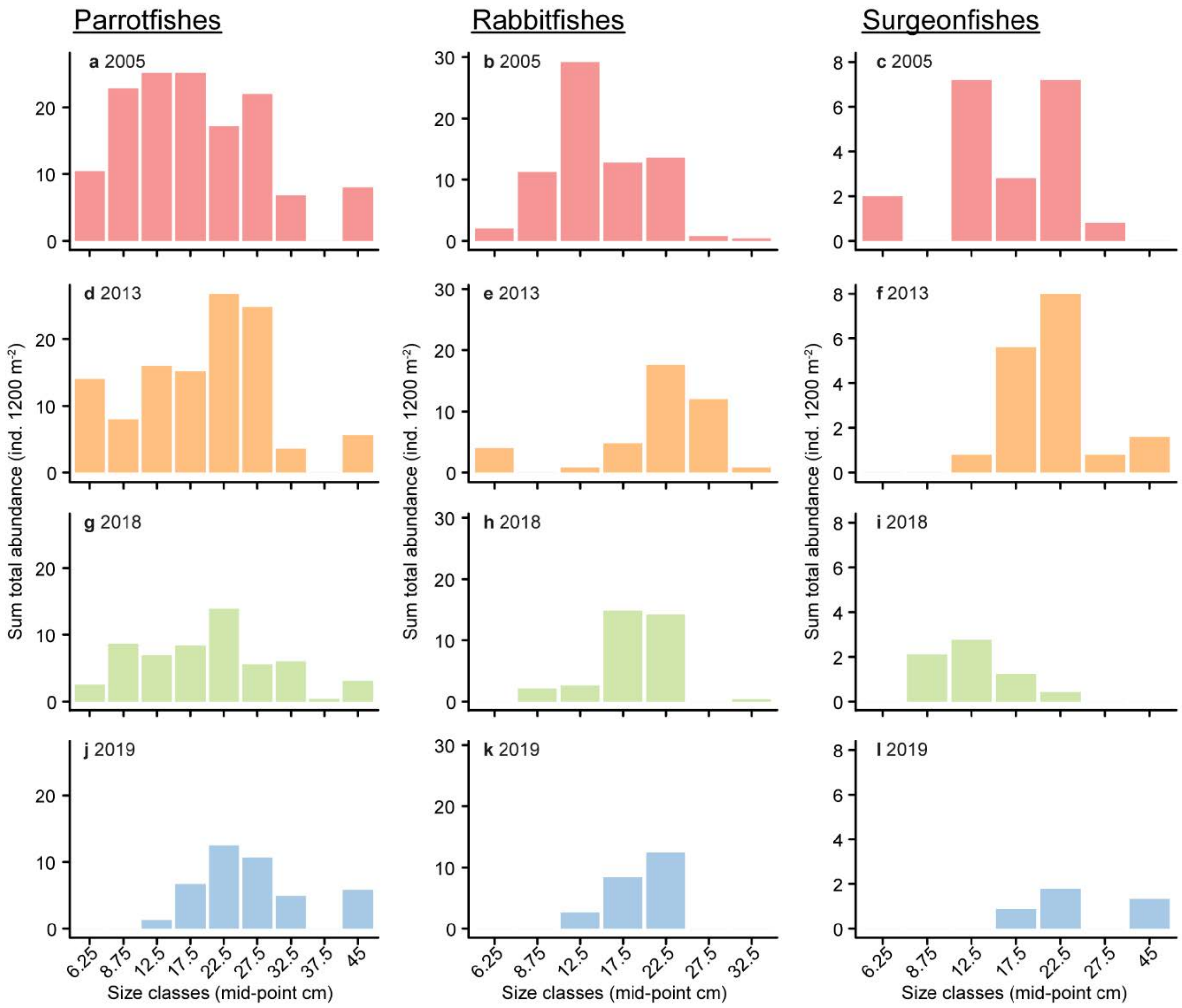

Figure F4 Size structure of the censused herbivorous fish community. Total abundance (abundance summed across transects) of the primary herbivorous fish groups (parrotfishes, rabbitfishes and surgeonfishes) across size classes and censused years in Pioneer Bay, Orpheus Island on the Great Barrier Reef.

