The ecological role of sediments on coral reefs

Thesis submitted by

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Statement on the contribution of others

This thesis includes some collaborative work with my supervisor, Professor David Bellwood, and colleague Dr. Andrew Hoey. In these collaborations I was responsible for the conception of the project, data collection, analysis and interpretation of data. My co-authors provided technical assistance, intellectual guidance, editorial assistance and financial support. Dr. Andrew Hoey provided video data of hawksbill turtles used in Chapter 3.2.

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Abstract

Sediments are deleterious to coral reefs, yet our understanding of how they actually damage reefs is somewhat limited. While effects on individual organisms, particularly those on the benthos, are well known (e.g. smothering, shading and abrasion) the role of sediment in mediating ecological processes, on which coral reefs depend, is less well understood. This thesis assesses the role of benthic sediments in mediating herbivory and detritivory by coral reef fishes, two vital processes on modern coral reefs.

Algal turfs can stabilise benthic sediments on coral reefs, yet sediment in these algal turfs can affect their palatability to fishes. In the first data chapter (Chapter 2), it seemed appropriate to assess the abundance of algal turfs, which together with detritus, infauna and sediment comprise the epilithic algal matrix (EAM). The simple question of how much EAM is present on a coral reef was rapidly confounded by the presence of 3-dimensional structure in the form of canopies. Canopies are common among autotrophs, increasing their access to light and thereby increasing competitive abilities. If viewed from above, however, canopies may conceal objects beneath them, creating a 'canopy effect'. Due to complexities in collecting 3-dimensional data, most ecosystem monitoring programmes reduce dimensionality when sampling, resorting to planar views. The resultant 'canopy effects' may bias data interpretation, particularly following disturbances. Canopy effects are especially relevant on coral reefs where coral cover is often used to evaluate and communicate ecosystem health. Canopies were found to hide benthic components including massive corals and, perhaps more importantly, algal turfs. These turfs stabilise benthic sediments on coral reefs and are often ignored by standard benthic sampling methods. As planar views are almost ubiquitously used to monitor disturbances, the loss of vulnerable canopy-forming corals may bias findings by presenting pre-existing benthic components as an altered system. Our reliance on planar views in monitoring ecosystems, especially coral cover on reefs, needs to be reassessed if we are to better understand the ecological consequences of ever more frequent disturbances.

In the second data chapter (Chapter 3), benthic sediment reductions were used to assess the role of sediment in suppressing reef fish herbivory across a depth gradient (reef base, crest and flat). Sediment suppressed herbivory across all reef zones. Even slight reductions on the reef crest, which had 35 times less sediment than the reef flat, resulted in over 1800 more herbivore bites (h^{-1} m^{-2}). The Acanthuridae (surgeonfishes) were responsible for over 80 per cent of all bites observed, and on the reef crest and flat took over 1500 more bites (h^{-1} m^{-2}) when sediment load was reduced. These findings highlight the role of natural sediment loads in shaping coral reef herbivory and suggest that changes in benthic sediment loads could directly impair reef resilience.

While conducting these experimental habitat manipulations to assess the roles of herbivorous reef fishes, green turtles (*Chelonia mydas*) showed responses remarkably similar to those of herbivorous fishes. Furthermore, while deploying macroalgal bioassays hawksbill turtles (*Eretmochelys imbricata*) were observed feeding. Reducing the sediment load of the epilithic algal matrix on a coral reef resulted in a forty-fold increase in grazing by green turtles. Hawksbill turtles were also observed to browse transplanted thalli of the macroalga *Sargassum swartzii* in a coral reef environment. These responses not only show strong parallels to herbivorous reef fishes, but also highlight that marine turtles actively, and intentionally, remove algae from coral reefs. When considering the size and potential historical abundance of marine turtles it appears that these potentially valuable herbivores may have been lost from many coral reefs before their true importance was understood.

In the third data chapter (Chapter 4), an experimental combination of caging and sediment addition treatments were used to investigate the effects of sediment pulses on herbivory and EAMs, and to determine whether sediment addition could trigger a positive-feedback loop, leading to deep, sediment-rich turfs. A 1-week pulsed sediment addition resulted in rapid increases in algal turf length with effects comparable to those seen in herbivore exclusion cages. Contrary to the hypothesised positive-feedback mechanism, benthic sediment loads returned to natural levels within 3 weeks, however, the EAM turfs remained almost 60%

longer for at least 3 months. While reduced herbivore density is widely understood to be a major threat to reefs, acute disturbances to reef sediments may elicit similar ecological responses in the EAM. With reefs increasingly threatened by both reductions in herbivore biomass and altered sediment fluxes, the development of longer turfs may become more common on coral reefs.

In the fourth data chapter (Chapter 5), off-reef sediment transport by the surgeonfish *Ctenochaetus striatus* (Acanthuridae) was quantified on the reef crest at Lizard Island, Great Barrier Reef. Three independent methods were implemented to estimate sediment ingestion rates. These considered (1) the bite rate and bite volume, (2) the defecation rate and faecal pellet size, and (3) the average gut contents and throughput rate. The 3 methods provided a broad range of estimates of sediment ingestion from 8.8 ± 2.4, to 66.1 ± 14.4 g $fish^{-1}$ d^{-1} (mean ± SE). Nevertheless, these estimates were comparable to rates of sediment ingestion by parrotfishes (Labridae), the other major sediment-moving group on reefs. Overall, 36.5% of all sediment ingested was transported from the upper reef crest into deeper water, equating to a removal rate of 28.6 ± 6.2 kg 100 m^{-2} yr^{-1} at the study site. By brushing the reef, *C. striatus* reduces the sediment loading in the epilithic algal matrix (EAM) while causing little damage to the algal turf. Reducing sediments in EAMs provides favourable settlement surfaces for benthic organisms and increases the palatability of the EAM to herbivorous reef fishes, thus supporting reef resilience. The ecological importance of *C. striatus*, which is abundant on reefs throughout the Indo-Pacific, appears to have been underestimated, particularly when considering reef sediment dynamics.

This thesis highlights the importance of benthic sediments in mediating grazing by both herbivorous fishes and macroherbivores. By making EAMs less palatable to herbivores, sediments reduce top down pressure controlling growth of algal turfs in the EAM and allows for the development of longer, apparently stable EAMs. By feeding on the reef crest and defecating off reef, some herbivorous and detritivorous reef fishes may reduce the levels of benthic sediment in reef crest EAMs, however, these fishes are also affected by the presence of

sediments, and as yet the thresholds at which this process will be affected are unknown. The roles of benthic sediments in mediating ecological processes on coral reefs appear far subtler yet more damaging than previously thought. While inundation by large quantities of sediment is undoubtedly deleterious to reefs, this thesis suggests that far smaller increases can have considerable impacts. By affecting ecological processes on which coral reefs rely (e.g. grazing), slight increases in benthic sediments erode the resilience of coral reefs. With sediment as such an important factor in maintaining ecological processes on coral reefs, the impacts of sediment can no longer be ignored when managing for coral reef resilience.

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Chapter 1: General introduction

Sediments have generally been considered to have deleterious impacts on coral reefs. The clearest examples of their effects have been seen in individual responses to increases (Fabricius et al. 2007). However, the broader effects of sediments are poorly understood. With this thesis I attempt to bridge this knowledge gap by investigating how benthic sediments on coral reefs (defined as inorganic material < 2mm diameter) affect the behaviour of herbivorous and detritivorous reef fishes and in turn, how this affects the application of the functional roles they play. By asking three simple questions about benthic sediments on coral reefs I will introduce the overlying themes of this thesis, and then present the overall aims and structure of the thesis to conclude this general introduction.

1.1 Where do reef sediments come from?

When considering sediments on coral reefs, both the public eye and management protocols tend to focus on direct anthropogenic inputs of sediment to coral reefs. Human activities such as coastal developments and land clearing release terrigenous sediments (sediments created on the land) into the marine environment (Fabricius 2005). Furthermore marine activities such as dredging and shipping (including ship groundings) can resuspend marine sediments, along with other benthic material such as terrigenous sediments and pollutants, allowing these materials to be transported to inshore reefs (Wolanski and Gibbs 1992; Erftemeijer et al. 2012). These activities are, without doubt, a major threat to marine ecosystems and are a key source of sediments to inshore reefs (Wolanski et al. 2005). They are, on the other hand, predominantly coastal and relatively localised. As such, these anthropogenic sediment releases are relatively easy to detect, study and prevent.

However, not all coral reefs are inshore, and many are at a considerable distance from human populations, leaving them less prone to coastal and anthropogenic sediment releases. These reefs still have sediments. In fact, sediments are a ubiquitous component of all coral reefs. Whilst hydrodynamic resuspension by storms and cyclones plays a role in getting existing sediments to these offshore reefs (Graus and Macintyre 1989; Larcombe and Carter 2004; Bak et al. 2005), a considerable proportion of their benthic sediments are produced *in situ*. The carbonate matrix from which reefs are created is continuously eroded into sediment by a variety of physical and biological forces. Whole coral colonies can become detached from the reef matrix under high hydrodynamic drag. While storms and tidal surges are the most common source of hydrodynamic forces great enough to dislodge colonies, some large branching coral colonies (especially tabulate *Acropora* spp.) provide enough cross sectional area, and henceforth drag, to be dislodged by relatively small hydrodynamic forces (Madin 2005; Madin and Connolly 2006). Dead and dislodged colonies undergo further erosion to rubble and eventually sediments.

Physical and chemical processes are important in coral reef taphonomy (the breakdown of organisms), however, biological erosion plays a considerable role (Wood 2011). A diverse assemblage of organisms, from microbes to large vertebrates, erodes the reef matrix. The most obvious bioeroding organisms on coral reefs are the parrotfishes (scarine labrids), with individuals of the largest species, *Bolbometopon muricatum* capable of removing over 5 tonnes of carbonate from reefs per year (Bellwood et al. 2003). Much of the eroded material is returned to reefs as sediment. This constant creation of sediment by biological and physical processes is the driver behind the ubiquity of sediments on all coral reefs, and the nature of this production may also determine their fates on coral reefs.

1.2 Where do reef sediments go?

In addition to producing sediments on coral reefs, hydrodynamics play an important role in their fate. Sediments are transported by resuspension or saltation and driven back from exposed reef crests. Depending on reef topography, this can result in a build-up of sediments on the reef flat, sometimes creating beaches or sand cays (Kench 1998; Kench and Brander 2006). The majority of sediments keep moving and are transported off the leeward side of the reef. While the sediment is being transported on reefs, a small proportion may be affected by further physical, chemical and biological erosion which can reduce particle size until the carbonate can be completely dissolved and lost from the benthos.

At any given time, a large quantity of sediment can be found on coral reefs. Sediments are found on hard substrates of all coral reefs, in crevices or sand patches but most commonly bound within the epilithic algal matrix (EAM). EAMs are composed of algal and cyanobacterial turfs, detritus, infaunal organisms and sediments (Wilson and Bellwood 1997). They are among the most common forms of benthic cover on coral reefs (Wismer et al. 2009), although their actual abundance is rarely quantified (Vroom 2011). They form a stable sediment reservoir as their complex 3-dimensional structure stabilises benthic sediments, sheltering them from hydrodynamic forces (Carpenter and Williams 1993; Airoldi et al. 1995; McClanahan 1997).

Whilst sediment trapped within the EAM can be removed by stochastic hydrodynamic events such as storms and cyclones (Roberts and Suhayda 1983), biological processes provide a constant, yet relatively poorly studied, background of sediment removal. Many fishes eat components of the EAM. Whether targeting invertebrates (Kramer et al. 2013a), detritus (Wilson et al. 2003) or algae (Fox and Bellwood 2007; Hoey and Bellwood 2008), fishes also ingest other components of the matrix, including sediment. In fact, relatively pristine herbivore populations can graze the entire EAM multiple times per year (Fox and Bellwood 2007) removing sediment as they do (Bellwood 1996), and several detritivorous species, including *Ctenochaetus striatus* (Acanthuridae) have specialised comb-like teeth (Purcell and Bellwood

1993), which are ideally suited for removing large quantities of detritius, but also sediment from the EAM, while leaving the algae intact. These factors are particularly important when combined with evidence that herbivorous and detritivorous fishes feed and defecate in different locations; often repeatedly using specific 'latrine' sites (Krone et al. 2008). While there is evidence to show that fish do transport sediments in this process (Bellwood 1995a), the absolute magnitude of this function has not been quantified for any fish species.

1.3 What do reef sediments do?

It is widely accepted that sediments are deleterious to coral reefs, however, their impacts across a range of spatio-temporal scales are not fully understood. At the scale of individual organisms the effects of sediment are relatively well documented, sediment deposited on benthic organisms including hard and soft corals, sponges, ascidians, algae and tridacnid clams rapidly results in signs of stress and/or mortality (Rogers 1990; Fabricius et al. 2007). At this 'physiological scale' sediment damages sessile organisms by smothering and shading (Rogers 1990; Erftemeijer et al. 2012) or promoting the growth of microbes leading to anoxia (Weber et al. 2012). Similarly, at much larger spatial and temporal scales, the roles of sediment are relatively well understood. Sediment can influence the development and distribution of entire reef systems (Woolfe and Larcombe 1999; Perry and Smithers 2010), and while reefs can exist in high sediment locations (Browne et al. 2012) their vertical accretion can be slowed, making them more prone to drowning during sea level rise (Blanchon and Shaw 1995).

At scales between the small 'physiological scale' and large 'geomorphic' or 'geological scales' (see Perry et al. 2008) discussed above, sediments also appear to be involved in ecological processes on coral reefs, however, considerably less is understood about the roles of sediment at this scale. Observing the impacts of sediments at this ecological scale is crucial in both understanding the ecological role of sediments on coral reefs and in providing useful information for ecosystem management. Ecological processes involve interactions between

multiple organisms and their environment, hence it is important to focus on spatial scales that incorporate more than individual organisms (i.e. the 'physiological scale' mentioned above), yet at very large spatial and temporal scales (i.e. geomorphic and geological scales) changes can happen too slowly and/or over too large an area to be effectively observed or managed.

While the information is relatively limited, sediments do appear to influence several key ecological processes on coral reefs. Recovery of reefs from disturbances can be impeded by sediments as the settlement of larval corals is inhibited by benthic sediments (Birrell et al. 2008). The loose matrix formed by the sediment covers the hard substrate and creates an unstable surface onto which larval corals cannot adhere (Rogers 1990; Babcock and Davies 1991; Sanders and Baron-Szabo 2005). Furthermore, benthic sediments limit the survival of newly settled corals, by smothering and abrading the corals tissues (Birrell et al. 2008). Indeed palaeoecological evidence suggests that increased sedimentation could be the ultimate cause of reef-wide degradation, with high sediment reefs unable to recover from disturbances (Blanchon and Shaw 1995; Blanchon 2010; Roff et al. 2013).

While settlement and survivorship of corals is undoubtedly a key process on coral reefs, it is, by no means the only ecosystem process on which coral reefs rely. Coral reef fishes play many crucial roles. Although high concentrations of suspended sediments from terrestrial sources may impair the settlement and survivorship of larval reef fishes on inshore reefs (Wenger et al. 2011, 2012), there is only a limited understanding of the roles of benthic sediments on coral reefs, particularly those away from terrestrial sources of sedimentation. What little information does exist, however, point to a negative impact of sediments on herbivory by coral reef fishes (Bellwood and Fulton 2008).

Herbivory is a critical process on coral reefs. By controlling algal development, herbivores maintain the resilience of reefs and allow them to recover from disturbances (Bellwood et al. 2004). On most 'healthy' coral reefs, herbivorous reef fishes are the most important group in this role. Natural and experimental reductions in herbivorous fish

abundances have repeatedly resulted in phase-shifts to macro-algal dominated states on coral reefs, highlighting their crucial role in this process (Burkepile and Hay 2006; Mumby 2006; Jessen and Wild 2013). Herbivory, however, is not a single process. A number of functional groups of reef fishes remove algae in fundamentally different ways and as such have different ecosystem impacts. Broadly these functional groups can be thought of as macroalgal browsers and benthic scrapers, excavators and grazers (Hoey and Bellwood 2009), with the latter three being the most relevant for this study as they target components of the EAM. In addition to herbivores being split by the functions they provide, there is an increasing body of evidence suggesting that high biodiversity does not engender high functional redundancy. Each function appears to be maintained by only a few key species (Bellwood et al. 2003; Hoey and Bellwood 2009). As such, disturbances need only affect these few key species to have dramatic effects on coral reef resilience. However, the effects of sediments on the function of herbivorous reef fishes is poorly understood.

While all coral reef EAMs contain sediments, it appears that this component could deter feeding by herbivorous reef fishes. Although anecdotal evidence of this has existed for some time (Choat 1991; Purcell and Bellwood 2001), the impacts of sediment on feeding by herbivores were not directly quantified until recently (Bellwood and Fulton 2008). Following removal of sediments from hydrodynamically exposed EAMs, herbivory increased almost four-fold and resulted in a 64% reduction in turf length in only four-hours. The study by Bellwood and Fulton (2008) was conducted at a limited spatial scale in only one reef zone, yet the magnitude of the effect of sediment removal was unexpected and highlights the potentially important role of sediments in suppressing herbivory, as such this study acted as the impetus for this thesis. There is a clear need to understand the role of fish-sediment interactions, especially at the ecological scale.

1.4 Aims

The broad aim of this thesis is: **"To investigate interactions between herbivorous reef fishes and sediments, and to therefore quantify their impact on ecological processes on coral reefs."** To accomplish this, a number of questions will be addressed across four data chapters.

Chapter 2 asks the question: "**How much EAM is on a coral reef?**" EAMs are potentially important sediment reservoirs on coral reefs, yet there is very little information on their abundance and cover on coral reefs. This chapter provides information on the prevalence of EAMs on coral reefs using a variety of previously untested metrics. Following this assessment of EAM cover, **Chapter 3** asks: "**How do reef herbivores respond to changes in EAM-bound sediments?**" and presents two studies that quantify increased herbivory following sediment removal. The sediment removals conducted for this chapter highlight that sediment suppresses herbivory by coral reef fishes whereas **Chapter 4** uses ecologically relevant sediment additions to ask "**Can reef-sediments induce coral reef phase-shifts?**" Finally, in **Chapter 5,** I ask whether any ecological processes can help coral reefs overcome the effects of sediments, to answer the question "**Can fish affect coral reef sediments?"**

Chapter 2: The roles of dimensionality, canopies and complexity in ecosystem monitoring

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2.1 Introduction

Worldwide, the increasing frequency and severity of ecosystem disturbances associated with changing climatic conditions and direct anthropogenic activities has increased the need for ecosystem monitoring. Effective monitoring programmes aim to detect disturbances in time to mitigate their impacts (Margules and Pressey 2000; Wilson et al. 2007a). To be effective, these monitoring programmes must be fast and cost-effective, as this facilitates repeated observations, a vital feature to detect changes in ecosystems. While a plethora of methods exist to monitor habitats across various ecosystems, one feature is almost universal among direct monitoring regimes regardless of ecosystem: the use of horizontal planar views in sampling. This standardises monitoring and provides rapid assessments of abundance or cover of organisms (Shuman and Ambrose 2003; Hill and Wilkinson 2004; Booth et al. 2008). A potential concern arises, however, as ecosystems are inherently 3-dimensional. By reducing dimensionality in monitoring we simplify data collection and analysis, but at what cost to the quality of data?

Obviously, recording 3-dimensional data from ecosystems is highly complex and increases the amount of time needed to sample. Reducing dimensionality in sampling is therefore justified if the increased speed and reduced cost improves the spatial and/or temporal resolution of the data being collected. Of the 3 dimensions, however, it has almost always been the vertical component that is discarded first, leaving the horizontal axes. The implications of this reliance on linear or planar views could affect the data collected in ecosystem monitoring, particularly with regards to the detection of disturbances in multi-layered ecosystems. Furthermore, as these methods have often been extended for use in more detailed ecological

studies, biases associated with reducing dimensionality could undermine our understanding of key ecological processes in complex ecosystems.

Alongside tropical rainforests, coral reefs are one of the most biodiverse ecosystems on the planet (Connell 1978). Furthermore, coral reefs are arguably the most threatened high biodiversity ecosystem. They are highly sensitive to physical and environmental perturbations (Berkelmans et al. 2004; Hoegh-Guldberg et al. 2007; Madin et al. 2008). As such, many monitoring programmes have been implemented, some over several decades (Hill and Wilkinson 2004; Wilkinson 2008). The methods used, therefore, are relatively well developed (Hill and Wilkinson 2004), and numerous detailed ecological studies have used similar methods in their data collection (Marshall and Baird 2000; Fox et al. 2003; Pratchett et al. 2011). Almost all of these methods, however, are based on horizontal linear or planar views, and the most commonly reported metric of reef health is coral cover (Wilkinson 2008; Vroom 2011). At present, the limitations of planar or linear views in coral reef studies are poorly understood. Given the fine scale, 3-dimensional structural complexity of corals, coral reefs represent an ideal model ecosystem to consider the effects of reduced dimensionality in sampling methods, and as such they are the primary focus of this study.

2.2 Potential problems with planar views

The use of planar views while studying and monitoring ecosystems has the potential to create problems falling into several general categories. The first problem is the development of a ‘methodological inertia’. The widespread and historical use of planar sampling techniques (e.g. Canfield 1941; Mcintyre 1953; Dayton 1971), like blinders on a horse, set a course for future studies to use similar methods. The simplicity of data collection and interpretation from planar views has exacerbated this problem. Such simple methods can easily be transposed between ecosystems (Schmid 1965; Gehlbach 1975; O’Neill et al. 1991) and in some cases the ecological or structural differences between these ecosystems may have been overlooked. Modern technologies such as still and video cameras, and even aerial and satellite surveys

(Seefeldt and Booth 2006; Booth et al. 2008; Dumas et al. 2009) have increased the amount of field data that can be collected, however, these images are almost exclusively planar. While the areas sampled may be bigger, the methods are essentially the same.

A second problem is that collecting 3-dimensional data is challenging. This is particularly the case where rapid and repeatable observations are needed, as per most monitoring programmes. Manual collection of 3 dimensional data is impractical. The use of stereoscopic images (Done 1981; Korpela 2004; Wakeford et al. 2008) and other recent developments allow some level of 3-dimensional sampling (Bythell et al. 2001; Harding and Carabajal 2005) but most of these technologies are not widely used in large-scale studies due to the complexity of data collection and analysis. As such, 3-dimensional ecosystems are most commonly monitored in 1- or 2-dimensions.

Potentially the biggest problem with planar views is that the vertical component of ecosystems is often lost during periods of ecological change. By overlooking the vertical relief of ecosystems no data on structural complexity can be derived. However, structural complexity is of considerable importance in facilitating the development of high biodiversity and resilience. A highly complex ecosystem provides cover for prey (Bartholomew et al. 2000; Grabowski 2004), allows predators to find effective ambush sites (Savino and Stein 1989), and increases environmental niches, reducing the severity of physical stresses (Kohn and Leviten 1976; O'Connor 1991). Furthermore, for coral reefs and rainforests alike, one of the most serious post-disturbance effects is the loss of structural complexity associated with the collapse of the biogenic habitat (Watling and Norse 1998; Laurance et al. 2002; Graham et al. 2006). Standard planar or linear views of ecosystems do not provide information on this property, thus their utility in documenting and understanding the effects of disturbance is limited.

2.3 The canopy effect

Autotrophs' need for light has led to the recurring development of large canopy shaped growth forms to both overtop competitors and increase the surface area exposed to light. These structures almost invariably become biogenic habitats themselves. Using planar or linear views to sample any of these habitats can cause a bias in sampling, in terms of a 'canopy effect'. Perhaps the best conceptual example of this would be from tropical rainforests. While planar views from aerial or satellite imaging provide useful information on the areas covered by these ecosystems, little data is provided on any organisms below the upper canopy as they are hidden beneath it. This effect is not, however, constrained to rainforests. In fact, if any observed substrate has 3-dimensional structure it is likely that the upper layers will obscure those below them. This effect is more acute if the upper layers occupy more horizontal space at elevation than they do beneath (i.e. form a canopy). Canopy effects, therefore, can potentially occur at any scale from microscopic samples in a Petri dish to satellite imaging of entire forest ecosystems.

In comparison to rainforests, coral reefs could be especially prone to canopy effects. Their relatively small vertical elevations mean that, unlike rainforests, we cannot easily observe the ecosystem from within, and as such the layered structure is easier to overlook. Furthermore, pronounced canopies, and the logistical challenges associated with accessing them accentuate this problem. As such, in this study we use data collected from coral reefs to explore and quantify the canopy effect with an emphasis on potential implications in monitoring disturbances.

2.4 Coral reefs and the 'canopy effect'

While it might be presumed that coral reefs are coral dominated, this is rarely the case (Vroom et al. 2006; Vroom 2011). Coral reefs are, of course, defined by the presence of scleractinian corals, but at present they rarely represent the primary benthic cover of these habitats. A meta-analysis revealed that the mean scleractinian coral cover on coral reefs from 88

locations worldwide was 25.9 ± 1.5 % (mean ± S.E.; data from: Wilkinson 2008; Australian Institute of Marine Science 2011). As the methods used to collect these data are entirely based upon linear or planar views, from reefs likely to be dominated by canopy-forming species, but without considering a canopy effect, the actual benthic cover of corals is likely to be much lower. Bare space is, however, almost non-existent on most reefs (Birrell et al. 2008; Braun et al. 2009; Vroom and Braun 2010) and, as such, the remaining three quarters of the benthos of coral reefs is relatively poorly understood (cf. Wilson et al. 2003; Vroom et al. 2006; Vroom 2011).

Although corals are arguably the most important organisms on coral reefs, especially in terms of growth and accretion, numerous other benthic organisms play measurable ecological roles on reefs (Jackson and Buss 1975; Moberg and Folke 1999; Diaz and Rützler 2001). Calcareous and filamentous algal turfs, for example, are ubiquitous components of coral reef flora, potentially occupying more of the reef than corals (Birrell et al. 2008; Vroom and Braun 2010; Vroom 2011). Calcareous turfs aid reef calcification (Heyward and Negri 1999; Perry et al. 2008; Diaz-Pulido et al. 2009), while filamentous turfs create an epilithic algal matrix (EAM) containing sediments, detritus and infaunal organisms (Wilson and Bellwood 1997), which can reduce the settlement and survivorship of coral larvae (Diaz-Pulido and McCook 2002; Birrell et al. 2008) and reduce the palatability of turfs to herbivores (Bellwood and Fulton 2008). The effects of algal turfs are becoming more apparent, yet their actual benthic cover on coral reefs is essentially unknown; we will provide a preliminary estimation of the benthic cover of algal turfs on coral reefs.