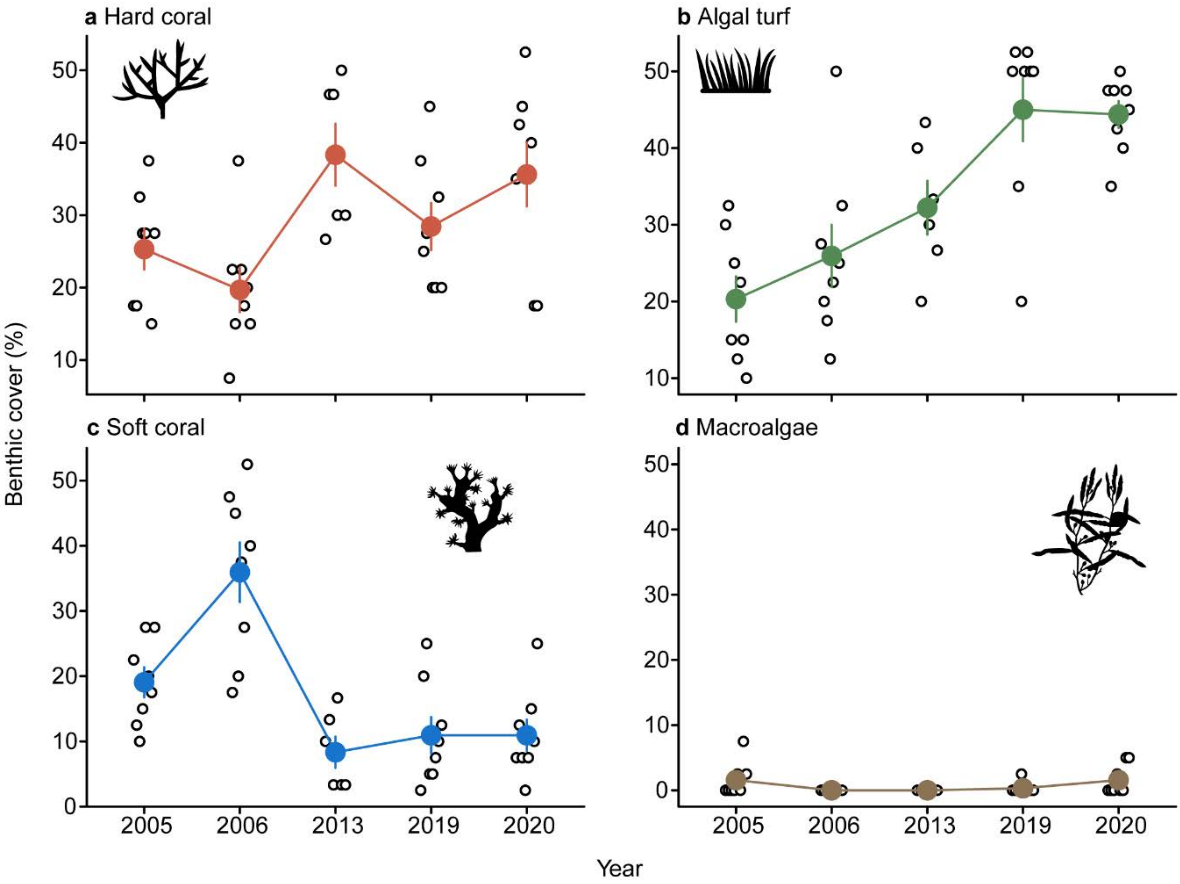

Figure F5 Changes in coral reef benthic cover through time. The mean (± SE) cover of a) hard corals, b) algal turfs, c) soft corals and d) macroalgae on the reef crest in Pioneer Bay, Orpheus Island. Open circles are the raw data points.