Coral reefs are not uniform. Scleractinian corals are phylogenetically and morphologically diverse and different growth forms often dominate different habitats. Exposed reef crests are often dominated by fast growing branching and tabulate corals (e.g. *Acropora* spp.), which form extensive canopies. More sheltered reefs can be dominated by slow growing massive colonies (e.g. *Porites* spp.), which, with mound shaped morphologies offer little canopy

cover. If canopy effects have measurable consequences they should be more pronounced on reefs dominated by branching and tabulate corals than those dominated by massive corals.

2.5 Methods

We applied three 20m linear transects along the same course: firstly, a planar point intercept transect (hereafter: planar transect) recording the apparent benthic cover visible from above (as would be seen in a photographic image of the reef) at 101 points 20cm apart, secondly a benthic point intercept transect (hereafter: benthic transect), identical to the planar transect except that the actual benthic cover of the consolidated reef matrix (i.e. the benthic cover beneath any overhangs or canopies) was recorded. A comparison of the first two methods highlights the magnitude of any canopy effect on that reef. Finally a chain intercept transect (hereafter: chain transect), which conforms to the benthos below the initial tapes provided both a measure of the vertical relief (rugosity; see McCormick 1994; Wilson et al. 2007b) and the benthic cover across both horizontal and vertical axes (Figure 2.1). These methods were employed on healthy *Acropora*- and *Porites*-dominated reefs (10 replicates at each reef) around Lizard Island on the northern Great Barrier Reef (Figure 2.2) to provide a basis on which to illustrate the canopy effect.

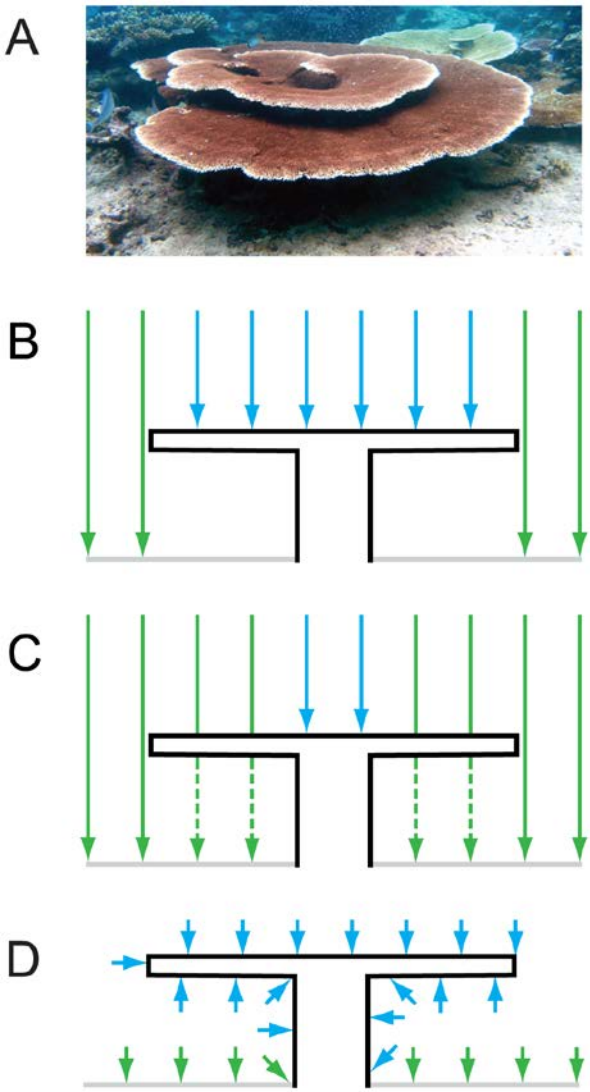

Figure 2.1 Sampling methods for estimating benthic cover of canopy-forming corals (**A**) A typical colony of *Acropora hyacinthus* on reefs at Lizard Island. (**B**), A schematic figure demonstrating intercepts (vertical lines; blue = coral, green = other benthos) on a planar transect, coral cover = 60%. (**C**), A schematic figure demonstrating benthic transects, here the dotted vertical lines indicate measurements made beneath the canopy; here coral cover = 20%. (**D**), A schematic figure demonstrating the chain transects, where lines indicate that measurements were made at set distances along a line that conforms to the outline of the coral; here coral cover = 68%.

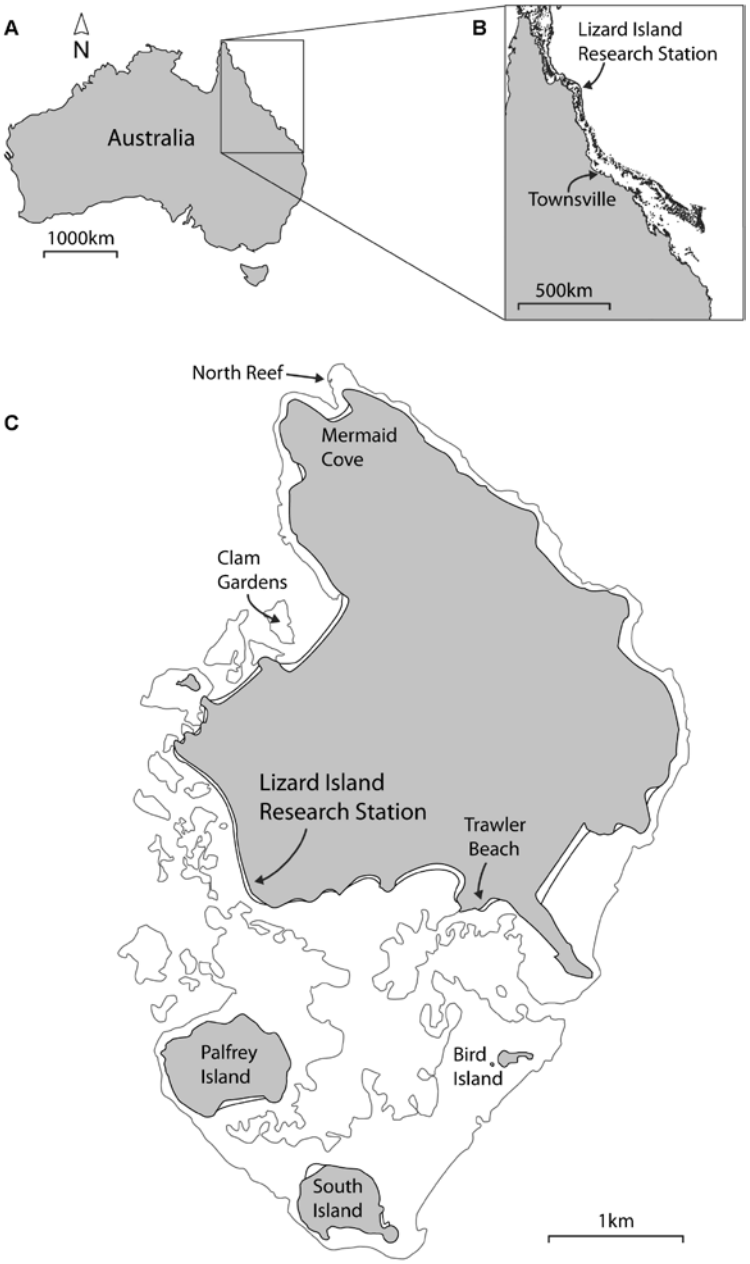

Figure 2.2 Site map of Lizard Island, on the Northern Great Barrier Reef, Australia. (**A**) Australia and (**B**) the relative position of Lizard Island. (**C**) All benthic censuses in this chapter and all field work in this thesis was conducted at Lizard Island Research Station. *Acropora* dominated reefs were at North Reef and between South and Palfrey Islands, *Porites* dominated reefs were at Clam Gardens and Trawler Beach.

2.6 The 'canopy effect' hides algae on coral reefs

Regardless of reef type or site, several patterns became apparent when the sampling methods were compared. Most striking is that, using standard planar transects, all reefs showed coral as the dominant benthic component (25.9±2.1% to 54.4±4.9%; mean ± S.E.) and algal turf (EAM) cover as the second most abundant (21.4±1.7% to 34.9±2.7%). Yet when considering cover beneath the canopy (using the benthic transects) a marked change can be seen on the *Acropora*-dominated reefs. The coral cover dropped by almost half from 53.5±2.6% planar cover to 27.7±2.3% in benthic cover. Concurrently, the cover of turf algae (EAM) increased by more than two thirds (from 26.7±2.6% to 44.7± 2.6%) becoming the dominant benthic cover on the reefs (Figure 2.3). The canopy effect essentially hides this portion of the benthos from planar views, and as such, it is overlooked in standard monitoring practices.

Surprisingly, the chain transects, which provide an indication of vertical relief and the surface area of each benthic component, did not provide greatly differing results of coral cover from the planar point intercept transects (coral cover from 29.1±1.5% to 49.0±3.9%). The 'double counting' of canopies increases the proportion of coral cover, much as the canopy effect artificially increases the proportion of the benthos seen to be canopies. While coral cover showed similar results between methods, some benthic components, such as calcareous algae, which tended to grow on vertical surfaces, showed significant differences between the benthic and chain transects (on average, chain transects provided estimates of calcareous algal cover 96.4±21.0% higher than planar transects; Figure 2.4).

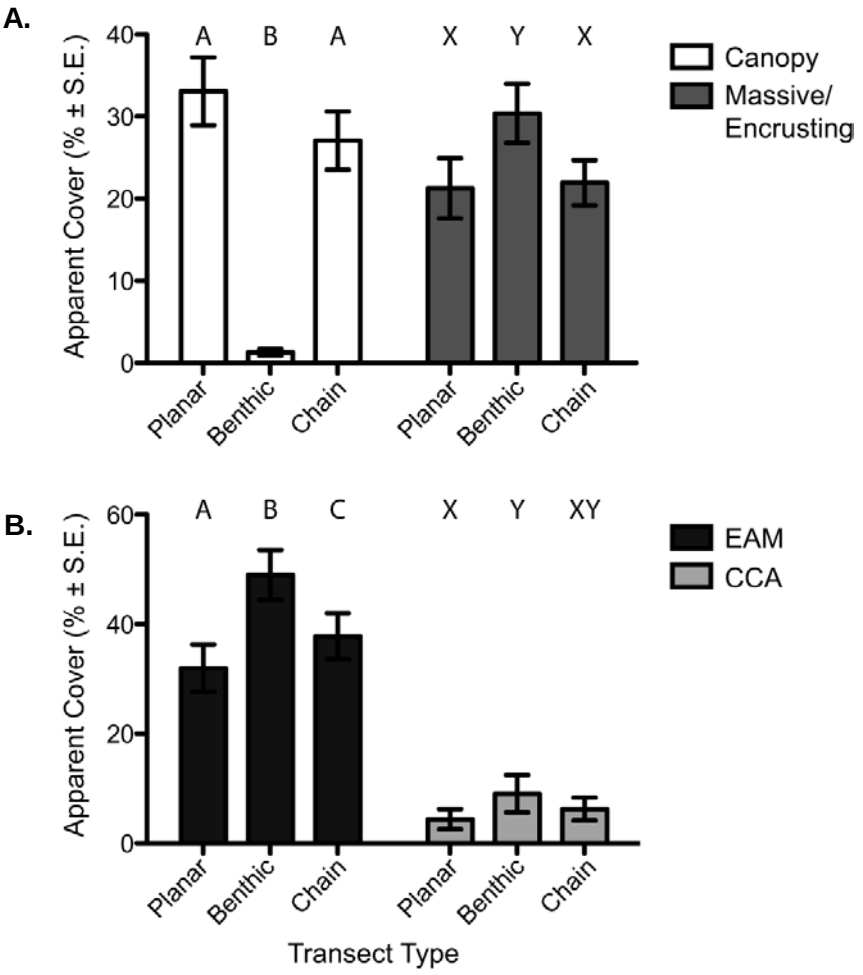

Figure 2.3 Benthic cover of algae and corals using three transect methods on an *Acropora*-dominated reef. (**A**) The estimated cover of corals on an *Acropora* dominated reef using the three different transect types; canopy forming taxa in white and benthic cover species in dark grey. (**B**) The estimated cover of algae on the same transects; black bars represent cover of epilithic algal matrix (EAM) and light grey, crustose coralline algae (CCA). A, B, C and X, Y, Z denote statistically different groupings (Repeated Measures ANOVA with Tukey Kramer post-hoc test, $\alpha = 0.05$).

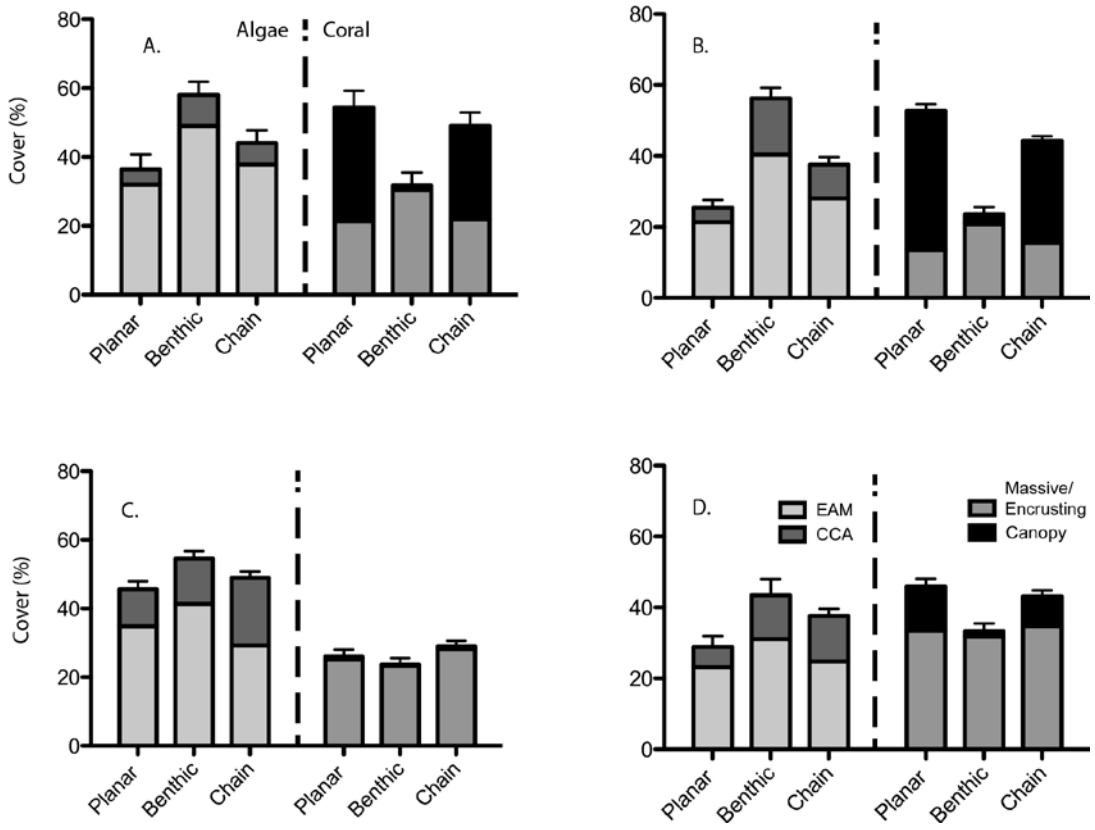

Figure 2.4 Results of the three transect types from four reefs around Lizard Island. (**A**) represents Mermaid Cove and (**B**) South-Palfrey, two *Acropora*-dominated reefs. (**C**) represents Clam Gardens and (**D**) Trawler Beach, two *Porites*-dominated reefs. The left hand portion of the graphs shows the algae recorded using the three methods (light grey = epilithic algal matrix, dark grey = crustose coralline algae). The right hand portion of the graphs shows the results for corals (mid-grey = massive and encrusting colonies, black = canopy-forming species). Notice the consistent decreases in canopy forming corals and subsequent algal increases (especially EAMs) with the benthic point intercept transect.

2.7 Calcification and the canopy effect

Different colony morphologies of corals provide very different functions on reefs. The planar methods used in most monitoring programmes provide only a limited ability to distinguish these functions. For example, the fast growth and high contribution to coral cover of canopy-forming corals are not necessarily related to the amount of carbonate they deposit on consolidated reef structures. Most canopy-forming species have low density, perforate branches that are easily removed by corallivores (Cole et al. 2008; Hoey and Bellwood 2008; Bellwood and Choat 2011) and hydrodynamic forces (Madin and Connolly 2006), with much of the carbonate being lost from the reef matrix. As such, with the possible exception of the dense stems of these colonies (Hughes 1987), canopy-forming corals provide a relatively small contribution to reef calcification yet they conceal massive corals and crustose coralline algae that deposit carbonate directly onto the reef matrix. High coral cover, therefore, does not mean high accretion rates (Vroom 2011). Furthermore, additions to reef carbonates as a result of rubble formation by high cover of canopy-forming corals (e.g. Perry and Smithers 2006) could be ecologically deleterious as the mobile substrate produced in this process can hinder recruitment of corals and subsequent reef recovery (Rasser and Riegl 2002; Fox et al. 2003; Wilson et al. 2006).

2.8 Disturbances and the canopy effect

The canopy effect, as demonstrated above, influences what we monitor on coral reefs. The overlooked understory has a markedly different composition to the canopy. If reefs were stable, this would result solely in a gap in our ecological understanding of reefs. However, reefs and other ecosystems are most often monitored to observe changes in ecosystem composition brought about by disturbances. The canopy effect is likely to play an important role in our ability to monitor the effects of, and recovery from these disturbances. This may be particularly important if there are differences in the way in which canopy and non-canopy components of the reef respond to disturbances.

2.9 Differential susceptibility and disturbances

Differences between coral colonies are more than morphological. Branching and tabulate taxa such as acroporids, which form the majority of the canopies studied herein, are also the most susceptible to environmental and physical disturbances (Hughes and Connell 1999; Linares et al. 2011). They are among the first corals to bleach under environmental stresses (Marshall and Baird 2000), often suffering considerable mortality (Baird and Marshall 2002). Physical disturbances also readily dislodge these colonies from the benthos (Madin and Connolly 2006) and many coral predators preferentially target these taxa (Cole et al. 2008; Brooker et al. 2010; Pratchett 2010). Massive colonies such as *Porites*, in contrast, are more tolerant to disturbances, being more hydrodynamically stable (Madin and Connolly 2006). They also bleach less readily (Baird & Marshall 2002), and are a less favoured prey of corallivores (e.g. Cole et al. 2008).

In almost all cases, canopy-forming corals are most severely affected following disturbances on coral reefs (Baird and Marshall 2002; Madin and Connolly 2006) and if the colony's skeleton is left intact following the disturbance they are quickly removed from the reef by biological and physical erosion (Bellwood et al. 2003; Mallela and Perry 2007; Madin et al. 2008). The increased susceptibility of coral canopies to disturbances may, therefore, create a bias when monitoring the effects of disturbance on coral reefs.

2.10 Canopy loss and coral cover

A simple conceptual model was created using the transect data to assess the magnitude of the canopy effect on *Acropora*-dominated reefs. The high susceptibility of canopy-forming corals to disturbances often results in extensive loss of these corals from reefs (Baird and Marshall 2002; Wilson et al. 2006; Pratchett et al. 2011). The model replicates this effect. The start point was set as the mean planar cover of algae and corals found on the two *Acropora*-dominated reefs in this study, using the planar transects. The cover of canopy-forming corals is

then reduced by 10% each generation for 62 generations (until canopy cover < 0.05%) to simulate a disturbance. Using the inverse of canopy cover and the data from the benthic transects, the apparent change in benthic cover is simulated. The cover of concealed benthic components (end point of the model) was based on the results of the benthic transects (Figure 2.5). A similar model was created using data from the *Porites*-dominated reefs.

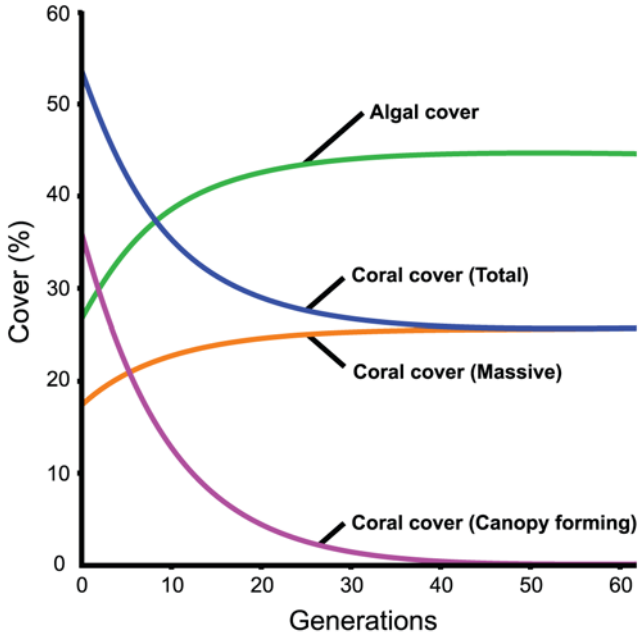

Figure 2.5 Conceptual model demonstrating the effect of canopy removal on an *Acropora*-dominated reef. Note the apparent increase in both algae (EAM) and massive corals simply as a result of the loss of the canopy. Start points are based on data collected using planar transects. Canopy-forming cover is reduced by 10% each generation. End points are based on data collected using benthic transects (with no remaining canopy).

As would be expected, on *Porites*-dominated reefs a total loss of canopy-forming corals causes relatively little change (Figure 2.6). Overtopping is rare on these reefs, as the colonies of massive corals are too large. The only effects seen with the loss of canopy-forming corals is an equivalent reduction of overall coral cover and similar apparent increase of EAM cover.

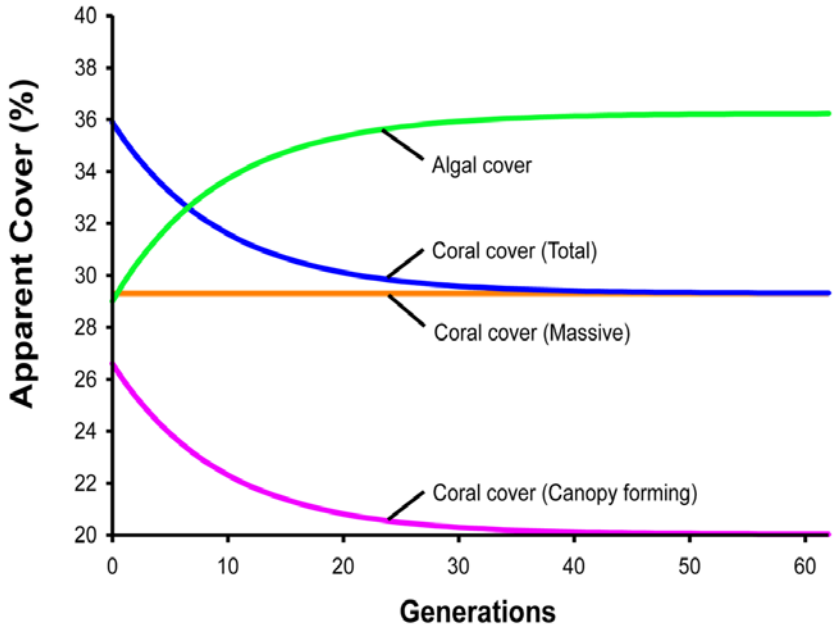

Figure 2.6 Conceptual model demonstrating the effect of canopy removal on a *Porites*-dominated reef. Start points are based on planar transect data. Canopy cover is reduced 10% each generation. End points are based on benthic transect data (with no remaining canopy). The 'loss' of canopy cover (difference between planar transects and benthic transects) was almost identical to the apparent increase in benthic algae (6.58% loss vs. 7.23% increase respectively).

In contrast, the effect on *Acropora*-dominated reefs is much greater (Figure 2.3). As canopy-forming corals are competitively dominant on these reefs, predominantly by overtopping other corals, there is a pronounced canopy effect. The loss of canopy-forming species most obviously reduces overall coral cover. However, an apparent 8.2% increase in the cover of massive corals was recorded. This increase indicates that almost a quarter of the space beneath coral canopies was occupied by massive coral colonies. The reported increase in massive coral cover is, therefore, an artefact of using sampling methods based on horizontal planar views in an ecosystem with pronounced canopy effects. However, there are further implications. The recorded loss of coral cover associated with the loss of the canopy is effectively cushioned as the massive colonies are revealed. As coral cover is among the most commonly reported metrics of reef health, the impacts of disturbances may, therefore, be under-reported using planar monitoring methods.

That coral cover provides a somewhat unrealistic measure of the effects of disturbances is not necessarily always this misleading, as most monitoring programmes record far more data than just coral cover. Although there is a clear trade-off between precision and spatio-temporal resolution, almost all coral monitoring programmes include at least some form of categorisation of the corals observed. Nevertheless, coral cover remains the most widespread metric for communicating reef health. Unfortunately, changing coral cover does not reveal the underlying mechanisms (e.g. recruitment limitation and/or adult mortality), nor can it identify the causes of disturbances. Furthermore, coral cover probably underestimates the magnitude of coral loss and the prevalence of other benthic components. There is the potential, therefore, that researchers may be led astray by just using planar data on reefs and in other 3-dimensional systems.

2.11 Canopy loss and algal cover

The removal of a canopy reveals the other benthic components, which on many reefs, including those selected for this case study, are primarily algal turfs (EAMs). Simulated removal of the canopy from *Acropora*-dominated reefs resulted in a 67% increase in cover of

EAMs (Figure 2.3). While phase-shifts to algal dominated states are among the most reported effects following disturbances on coral reefs (Hughes 1994; Diaz-Pulido et al. 2009; Norström et al. 2009) our results suggest that in some cases, apparent shifts could simply be due to the canopy effect, with the removal of the coral canopy unveiling a pre-existing algal-dominated state (e.g. Mumby 2009; Vroom 2011). No further ecological succession to an alternate stable ecosystem would be necessary to create an apparent phase-shift to EAMs (turfs) following the loss of these canopy-forming species. Furthermore, exposure of this EAM could possibly trigger an expansion of macroalgae (see Hughes 1994; Nyström et al. 2000; Bellwood et al. 2004; Norström et al. 2009).