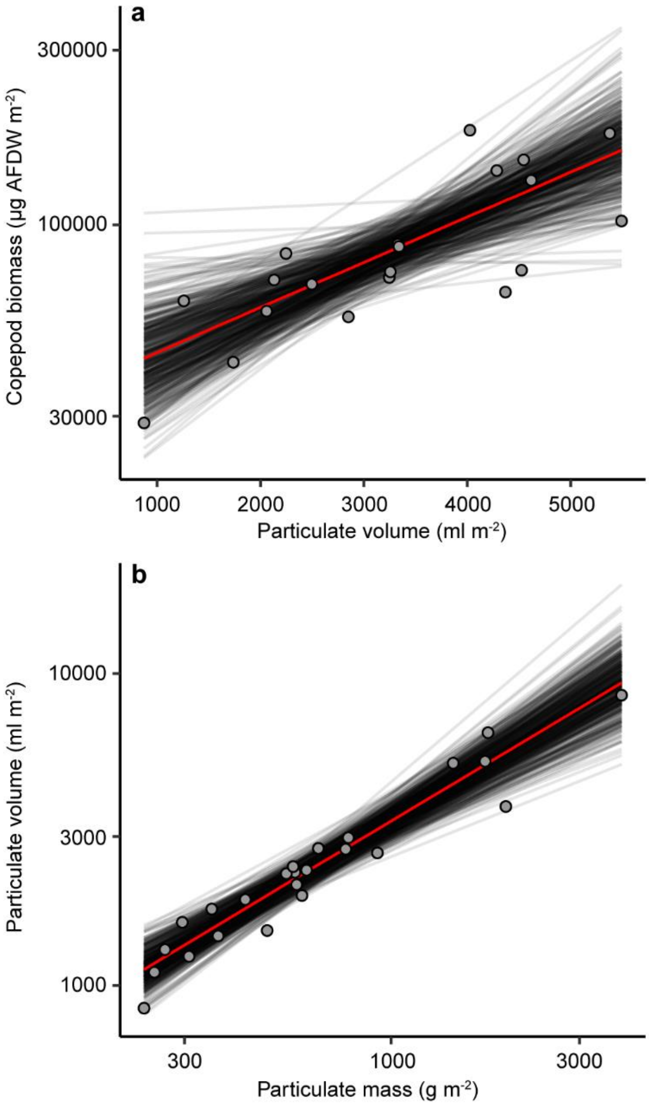

Figure F6 The relationship between a) particulate volume and harpacticoid copepod biomass within algal turfs, and b) particulate mass and particulate volume within algal turfs. The red lines indicate the mean predicted model fit from Bayesian generalised linear models. The black lines are based on 500 randomly selected model fits from the posterior distribution and the grey dots denote the raw data points.

Table F1 Prior values and chain details for the Bayesian models used in the study.

Response variable	Distribution	Prior information	Iterations	Thin	Chains	Warmup
Copepod biomass	Gamma (log-link)	Intercept (normal, 0, 10) Coefficients (normal, 0, 2.5) Auxiliary (exponential, 1)	3000	3	3	500
Particulate volume	Gamma (log-link)	Intercept (normal, 0, 10) Coefficients (normal, 0, 2.5) Auxiliary (exponential, 1)	3000	3	3	500
Herbivore abundance	Gamma (log-link)	Intercept (normal, 0, 10) Coefficients (normal, 0, 2.5) Auxiliary (exponential, 1)	3000	3	3	500
Herbivore biomass	Gamma (log-link)	Intercept (normal, 0, 10) Coefficients (normal, 0, 2.5) Auxiliary (exponential, 1)	3000	3	3	500
Herbivore biomass production	Gamma (log-link)	Intercept (normal, 0, 10) Coefficients (normal, 0, 2.5) Auxiliary (exponential, 1)	3000	3	3	500
Sediment mass	Gamma (log-link)	Intercept (normal, 0, 10) Coefficients (normal, 0, 2.5) Auxiliary (exponential, 1)	4000	4	3	750
Turf length	Gamma (log-link)	Intercept (normal, 0, 10) Coefficients (normal, 0, 2.5) Auxiliary (exponential, 1)	3000	3	3	500
Turf productivity	Gaussian (log-link)	Intercept (normal, 0, 10) Coefficients (normal, 0, 2.5) Auxiliary (exponential, 1)	4000	5	3	750

Table F2 Results of permutational analysis of multivariate dispersions conducted in the current study. df = degrees of freedom, SS = sum of squares.

Response variable	**Term**	**df**	**SS**	**Mean SS**	**F statistic**	***p* value**
Benthic function-space	Years	3	0.1243	0.0414	1.3296	0.2783
	Residuals	40	1.2467	0.0312		
Benthic function-space	Site	7	0.4302	0.0615	2.7334	<0.05
	Residuals	36	0.8095	0.0225		
Herbivore function-space	Years	3	0.4550	0.1517	2.8727	<0.05
	Residuals	44	2.3228	0.0528		
Herbivore abundance	Years	3	0.0148	0.0049	1.1578	0.3366
	Residuals	44	0.1875	0.0043		
Herbivore biomass	Years	3	0.0347	0.0116	2.4517	0.0759
	Residuals	44	0.2073	0.0047		

Table F3 Summary outputs of Bayesian models used in the study. Values are on the response scale and therefore an effect is apparent if the upper and lower CIs do not overlap 1. SE = standard error, CI = credibility interval