As discussed above, high benthic cover of EAMs has both positive and negative implications for coral reefs. Algal turfs in the EAM provide settlement cues for a variety of organisms including corals (Diaz-Pulido et al. 2010), and a habitat for infaunal detritivores, which provide a trophic pathway to recycle energy from the detritus (see Depczynski and Bellwood 2003; Wilson et al. 2003). Furthermore, well-grazed EAMs indicate high levels of herbivory by reef fish or invertebrates (see Bellwood et al. 2004). However, it is likely that a disturbance that removes a high percentage of branching corals is likely to involve multiple synergistic stressors (e.g. Wilson et al. 2006; Graham et al. 2011). Stressors that affect coral cover may have markedly different effects on the other benthic ecosystem components. The EAM, for example, is considerably more resilient than corals to most environmental perturbations (Hay 1981; Steneck and Dethier 1994; Diaz-Pulido and McCook 2002). Indeed, increased temperatures, sediment and nutrients; all stressors to corals, can be beneficial to the algal component of the EAM (Diaz-Pulido et al. 2007). Furthermore EAMs are tolerant of high sediment loads (Airoldi and Virgilio 1998; Birrell et al. 2008) and their complex structure slows surface flow and increases sediment deposition (Kendrick 1991; Carpenter and Williams 1993). Sediment loaded turfs inhibit the settlement of coral larvae (Birrell et al. 2008) and deter herbivores on coral reefs (Bellwood and Fulton 2008). The effects of multiple synergistic stressors might, therefore, increase the damage done to reefs not just in terms of the amount of

coral damaged but in reducing the recovery potential of reefs, even from an apparently pre-existing algal dominated state.

2.12 Which sampling method is best?

Each of the methods used in this study have benefits and drawbacks, which are important to consider before designing any study. Planar transects, for example, provide a focussed assessment of more susceptible, canopy-forming species (e.g. *Acropora* spp.). As such, planar transects allow rapid detection of disturbances, such as temperature anomalies, which will provoke stress responses (e.g. bleaching) or localised mortality of canopy-forming species (Hughes and Connell 1999; Marshall and Baird 2000; Linares et al. 2011). Furthermore, planar transects are quick and easy to complete, allowing high replication at any site. Underwater video and photographs can also be used to collect planar data even by inexperienced observers, with minimal training. However, the present study has revealed several drawbacks with this method. Apparent coral loss following major disturbances might be cushioned as less susceptible benthic corals are revealed. Also, by revealing pre-existing benthic communities, canopy loss could lead to misleading reports of phase-shifts with apparent increases in the cover of algae and massive corals (the changes are relative not actual). This method is excellent for studies of tabulate corals but has serious limitations for other benthic components.

Benthic transects provide useful information on the consolidated reef matrix, which has rarely been the focus of previous studies. This substrate is the ‘solid’ structure underlying the veneer of living corals. Calcification and accretion of the reef matrix allows reefs to maintain their depth with increases in sea-level (Blanchon and Shaw 1995), furthermore, the consolidated reef matrix is often entirely occupied by algae and other benthic organisms, which are often overlooked using planar methods (Birrell et al. 2008; Braun et al. 2009; Vroom and Braun 2010). This sampling method also benefits from being relatively straightforward, although video or photographic transects are probably not possible. Unfortunately, benthic transects provide little information on canopy forming species, and as such, are insensitive to the effects of

common disturbances (Hay 1981; Steneck and Dethier 1994; Marshall and Baird 2000; Diaz-Pulido and McCook 2002). Benthic transects, therefore, provide an accurate picture of reef composition in terms of the area of substratum occupied. Relatively insensitive to changes in canopy forming species, they more accurately portray the role of algae and other benthic organisms on the reef surface.

The chain transects might appear to provide a more balanced approach to benthic sampling as they concurrently assess both the canopy and benthos. In fact, from the perspective of a fish or settling coral planula, which rely on reef surface area for feeding or settlement respectively, it is perhaps the most relevant measure of reef cover. Furthermore, this is the only method, which includes 3-dimensions. However, for some ecological surveys, the double counting of canopies (i.e. including both the upper and lower surfaces) artificially increases the importance of canopy forming corals. Changes in coral cover of the sensitive, canopy-forming species is thus at risk of being over-reported after disturbances. Massive coral colonies, for example, contribute directly to calcification of the reef matrix but due to their low surface area their loss would not be reported to be as important as high surface area, but structurally delicate, canopy forming corals. The main disadvantage with chain transects is, however, logistical. The complexity of the methods means that replication at any site will suffer and less area will be surveyed. Furthermore, the sampling would rely on experienced observers and becomes much more challenging in adverse conditions (a fact to which the authors can attest).

It appears that a combination of survey methods may be most appropriate. For example, stratified sampling using planar and benthic transects together would allow some increased dimensionality with minimal extra effort. Furthermore the problems of the canopy effect could be overcome, as the cover beneath canopies is recorded and therefore can be included as a correction factor if any changes in canopy cover are observed. It must, however, be highlighted that this study is far from comprehensive and a great many more sampling methods currently exist (cf. Hill and Wilkinson 2004). Furthermore, new ecological studies will obviously demand the development of new sampling methods. Similarly, sampling in other ecosystems will require

different considerations. There is no simple answer to the question, “which sampling method is best?” The most important messages, highlighted by this study are 1) that it is important to match the census technique to the question and, 2) that it is of vital importance to critically evaluate what any method is actually estimating. The greatest danger is following methodological inertia, choosing methods simply because they have been used before.

2.13 Conclusions

The canopy effect has the potential to be pervasive in ecological survey techniques across ecosystems. It is most prevalent in systems dominated by canopy-forming autotrophs as in tropical forests and on coral reefs. The canopy effect, however, is particularly relevant for coral reefs where massive changes are predicted around the world. While planar transects are logistically practical and have a long history of use we must be careful to consider the hidden portions of the benthos, which have the potential to alter our interpretations of the status of ecosystems and how they respond to ever more frequent disturbances. The understories of reefs are not ecologically irrelevant, with diverse algal and coral communities, which, when compared to the canopies, have different susceptibilities and responses to disturbances. Therefore, the current ‘coral-centric’ view of coral reefs, which are often not numerically dominated by corals, might be misleading. A reliance on planar assessments of coral cover as a proxy for reef health should be reassessed. By looking at both planar and benthic cover we can begin to move beyond simple cover estimates to understand the processes that shape benthic configurations and better understand the impacts of the more frequent and severe disturbances that coral reefs are likely to suffer.

Chapter 3.1: Sediment suppresses herbivory across a coral reef depth gradient

Published in *Biology Letters* 8: 1016-1018 (Appendix 3.1.1)

3.1.1 Introduction

Sediments are a ubiquitous feature of coral reefs. Calcification by benthic organisms produces the carbonate reef matrix, which is then reduced to sediment by biological and physical erosion (Hutchings 1986; Scoffin 1992). While most of this sediment is transported off reefs (Bellwood 1995a; Kench 1998; Goatley and Bellwood 2010; Chapter 5), some remains trapped within the epilithic algal matrix (EAM; Wilson and Bellwood 1997). This composite of algal turfs, detritus, infauna and sediments is common to all reefs and is often the most common benthic component (Wismer et al. 2009; Goatley and Bellwood 2011; Vroom 2011; Chapter 2). While sediments provide an important function in reef accretion, infilling crevices and cementing the reef framework (Perry et al. 2012), recent evidence suggests that EAM-bound sediments suppress herbivory; a vital ecological function on coral reefs (Bellwood and Fulton 2008).

Coral reefs rely on a suite of ecological functions to maintain their resilience to disturbances. Among the most important functions is herbivory, provided mainly by herbivorous reef fishes. These fishes maintain algae as well cropped turfs and help in the prevention of, or recovery from, phase-shifts to macroalgal-dominated states (Bellwood et al. 2004; Hughes et al. 2007). Reduced herbivory due to overfishing, is well documented as a driver of macroalgal phase-shifts (Hughes et al. 2007; Mumby and Steneck 2008). However, it appears herbivory is also suppressed by sediments (Choat 1991; Bellwood and Fulton 2008), although the extent of this interaction is poorly understood. Currently our knowledge of the ecological impacts of sediments on herbivory is limited to just one reef zone; the reef flat, where

sediment loads are highest (Purcell and Bellwood 2001), and corals and herbivores least abundant (Hay et al. 1983; Fox and Bellwood 2007). Little is known about how sediments affect herbivory in other reef zones.

Typical coral reefs have a distinct base, slope, crest and flat (Figure 3.1.1a; Purcell & Bellwood 2001). The reef crest is normally the zone of highest wave action, accretion, productivity and herbivore activity (Steneck 1988; Fox and Bellwood 2007). While the reef crest is one of the most dynamic, and arguably, most important reef zones in terms of resistance and resilience to the effects of disturbances (Steneck 1988), little is known of the effects of sediment in this zone. From a physical perspective, the high hydrodynamic activity on the reef crest should keep benthic sediments low (Purcell and Bellwood 2001), however, sediment loads can change rapidly with natural or anthropogenic disturbances (Kench 1998; Esslemont et al. 2004) and, as such, have the potential to affect herbivory. Here we aim to assess sediment suppression of herbivory across a coral reef depth gradient including the reef base, crest and flat.

3.1.2 Methods

Experimental manipulations were conducted across a 300 m section of exposed reef, off Lizard Island in the northern Great Barrier Reef, Australia. Three reef zones were selected for comparisons: the reef flat, crest and base (Figure 3.1.1a). The reef flat at the study site has low complexity, few corals, a depth of 1-3 m, and is sheltered from breaking waves by the reef crest. The crest is 3-6 m deep, has the highest topographic complexity and relatively abundant corals, predominantly *Acropora* and *Pocillopora*. At the reef base, manipulations were conducted on the consolidated reef matrix just above the transition to sand at 12-15 m.

In each reef zone, twenty sediment samples were collected as a baseline, by haphazardly placing a 5.8×10^{-3} m^2 PVC ring on the EAM and collecting the enclosed sediment using an electric vacuum sampler (Purcell and Bellwood 2001).

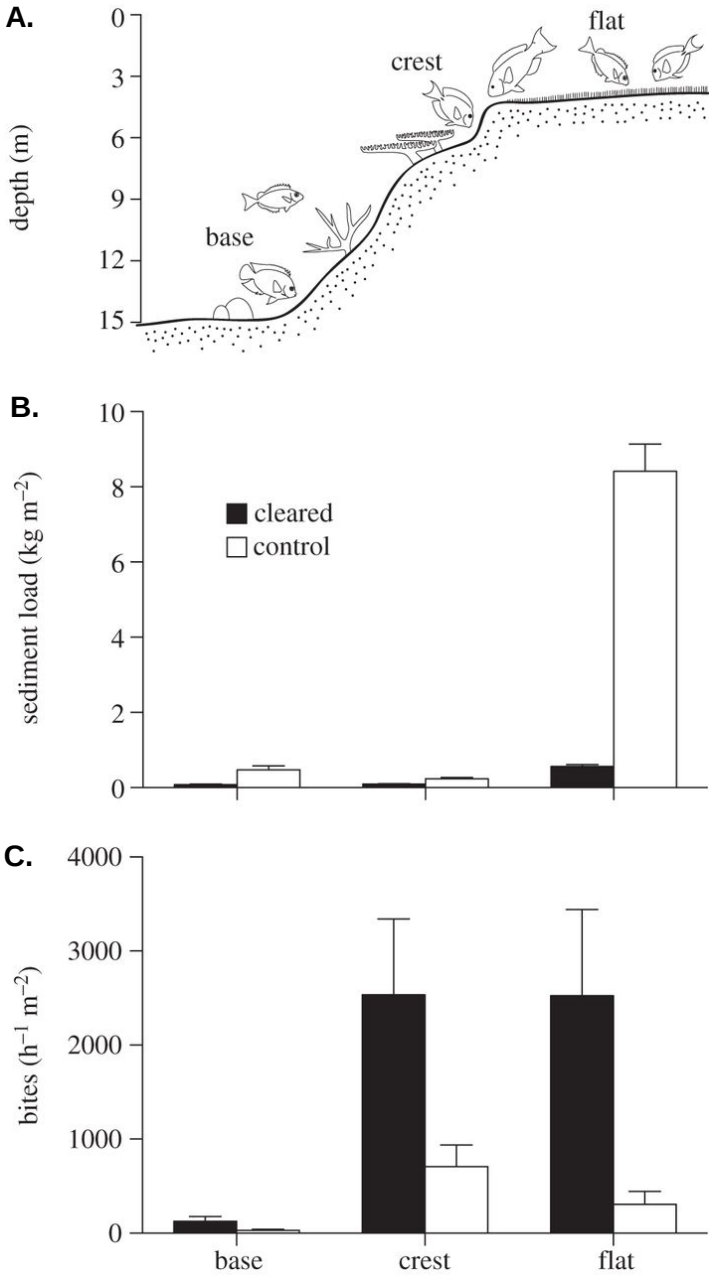

Figure 3.1.1 Reef profile and sediment loads before and after sediment reduction (**A**) A reef cross-section showing the location and depth of the zones used in this study. (**B**) Mean sediment loads (± S. E.) in the EAM before (white) and after (black) sediment reduction (n = 20 before and 10 after). (**C**) Mean number of bites (± S. E.) in cleared and control plots (black and white bars respectively) standardised to bites h^{-1} m^{-2}.

Manipulations were conducted by delineating haphazardly selected areas of EAM using a 1.5m x 1.5m PVC frame. Half of the frame was kept as a control plot and was covered in clear plastic sheeting to ensure that no sediment was disturbed. The other half was cleared of sediment using an airlift and compressed air gun (Bellwood and Fulton 2008). Benthic sediment loads in manipulated plots were reduced by 79.1 ± 9.4% (tested using the vacuum sampler as above; Figure 3.1.1b). Following sediment removal, a video camera was mounted on a tripod so that both the treatment and control plots were in view. The PVC frame was removed after 30 s of recording to allow initial calibration of the videos. The camera was left recording for at least 4 hours 30 minutes. Videos were viewed on a computer with the plots marked on an overlaid transparent film. Bites by herbivores (parrotfishes [scarine labrids], rabbitfishes [Siganidae], and surgeonfishes [Acanthuridae, and the detritivorous *Ctenochaetus*]) in both cleared and control plots were counted in the first 15 minutes of each hour, resulting in 1 hour of data per replicate. Subsampling in this manner was the most efficient means to collect sufficient data without temporally biasing the data. Due to logistical constraints the sampling was unbalanced between reef zones: 8, 5, and 6 replicate videos were recorded on the base, crest and flat, respectively. Overall bite rate data and the impact of individual taxa were analysed using analyses of variances (ANOVAs; Type II S.S. due to the unbalanced design; Langsrud 2003), fourth-root transformations were applied to ensure assumptions were met. All data are presented as means ± standard error throughout.

3.1.3 Results and Discussion

A total of 32,477 bites by herbivorous reef fishes were observed. Of these, 26,838 (82.6%) were in cleared plots (Figures 3.1.1c & 3.1.2). Sediment reductions resulted in higher herbivore feeding rates in all families in all three zones ($F_{1,108} = 5.2$, $p = 0.03$), although the extent of responses among reef zones differed (Figure 3.1.1; $F_{2,108} = 13.4$, $p < 0.0001$). We document a general response of increasing herbivory following sediment reduction across all

reef zones, which extends beyond previous observations in high sediment locations (where sediment loads are over 8 kg m^{-2}; Figure 3.1.1b, also see Bellwood and Fulton 2008).

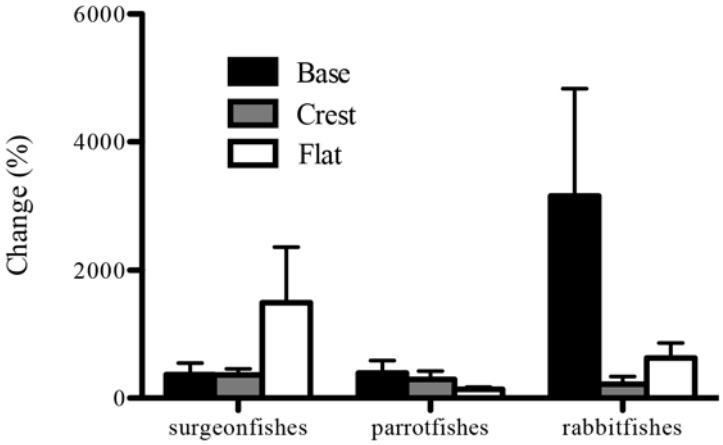

Figure 3.1.2 Relative responses of taxa to sediment reductions. Data are shown as mean percent differences in bites taken in cleared and adjacent control plots. Data were transformed (n + 1) to correct for issues with dividing by zero.

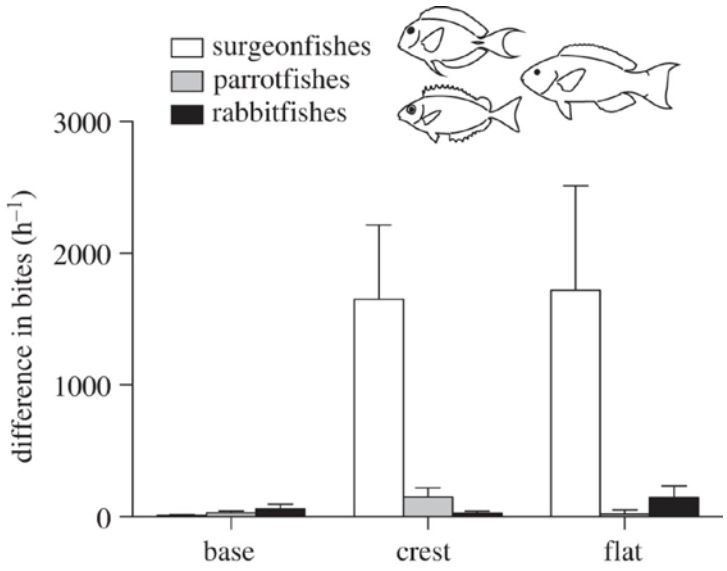

Figure 3.1.3 Mean additional bites by herbivorous reef fishes in cleared plots relative to adjacent control plots (± S. E.) for the three main fish taxa across the depth gradient: surgeonfishes (white), parrotfishes (grey) and rabbitfishes (black).

The effect of sediment removal on the reef crest is particularly surprising, as the crest sediment loads were the lowest detected in any reef zone, with only 237.8 ± 3.2 g m^{-2}; i.e. 35 times less than the reef flat (Figure 3.1.1b). It is well known that reef crests have the highest herbivore abundances and highest rates of herbivory (Hay et al. 1983; Steneck 1988; Fox and Bellwood 2007), explaining the high bite rates in the control plots. However, what was particularly striking was that a sediment reduction of less than 150 g m^{-2} on the crest had a comparable effect on herbivores as a reduction of over 7800 g m^{-2} on the flat. It appears that fishes may be far more sensitive to sediments on reefs than previously thought. Even small changes in sediment loads may therefore, fundamentally alter vital ecological processes on coral reefs.

When considering specific taxa, the surgeonfishes were responsible for the largest number of bites, taking 82.8% of all bites observed. The disparity in bites compared to the other taxa does not correspond with a faster bite rate, or higher abundance of surgeonfishes on the reef studied. Both are similar to those of parrotfish in this region (Choat et al. 2004; Goatley and Bellwood 2010; Cheal et al. 2012; Chapter 5). While the proportional response of the surgeonfishes to sediment reduction did not differ from the other taxa (Figure 3.1.2), the high number of bites by this taxon led to a considerable difference in the number of bites taken from cleared plots (Figure 3.1.3; ANOVA interaction: $F_{4,48} = 5.5$, $p = 0.004$; see Table 3.1.1). This probably corresponds with surgeonfishes' known preference of feeding on flat reef surfaces (Choat and Bellwood 1985), similar to those selected for this study. The surgeonfishes, it appears, are of considerable importance as herbivores of EAMs on low complexity surfaces on the crest and flat.

With regards to the other taxa, the parrotfishes showed the largest difference following sediment removal on the crest (Figure 3.1.2) reflecting earlier studies (Bellwood 1995a; Fox and Bellwood 2007), and emphasising the value of low sediment locations for these fishes. Rabbitfishes, in contrast, showed the largest response on the reef flat (notably *Siganus argenteus* and *S. spinus*) and base (predominantly *S. doliatus*) [ESM], reflecting reported

division within the family relating to morphological and behavioural attributes (Borsa et al. 2007).

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

Table 3.1.1: ANOVA (Type II S.S.) results of bite difference data per taxon (Figure 3.1.3). Data are fourth-root transformed.

	S.S.	d.f.	M.S.	*F*	*p*
Zone	11.029	2	5.514	4.417	0.017
Taxon	20.149	2	10.075	8.071	<0.001
Zone x Taxon	21.842	4	5.461	4.374	0.004
Error	59.920	48	1.248		

Chapter 3.2: The role of turtles as coral reef macroherbivores

Published in *PLoS One* 7: e39979 (Appendix 3.2.1)

3.2.1 Introduction

Herbivory is widely recognised as a vital process for the health and resilience of coral reefs (Hughes 1994; Burkepile and Hay 2008, 2010), mediating the competition for benthic space between algae and reef-building corals. When present in sufficient densities, herbivores can maintain algal communities in a cropped state, preventing the proliferation and expansion of macroalgal communities (Hughes et al. 2007; Mumby and Steneck 2008). However, reductions in herbivory through both small-scale experimental exclusions and regional-scale overfishing have demonstrated that, when released from top-down control, algal assemblages can shift from highly productive algal turfs to less productive, late successional stage macroalgae such as *Sargassum* (Hughes 1994; Hunter and Evans 1995; Ledlie et al. 2007; Rasher et al. 2012). As such, herbivores are widely viewed as a key component of the resilience of coral reefs (Bellwood et al. 2004; Nyström 2006). To date, quantitative studies of herbivory on coral reefs have focussed on the roles of fishes and/or urchins (McClanahan and Shafir 1990; Hughes et al. 2007; Hoey and Bellwood 2010). Few studies have considered the role of macroherbivores in coral reef ecosystem processes (Bjorndal and Jackson 2003; Bellwood et al. 2004).

Worldwide, almost all populations of marine macroherbivores have suffered drastic declines. For example, many marine turtle populations have been estimated to be below 10% of their historical baselines (Jackson 1997; Jackson et al. 2001), while estimates of sirenian (dugong and manatee) populations suggest they are less than 3.1% of baselines (Jackson et al. 2001; Marsh et al. 2005). By underestimating the historic anthropogenic impact on populations of sirenians and turtles, both the natural population densities and ecological roles of these

species have, until quite recently, been largely overlooked (Jackson 1997; Jackson et al. 2001; Marsh et al. 2005). At 'baseline' populations, many species of sea turtles may have had important ecological roles structuring their various prey communities (Bjorndal 1997). Hawksbill turtles, *Eretmochelys imbricata*, have been shown to structure sessile invertebrate communities (León and Bjorndal 2002; Obura et al. 2010; Wabnitz et al. 2010), while green turtles, *Chelonia mydas*, appear to have been the primary herbivores of seagrass beds in the Caribbean (Jackson 2001) and may still structure seagrass communities when they are abundant (Fourqurean et al. 2010).

Both green and hawksbill turtles have circumtropical distributions and occupy a range of habitats, including seagrass beds, coral and rocky reefs, and oceanic waters. Green turtles, while often considered to be consumers of seagrass (Thayer et al. 1984), can contain substantial proportions of macroalgae characteristic of reef environments in their stomachs (Forbes 1994; Read and Limpus 2002; Carrión-Cortez et al. 2010; Van Houtan et al. 2010). Reports of herbivory by adult hawksbill turtles are less common. Hawksbill turtles are primarily predators of sponges (Meylan 1988; León and Bjorndal 2002) or other sessile invertebrates (Stampar et al. 2007; Obura et al. 2010), but may also consume small amounts of algal material in some areas (Mayor et al. 1998; Alvarez 2000). In all cases it is not certain if the algae are directly targeted or if they are removed from the benthos or floating algal rafts. Hawksbill and green turtles frequent coral reefs throughout their range but their role as herbivores in these ecosystems remains poorly understood (Bellwood et al. 2004; Wabnitz et al. 2010).

Within coral reef systems herbivores may be broadly categorised into two functional groups (i.e., grazers and browsers) based on the algal material they remove and consequently the roles they perform in reef processes (Steneck 1988; Hoey and Bellwood 2011). Grazers typically feed on algal turfs or epilithic algal matrix (EAM; Wilson and Bellwood 1997) and play an important role in helping reefs to resist shifts to alternate states and reassemble following disturbances (Bellwood et al. 2004; Nyström 2006). In contrast, browsing taxa feed on leathery macroalgae and play a potentially critical role in the reversal of shifts to macroalgal-

dominance on coral reefs (Bellwood et al. 2006; Hoey and Bellwood 2011). On reefs, herbivorous species rarely fulfil both functional roles and there is often little redundancy within functional groups (Bellwood et al. 2004; Hoey and Bellwood 2009). Furthermore, recent studies have shown that many of these fishes have relatively small home ranges (< 10ha; Meyer and Holland 2005; Fox and Bellwood 2011; Marshell et al. 2011; Welsh and Bellwood 2011), suggesting their functional impact may be spatially restricted. The morphological and taxonomic distinctness of turtles might suggest that they could play unique roles on reefs. Using observations taken during experimental habitat manipulations and transplanted macroalgal assays we present evidence to highlight the potential roles of marine turtles as both algal turf grazers and macroalgal browsers in coral reef environments.

3.2.2 Methods

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

This study was conducted on the reefs surrounding Lizard Island (14°40'S 145°28'E), in the northern Great Barrier Reef (GBR; Figure 3.2.1). Two experimental manipulations: sediment reductions of algal turfs and macroalgal assays were performed to assess the ecological roles of coral reef grazers and browsers, respectively. While these experiments were primarily focused on the roles of herbivorous fishes (Hoey and Bellwood 2009), responses by marine turtles were also recorded and are reported herein. The sediment reductions were conducted on the exposed reef flat to the south-east of the island at a depth of 2-4 m, whilst the macroalgal transplants were conducted within six habitats of varying depth and wave exposure: the exposed reef crest (2-4 m depth), exposed reef flat (1-2 m), back reef (2-4 m), patch reef (4-6 m depth), sheltered reef flat (1-2 m) and sheltered reef base (6-8 m; Figure 3.2.1). See (Hoey and Bellwood 2009) for detailed description of habitats.

Figure 3.2.1 Site map, Lizard Island. The filled square represents the location of the sediment removal study, where green turtles (*Chelonia mydas*) were observed feeding. The filled circle to the north represents the sheltered reef base and to the south the back reef. At both sites hawksbill turtles (*Eretmochelys imbricata*) were observed feeding on transplanted *Sargassum* assays.

Sediment reduction

The exposed reef flat was selected as it has a high cover of EAM (Wismer et al. 2009; Hoey and Bellwood 2010) and is adjacent to the area of highest herbivory (i.e. exposed reef crest). The high sediment load of the EAM in this habitat has been proposed to limit grazing by reef fishes (Bellwood and Fulton 2008). Two adjacent 0.75 x 1.5 m plots that were devoid of

living coral and covered by EAM were temporarily delineated using a PVC frame. One of the plots was randomly selected and cleared of sediment using a compressed air powered airlift (hereafter 'cleared plot') while the adjacent plot was left undisturbed (hereafter 'control plot'). Underwater video cameras (Sony DCR-SR100 HDD cameras in Ikelite housings), mounted on tripods, were then deployed for three hours to record the feeding activity of herbivores on the cleared and control plots simultaneously. Filming was continuous for the 3-hour experimental period with the PVC frame and a small scale bar being placed on the focal plane of the EAM in the experimental plots for approximately 10 s allowing calibration of experimental plots and turtle sizes from the video footage. This procedure was repeated until ten replicate plots had been recorded. Replicate plots were separated by at least 10 m.