Response variable	**Distribution**	**Term**	**Estimate**	**SE**	**CI Low**	**CI High**
Copepod biomass	Gamma (log-link)	Intercept	33863.74	1.3229	19520.10	58133.65
		Particulate volume	1.0003	1.0001	1.0001	1.0004
Particulate volume	Gamma (log-link)	Intercept	17.7285	1.9200	4.8023	62.7287
		Particulate mass	2.1375	1.1060	1.7614	2.6090
Herbivore abundance	Gamma (log-link)	Intercept	19.1394	1.1923	13.8770	27.4230
		2013	0.7559	1.2759	0.4655	1.2148
		2018	0.4259	1.2733	0.2706	0.6866
		2019	0.3077	1.2826	0.1845	0.4929
Herbivore biomass	Gamma (log-link)	Intercept	4.3765	1.2149	3.0571	6.5986
		2013	1.0314	1.3086	0.6199	1.7951
		2018	0.5055	1.3131	0.2971	0.8434
		2019	0.6333	1.3194	0.3673	1.0777
Herbivore biomass production	Gamma (log-link)	Intercept	7.1991	1.1948	5.1357	10.1485
		2013	0.8945	1.2916	0.5261	1.4398
		2018	0.4257	1.2909	0.2639	0.7084
		2019	0.4965	1.2793	0.3045	0.8122
Sediment mass	Gamma (log-link)	Intercept	31.7112	1.6348	13.4939	93.4651
		2013	23.9494	1.9895	6.2951	81.8840
		2018	25.5698	1.9629	6.1590	79.1091
		2019	21.8139	1.9930	4.6223	68.7040
Turf length	Gamma (log-link)	Intercept	3.8784	1.1755	2.9128	5.4297
		2013	1.9120	1.2400	1.2755	2.8852
		2018	1.9370	1.2384	1.2964	2.9884
		2019	1.3830	1.2543	0.9089	2.2397
Turf productivity	Gaussian (log-link)	Intercept	0.7031	1.0556	0.6384	0.7731
		2013	0.3801	1.1102	0.3072	0.4586
		2018	0.3773	1.1018	0.3108	0.4473
		2019	0.3798	1.1023	0.3177	0.4562

Table F4 Results of permutational multivariate analysis of variance conducted in the current study. df = degrees of freedom, SS = sum of squares.

Response variable	Term	df	SS	Mean SS	F statistic	*p* value
Benthic function-space	2013	1	2.9768	2.9768	31.706	< 0.001
	2018	1	2.3841	2.3841	25.393	< 0.001
	2019	1	6.6894	6.6894	71.249	< 0.001
	Site	4	0.321	0.0803	0.855	0.5411
	Residuals	36	3.38	0.0939		
	Total	43	15.7513			
Herbivore function-space	2013	1	1.2175	1.2175	5.4217	< 0.05
	2018	1	0.6404	0.6404	2.8519	0.088
	2019	1	1.5688	1.5688	6.9863	< 0.01
	Residuals	44	9.8806	0.2246		
	Total	47	13.3073			
Herbivore abundance	2013	1	0.6932	0.6932	7.9999	< 0.001
	2018	1	0.2043	0.2043	2.3579	< 0.05
	2019	1	0.3497	0.3497	4.0363	< 0.01
	Residuals	44	3.8126	0.0867		
	Total	47	5.0598			
Herbivore biomass	2013	1	0.6740	0.6740	7.533	< 0.001
	2018	1	0.1746	0.1746	1.9518	0.0785
	2019	1	0.1652	0.1652	1.8466	0.0893
	Residuals	44	3.9369	0.0895		
	Total	47	4.9508			

Appendix G: Supporting information for chapter 9

Text G1 Sediment sampling and processing

Within a week of video recordings being taken, (sediments are temporally stable over week-month time scales [Gordon et al. 2016; Tebbett et al. 2018]), the sediments were sampled from hotspots and random locations. This was achieved by using an electronic vacuum sampler (modified after Purcell 1996; Kramer et al. 2012) to collect the sediments contained within a 58 cm^2 ring. Sampled surfaces were smooth, covered in algal turfs/CCA, and free of sediment retaining pits, macroalgae, and encrusting organisms. Following sample collection, the angle of each sampled surface was also recorded using an inclinometer.

Sediment samples were immediately fixed with 15 ml of 4% buffered formaldehyde to prevent the decay of organic detritus. Samples were then transferred into 9 l containers to settle and subsequently decanted until they could be held in 120 ml sample jars, leaving at least three hours between decants to allow particulate material >10 µm to settle (Purcell 1996). Samples were then standardised by wet sieving each through 2 mm stainless steel mesh. All inorganic particulate material less than 2 mm was considered sediment (sands, silts and clays; ISO 14688-1:2017). Each sample was then rinsed with freshwater three times to remove salts, allowing a standard (minimum 3 hour) sediment settling period between each rinse. Samples were then bleached to remove organic matter using 30% hydrogen peroxide (H_2O_2) for a minimum of two weeks. The samples were stirred and fresh H_2O_2 was added on a regular basis during this period. The samples were then dried to a constant weight at 60°C and their mass was recorded to yield information on total inorganic sediment load and organic detrital load. Methods for sediment processing follow Gordon et al. (2016).

Text G2 Nature of algal turf sediments at the study site

The study site between Palfrey and South Island contained a mean (± SE) algal turf sediment load of 157.8 ± 16.8 g m^{-2} across all surfaces sampled. Within this upper reef crest, algal turf sediment loads ranged from 8.5 to 984.9 g m^{-2}. 80 algal turf sediment samples were collected from the preferred feeding surface (i.e. algal turf/CCA-covered substratum <30° from horizontal) of *C. striatus*. Algal turf sediment loads on the preferred surfaces ranged from 14.25 to 984.9 g m^{-2}, with a mean load of 173.7 ± 20.8 g m^{-2}. These minimum, maximum and mean values of algal turf sediment loads on preferred feeding surfaces represented the values on which alternative algal turf sediment load frequency distributions were generated for modelling purposes.

Text G3 Percentage calculations

The results of this study include a number of percentages. The steps taken to calculate these are outlined below:

Reef area percentages

The coverage of different benthic categories, and the occurrence of different surface angles on the reef, were based on the 10 points generated for each of the 106 *C. striatus* individual bites examined (i.e. 1060 points over the reef). Whenever the chapter refers to benthic covering/surface angle as a percentage of reef area, or the percentage of area that bites occurred in, this refers to the percentage of points out of the original 1060 (i.e. all percentages are based on the entire reef being 100%) (Fig. G1). For example, when percentage of total reef area covered by a specific benthic covering and surface angle (e.g. horizontal algal turf/CCA cover) is referred to in the chapter this is based on the number of points (out of 1060) that satisfy both criteria: horizontal and algal turf/CCA. When the frequency distribution of algal turf sediment loads was considered (in the 5 different feeding rate bins) on a specific surface I could therefore also calculate the percentage of that surface that would be covered in a specific algal turf sediment load. For example, for the algal turf sediment distribution data if 50% was contained within the lowest bin, then 50% of the specific surface would have sediment loads that fell within that bin, and as I knew that the specific surface made up 25% of reef area (e.g. Fig. G1), I therefore calculated that the specific surface, with that specific sediment range, would make up 12.5% of total reef area assuming no interaction term (e.g. Fig. G1).

Feeding percentages

In a similar manner to the reef area percentages, all percentages related to the number of bites delivered by *C. striatus* were based on the 106 bites examined being 100% of feeding. In essence, at the coarsest level, 100% of bites (106 bites) are delivered in 100% of reef area (Fig. G1). From this data I could then work out the percentage of the 106 bites that fell on specific benthic coverings as I looked in more detail. When changing algal turf sediment loads were considered on a specific benthic surface at a specific angle, I knew what percentage of bites were delivered to those surfaces (e.g. 50%) (Fig. G1). Based on the feeding response model of *C. striatus* against algal turf sediment I could also calculate the relative frequency of bites at specific algal turf sediment loads. By combining this relative feeding frequency with percentage of bites actually delivered to the reef (i.e. bites out of 106) I could therefore calculate the likely percentage of bites that would be delivered at different algal turf sediment loads. For example, if 50% of total bites were delivered on a specific surface, and my models suggested that 75% of the total bites were likely to fall within a specific algal turf sediment bin on that surface, then 37.5% of the total bites delivered to the reef by *C. striatus* would fall on such surfaces at such algal turf sediment loads (Fig. G1). As I also had the percentage occurrence of such surfaces (as outlined above) I could therefore present data on the percentage of bites delivered by *C. striatus* against the percentage of reef area covered by the matching surface assuming no interaction (Fig. G1).

References

Gordon SE, Goatley CHR, Bellwood DR (2016) Composition and temporal stability of turf sediments on inner-shelf coral reefs. Mar Pollut Bull 111:178–183

Kramer MJ, Bellwood DR, Bellwood O (2012) Cryptofauna of the epilithic algal matrix on an inshore coral reef, Great Barrier Reef. Coral Reefs 31:1007–1015

Purcell SW (1996) A direct method for assessing sediment load in epilithic algal communities. Coral Reefs 15:211–213

Tebbett SB, Bellwood DR, Purcell SW (2018) Sediment addition drives declines in algal turf yield to herbivorous coral reef fishes: implications for reefs and reef fisheries. Coral Reefs 37:929–937