The lengths of algal turfs within the plots were measured before and after the 3-hour experimental period prior to sediment removal. The heights of 20 randomly selected algal filaments were measured from both the cleared and control plots using the depth probe of vernier callipers. Data were analysed using a two-way fixed factor analysis of variance (ANOVA) treating turf filaments as replicates, followed by residual analysis to ensure assumptions of the test were met.

Macroalgal assays

To quantify browsing intensity across the six habitats a series of macroalgal assays were conducted. *Sargassum swartzii* (Ochrophyta: Phaeophyceae) was collected from an inshore reef in the Turtle Island Group (28 km west of Lizard Island). Similarly sized thalli (mean weight [± S.E.] = 363.6 ± 4.7 g) were transplanted to each of two haphazardly selected sites within each of the six habitats for 8-hours (approx. 07:30–15:30). Adjacent sites within each habitat were separated by a minimum of 50 m. Underwater video cameras (Sony DCR-SR100 HDD camera in Ikelite housing) mounted on concrete blocks were used to record feeding activity on the transplanted *Sargassum* for the 8-h experimental period within each habitat (detailed description in Hoey and Bellwood 2009).

Video Analyses

The video footage from both experimental manipulations was examined and all bites by turtles on the EAM within the cleared and control plots, and the transplanted *S. swartzii* thalli, were recorded. Turtles were identified to species and size (straight carapace length, SCL) was estimated. Throughout this study, results are presented as means ± standard error.

3.2.3 Results

Reducing the sediment loads in the EAM on the exposed reef flat resulted in over forty times more grazing pressure on algal turfs by the green turtle, *Chelonia mydas* (Figure 3.2.2a). In total 585 bites were recorded over nine feeding bouts on three of the ten experimental plots. Each feeding bout lasted approximately four and a half minutes (4:36±0:42; see Appendix 3.2.2); between bouts the turtles were observed to remain near the plots but did not feed. Where turtles fed, grazing was overwhelmingly on the cleared plots (98.0±0.7% of bites; Figure 3.2.2b). Size estimates of the green turtles observed feeding revealed at least three turtles were feeding on the plots, with a mean length of 56.0±4.5 cm (SCL).

The higher herbivory resulted in a 21.2% reduction in algal turf height in the three cleared plots grazed by turtles in just three hours (Figure 3.2.2c; significant interaction term: $F_{1, 232}=6.47$, $p=0.01$). Grazing by both herbivorous fishes and green turtles will have contributed to this reduction and it is impossible to attribute the cause of the reduction to either group, in fact, the reduction observed did not differ from that seen in plots without turtles (21.4%). Herbivorous reef fish, however, appeared to be deterred by the presence of turtles, and as such, the presence of a single turtle appeared to have comparable effects to multiple reef fishes. The large size and large number of bites made by turtles might indicate a possibly important role.

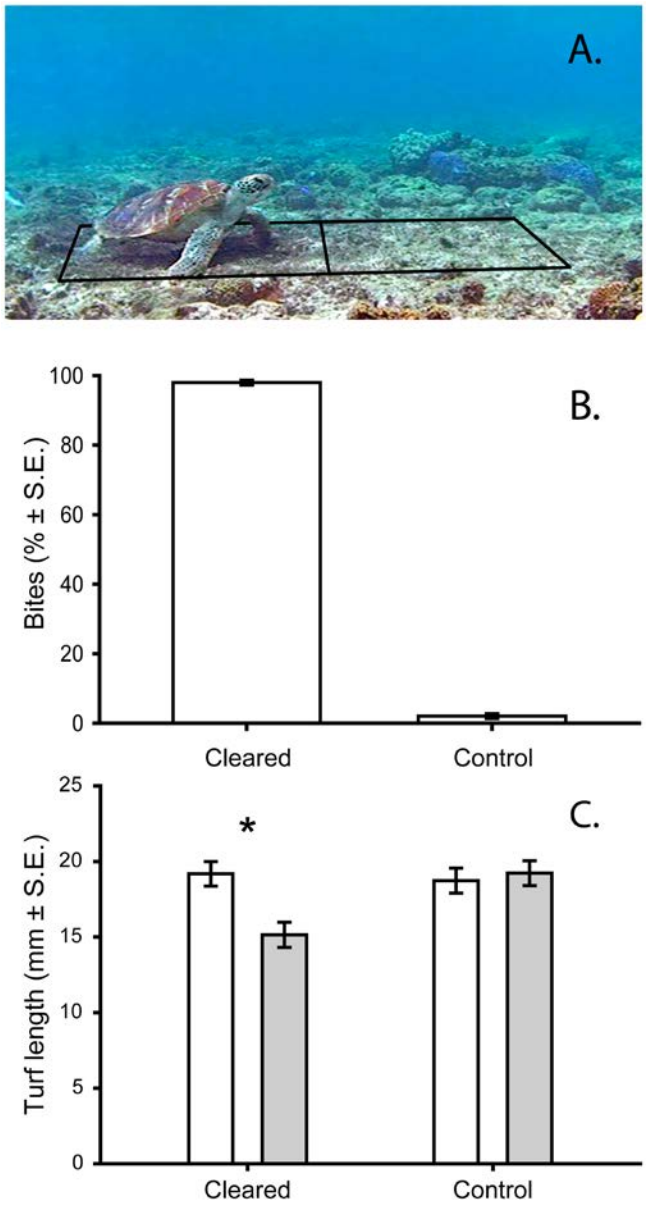

Figure 3.2.2 Grazing by the green turtle (*Chelonia mydas*) on sediment reduced plots. (**A**) Image capture of a green turtle feeding on the experimental sediment clearance plot. The lines represent the boundaries of the two adjacent plots: the sediment clearance plot to the left, and the control plot to the right. (**B**) The proportion of bites made in the cleared and control plots by green turtles during the three-hour experimental period (n = 3 plots). (**C**) The reduction in turf length observed in three hours in the cleared and control plots respectively. White bars represent the mean initial length and grey the mean final length (n = 3 plots for each treatment), * indicates a significant difference (Tukey's HSD).

Analysis of 288 hours of video footage of the *S. swartzii* assays across the six habitats revealed that while most browsing was by fishes, two turtles were recorded feeding on the *Sargassum*. Both were hawksbill turtles, *E. imbricata*, (approx. 58 cm SCL), with one being recorded to feed on *Sargassum* in the back reef habitat, and the other in the sheltered reef base (Figures 3.2.1, 3.2.3; Appendices 3.2.3, 4). On each occasion the turtles took three bites from the *Sargassum*.

Figure 3.2.3 A hawksbill turtle (*Eretmochelys imbricata*) feeding on a transplanted thallus of the brown macroalga *Sargassum swartzii*.

3.2.4 Discussion

Our results provide observational evidence that marine turtles may function as both grazing and browsing herbivores on coral reefs. Collectively, green and hawksbills turtles displayed responses to sediment reductions of algal turfs and macroalgal assays that were remarkably similar to those of herbivorous fishes. While we were unable to isolate the effects of turtles from those of fishes in reducing the algal biomass, our observations clearly show that marine turtles are actively targeting and removing both algal turfs and leathery macroalgae from

coral reef habitats. We postulate that, in doing so, turtles may potentially play a role in important ecological processes on coral reefs.

Numerous studies have advocated the importance of herbivory to reef health and resilience, focusing on the roles performed by herbivorous fishes (Bellwood et al. 2004; Hughes et al. 2007; Burkepile and Hay 2008, 2010; Hoey and Bellwood 2009, 2010). Fishes, while undoubtedly playing a key role in reef processes, lack some important morphological and behavioural traits of larger organisms. Larger animals, having larger mouths, usually take larger, more forceful, bites, and as such may be expected to have greater functional impacts (Bonaldo and Bellwood 2008; Bellwood et al. 2012). While the general scarcity of macroherbivores reduces the net benefits of size, larger individuals can offer greater ecological benefits in terms of mobility and may complement the roles of herbivorous fishes and urchins on coral reefs.

Ecological resilience may derive from overlapping function within scales, and reinforcement across scales (Peterson et al. 1998). Within coral reef systems, even some of the largest herbivorous reef fishes have relatively small home ranges. For example, the grazing steephead parrotfish, *Chlorurus microrhinos* (maximum length 80 cm) has a home range of less than 1 ha (Welsh and Bellwood 2011) and large browsing herbivores, such as the bluespine unicornfish, *Naso unicornis* (maximum length 70 cm) maintain home ranges well under 10 ha (Meyer and Holland 2005; Marshell et al. 2011). As such, the ability of herbivorous reef fishes to respond to phase shifts appears somewhat limited by their spatial distribution; truly wide-ranging or roving reef herbivores may be rarer than previously assumed. Marine turtles, however, have far larger home ranges (over 3900 ha; Seminoff et al. 2002a) and often undergo large migrations (Limpus et al. 1992; Luschi et al. 1996; Lahanas et al. 1998). We suggest that, regardless of phylogeny, large mobile herbivores with large home ranges could play any ecological roles on reefs at a broad scale, providing a function not yet observed on reefs.

Grazing by green turtles, Chelonia mydas on coral reefs

Green turtles made over forty times more bites on plots of algal turfs (EAMs) that had been subject to artificial sediment reduction than those with natural sediment loads. The observed behaviour of green turtles mirrors that seen by fishes in the only other study using sediment reductions on coral reefs (Bellwood and Fulton 2008). Why sediment suppresses herbivory is unclear, but is likely to be associated with diminished accessibility of resources and reduced energy uptake per bite (Choat 1991; Purcell and Bellwood 2001). Regardless of the cause, it appears that natural sediment loads in coral reef EAMs are enough to suppress herbivory on coral reefs across multiple herbivorous taxa.

The large size of green turtles compared to herbivorous reef fishes suggests they could play a greater functional role per-individual than herbivorous fishes. However, as turtles were not observed to respond differently to fishes, well-grazed reefs may not gain any potential benefits from increased turtle grazing. Larger turtle populations might not act as an alternative to current management techniques, only to supplement them.

Green turtles are well known as herbivores (Table 3.2.1), however most studies have used gut contents data to determine what algae the turtles have consumed. While analysis of gut contents clearly indicates what the study animal has ingested, it provides no indication of the source of the prey. As such, the propensity of green turtles to feed on coral reefs has remained unclear. The source of ingested algae could have been non-reefal hard substrates or flotsam. Furthermore, grazing of algal turfs is likely to be under-reported in gut contents analyses, as algal filaments are small and difficult to identify. Our observations demonstrate that green turtles do actively consume turf algae from coral reef environments. Furthermore they respond to turf-associated sediment in a manner comparable to fishes (Bellwood and Fulton 2008).

Table 3.2.1: Summary of previous dietary studies of the green turtle, *Chelonia mydas*. Values represent percent volume of each dietary category. Where quantitative estimates were not available †† indicates the dominant component, and * indicates presence as a minor component.

				Macroalgae						
Life stage	**Method**	**Sample Size**	**Seagrass**	**Chlorophyta**	**Rhodophyta**	**Phaeophyta**	**Sponge**	**Other Invertebrate**	**Location**	**Source**
Juvenile	Lavage	113	59.7	9.3	26.3				Moreton Banks, Queensland	Read & Limpus 2002
Juvenile	Lavage	127	25.5	14.3	62.7	1.8			Flathead Gutter, Queensland	Read & Limpus 2002
Juvenile	Lavage	20	45.7		47.3			6.8	Moreton Bay, Queensland	Brand-Gardner et al. 1999
Juvenile	Lavage	40	0.1	4	89.9	0.7	0.4	0.8	Florida	Gilbert et al. 2008
Juvenile	Lavage	108	81.8	0.5	13.9	0.9		0.5	Green Island, GBR	Fuentes et al. 2006
Subadult	Lavage	15		49.4	49.9		0.6		Baja California, Mexico	Lopez-Mendilaharsu et al. 2008
Subadult	Lavage	191	2.1	11.6	78	1.7		0.9	Hawaii	Arthur & Balazs 2008
Subadult /Adult	Lavage	146	85.5	< 1.0	9.4	< 1.0	< 1.0	1.3	Shoalwater Bay, Qld	Arthur et al. 2009
Subadult /Adult	Stomach content	243	88.6	3.1	4.8	0.3	0.9	0.4	Nicaragua	Mortimer 1981
Subadult /Adult	Lavage	408		30	38.6	29.5			Heron Island, GBR	Forbes 1996
Subadult /Adult	Stomach content	9	> 50	ca 15		ca 10			Oman	Ross 1985
Subadult /Adult	Crop contents	372	ca 4	ca 20	ca 65	ca 7			Kane'ohe Bay, Hawaii	Russell & Balazs 2009
Subadult /Adult	Lavage & faecal	101		4.4	90			2.9	Gulf of California, Mexico	Seminoff et al. 2002
Subadult Adult	Lavage	65		43.3	33.1	5.8		8.8	Galapagos Islands	Carrion-Cortez et al 2010
Adult	Stomach content	1		††		*			Tokelau	Balazs 1983

Browsing by hawksbill turtles, Eretmochelys imbricata on coral reefs

Although few bites were videoed, the evidence presented herein supports previous observations by the authors of turtles feeding on leathery macroalgae on both algal dominated inshore reefs and offshore coral dominated reefs on the GBR. Previous studies using gastric lavages or dissections have demonstrated that sponges and other sessile invertebrates account for over 95% of the diet of *E. imbricata*, with macroalgae only representing a very minor component (Table 3.2.2). However, similarly to those for green turtles, these studies do not provide information on the source of the small proportions of macroalgae ingested by hawksbill turtles, which could have been ingested incidentally when feeding on sponges or from floating algal mats. Our observations indicate that adult hawksbill turtles may be actively targeting and ingesting leathery macroalgae when available on coral reefs.

Table 3.2.2: Summary of previous dietary studies of the hawksbill turtle, *Eretmochelys imbricata*. Values represent percent volume of each dietary category. Where quantitative estimates were not available †† indicates the dominant component, and * indicates presence as a minor component.

				Macroalgae						
Life stage	**Method**	**Sample Size**	**Seagrass**	**Chlorophyta**	**Rhodophyta**	**Phaeophyta**	**Sponge**	**Other Invertebrate**	**Location**	**Source**
Juvenile	Photograph	NA					††	*	Cayman Islands	Blumenthal et al. 2009
Subadult /Adult	Stomach content	64					95.3		Caribbean	Meylan 1988
Subadult /Adult	Lavage	75					††	*	Puerto Rico	van Dam & Diez 1997
Subadult /Adult	Lavage	18		1.6	3.8	0.2	0.4	94	US Virgin Islands	Mayor et al 1998
Subadult /Adult	Lavage	146		1.2	2.1	0.7	91.6	4.8	Cuba	Alvarez 2000
Adult	Direct Observation	1						††	Southeastern Brazil	Stampar et al. 2007
Adult	Direct Observation	1						††	Aldabra Atoll	Obura et al 2010

Historical roles, shifting baselines and generalist herbivory

The concept of shifting baselines on reefs (Pauly 1995; Sheppard 1995) is of particular relevance when considering macroherbivores as they show some of the quickest declines after human exploitation (Pandolfi et al. 2003). Marine turtles, along with most marine macrofauna have been hunted for considerably longer than their populations have been monitored; as such, estimates of historical populations are hard to derive and highly variable (Jackson 1997; Jackson et al. 2001; McClenachan et al. 2006).

Regardless of the actual figures, turtle populations have suffered considerable depletion worldwide (Allen 2007; Chaloupka et al. 2008; Great Barrier Reef Marine Park Authority 2009). Only after the depletion of Caribbean green turtle populations did their role as the principal grazer of seagrass communities become apparent (cf. Thayer et al. 1984). Some modern populations of turtles can control and even overgraze some marine habitats (Fourqurean et al. 2010), further highlighting that even at low densities turtles have the potential to play significant roles in marine ecosystems.

We speculate that, although each species was only seen to feed on one functional group of algae (green turtles on EAMs and hawksbills on leathery macroalgae), and in combination with previous reports of the diets of marine turtles (Appendices 3.2.5, 3.2.6), contrary to most fish taxa, marine turtles might represent a trophically flexible group of herbivores on coral reefs. As the resilience of coral reefs is often reliant on numerous roles provided by individual species or small functional groups (Nyström 2006; Fox and Bellwood 2008; Hoey and Bellwood 2009), large generalist herbivores would be particularly valuable, as they would provide a measure of redundancy across a wide array of functions. Reported dietary shifts with changes in prey abundances by turtles highlight their potential as ecological stand-ins (Russell and Balazs 2009). At current population densities, however, the scarcity of turtles means that, even if turtles were generalist herbivores they would be unlikely to be able to replace any lost ecosystem function. Furthermore, the capacity for fishes to take over the roles of turtles is limited (Bellwood et al. 2006). Of the 60-70 species of nominally herbivorous fishes found on the Great Barrier Reef

less than 10 have been found to feed on leathery macroalgae, and in each case they have highly restricted diets (Choat et al. 2002; Bellwood et al. 2006). Turtles may, therefore, provide a unique combination of size, mobility and dietary flexibility that is unlikely to be matched by fishes.

While recent conservation efforts have yielded encouraging results (Chaloupka et al. 2008), threats to turtles are not restricted to hunting and bycatch. Changing environmental conditions and sea level rise are a particular threat to turtles, which are reliant on specific nesting beaches and have temperature dependent sex ratios (Pike and Stiner 2007; Fuentes et al. 2010, 2011). These threats are far more challenging to manage than those from exploitation and the future for turtle populations remains uncertain. The population declines and continuing threats to marine turtles may, therefore, mean that coral reefs might have lost, what may be, their largest generalist macroherbivores before their role was fully understood.

Chapter 4: Ecological consequences of sediment on high-energy coral reefs

Published in *PLoS One* 8: e77737 (Appendix 4.1)

4.1 Introduction

Coral reefs are among the most biodiverse ecosystems on the planet. Despite the ecological and physical complexity associated with this biodiversity, they are remarkably fragile. The increasing rate of disturbances associated with climate change and other anthropogenically induced stressors has repeatedly highlighted that acute stressors can have long lasting impacts (Nyström et al. 2000; Norström et al. 2009). For example, temperature anomalies lasting for very short periods can result in bleaching events, which have long-term effects at reef-wide scales (Hoegh-Guldberg et al. 2007). While temperature anomalies might be the best understood, there are many other acute threats to coral reefs. These include storms, freshwater inundation and, potentially, sediments.

The source of sediment on coral reefs affects its physical and chemical properties. Fine marine (primarily carbonate) and terrigenous (primarily silicate) sediments can be transported long distances in suspension and/or driven by hydrodynamic activity (Alongi and Mckinnon 2005). While these sediments can be particularly deleterious to coral reefs, blocking light penetration and, upon settling, producing blankets of smothering silt (Erftemeijer et al. 2012), their affects tend to be best-documented on near-shore reefs (Fabricius et al. 2005). The proximity to the sources of terrigenous sediments and shallow waters allow sediments to be effectively resuspended and transported to these reefs (Alongi and Mckinnon 2005). On reefs further from shore, however, most sediment is produced *in situ* as the reef matrix is eroded into sediments by physical, biological and, chemical processes (Scoffin 1992).

While benthic sediments are highly dynamic on offshore coral reefs (Kench 1998; Kench and Brander 2006), the continual production of sediments through erosion is often balanced by hydrodynamically driven losses to deep water or accretion into cays or beaches (Kench 1998). As such, although the sediment is constantly moving, the system remains in a state of dynamic stability (Bellwood and Fulton 2008; Goatley and Bellwood 2012; Chapter 3.1), with all but the most severe perturbations being short lived (Scoffin 1993).

On hard coral reef substrata some sediment exists in sand patches, but a large proportion of the benthic sediment is bound within algal turfs (Purcell 2000; Birrell et al. 2005; Goatley and Bellwood 2010, 2011, 2012; Chapters 2, 3.1 and 5). The turfs also trap detritus and provide habitat for infaunal organisms (Kramer et al. 2012; Kramer 2013b). Together, these components form an epilithic algal matrix (EAM; Wilson and Bellwood 1997); a ubiquitous feature of coral reefs, often occupying more benthic space than corals (Goatley and Bellwood 2011; Vroom 2011; Chapter 2). On the Great Barrier Reef, EAMs cover between 18 and 59% of the reef surface (Wismer et al. 2009). While EAMs can play positive roles on coral reefs, with some components providing settlement cues for corals (Diaz-Pulido et al. 2010) and others directly adding to carbonate accretion (Chisholm 2003), they also have several deleterious impacts. Algae within the EAMs can compete with corals for space (McCook et al. 2001; Diaz-Pulido et al. 2009), increase sediment deposition (Eckman et al. 1989; Carpenter and Williams 1993) and reduce the settlement success and survivorship of juvenile corals (Nugues and Roberts 2003; Birrell et al. 2008). The algal turfs in EAMs can also represent an early stage in successional growth of macroalgae on reefs (Burkepile and Hay 2010; Hixon and Brostoff 2013).

On ‘healthy’ coral reefs, EAMs are maintained as well-cropped productive turfs by herbivores, usually reef fishes (Bellwood et al. 2004). The intensity of herbivory by fishes on these reefs can control the growth of algae (Hughes et al. 2007; Burkepile and Hay 2008; Bonaldo and Bellwood 2011). While herbivory is clearly a vital function on coral reefs, recent evidence suggests that sediments may affect reef fish communities (Mallela et al. 2007; Cheal et al. 2013), and furthermore, sediments trapped in the EAM can deter herbivores from feeding

(Bellwood and Fulton 2008; Goatley and Bellwood 2012; Chapter 3.1). Sediment reductions result in almost instantaneous increases in rates of reef fish herbivory and measurable declines in algal turf length in less than four hours (Bellwood and Fulton 2008). The increased herbivory with reduced sediment loads indicates that trapped sediments actively deter herbivores, however, evidence for sediment suppression of herbivory remains almost entirely based on sediment removal experiments, which report increasing herbivory following sediment reductions (Bellwood and Fulton 2008; Goatley and Bellwood 2012; Chapter 3.1). Yet questions remain: *a*) will an increase in sediments produce similar changes in herbivory? And *b*) are these effects long-lasting or temporary? This is particularly interesting as increased sediments are believed to pose an ongoing threat to coral reefs (Fabricius 2005; Erftemeijer et al. 2012).

The interactions between benthic sediment and herbivory suggest the possibility of a positive feedback loop. Any disturbance leading to increased EAM sediment load, such as exposure to a sediment plume from storms, flooding or dredging could deter herbivores. The reduced top down pressure on the EAM is likely to result in an increase in EAM length (Bellwood and Fulton 2008), allowing further sediment trapping (Carpenter and Williams 1993; Bonaldo and Bellwood 2011). The potential result is a self-sustaining, long, sediment-rich EAM, unpalatable to herbivores. Using a combination of herbivore exclusion cages and pulsed sediment additions we attempt to initiate this positive feedback and generate a deep, sediment-rich EAM. In doing so, we will provide information on the relative impacts of sediment pulses and herbivore removal on coral reef resilience.

4.2 Methods

Experimental manipulations were conducted at two sites on the exposed reef crest southeast of Lizard Island in the northern section of the Great Barrier Reef, Australia. The experiment was conducted between December and March, in the southern hemisphere summer.

The sites had similar topographies, were at a depth of 2-4 m, and separated by over 800 m. Sites were characterised by sparse coral colonies, separated by expanses of short well-cropped EAMs on a flat, low-complexity reef matrix. At each site, six fully caged, six open (uncaged) and six partially caged 1 m^2 plots were haphazardly delineated on the flat EAM. Full cages were constructed of a steel bar frame, 25 cm high, enclosing the 1 m^2 plot, attached to the reef using epoxy putty and enclosed with galvanised 4 cm wire mesh. Partial cages were constructed of vertical panels identical to those used in the fully caged treatments and were deployed to control for any effect of the cage treatments on the EAM or sediment, while allowing herbivores access to graze the EAM.

Half of the plots in each cage treatment were subjected to an experimental sediment addition. In these addition plots, a sediment load of 8.6 kg m^{-2} was maintained for one week. This sediment load was equivalent to that on the adjacent reef flat (approximately 40 m leeward of the crest), which was determined by weighing dried sediment samples collected using an electric vacuum sampler from 20 replicate 5.8×10^{-3} m^2 rings (see Purcell 1996). The sediment for treatments was collected from a reef-margin sand apron and had a similar particle size profile to that found on the reef flat. When evenly spread, the 8.6 kg of sediment covered the 1 m^2 plot to a depth of 15 mm. Sediment was added daily to each plot to maintain this depth for one week, simulating an acute sedimentation event. Then the plots were left undisturbed for the remainder of the three-month experimental period.

The sediment depth and EAM turf length in each plot were recorded using the depth probe of vernier calipers (n = 20 reps for each plot). Measurements were made as sediment was initially manipulated (T_0), then at weekly intervals for 6 weeks post-manipulation ($T_{1\text{-}6}$), and again after three months (T_7).

EAM turf length data were standardised to percent increase over initial turf length (at T_0) correcting for initial variation among plots. The data were then analysed using 2- and 3-way analyses of variances (ANOVAs) of the T_7 data. Site was categorised as a random factor and

was found to have no significant effect or interaction. It was therefore pooled to increase the power of the analysis (Vergés et al. 2012; Fox and Bellwood 2013). Data normality was assessed using residuals plots and square-root transformations were applied where necessary. To allow data transformation for statistical analyses, negative percent EAM turf length values were removed by the addition of a constant to all data. Time series data were analysed using 2- and 3-way repeated measures ANOVAs (RM ANOVAs). Multivariate comparisons (Pillai's Trace; RM MANOVAs) were used if assumptions of sphericity were violated.

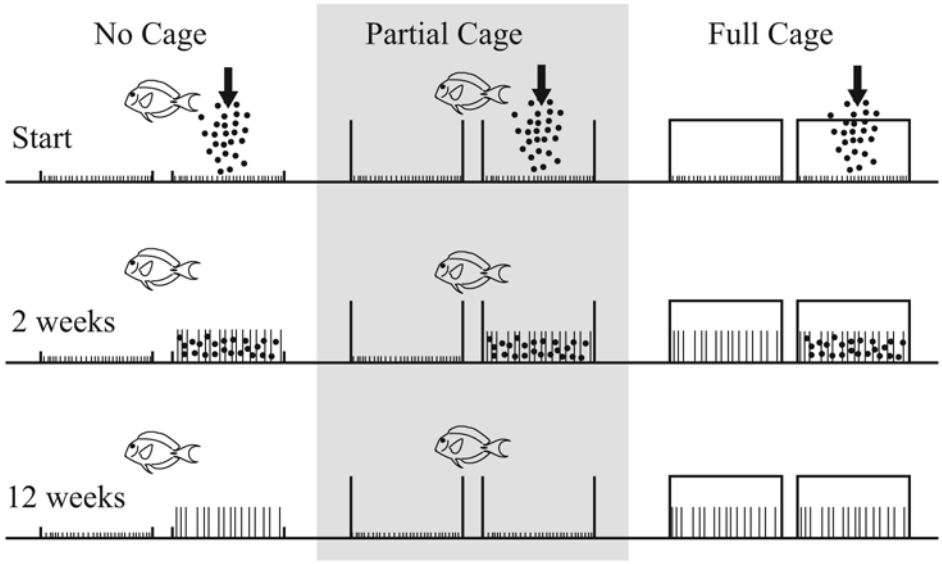

Figure 4.1 The effects of the experimental manipulations, at sediment addition, 2 and 12 weeks. Black circles represent added sediment and vertical lines the relative length of turfs in the EAM. Fishes indicate where herbivores had access to the plots.

4.3 Results

After three months (T_7) the greatest increase in the length of algae in the EAM was seen in the caged plots and a significant difference in turf length was observed between the caged and open plots (Figure 4.1; 3-way ANOVA on square root transformed data: $F_{2,24} = 7.32$, $P = 0.003$). While no other factors or interactions were significant (Appendix 4.2), a Fisher's least significant difference (LSD) post-hoc test revealed two groupings in the caging × sediment treatment interaction (Figure 4.2). Without sediments, a clear cage effect was observed. Algal

length increased by 58.9%; no response was seen in the open or partial cages.

Sediment additions to caged and partially caged plots resulted in no observable differences to the EAM when compared to the corresponding natural sediment plots. Sediment additions to the open plots, however, resulted in remarkable EAM turf algae growth, i.e., over 435% greater than observed on open, natural sediment treatment plots (Figure 4.2).

The time series data showed an initial rapid increase in turf length followed by an apparent asymptote after approximately three weeks (Figure 4.3). Data differed significantly over time (RM MANOVA; Pillai's Trace = 0.647, $F_{6,25} = 7.639$, $P < 0.0001$) and in the time × caging interaction (Pillai's Trace = 0.636, $F_{12,52} = 2.022$, $P = 0.041$). No other factors showed significant interactions (Appendix 4.3).

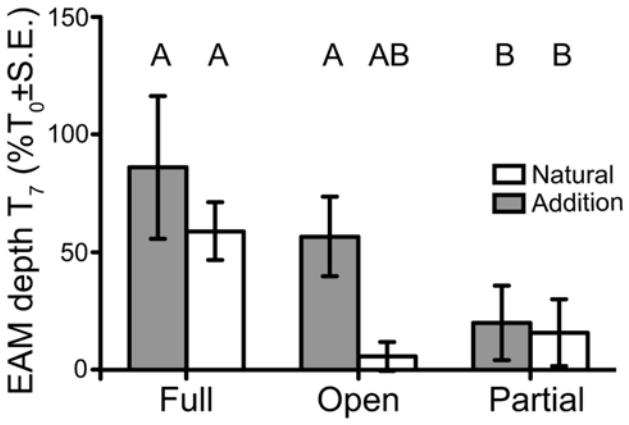

Figure 4.2 EAM turf lengths at T_7 (3 months post sediment addition). Filled bars represent sediment addition treatments and open bars natural sediment treatments. A and B denote significant groupings (Fisher's LSD). Data are shown as percentage of $T_0 \pm$ standard error, sites are pooled, therefore n = 6 replicates for each.

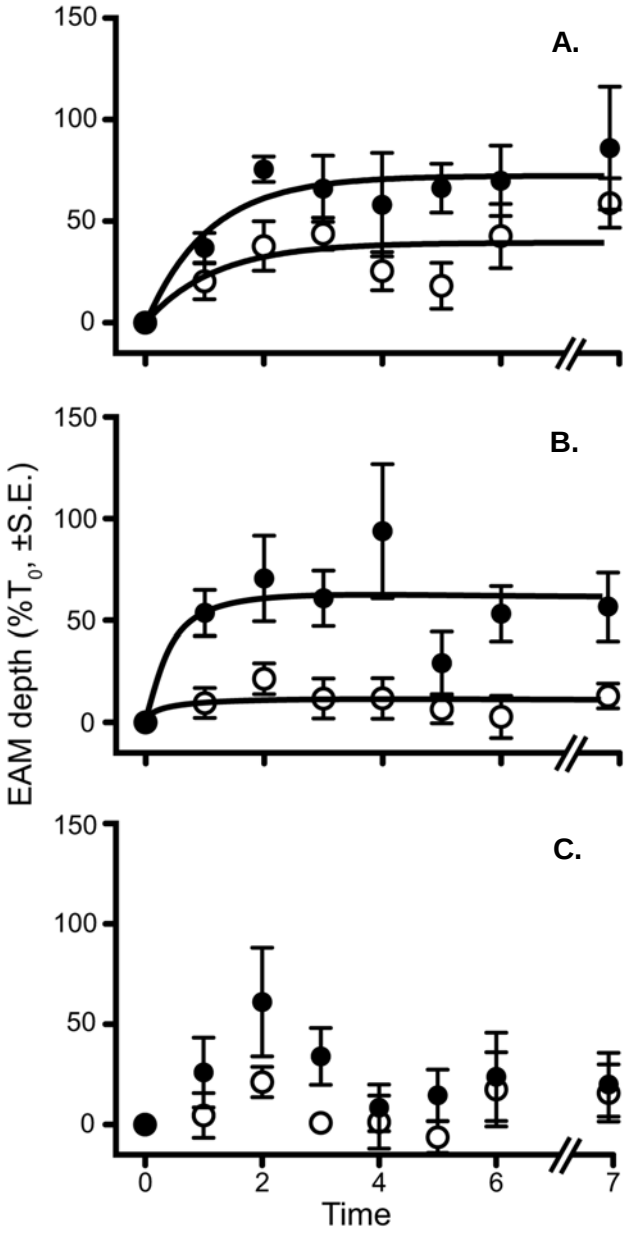

Figure 4.3 EAM turf length over time. Data are pooled between sites and standardized as percentage of T_0. Filled circles represent sediment addition, open circles represent natural sediment loads. Time is measured in weeks except T_7, which is three months after T_0. (**A**) shows the responses of the caged plots, (**B**) the open plots, and (**C**) the partially caged plots. Data are shown as percentage of $T_0 \pm$ standard error, with sites pooled, n = 6 replicates for each point. The lines fitted follow a one-phase decay model where appropriate.

Direct measurements of the sediment loads in the EAMs were conducted alongside measurements of the EAM turf length. Unlike the turf length, sediment rapidly declined in all treatments to levels indistinguishable from natural sediment loads within three weeks (Figure 4.4; Appendix 4.4).

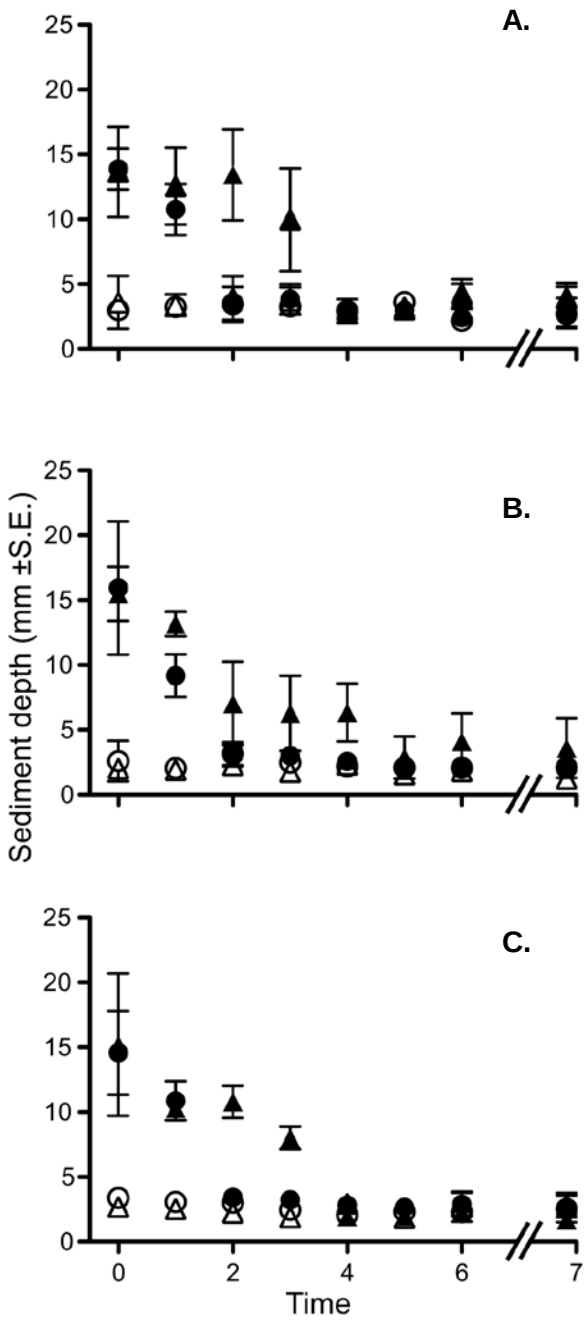

Figure 4.4 Sediment depth over time. Filled points represent sediment addition treatments, open points represent natural sediment treatments. Circles represent data from site 1, and triangles site 2. Time is measured in weeks except T_7, which is three months after T_0. (**A**) shows data from the caged plots, (**B**) the open plots, and (**C**) the partially caged plots. Data are shown as mean depth in mm ± standard error, n = 3 replicates for each.

4.4 Discussion

We found that a one-week pulsed increase in sediment loads resulted in significant and sustained (3-month) increases in the length of turfs in EAMs on a coral reef (Figure 4.1). However, our results provide only limited support for the existence of the proposed positive feedback loop. Although the length of turfs increased, high hydrodynamic activity on the crest (e.g. Fulton and Bellwood 2005) quickly removed sediment from the turfs and the predicted deep, sediment-rich turfs were not formed. Increased EAM turf length did not appear to require high sediment loads.

The EAMs on the exposed crest used in this study are heavily grazed by coral reef fishes, which maintain short, productive algal turfs (Hoey and Bellwood 2008). Previous studies have demonstrated that when EAM with long turfs are transplanted from the reef flat (low herbivore pressure) to the crest (high herbivore pressure) they are rapidly consumed by fishes (Purcell 2000; Bonaldo and Bellwood 2011). It was, therefore, expected that any sediment-induced increase in the length of EAM turfs would be rapidly reversed as sediments returned to normal levels, as a result of hydrodynamic activity, releasing the algae from any sediment-induced suppression of herbivory (e.g. (Bellwood and Fulton 2008; Goatley and Bellwood 2012; Chapter 3.1). This was not the case.

The EAMs in the present study grew in response to reduced herbivory (cages), increased sediments, or a combination of these factors. Growth in the cages was probably a result of the reduction in grazing (Hughes et al. 2007; Bonaldo and Bellwood 2011). While sediment addition may increase algal turf length as a result of the algae investing greater energy resources in linear extension to reach light (Prathep et al. 2003) and/or increased availability of nutrients desorbed from the sediment (Entsch et al. 1983; Purcell 2000). In both cage and sediment treatments the algal growth was rapid and occurred soon after the initial manipulations were made, while any added sediment was still present. The growth of the EAMs slowed rapidly as sediment loads diminished. Notably, there was no growth of macroalgae, only an increase in turf length. Whether the time for macroalgal development was insufficient, if propagules or

juveniles were absent or if the high hydrodynamic activity at this site limited development of macroalgae (Fulton and Bellwood 2005; Bellwood and Fulton 2008), the key result is that responses of algal turfs with artificially reduced herbivory (cages) were comparable to those with increased sediment loads.

Remarkably, after the initial growth of the algal filaments the new, longer, EAMs remained for at least three months in both caged and open plots. The three treatments followed different trajectories: (1) by reducing herbivory, cages maintained a long EAM regardless of sediments (as in previous studies, e.g. Burkepile and Hay 2008, 2010). (2) In open plots, EAMs likewise remained long, but only if exposed to sediment. This was particularly striking given the rapid loss of sediment. It may be that the vertical distribution of the remaining sediments through the EAM plays an important role in deterring herbivores, or that changes in the microbial community (Barott et al. 2011, 2012) or detrital load of the turfs (Wilson 2002) made them less palatable to herbivores. The methods used in this study, however, could not detect any of these factors and, as such, further study is necessary to determine what is underpinning this stability. However, the lack of recovery is worrying as it highlights that reefs are slow to recover from sediment-induced disturbances, even short, 'pulsed' events. (3) The partially caged plots followed similar initial growth trajectories to their equivalent open plots, however, the longer EAMs appeared to 'recover' (i.e. reduce in length) as sediment was removed. The apparent 'recovery' of the EAM in the partial cages was unexpected. It was expected that, as herbivores had access to the benthos, the EAMs would follow the responses seen in the open plots. However, this difference appears to be a result of increased herbivory in the partial cages. The partial cages increased topographic complexity, and provided shelter for a range of reef herbivores allowing localised increases in grazing (cf. Madin et al. 2011; Vergés et al. 2011; Welsh and Bellwood 2011; Downie et al. 2013).

We found that the growth of EAMs after a one-week sediment pulse was equivalent to, or greater than, that seen in simulated herbivore removals using cages. While increased sediment is often considered deleterious to reefs, most information pertaining to its effects are at a

physiological scale, considering the impact on individual organisms (Fabricius et al. 2007); little is known about how sediments affect the broader ecosystem functions on which coral reefs rely (Airoldi et al. 2008). At physiological scales, sediments have deleterious impacts on almost all benthic reef taxa (Fabricius et al. 2007), however the role of sediments in mediating reef processes is currently limited to studies addressing the impact of sediment laden EAMs in driving settlement and survivorship of corals. While some algae within EAMs may induce settlement (Diaz-Pulido et al. 2010) increased sediments result in reduced settlement of reef corals as they create a mobile substrate, preventing access to the consolidated reef matrix (Birrell et al. 2005, 2008). Furthermore, benthic sediments reduce survival of post-settlement corals particularly during their early development, presumably due to abrasion and shading (Babcock and Mundy 1996; Birrell et al. 2008). In addition to affecting benthic coral reef organisms, our findings suggest that increased sediments might suppress herbivory resulting in the development and persistence of longer EAMs driving further implications for reef ecosystems. Reduced herbivory through increased fishing pressure is widely publicised as a major threat to coral reefs on a global scale (Hughes et al. 2003), but it appears that short-term increases in sediment release or resuspension through anthropogenic activities (e.g. Mcculloch et al. 2003; Fabricius 2005; Erftemeijer et al. 2012) have the potential to have similar effects at localised scales.

The manipulation used in this study is comparable to that of other short-term (acute) perturbations caused by natural or anthropogenic disturbances. Storms and cyclones can move sediment from areas with high natural loads, such as lagoons or reef flats, which, as with this study site, may be only a few tens of meters away (Purcell and Bellwood 2001). Storms can also increase runoff to inner and mid-shelf reefs (Gagan et al. 1988; Kench 1998; Kench and Brander 2006). Similarly, anthropogenic sediment perturbations caused by dredging and other shallow-water maritime activities can resuspend sediments (Wolanski and Gibbs 1992; Esslemont et al. 2004; Erftemeijer et al. 2012). These events may all generate long EAMs similar to those seen after the experimental sediment manipulation. An even greater impact may be observed if these

events happen in succession, without sufficient recovery time. The longer EAMs generated in this study persisted for at least 3 months, with no obvious sign of recovery. If disturbances increasing sediment loads occurred more often than this, there is the risk that the turfs may grow longer still and persist for longer periods. An assessment of the recovery time is necessary to assess whether such a ratchet effect (*sensu* Birkeland 2004) is likely to lead to the disruption of ecological processes on reefs.

It is essential to note that our observations are of the effects of 'natural' carbonate dominated sediments, which characterise offshore coral reefs. The disturbance induced by this study, therefore, represents the best-case scenario for the effects of sediments on reefs. Terrigenous sediments, with higher silicate and nutrient loads alongside a high likelihood of associated pollutants (e.g. from metals, chemical fertilisers and pesticides), are likely to have even greater impacts (Devlin and Brodie 2005; Fabricius 2005).

Although our study did not find evidence to support the existence of a positive feedback leading to sediment-laden turfs, a clear and lasting effect was observed following an acute disturbance, with the development of a long-turfed EAM. Longer EAMs on reefs have the potential to reduce coral settlement (Birrell et al. 2008), provide inferior grazing surfaces for fishes (Bellwood and Fulton 2008; Goatley and Bellwood 2012; Chapter 3.1), and present an ecologically and economically less-desirable state (Norström et al. 2009). The development of these long EAMs appears to be driven by increases in both benthic sediments and reductions in herbivory. In a world where reefs are affected by increasingly unpredictable climatic conditions and chronic reductions in herbivore abundances, these longer EAMs are likely to become an increasingly common feature on coral reefs.

Chapter 5: Biologically mediated sediment fluxes on coral reefs: sediment removal and off-reef transportation by the surgeonfish *Ctenochaetus striatus*

Published in *Marine Ecology Progress Series* 415: 237-245 (Appendix 5.1)

5.1 Introduction

The ecological impacts of sediments on coral reefs are of considerable importance to reef resilience and development over almost all spatial and temporal scales. Impacts of altered sedimentation can be noted in individual organisms in a matter of hours or days (Rogers 1983; Fabricius et al. 2007; Bellwood and Fulton 2008), whilst longer-term changes in sedimentation patterns can control the development of entire reef systems over geological time (Blanchon and Shaw 1995; Airoldi 2003; Perry et al. 2008). Some effects of sedimentation seem beneficial (Adams et al. 2009), however, the majority are deleterious. The negative effects of increased sediment loads range from altered feeding patterns in corals and fishes (Anthony and Fabricius 2000; Bellwood and Fulton 2008) to reduced reef accretion rates during times of sea level rise, ultimately leading to the drowning of entire reefs (Blanchon and Shaw 1995).

Many studies of marine sedimentation have focussed on changing coastal land use patterns and the effects of associated increases in terrigenous sediment output (e.g. Neil et al. 2002; McCulloch et al. 2003; Fabricius 2005). Factors affecting sedimentation on reefs less impacted by coastal inputs, such as oceanic reefs or those in mid- or outer-shelf regions (Larcombe and Woolfe 1999) have been the subjects of less investigation.

Studies considering sedimentation on these more isolated reefs have traditionally been made from either a physiological or a geological approach, the former considering the effects of sediment on reef biota and the latter studying the physical processes involved in the production, taphonomy (the breakdown of biogenic structures) and eventual fates of reef sediments. Few studies have provided information to link the two disciplines at an ecological scale. Nevertheless, ecological studies are vital as they help to identify the mechanisms that bestow coral reef resilience at a scale where changes can be both detected and managed (e.g. Airoldi 2003; Bellwood et al. 2004; Airoldi et al. 2008; Bellwood and Fulton 2008).

At an ecological scale, studies of sea urchins (Echinoidea) and parrotfishes (Labridae) have proved to be the most illuminating and their roles in bioerosion (Bellwood 1995b; Bruggemann et al. 1996; Carreiro-Silva and McClanahan 2001) and taphonomy (Lipps 1988; Scoffin 1992; Bellwood 1996) are now routinely incorporated in 'more-geological' models (e.g. Scoffin 1992; Bak 1994; Mallela and Perry 2007). Parrotfishes also influence sediment resuspension (Yahel et al. 2002) and transport (Bellwood 1995a) on reefs and as these processes are yet to be incorporated into reef carbonate budgets they represent an unconsidered mechanism of biologically mediated sediment flux on coral reefs.

While the previously mentioned studies provide a useful starting point, to date, the study of biologically mediated sediment flux by fishes on coral reefs has been limited to the parrotfishes. Some members of this taxon defecate away from their feeding areas, in deeper water, thus transporting sediment off reefs in the process (Bellwood 1996). While parrotfishes might be the most important group involved in biologically mediated sediment flux, many other fish taxa feed on constituents of sediment-laden epilithic algal matrices (EAMs) and whether these fish are targeting detritus, infaunal organisms or the turfs themselves, some sediment is likely to be ingested as they feed. The impact of these fishes on reef sediment dynamics is currently unknown.

Of the fishes feeding on Indo-Pacific EAMs, the lined bristletooth, *Ctenochaetus striatus* (Acanthuridae) stands as one of the most likely candidates for being important in

biological sediment flux. These fish are abundant on most Indo-Pacific coral reefs and are frequently the most abundant large roving herbivore/detritivore (Choat and Bellwood 1985; Trip et al. 2008). They have a relatively high feeding rate and gut throughput rate (Polunin et al. 1995; Choat et al. 2004) and a diet that is comprised of fine particulates including sediment (Choat and Bellwood 1985; Choat 1991), which is removed using highly modified brush-like teeth (Purcell and Bellwood 1993). Furthermore, *C. striatus* defecate away from their primary feeding surface and often repeatedly defecate in the same location, transporting sediment away from their feeding surfaces in the process (Bellwood 1995a; Krone et al. 2008). To assess the potential importance of this species in biologically mediated sediment flux on Indo-Pacific coral reefs this study will quantify the amount and direction of sediment transported by *C. striatus* on a mid-shelf reef on the Great Barrier Reef, Australia.

5.2 Methods

Study location

Research was conducted at Lizard Island in the northern section of the Great Barrier Reef (GBR). Two sites were chosen along the fringing reef to the south of the island. The sites are at an oblique angle to the prevailing south-easterly winds in the region, leading to a moderate hydrodynamic exposure. As *Ctenochaetus striatus* are most abundant on reef crests this zone was the focus of the study at both sites. Within the reef crest, three habitats: Upper, Mid and Lower were considered, to assess how *C. striatus* drives sediment fluxes within the reef crest. These habitats were clearly defined: the upper consisting of a primarily horizontal reef matrix 0.5-2m deep, the mid a sloping region to from 2-4m deep and the lower a primarily horizontal, rubble dominated surface 4-6m deep.

Sediment ingestion by Ctenochaetus striatus

Initially the amount of sediment removed from the reef crest by *Ctenochaetus striatus* was estimated using three methods. The results were then compared to consider the reliability of the methods used. The most reliable method was then used to calculate sediment transport and the overall importance of *C. striatus* in sediment transport on coral reefs.

1. Bite rates and bite volume

The first method used to estimate sediment uptake by *Ctenochaetus striatus* was a video-based focal animal approach. To randomise the selection of fishes, the first fish seen after a 1 minute timed swim was selected. To simplify analyses only the most abundant size class of fish (200 ± 50mm total length) were selected. This omitted only a few small individuals. The activities of the fish were recorded for five to ten minutes using an underwater video camera. Over both sites, a total of 170 videos were recorded over 13 days. All videos were viewed in slow motion to accurately count the number of bites the fish made on the benthos, then again at full speed to time how long the fish was visible in the frame, allowing an accurate calculation of bite rate to be made. To test the efficacy of the method, 10 of the videos were recorded while a second observer counted bite rates of the same fish *in situ*. All videos and observations were undertaken prior to collections. The videos were used for three purposes.

First, 65 videos were recorded during the day (10:00-16:00) to estimate a bite rate over the majority of the feeding day for *Ctenochaetus striatus*. Second, to measure the length of the feeding day, 18 videos were recorded just prior to sunset (17:11-18:31). This allowed any reduction in bite rate and the cessation of feeding to be determined. Finally, a further 87 videos were recorded from sunrise until the first defecation was observed (06:12-09:33). A regression of mean bite rate over time (standardised to minutes after sunrise) allowed the number of bites made at any time prior to first defecation to be estimated. This increased the accuracy of the

estimate of the total number of bites made per day by *C. striatus* and enabled an estimate of the size of each bite to be made using the gut contents of fish collected prior to the first defecation.

To estimate the size of each bite 3 fish were collected using spears prior to commencement of feeding and 11 fish were collected after first feeding but before first defecation. The time that each fish was collected was noted. The gut contents were removed and bleached using 10% sodium hypochlorite solution (following Bellwood 1996) to remove all organic materials, leaving just the ingested sediments. Following bleaching and rinsing, the samples were dried to constant weight at 40˚C and weighed. The time that the fish was collected was then plotted on the bite rate increase regression (above) to estimate the number of bites taken. The mass of sediment in the guts was divided by the number of bites to provide an estimate of the mass of sediment ingested per bite. The 3 fish collected prior to first feeding were used to correct for the trace amount of sediment that remained in the gut from the previous day's feeding. The number of bites made by *C. striatus* each day was multiplied by the mass of sediment ingested per bite to provide the first estimate of daily sediment ingestion. For this and all subsequent methods, compound variances were calculated, where necessary, using a two term Goodman's estimator following Marnane and Bellwood (2002).

2. Defecation rate and faecal pellet size

The second method used to estimate sediment transport by *Ctenochaetus striatus* considered the mean defecation rates and faecal pellet sizes. The defecation rate was derived from the 65 videos recorded during the day and the mean mass of faecal pellets was calculated from 30 pellets collected *in situ*. To collect the faecal pellets, fish were followed using SCUBA until they were seen to defecate. Intact pellets were collected from the reef surface, stored in zip-lock bags then bleached, rinsed and dried following the protocol outlined above, any pellet that could not be collected intact was rejected. The mean mass of sediment produced per minute was then multiplied by the number of minutes between the first observed defecation and sunset to provide the second estimate of sediment ingestion by *Ctenochaetus striatus*.

3. Gut contents and throughput rate

Twenty-two *Ctenochaetus striatus* from the most abundant size class (200 ± 50mm standard length) were collected by spear from the study sites at Lizard Island in the early afternoon. The gut contents were removed and bleached as above. The contents of the entire gastrointestinal tract were weighed and the mean gut sediment content was calculated. Multiplying the mean mass of sediment from full guts by the estimated gut throughput rates of *C. striatus* (Polunin et al. 1995 [5.5 day^{-1}]) provided the third estimate of daily sediment ingestion.

Sediment transport by Ctenochaetus striatus

The 65 videos recorded during the day were reanalysed, recording the location of the first bite of any *C. striatus*. Using just the first viewed bite of each fish removes any issues of non-independence in the analysis as every bite used was made by a different individual. The same method was used to assess defecations by *C. striatus*. The proportion of bites and defecations among the three reef crest habitats was then calculated to reveal patterns of sediment transport. These data, combined with the daily bite rate and bite volume estimates, were used to calculate the sediment transported per fish per day (g $fish^{-1}$ day^{-1}).