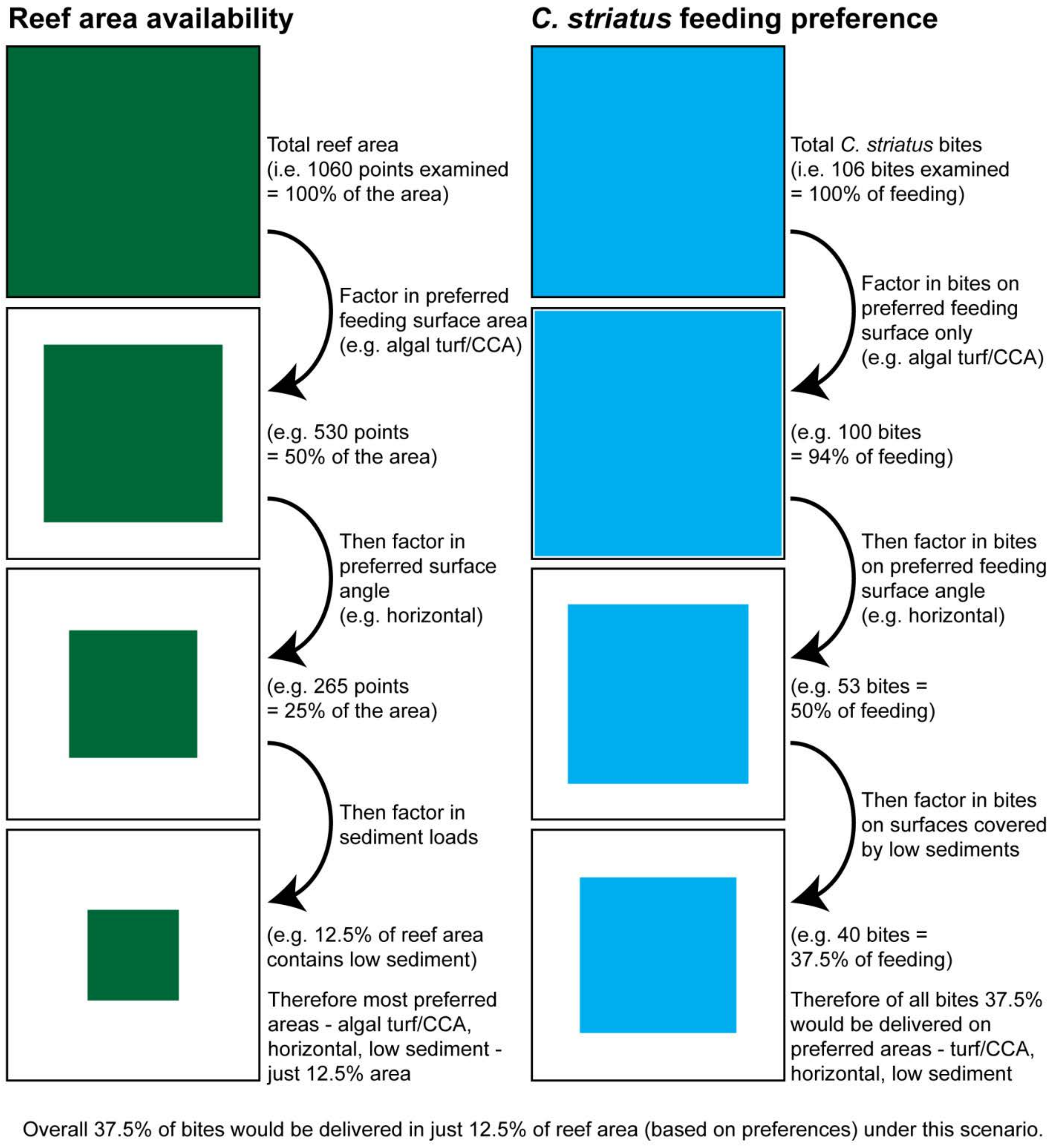

Figure G1 A conceptual outline of how percentage of *C. striatus* feeding as a percentage of reef area was calculated in the current study. The area of the coloured squares is scaled by the percent of the total (the top square in each case represents the total i.e. 100%).

Table G1 Comparison of models used to examine differences in algal turf sediment loads across surface angles in *Ctenochaetus striatus* feeding hotspots and on randomly sampled surfaces. Models are compared using the corrected Akaike Information Criterion (AICc). Shown are number of parameters (k), model maximum log-likelihood (logLik), AICc, change in AICc (Δ) and AICc weight (wAICc).

Model	**Variables**	**k**	**logLik**	**AICc**	**Δ**	**wAICc**
Sediment load	Angle × Type	7	-565.483	1146.5	0.00	0.897
	Angle + Type	6	-568.906	1151.0	4.44	0.097
	Type	5	-572.967	1156.7	10.22	0.005
	Angle	5	-576.412	1163.6	17.11	0.00
	Null	4	-580.969	1170.5	23.95	0.00

Table G2 Summary of model results used to examine differences in algal turf sediment loads across surface angles in *Ctenochaetus striatus* feeding hotspots and on randomly sampled surfaces. SE = standard error.

Response variable	**Model used**	**Predictor variable**	**Estimate**	**SE**	***t* value**	***p* value**
Sediment load	Gamma GLMM	Intercept	5.5973	0.2563	21.842	< 0.001
		Angle	-0.0053	0.0077	-0.691	0.49
		Random	1.6262	0.3178	5.118	< 0.001
		Angle:Random	-0.0310	0.012	-2.576	< 0.05

Table G3 Summary of model results used to examine relationships between algal turf sediments and other components of the epilithic algal matrix. Gamma distributions use a *t* value, Beta distributions use a *z* value. SE = standard error.

Response variable	**Model used**	**Predictor variable**	**Estimate**	**SE**	***t/z* value**	***p* value**
Detritus load	Gamma GLM	Intercept	0.5025	0.1609	3.1220	< 0.01
		Log(sediment)	0.4232	0.0335	12.6490	< 0.001
Detritus proportion	Beta GLM	Intercept	0.2704	0.1583	1.7080	0.09
		Log(sediment)	-0.5263	0.0354	-14.8550	< 0.001
Turf length	Gamma GLM	Intercept	-0.0692	0.1314	-0.5260	0.6
		Log(sediment)	0.2236	0.0273	8.1810	< 0.001

Appendix H: List of publications arising from this thesis

1. **Tebbett SB**, Bellwood DR (2019) Algal turf sediments on coral reefs: what's known and what's next. Mar Pollut Bull 149:110542
2. **Tebbett SB**, Streit RP, Bellwood DR (2020) A 3D perspective on sediment accumulation in algal turfs: implications of coral reef flattening. J Ecol 108:70-80
3. **Tebbett SB**, Bellwood DR (2020) Sediments ratchet-down coral reef algal turf productivity. Sci Total Environ 713:136709
4. **Tebbett SB**, Goatley CHR, Streit RP, Bellwood DR (2020) Algal turf sediments limit the spatial extent of function delivery on coral reefs. Sci Total Environ 734:139422
5. **Tebbett SB**, Bellwood DR (2021) Algal turf productivity on coral reefs: a meta-analysis. Mar Environ Res 168:105311
6. **Tebbett SB**, Morais RA, Goatley CHR, Bellwood DR (2021) Collapsing ecosystem functions on an inshore coral reef. J Environ Manage 289:112471
7. **Tebbett SB**, Morais J, Bellwood DR (2022) Spatial patchiness in change, recruitment, and recovery on coral reefs at Lizard Island following consecutive bleaching events. Mar Environ Res 173:105537
8. **Tebbett SB**, Connolly SR, Bellwood DR (*In Review*) Benthic composition changes on coral reefs at global scales. Nat Ecol Evol

Appendix I: Publications during candidature not arising from this thesis

1. Latrille FX, **Tebbett SB**, Bellwood DR (2019) Quantifying sediment dynamics on an inshore coral reef: putting algal turfs in perspective. Mar Pollut Bull 141:404-415

2. Bellwood DR, Pratchett MS, Morrison TH, Gurney GG, Hughes TP, Álvarez-Romero JG, Day JC, Grantham R, Grech A, Hoey AS, Jones GP, Pandolfi JM, **Tebbett SB**, Techera E, Weeks R, Cumming GS (2019) Coral reef conservation in the Anthropocene: confronting spatial mismatches and prioritizing functions. Biol Conserv 236:604-615

3. Wismer S, **Tebbett SB**, Streit RP, Bellwood DR (2019) Young fishes persist despite coral loss on the Great Barrier Reef. Commun Biol 2:456

4. **Tebbett SB**, Hoey AS, Depczynski M, Wismer S, Bellwood DR (2020) Macroalgae removal on coral reefs: realised ecosystem functions transcend biogeographic locations. Coral Reefs 39:203-214

5. Chase TJ, Pratchett MS, Hein MY, McWilliam MJ, **Tebbett SB**, Hoogenboom MO (2020) Damselfishes alleviate the impacts of sediments on host corals. R Soc Open Sci 7:192074

6. **Tebbett SB**, Chase TJ, Bellwood DR (2020) Farming damselfishes shape algal turf sediment dynamics on coral reefs. Mar Environ Res 160:104988

7. Oakley-Cogan A, **Tebbett SB**, Bellwood DR (2020) Habitat zonation on coral reefs: structural complexity, nutritional resources and herbivorous fish distributions. PLoS One 15:e0233498

8. Bellwood DR, Hemingson CR, **Tebbett SB** (2020) Subconscious biases in coral reef fish studies. Bioscience 70:621-627

9. Schlaefer JA, **Tebbett SB**, Bellwood DR (2021) The study of sediments on coral reefs: a hydrodynamic perspective. Mar Pollut Bull 169:112580

10. Morais J, Morais RA, Pratchett MS, **Tebbett SB**, Bellwood DR (2021) Dangerous demographics in post-bleach corals: boom-bust vs. protracted declines. Sci Rep 11: 18787