The abundance of *Ctenochaetus striatus* at the study sites was determined from underwater visual censuses along the crest at Sites A and B (50x4m belt transects, n_{total} = 14), following the pre-set distance method of Fulton et al. (2001).

Benthic sediments were collected from the crest habitats using an electric vacuum sampler and subsequently bleached and weighed (following Bellwood 1996; Purcell 1996). Sediments were collected from 10 replicate 5.8 $x10^{-3}$ m^2 rings at each crest habitat at each site. When combined with the daily bite rate and bite volume estimates, these data provided estimates of total sediment flux mediated by the populations of *Ctenochaetus striatus* at the

study sites. The potential clearance rate of sediment from the habitats driven by *C. striatus* was also estimated.

5.3 Results

To validate the methods used in this study, data collected from video based focal animal surveys were compared to those collected *in situ* by a diver. The video based approach revealed a considerably higher bite rate than the diver based bite rate estimation ($t_9 = 5.16$, $p < 0.001$) with rates of 16.8 ± 2.7 bites min^{-1} versus 8.5 ± 1. 5 bites min^{-1} (mean ± S.E.) respectively. The video based approach also allowed fishes to be followed for longer periods, as divers commonly lost track of fish when they paused to record data. For these reasons, all observation data for this study were collected using video based approaches. All values presented are as means ± standard error, or where necessary, mean ± Goodman's estimator of compound variance.

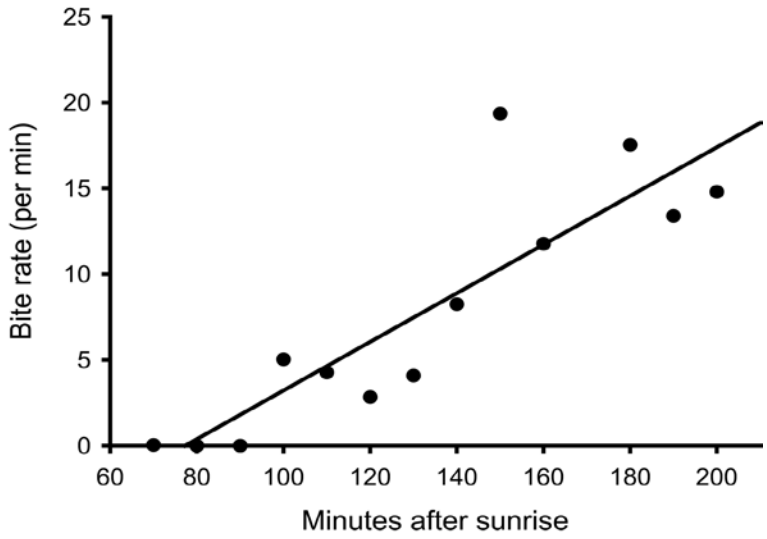

Figure 5.1 Regression of mean bite rate per 10-minute interval by *Ctenochaetus striatus*, standardised to minutes after sunrise. $y = 0.1418x - 10.959$, $r^2 = 0.76$.

Sediment ingestion by Ctenochaetus striatus

1. Bite rates and bite volume

Initially the number of bites made by an individual *Ctenochaetus striatus* per day was estimated. The average day length at Lizard Island is 728 minutes. Three sections of the feeding day were considered: (1) the commencement of feeding until first defecation, (2) the main part of the feeding day and (3) the cessation of feeding.

To calculate the number of bites made before the first defecation a regression of mean bite rates per 10-minute intervals was made from the videos recorded from sunrise to the time of first defecation ($y = 0.14x - 10.96$, $r^2 = 0.72$; Figure 5.1). This revealed that on average *Ctenochaetus striatus* make 933 bites prior to defecation, which occurs approximately 192 minutes after sunrise (09:33 during the study).

Following the first defecation the average bite rate of *Ctenochaetus striatus* was calculated using the videos recorded throughout the day. Bite rates during the day were found to differ between the sites ($t_{63} = 2.72$, $p < 0.01$). Fish at Site A showed bite rates of 15.4 ± 1.4 bites min^{-1} compared to 21.2 ± 1.6 bites min^{-1} at Site B. In the 536 minutes between the first defecation and sunset, individual *C. striatus* made 8275.8 ± 745.0 bites at Site A and 11379.3 ± 830.8 bites at Site B.

Feeding rates did not decline towards the end of the day (Figure 5.2). Instead, fish were observed to cease feeding abruptly at dusk and seek refuge in crevices in the reef. For this reason the end of the feeding day was considered as sunset. Using the data above, an average of the total number of bites made by individual *Ctenochaetus striatus* was calculated. The mean values were found to be 9208.8 ± 745.0 and 12312.3 ± 830.8 bites per day at Sites A and B respectively.

The mass of sediment ingested per bite by *Ctenochaetus striatus* was estimated. Prior to feeding, the mean residual sediment in the gut was found to be 0.19 ± 0.02 g. The number of bites made by each fish was calculated using the regression of feeding rate increase from sunrise

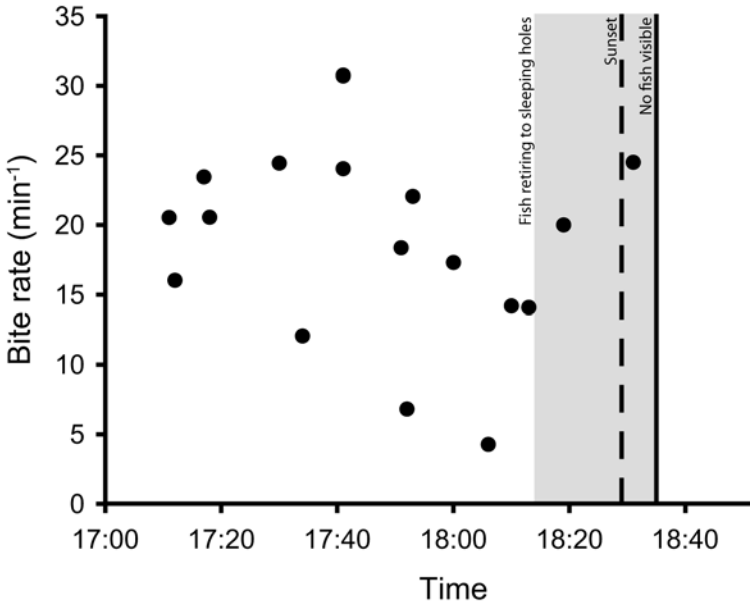

Figure 5.2 Feeding rates of *Ctenochaetus striatus* at the end of the feeding day. Each point is the bite rate determined from a single fish observed on video for a minimum of five minutes. Linear regression was not significant. The grey bar represents the time over which fish abundances were observed to decline (fish retired to sleeping holes). The dotted line represents sunset on the sampling day and the solid line the point after which no fish were visible on the reef (all retired to sleeping holes).

(above). After correcting for residual gut sediments, the mass of sediment contained in the guts of the 11 fish collected prior to their first defecation was divided by the number of bites made, resulting in a mean mass of sediment ingested per bite of 1.0 ± 0.3 mg. Thus, the mean mass of sediment ingested by each fish was estimated to be 8.8 ± 2.4 g day^{-1} and 11.8 ± 3.3 g day^{-1} at sites A and B respectively, using the first method (Figure 5.3).

2. Defecation rate and faecal pellet size

The average number of defecations made per day by *Ctenochaetus striatus* was calculated from the video data. This revealed defecation rates of 0.19 ± 0.04 min^{-1} and 0.07 ± 0.02 min^{-1} for Sites A and B respectively. Using the time between sunrise and first defecation

and the mean day length at Lizard Island the length of a defecation day was calculated to be 536 minutes. *C. striatus* therefore defecated on average 101.1 ± 19.8 and 37.7 ± 10.3 times per day at Sites A and B respectively.

The mean mass of sediment in a faecal pellet was calculated from the 30 collected pellets and multiplied by the number of defecations made per day. No difference in the mass of sediment per pellet was found between the sites so the data were pooled. Each pellet contained 0.7 ± 0.1 g of sediments resulting in an estimated sediment ingestion by *Ctenochaetus striatus* of 66.1 ± 14.4 g day^{-1} and 24.7 ± 7.1 g day^{-1} at Sites A and B respectively, using the second method (Figure 5.3).

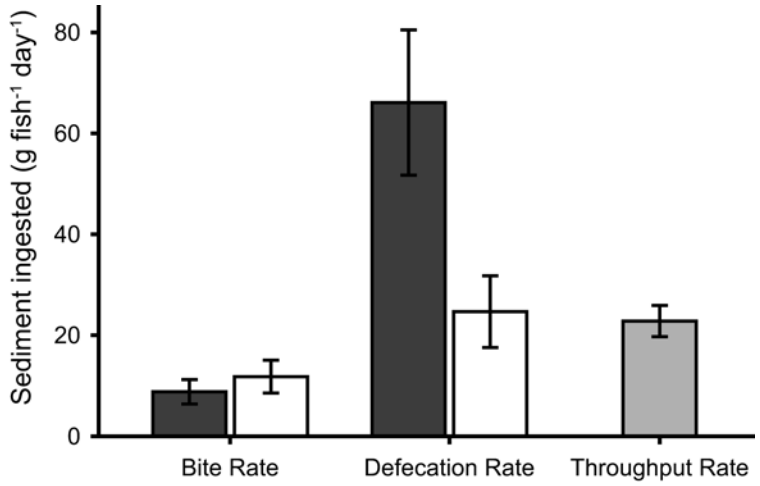

Figure 5.3 The estimated mass of sediment ingested by *Ctenochaetus striatus* per day using the three methodologies employed in this study: (1) bite rate and bite volume, (2) defecation rate and faecal pellet size and (3) average gut contents and throughput rate. Shaded bars represent Site A, open bars Site B. The average gut contents and throughput rate model is represented by specimens collected from both sites (sites did not differ significantly) to minimise the number of fish collected at either.

3. Gut contents and throughput rate

The mean volume of sediment found in the guts of the 22 *Ctenochaetus striatus* collected during the day was 4.2 ± 0.6 g (sites were not significantly different). Using published gut throughput rates (5.5 times per day) this produced an estimated sediment removal rate of 22.8 ± 3.1 g day^{-1} by each *C. striatus* (Figure 5.3).

Sediment transport by Ctenochaetus striatus

Bites were predominantly taken from the upper reef crest (45.9%) while defecations occurred most frequently at the lower reef crest (45.0%; Figure 5.4a), with 79.6% of defecations occurring away from the upper reef crest. In total, 36.5% of all sediment ingested by *Ctenochaetus striatus* was transported from the upper reef crest to deeper habitats. Using the estimated volume of sediment ingested by *C. striatus* from the defecation rate model revealed that each fish at Site A transported 24.3 ± 5.3 g day^{-1} away from the upper reef crest compared to 9.1 ± 2.6 g day^{-1} at Site B.

C. striatus may also act to move sediments from areas of high hydrodynamic exposure to sheltered locations, with 60.0% of defecations observed to occur in overhangs, crevices or caves. This is likely to be an underestimate as *C. striatus* was repeatedly observed to defecate in cryptic areas, which could only be detected after the event, by observing the faecal pellet.

The abundances of *Ctenochaetus striatus* at Sites A and B were found to be 3.2 ± 0.5 and 5.8 ± 0.9 fish per 100 m^2 respectively. With this abundance, *C. striatus* has the potential to transport 28.6 ± 6.2 kg $100m^{-2}$ yr^{-1} and 19.2 ± 5.5 kg $100m^{-2}$ yr^{-1} at Sites A and B respectively (using the defecation rate model transport estimates).

The weights of reef sediments collected using the electronic vacuum sampler did not differ between sites, thus the results were pooled. The mean sediment load of the upper reef crest was 75.5 ± 14.0 g m^{-2} increasing to 901.7 ± 184.6 g m^{-2} at the lower crest ($F_{2,57}$ = 14.97, p <0.0001; Figure 5.4b). Without considering sediment inputs, the feeding of *Ctenochaetus*

striatus therefore equates to the complete removal of sediments from the upper reef crest EAM 3.8 ± 0.8 times per year and 2.5 ± 0.7 times per year at Sites A and B, respectively.

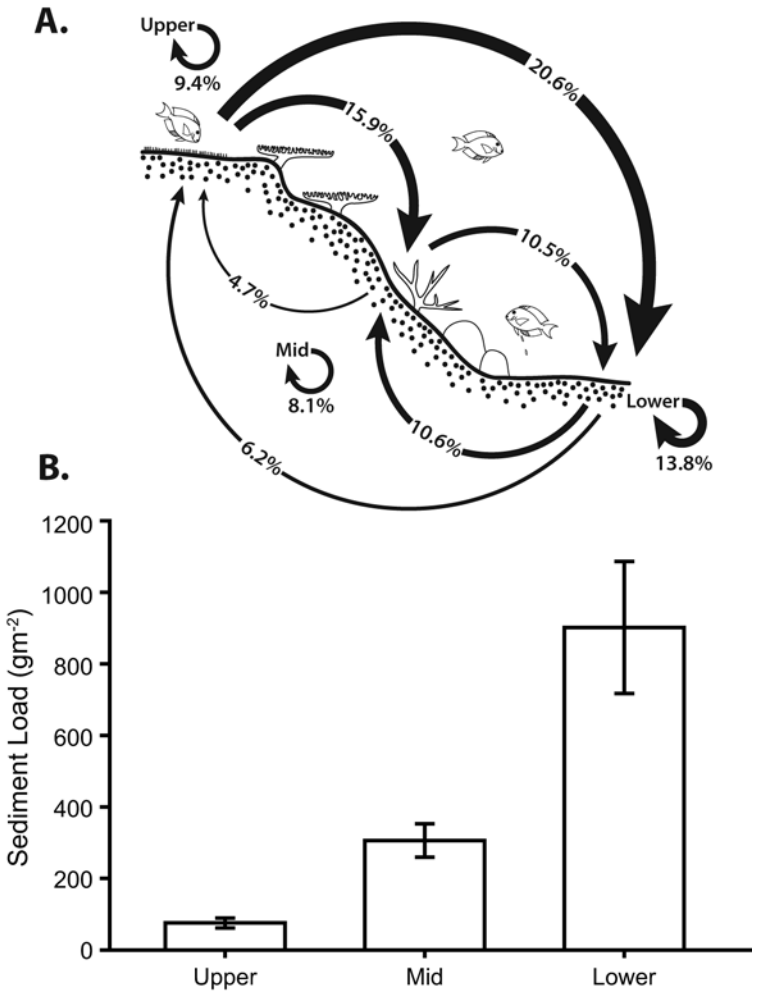

Figure 5.4 Sediment transport by *Ctenochaetus striatus* on the reef crest. (**A**) Arrow values represent the percent of total ingested sediment that is transported between habitats. (**B**) The mean benthic sediment load (g m^{-2} ± S.E.) in the three reef crest habitats (n = 20 for each habitat).

5.4 Discussion

Off-reef sediment flux mediated by the lined bristletooth, *Ctenochaetus striatus* (Acanthuridae) was quantified at Lizard Island, northern Great Barrier Reef. Although a tendency to defecate away from feeding areas has been documented for *C. striatus* (Krone et al. 2008) its role in biologically mediated sediment flux on coral reefs has not previously been quantified.

Sediment transport and its effects

Ctenochaetus striatus feeds primarily on the upper reef crest. Although it probably targets detritus (Purcell and Bellwood 1993) it ingests sediments in the process. It then moves into deeper waters to defecate, depositing the sediments, often in locations sheltered from hydrodynamic exposure. Remarkably, the quantities of sediment ingested by each *C. striatus* (8.8 ± 2.4 to 66.1 ± 14.4 g fish^{-1} day^{-1}) are broadly comparable with the quantity of existing sediments reworked by even large excavating parrotfishes such as *Chlorurus microrhinos* and *Ch. sordidus* (Labridae; 68.6 ± 21.6 g and 24.1 ± 7.4 g fish^{-1} day^{-1}, respectively; Bellwood 1996). This is particularly striking, as these parrotfishes are up to 26 times heavier than *C. striatus* (Choat et al. 2004). Even accounting for underestimation by visual observers in parrotfish studies, and using the methods that provide the lowest estimates of sediment ingestion by *C. striatus*, such as the bite rate and bite volume model, the high abundances of *C. striatus* on Indo-Pacific coral reefs (Choat and Bellwood 1985; Sluka and Miller 2001) ensure that *C. striatus* remain of considerable potential importance in reef sediment dynamics.

The ecological impact of *Ctenochaetus striatus* is very different to that of the parrotfishes. While even small *Scarus* sp. leave clearly visible grazing scars where the reef matrix is exposed (Bonaldo and Bellwood 2008, 2009), *C. striatus* feeds in an essentially non-destructive manner using its bristle-like teeth to sweep detritus from the EAM, simultaneously ingesting sediments (Purcell and Bellwood 1993; Krone et al. 2008). This method of feeding is

very unusual in reef fishes. Even amongst acanthurids, sweeping detritus from EAMs is unique to *Ctenochaetus* sp., with superficially similar *Acanthurus* sp. cropping algae with blade like teeth (Choat 1991). The only reef fishes to feed in a similar manner on coral reefs are salariin blennies (Blennidae; Wilson 2000), which have no taxonomic links with the other reef herbivores (Smith and Wheeler 2006). Removing sediments without significant bioerosion may benefit reefs by reducing sediment-induced stress on corals without reducing carbonate accretion rates (cf. Mallela and Perry 2007).

Furthermore, by sweeping sediments from the EAM, feeding by *Ctenochaetus striatus* may act to increase reef fish herbivory; a critical process on coral reefs (e.g. Bellwood et al. 2004). Experimental sediment removal from EAMs at Lizard Island resulted in 3.8-fold increases in herbivore feeding rates over short time periods (Bellwood and Fulton 2008). The cause of this behaviour is currently unknown, but may be due to diminished accessibility or utility of resources in the EAM when sediment is present (Purcell and Bellwood 2001). Decreased light attenuation in the EAM by reducing sediments may also provide a more nutritious prey for herbivores (e.g. Polunin and Klumpp 1989). Regardless of the mechanism, by reducing sediment loads, *C. striatus* appears to increase the palatability of EAMs to grazing herbivorous reef fishes, increasing the impact of this vital functional group.

EAMs, consisting of algal turfs and associated organic and inorganic components (Wilson and Bellwood 1997) are ubiquitous on coral reefs and differences in their composition can have important effects on benthic communities. Sediment free algal turfs in the EAM, for example, can promote coral settlement (Diaz-Pulido et al. 2010). However, as the EAM traps sediments without suffering damage (Airoldi et al. 1996; Purcell 2000) there may be negative effects. Although adult coral colonies can outcompete EAMs (McCook 2001), sediment accumulation can prevent coral recruitment (Birrell et al. 2008). By reducing trapped sediment, *Ctenochaetus striatus* may play an important role, providing favourable settlement surfaces for sessile benthic organisms, thus increasing the potential for reefs to recover from disturbances. *C. striatus* may, therefore, increase reef resilience.

Comparison of methods

When considering the advantages of the three methods, the defecation rate and faecal pellet size approach has advantages over the other two models employed. This is not due to the fact that it predicts the largest effect by *Ctenochaetus striatus* but that the model is reliant on fewer variables than the bite rate and bite volume model, and suffers from fewer sources of error. This approach is also non-destructive (no fish need be sacrificed) and entirely based on data collected by the authors at the study site, rather than published values from other locations, like the gut contents and throughput rate method. Furthermore, any errors accrued using the defecation rate and faecal pellet size approach tend to be conservative, as it is difficult to collect all faecal pellets intact. The volume of sediment in a faecal pellet is likely to be an underestimate as some sediment may have been left on the reef. Likewise, the defecation rate is also likely to be an underestimate as during faecal pellet collections *C. striatus* were often seen to defecate in cryptic environments in the reef (crevices and caves), which could only be detected after the event by looking for the faecal pellet. These events would have been missed by observers or video analyses. This observation may help to explain the site effect found using this method, as site B had greater topographic complexity and more "cryptic" defecation locations. Defecation events may have been missed at site B. The final reason we believe this approach to be conservative is that it makes no allowance for material lost (defecated) during the night. Despite the errors resulting in underestimates, this method consistently gives the highest values. Errors for the other methods may be positive or negative making the results more complex to interpret. Given the above, subsequent analyses of the volume of sediment ingested were based on estimates derived from the defecation rate and faecal pellet size approach.

The defecation rate and faecal pellet method, although applicable here, might have limitations if applied to other taxa. The faecal pellets of *C. striatus* are relatively unusual amongst herbivores on coral reefs in that they remain consolidated for some time after defecation, allowing them to be collected. This method would, unfortunately, be impractical in

studying parrotfishes, which produce rapidly dispersing clouds of faeces (Sazima et al. 2005). Nonetheless, as the defecation rate and faecal pellet size method produced results considerably larger than those from the other methods one may have to take care when using estimates that rely on gut filling or throughput estimates. Based on the current study, they may considerably underestimate sediment throughput.

Biologically mediated sediment flux on coral reefs

The importance of the ecological roles played by sediments on coral reefs is gradually becoming more apparent. Where biologists have repeatedly shown the deleterious physiological effects of increased sediments on individual benthic organisms (e.g. Fabricius et al. 2007) and geologists have shown the broad scale implications of sedimentation in controlling the development, distribution and fate of coral reefs (e.g. Blanchon and Shaw 1995), there has been a shortage of studies that link these fields. Ecological studies, which incorporate both the biological and physical components of the ecosystem, bridge this knowledge gap and provide valuable insights into processes contributing to reef resilience.

The present study and the few other studies considering biologically mediated sediment flux on coral reefs (Bellwood 1995a, 1995b; Krone et al. 2008) have each revealed an unexpected biological contribution to reef sediment dynamics. But these cover a small number of species over small spatial scales. Future studies must consider the interactions between sediments and reef organisms across larger spatial scales, in particular considering marine and terrigenous sedimentation gradients. Sediments play a crucial role in reef development and maintenance, but the extent to which this is due to direct impacts (smothering, light attenuation etc.) or indirect impacts, such as mediating critical ecosystem functions (herbivory, recruitment etc.), is at present, unknown. Currently, sediment is generally considered harmful to coral reefs. Sediment is a ubiquitous feature of coral reefs. Indeed, its presence in the EAM means that it is a significant component of the most abundant benthic substratum type on reefs (Wismer et al. 2009). That it can have a negative influence is well understood; the key question is, how much

sediment is too much and what are the implications for coral reefs during a time of climate instability and change.

5.5 Conclusion

By sweeping sediments from the EAM, *Ctenochaetus striatus* reduces reef sediment loading while causing little damage to the algal turf. Furthermore, sediment is moved off-reef increasing sediment in deep areas and reducing sediments on exposed areas. As a consequence, feeding by *C. striatus* may increase the attractiveness of upper reef crest EAM to reef herbivores and provide more suitable settlement surfaces for sessile benthic organisms, thus supporting reef resilience and their ability to recover from disturbances. The mass of sediment removed per individual *C. striatus* is comparable to even that of large parrotfishes. Given the wide distribution and high abundance of *C. striatus* on Indo-Pacific coral reefs it is apparent that *C. striatus* may play a major role in reef sediment dynamics. Indeed, sediment removal may represent a key functional role on coral reefs and *C. striatus* a critical functional group.

Chapter 6: Concluding discussion

Understanding how disturbances affect ecological processes on coral reefs is a critical factor in managing for coral reef resilience. This thesis has highlighted that even small changes in benthic sediment loads rapidly alter the behaviour of herbivorous reef fishes (Goatley and Bellwood 2012; Chapter 3.1) and even larger macroherbivores (Goatley et al. 2012; Chapter 3.2). These short term changes however can have long term consequences for coral reefs (Goatley and Bellwood 2013; Chapter 4), with the development of apparently stable, long algal turfs in the epilithic algal matrix (EAM), which are unpalatable to herbivores. Even slight increases in benthic sediments, therefore, could have considerable implications to a coral reef, particularly as EAMs cover the majority of the benthos (Goatley and Bellwood 2011; Chapter 2). Grazing reef fishes such as the bristletooth surgeonfish, *Ctenochaetus striatus* could confer some degree of protection from the effects of changing benthic sediment loads, by transporting some of the material into deeper water (Goatley and Bellwood 2010; Chapter 5), however, as these fishes may be affected by increases in benthic sediment loads (Goatley and Bellwood 2013; Chapter 4) it seems more likely that the role played by these fishes is to maintain resilience in a stable system, rather than facilitate recovery from disturbances.

By answering the four questions proposed in the introduction (Chapter 1) this thesis has offered a new perspective on the ecological role of sediments on coral reefs:

Question 1: "**How much EAM is on a coral reef?**" EAM is important as a sediment reservoir on coral reefs. By reducing flow rates, producing a fluid boundary layer, sediment deposition can be increased (Kendrick 1991; Carpenter and Williams 1993; Shashar et al. 1996) and subsequently benthic sediments stabilised (Airoldi 1998; Purcell 2000; Birrell et al. 2005). EAM is likely to be the dominant benthic component on most coral reefs, however, it is rarely recorded in benthic censuses (Chapter 2). Furthermore, even if they were counted, the perspective of the observer has the potential to greatly affect the results recorded. Chapter two

highlights the prevalence of EAMs on coral reefs, and shows that even on reefs with high coral cover, the consolidated reef matrix below coral canopies is most often covered with EAM.

Whilst the primary implications of this study highlighted the potential for erroneously reporting phase shifts to macro-algal dominance following the loss of a canopy, it also revealed that on reefs dominated by canopy forming corals, estimating any form of benthic cover is highly complex. If considering planar views, EAM may be only a minor component of benthic cover; the higher the coral cover, the lower the EAM cover. On the coral rich reef crests on Lizard Island, this method recorded around 27% cover of EAM. However, when considering the consolidated reef matrix below canopies, EAM became the dominant benthic component with around 45% of the benthos covered.

The simple answer to the question of how much EAM is on coral reefs, appears to be affected by the observer's perspective; even on high coral cover reefs it can vary from 27 to 45%. However, in all cases it is more than traditionally expected. The main conclusion that can be drawn from chapter two is that: a) EAMs have typically been overlooked as a benthic component on coral reefs; b) lack of aesthetic appeal is not related to a lack of ecological relevance (cf. Vroom 2011), with EAM acting as both a source of food and a sediment reservoir on coral reefs and c) EAM is abundant on coral reefs and is likely to be of considerable importance to coral reef ecology.