11. Pessarrodona A, **Tebbett SB**, Bosch NE, Bellwood DR, Wernberg T (2022) High herbivory despite high sediment loads on a fringing coral reef. Coral Reefs 41:161-173

12. **Tebbett SB**, Siqueira AC, Bellwood DR (2022) The functional roles of surgeonfishes on coral reefs: past, present and future. Rev Fish Biol 32:387-439

13. Crisp SK, **Tebbett SB**, Bellwood DR (2022) A critical evaluation of benthic phase shift studies on coral reefs. Mar Environ Res 178:105667

14. Bowden CL, Streit RP, Bellwood DR, **Tebbett SB** (2022) A 3D perspective on sediment turnover and feeding selectivity in blennies. Mar Pollut Bull 180:113799

15. **Tebbett SB**, Sgarlatta MP, Pessarrodona A, Vergés A, Wernberg T, Bellwood DR (2022) How to quantify algal turf sediments and particulates on tropical and temperate reefs: an overview. Mar Environ Res 179:105673

16. Scott ME, **Tebbett SB**, Whitman KL, Thompson CA, Mancini FB, Heupel MR, Pratchett MS (*In Review*) Variation in abundance, diversity and composition of coral reef fishes with increasing depth at a submerged shoal in the northern Great Barrier Reef. Rev Fish Biol

17. Arjunwadkar CV, **Tebbett SB**, Bellwood DR, Bourne DG, Smith HA (*In Review*) Algal turf structure and composition vary with particulate loads on coral reefs. Mar Pollut Bull

18. Schlaefer JA, **Tebbett SB**, Bowden CL, Collins WP, Duce S, Hemingson CR, Mihalitsis M, Morais J, Morais RA, Siqueira AC, Streit RP, Swan S, Valenzuela J, Bellwood DR (*In Review*) A snapshot of sediment dynamics on an inshore coral reef. Mar Pollut Bull

19. **Tebbett SB**, Crisp SK, Evans RD, Fulton CJ, Pessarrodona A, Wernberg T, Wilson SK, Bellwood DR (*In Review*) Are regime shifts an appropriate indicator of decline on coral reefs? Proc Natl Acad Sci USA

20. Morais J, Morais RA, **Tebbett SB**, Bellwood DR (*In Review*) On the fate of dead coral colonies. Funct Ecol

21. **Tebbett SB**, Bellwood DR, Johnson ER, Chase TJ (*In Review*) Algal turfs as a sink for sediment-bound heavy metals on coral reefs. Mar Pollut Bull

22. **Tebbett SB**, Sreit RP, Morais J, Schlaefer JA, Swan S, Bellwood DR (*In Review*) Benthic cyanobacterial mat formation during severe coral bleaching at Lizard Island: the mediating role of water currents. Mar Environ Res

Appendix J: Storage locations of data arising from this thesis

Chapter 2: Sources of, and relevant links to, all data locations for this chapter are listed in Appendix A: Text A2

Chapter 3: Tebbett, Sterling; Morais, Juliano; Bellwood, David (2021): Data from: Spatial patchiness in change, recruitment, and recovery on coral reefs at Lizard Island following consecutive bleaching events. James Cook University. https://doi.org/10.25903/3bzv-1y39

Chapter 4: Tebbett, Sterling; Bellwood, David (2021): Data from: Algal turf sediments on coral reefs: what's known and what's next. James Cook University. https://doi.org/10.25903/8t81-t071

Chapter 5: Tebbett, Sterling; Streit, Robert; Bellwood, David (2019): Data from: A 3D perspective on sediment accumulation in algal turfs: implications of coral reef flattening. James Cook University. https://doi.org/10.25903/5d0ada7f84903

Chapter 6: Tebbett, Sterling; Bellwood, David (2021): Data from: Sediments ratchet-down coral reef algal turf productivity. James Cook University. https://doi.org/10.25903/834y-dd78

Chapter 7: Tebbett, Sterling; Bellwood, David (2021): Data from: Algal turf productivity on coral reefs: a meta-analysis. James Cook University. https://doi.org/10.25903/y12c-xd63

Chapter 8: Tebbett, Sterling; Morais, Renato; Goatley, Christopher; Bellwood, David (2021): Data from: Collapsing ecosystem functions on an inshore coral reef. James Cook University. https://doi.org/10.25903/as5q-yn02

Chapter 9: Tebbett, Sterling; Goatley, Christopher; Streit, Robert; Bellwood, David (2021): Data from: Algal turf sediments limit the spatial extent of function delivery on coral reefs. James Cook University. https://doi.org/10.25903/mrre-wh52