Question 2: "**How do reef herbivores respond to changes in EAM-bound sediments?**" Even slight changes in benthic sediment loads may critically alter the feeding behaviour of herbivorous reef fishes. In chapter 3.1 I highlighted that removing less than 150 g of sediment from a square metre of reef crest EAM resulted in considerable increases in herbivory. Even this small removal resulted in 1800 more bites per hour on the reef crest. While conducting the study, at least three green turtles (*Chelonia mydas*) were observed to preferentially feed on the sediment reduced plots. 98% of 585 bites taken by the turtles were in sediment-reduced plots (Chapter 3.2). Sediment removals, like those conducted in this thesis,

are not intended to simulate real world events. They are a tool to show that grazing herbivores prefer feeding on areas with reduced sediment loads. It is far more important to understand the impacts of increased benthic sediments. Recording reduced feeding from already low background rates is more challenging, but more valuable in understanding the likely role of sediment on coral reefs.

Question 3: "**Can reef-sediments induce coral reef phase-shifts?**" While the study presented in chapter four did not show definite evidence of a phase-shift, a pulsed sediment addition resulted in a sustained increase in EAM length. Algal turfs grew by almost 60% while increased sediment was present. Hydrodynamic activity on the reef crest cleared sediment to undetectable levels after approximately two weeks and as such, a quick recovery of algal turf lengths was expected. This was not observed. While the lack of a phase-shift to a long, sediment-rich turf can be seen as positive, the fact that the longer algae generated by a short-lived sediment pulse did not recover for at least three months is worrying and suggests that the effects of sediments on coral reef EAMs are more complex than previously thought.

Question 4: "**Can fish affect coral reef sediments?"** While parrotfishes are well known to transport sediment (Bellwood 1995a) no studies have considered the effects of other herbivorous or detritivorous fishes on coral reefs. Chapter 5 shows that *Ctenochatus striatus* (Acanthuridae), which is among the most abundant herbivores/detritivores on coral reefs, transports approximately 9kg of sediment off the reef crest per individual per year. When their abundance is considered, *Ctenochaetus striatus* transport as much sediment as even large parrotfishes (Bellwood 1995a). While the comb-like dentition of this species is likely to increase its ability to ingest sediments from EAMs, any fish feeding on components of the EAM are likely to incidentally ingest sediments while feeding.

Biologically mediated sediment transport might play an important role in maintaining the dynamic stability of benthic sediments on coral reefs (the sediment particles changing, but the loads remaining constant), and in so doing, helping maintain a resilient ecosystem. However

the ability of fishes to help a reef to recover following an increase in benthic sediments (whether pulsed or chronic) is unknown. Feeding by all herbivorous and detritivorous fishes increased following sediment removals (Goatley and Bellwood 2012; Chapter 3.1) suggesting that all prefer low sediment feeding surfaces. If sediment increases were to deter feeding by fishes such as *Ctenochaetus* the loss of a biological mechanism for sediment removal may in fact compound the effects of the original sediment increase.

These four questions were posed to accomplish the overall aim of this thesis: "to investigate interactions between herbivorous reef fishes and sediments, and to therefore quantify their impact on ecological processes on coral reefs." For the most part this thesis has accomplished these aims; small changes in benthic sediment loads have been conclusively shown to affect herbivory, a critical ecosystem process on coral reefs, with measurable and long lasting consequences of sediment additions. This suggests that sediment is an important component of coral reef ecology, and should be considered when managing coral reefs. However, as with all research, further questions about the precise nature of the interactions between coral reef herbivores, the EAM and benthic sediments have arisen. From the results of this thesis it appears that there are several crucial factors, which must be considered with regards to the ecological role of sediments on coral reefs.

All sediments are not 'sediments'

The studies conducted for this thesis were conducted on a mid-shelf island on the GBR. While many of the effects of sediment may be universal, sediments are not uniform in their physical and chemical properties. On offshore reefs, sediments are primarily biogenic (i.e. created by reef organisms) and composed of calcium carbonate, although some siliceous sediments may be present from geological features such as islands or biogenic production from sponges (Rützler and Macintyre 1978). Inshore reefs are subject to greater terrigenous inputs

and therefore can have far higher proportions of silicates alongside considerably different particle size regimes.

In addition to differences in chemical composition, shelf position may affect the sizes of sediment granules differently. Offshore sediments produced *in situ* can be much larger than those from terrigenous sources, which are transported in suspension, and hence have small grain sizes. The size of sediment grains can considerably change the effects it has. Larger grains are less likely to be moved by hydrodynamic forces and are more abrasive to the benthos and/or the digestive systems of any organism that ingests them (Choat 1991). However, they generally do not pack tightly together and as such are less likely to smother the benthos. Conversely, fine terrigenous sediments are easily transported in suspension and are less abrasive. However, once they settle they can form a blanket that prevents transfer of nutrients and gases to the benthos, effectively smothering them. Understanding the effects of the physical and chemical properties of sediments on reef fishes and benthic organisms is crucial if we are to manage sediment output and its impacts on coral reefs. By highlighting the potentially subtle nature of interactions between sediments and ecological processes on coral reefs this thesis has paved the way for these future studies.

All Coral reefs are not 'coral reefs'

Ecosystems created by scleractinian corals are considered coral reefs just as ecosystems dominated by trees are considered forests. However, while it is widely understood that there are many different kinds of forest (e.g. rainforest, cloud forest, sclerophyll, mallee etc.), no such subcategories are in common use for coral reefs. This can lead to a preconception of coral reefs as ecologically homogenous ecosystems. This is not the case.

One of the primary reasons that some coral reefs can survive in high sediment environments is that these reefs are comprised of a fundamentally different assemblage of organisms to those away from sources of terrigenous sediments. Through its physiological and

ecological impacts sediment drives distributions of organisms on coral reefs. High sediment reefs have higher abundances of benthic organisms tolerant of low light conditions and able to shed sediments from their tissues (Stafford-Smith and Ormond 1992; Sofonia and Anthony 2008). While there is an understanding of the effects of sediments in mediating the distributions and abundances of benthic organisms (Done 1982; Acevedo et al. 1989; Larcombe et al. 2001; Wismer et al. 2009), until recently, little was known about the effect of sediments on the distribution of reef fishes.

It is increasingly evident that sediments may affect the distributions of fish communities. Distributions of several herbivorous and detritivorous fish taxa correlate with suspended sediment loads (Cheal et al. 2012). Reefs with high suspended sediment loads often lack many acanthurid species including *Ctenochaetus striatus*, a fish that may facilitate herbivory by reducing benthic sediments (Chapter 5). While this thesis focuses on the impacts of benthic sediments, suspended sediments may have similar influences on reef fishes. Suspended sediments have to be fine grained to remain in suspension, yet in calm conditions may settle on the benthos. No broad scale assessment of links between benthic and suspended sediment loads has been conducted. An understanding of these links is crucial, as this thesis has highlighted the importance of benthic sediments in coral reef ecology, yet current monitoring only considers turbidity/suspended sediment loads.

The dynamics of sedimentation

The size of pulses, the duration of sedimentation events and the effects of hydrodynamics will all greatly alter how sediments interact with coral reef ecosystems. Mechanisms of sediment creation will affect the chemical composition, size structure and mechanism of transport of sediments to coral reefs. In conjunction with a further understanding of the effects of sediment composition on ecological processes, and how the composition of coral reef communities affects their responses it is crucial to understand how the duration and frequency of changes in sedimentation affects ecological processes.

Thresholds at which changes in benthic sediment have effects on coral reefs are unknown, however evidence suggests that even slight changes may have considerable impacts. Perhaps the most useful lesson from the studies conducted in this thesis has been that it is not high sediment loads that affects ecological processes, rather it is changes in sediment that alters ecosystems. All manipulations of benthic sediment conducted in this thesis resulted in significant impacts on ecological processes on coral reefs. As such, future studies may have to be conducted using far finer margins to address how reefs will tolerate increases in benthic sediments.

The future of reefs with sediments

The effects of changing climate, ocean acidification and direct anthropogenic impacts are likely to result in further losses in coral cover on a world-wide scale. There is no such thing as bare space on a coral reef and, as such, the most likely contender to replace benthic cover, following any loss of corals, is EAM (Chapter 2). It is unlikely that functional herbivory will increase in response to increased EAM cover, as coral reef herbivores rarely appear to be resource limited (Shulman 1984). Furthermore, loss of corals can reduce topographic complexity (Graham et al. 2006) with resulting reductions in fish abundance. Increased areas of EAM, therefore, may not be able to be grazed as readily as those on reefs today. This points to the risk of more and longer EAMs. Longer turfs have the potential to trap more sediments than their shorter counterparts. This is particularly worrying, because with increased intensity and frequency of storms, increased runoff as a consequence of larger coastal populations, and potential increases in *in situ* sediment production on reefs, as the remaining coral skeletons are eroded, there is the potential for increased sediment supply to reefs, particularly those near shore.

In addition to the potential for more EAMs being present to trap sediments, climate change may drive the creation of more sediment for the EAMs to trap. The frequency and severity of storms and cyclones is predicted to increase with the changing climate (Emanuel

2005; Knutson et al. 2010). Offshore reefs may suffer increased sediment production through breakage of coral colonies (Madin 2005; Madin and Connolly 2006; Madin et al. 2008), while inshore reefs may suffer increased sediment flux through resuspension (Gagan et al. 1988; Orpin and Ridd 2012) and increased runoff with flooding (Rogers 1990; Larcombe and Woolfe 1999; Fabricius 2005; Haapkylä et al. 2011). Managing anthropogenic climate change is proving to be a seemingly insurmountable challenging on a global scale, and as such we should prepare for potential increases in sediment supply to coral reefs.

What can be managed however are direct anthropogenic inputs of sediment to coral reef areas. By reducing these direct inputs we minimise the effects of sediment to reefs, while long-term practices can be set up to manage the effects of climate change. Farming practices and land clearing are relatively easy to manage (compared to climate change) and have shown promising improvements in sediment output (at least in terms of suspended sediments; Reef Water Quality Protection Plan 2013). Coastal development however has the potential to be a much greater threat. Port developments and expansion of coastal settlements with associated dredging can result in the release and resuspension of large quantities of sediments. A more thorough understanding of the ecological roles of sediment on coral reefs should be gained before these activities occur in the vicinity of coral reefs.

Management practices that consider the role of sediments in mediating ecological processes on coral reefs are crucial. Negative effects of sediments have, as yet, been measured by their impacts on individual organisms. While the death of coral colonies, fish or marine megafauna associated increased sediments is highly undesirable, and often appears in headlines, by affecting ecological processes, sediments may have far more damaging impacts to coral reefs. The processes that underpin diversity and resilience on coral reefs are complex and intertwined. The preliminary work in this thesis suggests that the roles of sediment in these processes are far from simple and that any change in benthic sediments on coral reefs has the potential to have unexpected and potentially long-term consequences.

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Appendix

Appendix 2.1: The Roles of Dimensionality, Canopies and Complexity in Ecosystem Monitoring. Availiable at:

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The Roles of Dimensionality, Canopies and Complexity in Ecosystem Monitoring

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Abstract

Canopies are common among autotrophs, increasing their access to light and thereby increasing competitive abilities. If viewed from above canopies may conceal objects beneath them creating a 'canopy effect'. Due to complexities in collecting 3-dimensional data, most ecosystem monitoring programmes reduce dimensionality when sampling, resorting to planar views. The resultant 'canopy effects' may bias data interpretation, particularly following disturbances. Canopy effects are especially relevant on coral reefs where coral cover is often used to evaluate and communicate ecosystem health. We show that canopies hide benthic components including massive corals and algal turfs, and as planar views are almost ubiquitously used to monitor disturbances, the loss of vulnerable canopy-forming corals may bias findings by presenting pre-existing benthic components as an altered system. Our reliance on planar views in monitoring ecosystems, especially coral cover on reefs, needs to be reassessed if we are to better understand the ecological consequences of ever more frequent disturbances.

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Introduction

Worldwide, the increasing frequency and severity of ecosystem disturbances associated with changing climatic conditions and direct anthropogenic activities has increased the need for ecosystem monitoring. Effective monitoring programmes aim to detect disturbances in time to mitigate their impacts [1,2]. To be effective, these monitoring programmes must be fast and cost-effective, as this facilitates repeated observations, a vital feature to detect changes in ecosystems. While a plethora of methods exist to monitor habitats across various ecosystems, one feature is almost universal among direct monitoring regimes regardless of ecosystem: the use of horizontal planar views in sampling. This standardises monitoring and provides rapid assessments of abundance or cover of organisms [3–5]. A potential concern arises, however, as ecosystems are inherently 3-dimensional. By reducing dimensionality in monitoring we simplify data collection and analysis, but at what cost to the quality of data?

Obviously, recording 3-dimensional data from ecosystems is highly complex and increases the amount of time needed to sample. Reducing dimensionality in sampling is therefore justified if the increased speed and reduced cost improves the spatial and/or temporal resolution of the data being collected. Of the 3 dimensions, however, it has almost always been the vertical component that is discarded first, leaving the horizontal axes. The implications of this reliance on linear or planar views could affect the data collected in ecosystem monitoring, particularly with regards to the detection of disturbances in multi-layered ecosystems. Furthermore, as these methods have often been extended for use in more detailed ecological studies, biases associated with reducing dimensionality could undermine our understanding of key ecological processes in complex ecosystems.

Alongside tropical rainforests, coral reefs are one of the most biodiverse ecosystems on the planet [6]. Furthermore, coral reefs are arguably the most threatened high biodiversity ecosystem. They are highly sensitive to physical and environmental perturbations [7–9]. As such, many monitoring programmes have been implemented, some over several decades [4,10]. The methods used, therefore, are relatively well developed (e.g. [4]), and numerous detailed ecological studies have used similar methods in their data collection [11–13]. Almost all of these methods, however, are based on horizontal linear or planar views, and the most commonly reported metric of reef health is coral cover [10,14]. At present, the limitations of planar or linear views in coral reef studies are poorly understood. Given the fine scale, 3-dimensional structural complexity of corals, coral reefs represent an ideal model ecosystem to consider the effects of reduced dimensionality in sampling methods, and as such they are the primary focus of this study.

Potential problems with planar views

The use of planar views while studying and monitoring ecosystems has the potential to create problems falling into several general categories. The first problem is the development of a 'methodological inertia'. The widespread and historical use of planar sampling techniques (e.g. [15–17]), like blinders on a horse, set a course for future studies to use similar methods. The

simplicity of data collection and interpretation from planar views has exacerbated this problem. Such simple methods can easily be transposed between ecosystems [18–20] and in some cases the ecological or structural differences between these ecosystems may have been overlooked. Modern technologies such as still and video cameras, and even aerial and satellite surveys (e.g. [5,21–22]) have increased the amount of field data that can be collected, however, these images are almost exclusively planar. While the areas sampled may be bigger, the methods are essentially the same.

A second problem is that collecting 3-dimensional data is challenging. This is particularly the case where rapid and repeatable observations are needed, as per most monitoring programmes. Manual collection of 3 dimensional data is impractical. The use of stereoscopic images [23–25] and other recent developments allow some level of 3-dimensional sampling [26,27] but most of these technologies are not widely used in large-scale studies due to the complexity of data collection and analysis. As such, 3-dimensional ecosystems are most commonly monitored in 1- or 2-dimensions.

Potentially the biggest problem with planar views is that the vertical component of ecosystems is often lost during periods of ecological change. By overlooking the vertical relief of ecosystems no data on structural complexity can be derived. However, structural complexity is of considerable importance in facilitating the development of high biodiversity and resilience. A highly complex ecosystem provides cover for prey [28,29], allows predators to find effective ambush sites [30], and increases environmental niches, reducing the severity of physical stresses (e.g. [31,32]). Furthermore, for coral reefs and rainforests alike, one of the most serious post-disturbance effects is the loss of structural complexity associated with the collapse of the biogenic habitat [33–35]. Standard planar or linear views of ecosystems do not provide information on this property, thus their utility in documenting and understanding the effects of disturbance is limited.

The Canopy Effect

Autotrophs' need for light has led to the recurring development of large canopy shaped growth forms to both overtop competitors and increase the surface area exposed to light. These structures almost invariably become biogenic habitats themselves. Using planar or linear views to sample any of these habitats can cause a bias in sampling, in terms of a 'canopy effect'. Perhaps the best conceptual example of this would be from tropical rainforests. While planar views from aerial or satellite imaging provide useful information on the areas covered by these ecosystems, little data is provided on any organisms below the upper canopy as they are hidden beneath it. This effect is not, however, constrained to rainforests. In fact, if any observed substrate has 3-dimensional structure it is likely that the upper layers will obscure those below them. This effect is more acute if the upper layers occupy more horizontal space at elevation than they do beneath (i.e. form a canopy). Canopy effects, therefore, can potentially occur at any scale from microscopic samples in a Petri dish to satellite imaging of entire forest ecosystems.

In comparison to rainforests, coral reefs could be especially prone to canopy effects. Their relatively small vertical elevations mean that, unlike rainforests, we cannot easily observe the ecosystem from within, and as such the layered structure is easier to overlook. Furthermore, pronounced canopies, and the logistical challenges associated with accessing them accentuate this problem. As such, in this study we use data collected from coral reefs to explore and quantify the canopy effect with an emphasis on potential implications in monitoring disturbances.

Coral reefs and the 'canopy effect'

While it might be presumed that coral reefs are coral dominated, this is rarely the case [14,36]. Coral reefs are, of course, defined by the presence of scleractinian corals, but at present they rarely represent the primary benthic cover of these habitats. A meta-analysis revealed that the mean scleractinian coral cover on coral reefs from 88 locations worldwide was 25.9±1.5% (mean ± S.E.; data from [10,37]). As the methods used to collect these data are entirely based upon linear or planar views, from reefs likely to be dominated by canopy-forming species, but without considering a canopy effect, the actual benthic cover of corals is likely to be much lower. Bare space is, however, almost non-existent on most reefs [38–40] and, as such, the remaining three quarters of the benthos of coral reefs is relatively poorly understood (cf. [14,36,41]).

Although corals are arguably the most important organisms on coral reefs, especially in terms of growth and accretion, numerous other benthic organisms play measurable ecological roles on reefs [42–44]. Calcareous and filamentous algal turfs, for example, are ubiquitous components of coral reef flora, potentially occupying more of the reef than corals [14,38,40]. Calcareous turfs aid reef calcification [45–47], while filamentous turfs create an epilithic algal matrix (EAM) containing sediments, detritus and infaunal organisms [48], which can reduce the settlement and survivorship of coral larvae [38,49] and reduce the palatability of turfs to herbivores [50]. The effects of algal turfs are becoming more apparent, yet their actual benthic cover on coral reefs is essentially unknown; we will provide a preliminary estimation of the benthic cover of algal turfs on coral reefs.

Coral reefs are not uniform. Scleractinian corals are phylogenetically and morphologically diverse and different growth forms often dominate different habitats. Exposed reef crests are often dominated by fast growing branching and tabulate corals (e.g. *Acropora* spp.), which form extensive canopies. More sheltered reefs can be dominated by slow growing massive colonies (e.g. *Porites* spp.), which, with mound shaped morphologies offer little canopy cover. If canopy effects have measurable consequences they should be more pronounced on reefs dominated by branching and tabulate corals than those dominated by massive corals.

Methods

We applied three linear transects along the same course: firstly, a planar point intercept transect (hereafter: planar transect) recording the apparent benthic cover visible from above (as would be seen in a photographic image of the reef) at set intervals, secondly a benthic point intercept transect (hereafter: benthic transect), identical to the planar transect except that the actual benthic cover of the consolidated reef matrix (i.e. the benthic cover beneath any overhangs or canopies) was recorded. A comparison of the first two methods highlights the magnitude any canopy effect on that reef. Finally a chain intercept transect (hereafter: chain transect), which conforms to the benthos below the initial tapes provides both a measure of the vertical relief (rugosity; see [51–52]) and the benthic cover across both horizontal and vertical axes (Figure 1). These methods were employed on healthy *Acropora*- and *Porites*-dominated reefs around Lizard Island on the northern Great Barrier Reef to provide a basis on which to illustrate the canopy effect.

Results

The 'canopy effect' hides algae on coral reefs

Regardless of reef type or site, several patterns became apparent when the sampling methods were compared. Most striking is that,

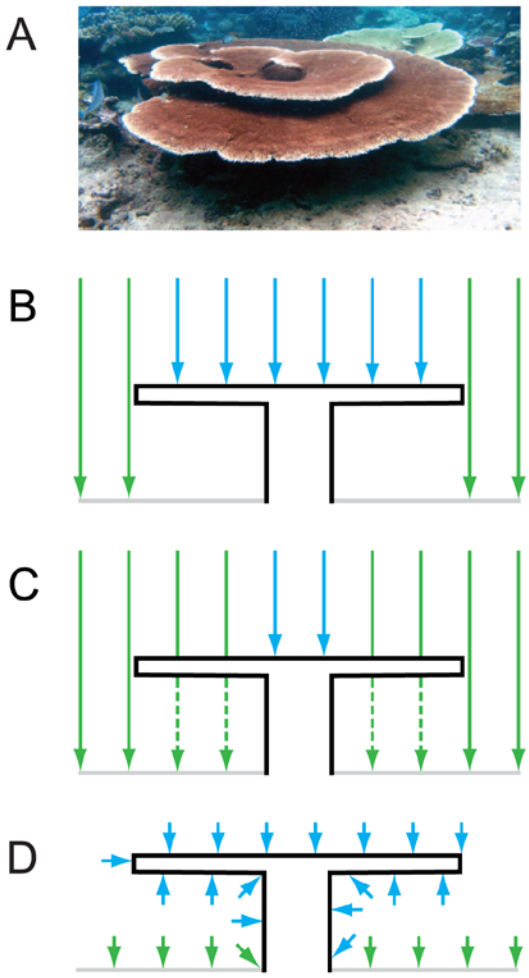

Figure 1. Sampling methods for estimating benthic cover of canopy-forming corals. (**A**) A typical colony of *Acropora hyacinthus* on reefs at Lizard Island. (**B**), A schematic figure demonstrating intercepts (vertical lines; blue = coral, green`other benthos) on a planar transect, coral cover = 60%. (**C**), A schematic figure demonstrating benthic transects, here the dotted vertical lines indicate measurements made beneath the canopy; here coral cover = 20%. (**D**), A schematic figure demonstrating the chain transects, where lines indicate that measurements were made at set distances along a line that conforms to the outline of the coral; here coral cover = 68%.
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using standard planar transects, all reefs showed coral as the dominant benthic component (25.9±2.1% to 54.4±4.9%; mean ± S.E.) and algal turf (EAM) cover as the second most abundant (21.4±1.7% to 34.9±2.7%). Yet when considering cover beneath the canopy (using the benthic transects) a marked change can be seen on the *Acropora*-dominated reefs. The coral cover dropped by almost half from 53.5±2.6% planar cover to 27.7±2.3% in benthic cover. Concurrently, the cover of turf algae (EAM) increased by more than two thirds (from 26.7±2.6% to 44.7±2.6%) becoming the dominant benthic cover on the reefs (Figure 2). The canopy effect essentially hides this portion of the benthos from planar views, and as such, it is overlooked in standard monitoring practices.

Surprisingly, the chain transects, which provide an indication of vertical relief and the surface area of each benthic component, did not provide greatly differing results of coral cover from the planar point intercept transects (coral cover from 29.1±1.5% to 49.0±3.9%). The 'double counting' of canopies increases the proportion of coral cover, much as the canopy effect artificially increases the proportion of the benthos seen to be canopies. While coral cover showed similar results between methods, some benthic components, such as calcareous algae, which tended to grow on vertical surfaces, showed significant differences between the benthic and chain transects (on average, chain transects provided estimates of calcareous algal cover 96.4±21.0% higher than planar transects; Figure S1).

Discussion

Calcification and the canopy effect

Different colony morphologies of corals provide very different functions on reefs. The planar methods used in most monitoring programmes provide only a limited ability to distinguish these functions. For example, the fast growth and high contribution to coral cover of canopy-forming corals are not necessarily related to the amount of carbonate they deposit on consolidated reef structures. Most canopy-forming species have low density, perforate branches that are easily removed by corallivores [53–55] and hydrodynamic forces [56], with much of the carbonate being lost from the reef matrix. As such, with the possible exception of the dense stems of these colonies [57], canopy-forming corals provide a relatively small contribution to reef calcification yet they conceal massive corals and crustose coralline algae that deposit carbonate directly onto the reef matrix. High coral cover, therefore, does not mean high accretion rates [14]. Furthermore, additions to reef carbonates as a result of rubble formation by high cover of canopy-forming corals (e.g. [58]) could be ecologically deleterious as the mobile substrate produced in this process can hinder recruitment of corals and subsequent reef recovery [12,59,60].

Disturbances and the Canopy Effect

The canopy effect, as demonstrated above, influences what we monitor on coral reefs. The overlooked understory has a markedly different composition to the canopy. If reefs were stable, this would result solely in a gap in our ecological understanding of reefs. However, reefs and other ecosystems are most often monitored to observe changes in ecosystem composition brought about by disturbances. The canopy effect is likely to play an important role in our ability to monitor the effects of, and recovery from these disturbances. This may be particularly important if there are differences in the way in which canopy and non-canopy components of the reef respond to disturbances.

Differential susceptibility and disturbances

Differences between coral colonies are more than morphological. Branching and tabulate taxa such as acroporids, which form the majority of the canopies studied herein, are also the most susceptible to environmental and physical disturbances [61,62]. They are among the first corals to bleach under environmental stresses [11], often suffering considerable mortality [63]. Physical disturbances also readily dislodge these colonies from the benthos [56] and many coral predators preferentially target these taxa [53,64,65]. Massive colonies such as *Porites*, in contrast, are more

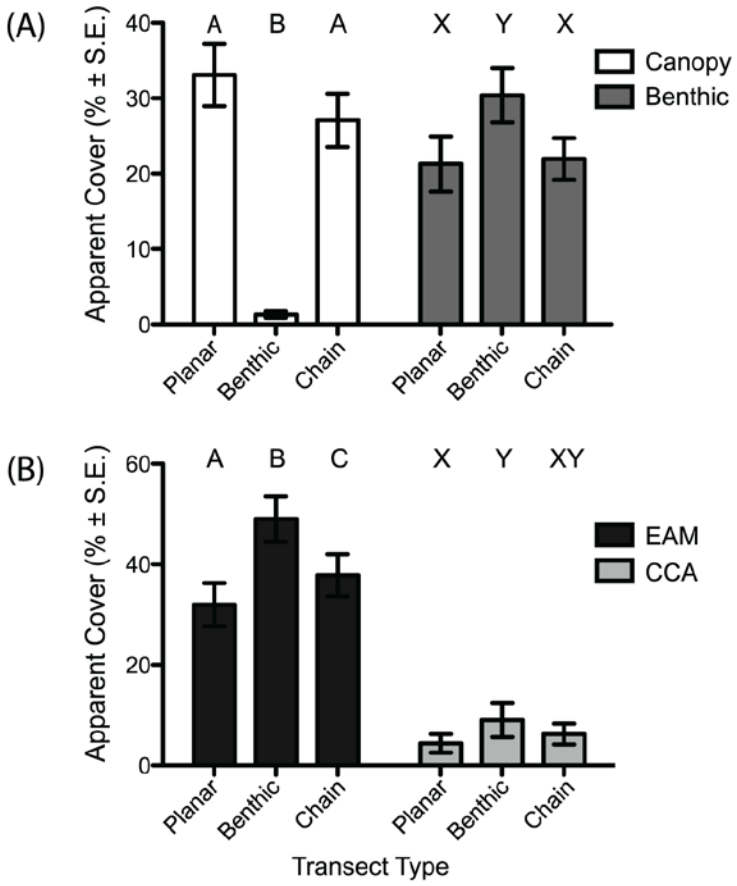

Figure 2. Benthic cover of algae and corals using three transect methods on an *Acropora*-dominated reef. (A) The estimated cover of corals on an *Acropora* dominated reef using the three different transect types; canopy forming taxa in white and benthic cover species in dark grey. **(B)** The estimated cover of algae on the same transects; black bars represent cover of epilithic algal matrix (EAM) and light grey, crustose coralline algae (CCA). A, B, C and X, Y, Z denote statistically different groupings (Repeated Measures ANOVA with Tukey Kramer post-hoc test, $\alpha = 0.05$).
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tolerant to disturbances, being more hydrodynamically stable [56]. They also bleach less readily [63], and are a less favoured prey of corallivores (e.g. [53]).

In almost all cases, canopy-forming corals are most severely affected following disturbances on coral reefs [56,63] and if the colony's skeleton is left intact following the disturbance they are quickly removed from the reef by biological and physical erosion [9,66,67]. The increased susceptibility of coral canopies to disturbances may, therefore, create a bias when monitoring the effects of disturbance on coral reefs.

Canopy loss and coral cover

A simple conceptual model was created using the transect data to assess the magnitude of the canopy effect on *Acropora*-dominated reefs. The high susceptibility of canopy-forming corals to disturbances often results in extensive loss of these corals from reefs [13,60,63]. The model replicates this effect. The start point was set as the mean planar cover of algae and corals found on the two *Acropora*-dominated reefs in this study, using the planar transects. The cover of canopy-forming corals is then reduced by 10% each generation for 62 generations (until canopy cover <0.05%) to simulate a disturbance. Using the inverse of canopy cover and the data from the benthic transects, the apparent change in benthic cover is simulated. The cover of concealed benthic components (end point of the model) was based on the results of the benthic transects (Figure 3). A similar model was created using data from the *Porites*-dominated reefs.

As would be expected, on *Porites*-dominated reefs a total loss of canopy-forming corals causes relatively little change (Figure S2). Overtopping is rare on these reefs, as the colonies of massive corals are too large. The only effects seen with the loss of canopy-forming corals is an equivalent reduction of overall coral cover and similar apparent increase of EAM cover.

In contrast, the effect on *Acropora*-dominated reefs is much greater (Figure 3). As canopy-forming corals are competitively dominant on these reefs, predominantly by overtopping other corals, there is a pronounced canopy effect. The loss of canopy-forming species most obviously reduces overall coral cover.

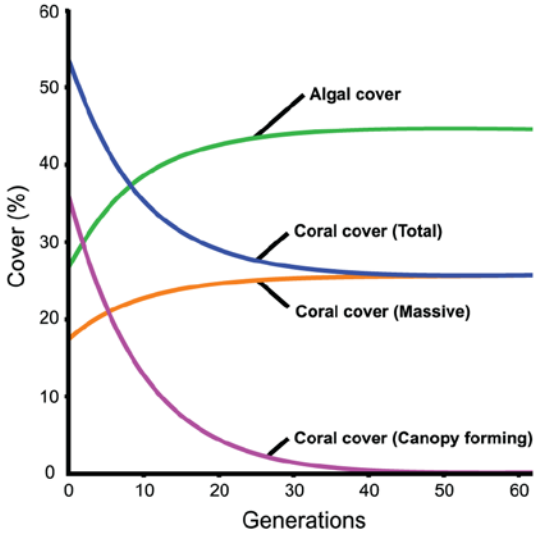

Figure 3. Conceptual model demonstrating the effect of canopy removal on an *Acropora*-dominated reef. Note the apparent increase in both algae (EAM) and massive corals simply as a result of the loss of the canopy. Start points are based on data collected using planar transects. Canopy-forming cover is reduced by 10% each generation. End points are based on data collected using benthic transects (with no remaining canopy).
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However, an apparent 8.2% increase in the cover of massive corals was recorded. This increase indicates that almost a quarter of the space beneath coral canopies was occupied by massive coral colonies. The reported increase in massive coral cover is, therefore, an artefact of using sampling methods based on horizontal planar views in an ecosystem with pronounced canopy effects. However, there are further implications. The recorded loss of coral cover associated with the loss of the canopy is effectively cushioned as the massive colonies are revealed. As coral cover is among the most commonly reported metrics of reef health, the impacts of disturbances may, therefore, be under-reported using planar monitoring methods.

That coral cover provides a somewhat unrealistic measure of the effects of disturbances is not necessarily always this misleading, as most monitoring programmes record far more data than just coral cover. Although there is a clear trade off between precision and spatio-temporal resolution almost all coral monitoring programmes include at least some form of categorisation of the corals observed. Nevertheless, coral cover remains the most widespread metric for communicating reef health. Unfortunately, changing coral cover does not reveal the underlying mechanisms (e.g. recruitment limitation and/or adult mortality), nor can it identify the causes of disturbances. Furthermore, coral cover probably underestimates the magnitude of coral loss and the prevalence of other benthic components. There is the potential, therefore, that researchers may be led astray by just using planar data on reefs and in other 3-dimensional systems.

Canopy loss and algal cover

The removal of a canopy reveals the other benthic components, which on many reefs, including those selected for this case study, are primarily algal turfs (EAMs). Simulated removal of the canopy from *Acropora*-dominated reefs resulted in a 67% increase in cover of EAMs (Figure 3). While phase-shifts to algal dominated states are among the most reported effects following disturbances on coral reefs [47,68,69] our results suggest that in some cases, apparent shifts could simply be due to the canopy effect, with the removal of the coral canopy unveiling a pre-existing algal-dominated state (e.g. [14,70]. No further ecological succession to an alternate stable ecosystem would be necessary to create an apparent phase-shift to EAMs (turfs) following the loss of these canopy-forming species. Furthermore, exposure of this EAM could possibly trigger an expansion of macroalgae (see [68,69,71,72]).

As discussed above, high benthic cover of EAMs has both positive and negative implications for coral reefs. Algal turfs in the EAM provide settlement cues for a variety of organisms including corals [73], and a habitat for infaunal detritivores, which provide a trophic pathway to recycle energy from the detritus (see [41,74]). Furthermore, well-grazed EAMs indicate high levels of herbivory by reef fish or invertebrates (see [72]). However, it is likely that a disturbance that removes a high percentage of branching corals is likely to involve multiple synergistic stressors (e.g. [60,75]). Stressors that affect coral cover may have markedly different effects on the other benthic ecosystem components. The EAM, for example, is considerably more resilient than corals to most environmental perturbations [49,76,77]. Indeed, increased temperatures, sediment and nutrients; all stressors to corals, can be beneficial to the algal component of the EAM [78]. Furthermore EAMs are tolerant of high sediment loads [38,79] and their complex structure slows surface flow and increases sediment deposition [80,81]. Sediment loaded turfs inhibit the settlement of coral larvae [38] and deter herbivores on coral reefs [50]. The effects of multiple synergistic stressors might, therefore, increase the damage done to reefs not just in terms of the amount of coral damaged but in reducing the recovery potential of reefs, even from an apparently pre-existing algal dominated state.

Which sampling method is best?

Each of the methods used in this study have benefits and drawbacks, which are important to consider before designing any study. Planar transects, for example, provide a focussed assessment of more susceptible, canopy-forming species (e.g. *Acropora* sp.). As such, planar transects allow rapid detection of disturbances, such as temperature anomalies, which will provoke stress responses (e.g. bleaching) or localised mortality of canopy-forming species [11,61,62]. Furthermore, planar transects are quick and easy to complete, allowing high replication at any site. Underwater video and photographs can also be used to collect planar data even by inexperienced observers, with minimal training. However, the present study has revealed several drawbacks with this method. Apparent coral loss following major disturbances might be cushioned as less susceptible benthic corals are revealed. Also, by revealing pre-existing benthic communities, canopy loss could lead to misleading reports of phase-shifts with apparent increases in the cover of algae and massive corals (the changes are relative not actual). This method is excellent for studies of tabulate corals but has serious limitations for other benthic components.

Benthic transects provide useful information on the consolidated reef matrix, which has rarely been the focus of previous studies. This substrate is the 'solid' structure underlying the veneer of living corals. Calcification and accretion of the reef matrix allows reefs to maintain their depth with increases in sea-level [82], furthermore, the consolidated reef matrix is often entirely occupied by algae and other benthic organisms, which are often overlooked using planar methods [38–40]. This sampling method also benefits from being relatively straightforward, although video or photographic tran-

sects are probably not possible. Unfortunately, benthic transects provide little information on canopy forming species, and as such, are insensitive to the effects of common disturbances [11,49,76,77]. Benthic transects, therefore, provide an accurate picture of reef composition in terms of the area of substratum occupied. Relatively insensitive to changes in canopy forming species, they more accurately portray the role of algae and other benthic organisms on the reef surface.

The chain transects might appear to provide a more balanced approach to benthic sampling as they concurrently assess both the canopy and benthos. In fact, from the perspective of a fish or settling coral planula, which rely on reef surface area for feeding or settlement respectively, it is perhaps the most relevant measure of reef cover. Furthermore, this is the only method, which includes 3-dimensions. However, for some ecological surveys, the double counting of canopies (i.e. including both the upper and lower surfaces) artificially increases the importance of canopy forming corals. Changes in coral cover of the sensitive, canopy-forming species is thus at risk of being over-reported after disturbances. Massive coral colonies, for example, contribute directly to calcification of the reef matrix but due to their low surface area their loss would not be reported to be as important as high surface area, but structurally delicate, canopy forming corals. The main disadvantage with chain transects is, however, logistical. The complexity of the methods means that replication at any site will suffer and less area will be surveyed. Furthermore, the sampling would rely on experienced observers and becomes much more challenging in adverse conditions (a fact to which the authors can attest).

It appears that a combination of survey methods may be most appropriate. For example, stratified sampling using planar and benthic transects together would allow some increased dimensionality with minimal extra effort. Furthermore the problems of the canopy effect could be overcome, as the cover beneath canopies is recorded and therefore can be included as a correction factor if any changes in canopy cover are observed. It must, however, be highlighted that this study is far from comprehensive and a great many more sampling methods currently exist (cf. [4]). Furthermore, new ecological studies will obviously demand the development of new sampling methods. Similarly, sampling in other ecosystems will require different considerations. There is no simple answer to the question, "which sampling method is best?" The most important messages, highlighted by this study are 1) that it is important to match the census technique to the question and, 2) that it is of vital importance to critically evaluate what any method is actually estimating. The greatest danger is following methodological inertia, choosing methods simply because they have been used before.

Conclusions

The canopy effect has the potential to be pervasive in ecological survey techniques across ecosystems. It is most prevalent in systems dominated by canopy-forming autotrophs as in tropical forests and on coral reefs. The canopy effect, however, is particularly relevant for coral reefs where massive changes are predicted around the world. While planar transects are logistically practical and have a long history of use we must be careful to consider the hidden portions of the benthos, which have the potential to alter our interpretations of the status of ecosystems and how they respond to ever more frequent disturbances. The understories of reefs are not ecologically irrelevant, with diverse algal and coral communities, which, when compared to the canopies, have different susceptibilities and responses to disturbances. Therefore, the current 'coral-centric' view of coral reefs, which are often not numerically dominated by corals, might be misleading. A reliance on planar assessments of coral cover as a proxy for reef health should be reassessed. By looking at both planar and benthic cover we can begin to move beyond simple cover estimates to understand the processes that shape benthic configurations and better understand the impacts of the more frequent and severe disturbances that coral reefs are likely to suffer.

Ethics Statement

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

Supporting Information

Figure S1 Results of the three transect types from four reefs around Lizard Island. A. represents Mermaid Cove and **B.** South-Palfrey, two *Acropora*-dominated reefs. **C.** represents Clam Gardens and **D.** Trawler Beach, two *Porites*-dominated reefs. The left hand portion of the graphs shows the algae recorded using the three methods (light grey = epilithic algal matrix, dark grey = crustose coralline algae). The right hand portion of the graphs shows the results for corals (mid-grey = massive and encrusting colonies, black = canopy-forming species). Notice the consistent decreases in canopy forming corals and subsequent algal increases (especially EAMs) with the benthic point intercept transect.
(PDF)

Figure S2 Conceptual model demonstrating the effect of canopy removal on a *Porites*-dominated reef. Start points are based on planar transect data. Canopy cover is reduced 10% each generation. End points are based on benthic transect data (with no remaining canopy). The 'loss' of canopy cover (difference between planar transects and benthic transects) was almost identical to the apparent increase in benthic algae (6.58% loss vs. 7.23% increase respectively).
(PDF)

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Author Contributions

Conceived and designed the experiments: CHRG DRB. Performed the experiments: CHRG. Analyzed the data: CHRG DRB. Contributed reagents/materials/analysis tools: DRB. Wrote the paper: CHRG DRB.

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Appendix 3.1.1: Sediment suppresses herbivory across a coral reef depth gradient.

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Sediment suppresses herbivory across a coral reef depth gradient

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

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

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Appendix 3.2.1: The role of turtles as coral reef macroherbivores. Available at:

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PLoS one

The Role of Turtles as Coral Reef Macroherbivores

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Abstract

Herbivory is widely accepted as a vital function on coral reefs. To date, the majority of studies examining herbivory in coral reef environments have focused on the roles of fishes and/or urchins, with relatively few studies considering the potential role of macroherbivores in reef processes. Here, we introduce evidence that highlights the potential role of marine turtles as herbivores on coral reefs. While conducting experimental habitat manipulations to assess the roles of herbivorous reef fishes we observed green turtles (*Chelonia mydas*) and hawksbill turtles (*Eretmochelys imbricata*) showing responses that were remarkably similar to those of herbivorous fishes. Reducing the sediment load of the epilithic algal matrix on a coral reef resulted in a forty-fold increase in grazing by green turtles. Hawksbill turtles were also observed to browse transplanted thalli of the macroalga *Sargassum swartzii* in a coral reef environment. These responses not only show strong parallels to herbivorous reef fishes, but also highlight that marine turtles actively, and intentionally, remove algae from coral reefs. When considering the size and potential historical abundance of marine turtles we suggest that these potentially valuable herbivores may have been lost from many coral reefs before their true importance was understood.

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Introduction

Herbivory is widely recognised as a vital process for the health and resilience of coral reefs [1–3], mediating the competition for benthic space between algae and reef-building corals. When present in sufficient densities herbivores can maintain algal communities in a cropped state, preventing the proliferation and expansion of macroalgal communities [4,5]. However, reductions in herbivory through both small-scale experimental exclusions and regional-scale overfishing have demonstrated that, when released from top-down control, algal assemblages can shift from highly productive algal turfs to less productive, late successional stage macroalgae such as *Sargassum* [1,6–8]. As such, herbivores are widely viewed as a key component of the resilience of coral reefs [9,10]. To date, quantitative studies of herbivory on coral reefs have focussed on the roles of fishes and/or urchins [4,11,12]. Few studies have considered the role of macroherbivores in coral reef ecosystem processes [9,13].

Worldwide, almost all populations of marine macroherbivores have suffered drastic declines. For example, many marine turtle populations have been estimated to be below 10% of their historical baselines [14,15], while estimates of sirenian (dugong and manatee) populations suggest they are less than 3.1% of baselines [15,16]. By underestimating the historic anthropogenic impact on populations of sirenians and turtles, both the natural population densities and ecological roles of these species have, until quite recently, been largely overlooked [14–16]. At 'baseline' populations, many species of sea turtles may have had important ecological roles structuring their various prey communities [17]. Hawksbill turtles *Eretmochelys imbricata*, have been shown to structure sessile invertebrate communities [18–20], while green turtles, *Chelonia mydas*, appear to have been the primary herbivores of seagrass beds in the Caribbean [21] and may still structure seagrass communities when they are abundant [22].

Both green and hawksbill turtles have circumtropical distributions and occupy a range of habitats, including seagrass beds, coral and rocky reefs, and oceanic waters. Green turtles, while often considered to be consumers of seagrass [23], can contain substantial proportions of macroalgae characteristic of reef environments in their stomachs [24–27]. Reports of herbivory by adult hawksbill turtles are less common. Hawksbill turtles are primarily predators of sponges [18,28] or other sessile invertebrates [19,29], but may also consume small amounts of algal material in some areas [30,31]. In all cases it is not certain if the algae are directly targeted or if they are removed from the benthos or floating algal rafts. Hawksbill and green turtles frequent coral reefs throughout their range but their role as herbivores in these ecosystems remains poorly understood [9,20].

Within coral reef systems herbivores may be broadly categorised into two functional groups (i.e., grazers and browsers) based on the algal material they remove and consequently the roles they perform in reef processes [32,33]. Grazers typically feed on algal turfs or epilithic algal matrix (EAM; [34]) and play an important role in helping reefs to resist shifts to alternate states and reassemble following disturbances [9,10]. In contrast, browsing taxa feed on leathery macroalgae and play a potentially critical role in the reversal of shifts to macroalgal-dominance on coral reefs [33,35]. On reefs, herbivorous species rarely fulfil both functional roles and there is often little redundancy within functional groups [9,36]. Furthermore, recent studies have shown that many of these fishes have relatively small home ranges

(<10ha; [37–40]), suggesting their functional impact may be spatially restricted. The morphological and taxonomic distinctness of turtles might suggest that they could play unique roles on reefs. Using observations taken during experimental habitat manipulations and transplanted macroalgal assays we present evidence to highlight the potential roles of marine turtles as both algal turf grazers and macroalgal browsers in coral reef environments.

Methods

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

This study was conducted on the reefs surrounding Lizard Island (14°40′S 145°28′E), in the northern Great Barrier Reef (GBR; Fig 1). Two experimental manipulations: sediment reductions of algal turfs and macroalgal assays were performed to assess the ecological roles of coral reef grazers and browsers, respectively. While these experiments were primarily focused on the roles of herbivorous fishes [36], responses by marine turtles were also recorded and are reported herein. The sediment reductions were conducted on the exposed reef flat to the south-east of the island at a depth of 2–4 m, whilst the macroalgal transplants were conducted within six habitats of varying depth and wave exposure: the exposed reef crest (2–4 m depth), exposed reef flat (1–2 m), back reef (2–4 m), patch reef (4–6 m depth), sheltered reef flat (1–2 m) and sheltered reef base (6–8 m; Fig 1). See [36] for detailed description of habitats.

Sediment Reduction

The exposed reef flat was selected as it has a high cover of EAM [12,41] and is adjacent to the area of highest herbivory (i.e. exposed reef crest). The high sediment load of the EAM in this habitat has been proposed to limit grazing by reef fishes [42]. Two adjacent 0.75×1.5 m plots that were devoid of living coral and covered by EAM were temporarily delineated using a PVC frame. One of the plots was randomly selected and cleared of sediment using a compressed air powered airlift (hereafter 'cleared plot') while the adjacent plot was left undisturbed (hereafter 'control plot'). Underwater video cameras (Sony DCR-SR100 HDD cameras in Ikelite housings), mounted on tripods, were then deployed for three hours to record the feeding activity of herbivores on the cleared and control plots simultaneously. Filming was continuous for the 3-hour experimental period with the PVC frame and a small scale bar being placed on the focal plane of the EAM in the experimental plots for approximately 10 s allowing calibration of experimental plots and turtle sizes from the video footage. This procedure was repeated until ten replicate plots had been recorded. Replicate plots were separated by at least 10 m.

The lengths of algal turfs within the plots were measured before and after the 3-hour experimental period. The heights of 20 randomly selected algal filaments were measured from both the cleared and control plots using the depth probe of vernier callipers. Data were analysed using a two-way fixed factor analysis of variance (ANOVA) followed by residual analysis to ensure assumptions of the test were met.

Macroalgal Assays

To quantify browsing intensity across the six habitats a series of macroalgal assays were conducted. *Sargassum swartzii* (Ochrophyta: Phaeophyceae) was collected from an inshore reef in the Turtle Island Group (28 km west of Lizard Island). Similarly sized thalli (mean weight [± S.E.] = 363.6±4.7 g) were transplanted to each of two haphazardly selected sites within each of the six habitats for 8-hours (approx. 07:30–15:30). Adjacent sites within each habitat were separated by a minimum of 50 m. Underwater video cameras (Sony DCR-SR100 HDD camera in Ikelite housing) mounted on concrete blocks were used to record feeding activity on the transplanted *Sargassum* for the 8- h experimental period within each habitat (see [36] for detailed description).

Figure 1. Site map. The filled square represents the location of the sediment removal study, where green turtles (*Chelonia mydas*) were observed feeding. The filled circle to the north represents the sheltered reef base and to the south the back reef. At both sites hawksbill turtles (*Eretmochelys imbricata*) were observed feeding on transplanted *Sargassum* assays.
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Video Analyses

The video footage from both experimental manipulations was examined and all bites by turtles on the EAM within the cleared and control plots, and the transplanted *S. swartzii* thalli, were recorded. Turtles were identified to species and size (straight carapace length, SCL) was estimated. Throughout this study, results are presented as means ± standard error.

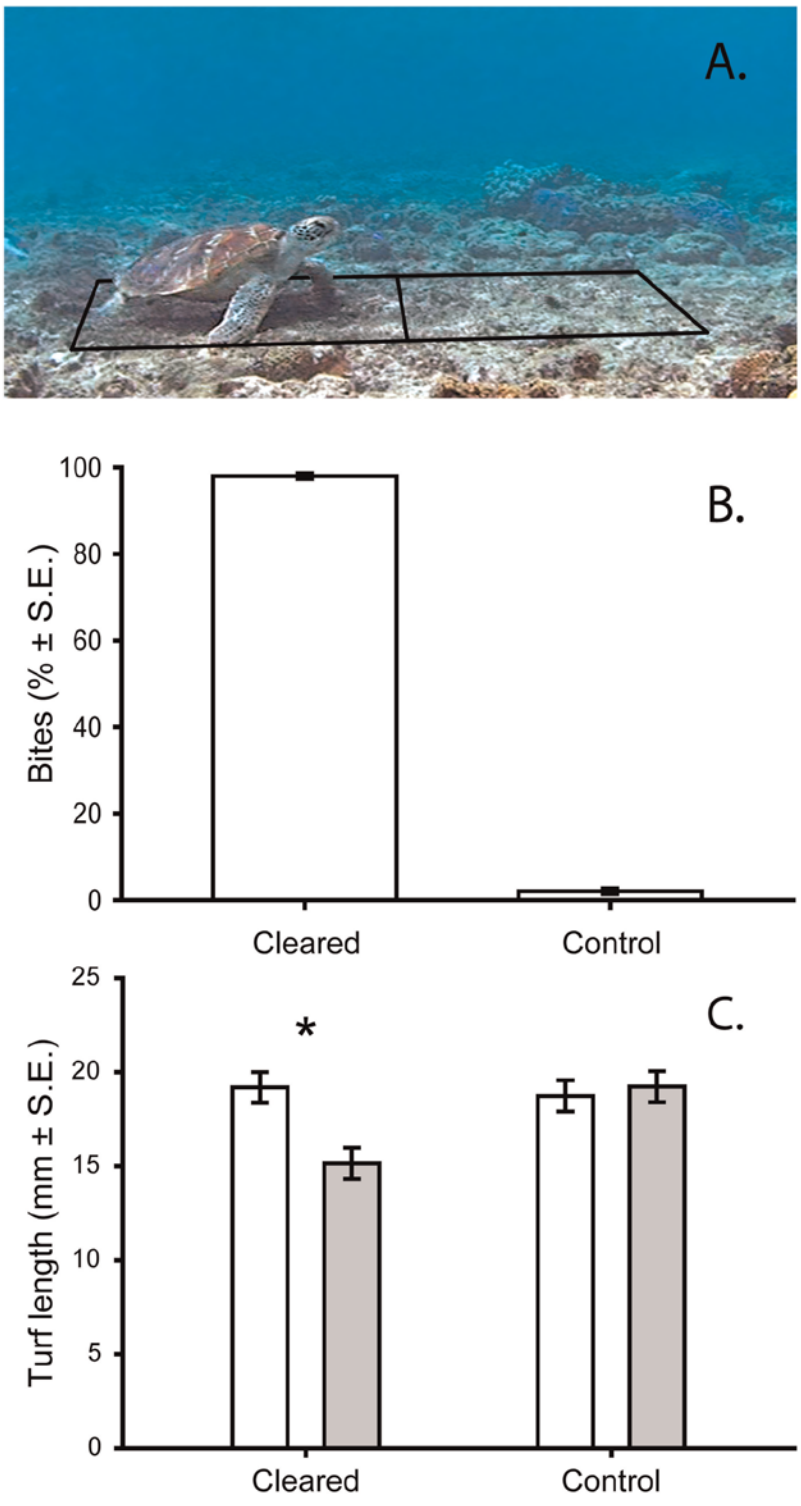
A.
B.
Bites (% ± S.E.)
100
80
60
40
20
0
Cleared
Control
C.
Turf length (mm ± S.E.)
25
20
15
10
5
0
*
Cleared
Control

Figure 2. Grazing by the green turtle (*Chelonia mydas*) on sediment reduced plots. A Image capture of a green turtle feeding on the experimental sediment clearance plot. The lines represent the boundaries of the two adjacent plots: the sediment clearance plot to the left, and the control plot to the right. **B** The proportion of bites made in the cleared and control plots by green turtles during the three-hour experimental period (n = 3 plots). **C** The reduction in turf length observed in three hours in the cleared and control plots respectively. White bars represent the mean initial length and grey the mean final length (n = 3 plots for each treatment), * indicates a significant difference (Tukey's HSD).
doi:10.1371/journal.pone.0039979.g002

Results

Reducing the sediment loads in the EAM on the exposed reef flat resulted in over forty times more grazing pressure on algal turfs by the green turtle, *Chelonia mydas* (Fig. 2a). In total 585 bites were recorded over nine feeding bouts on three of the ten experimental plots. Each feeding bout lasted approximately four and a half minutes (4:36±0:42; see video S1); between bouts the turtles were observed to remain near the plots but did not feed. Where turtles fed, grazing was overwhelmingly on the cleared plots (98.0±0.7% of bites; Fig. 2b). Size estimates of the green turtles observed feeding revealed at least three turtles were feeding on the plots, with a mean length of 56.0±4.5 cm (SCL).

The higher herbivory resulted in a 21.2% reduction in algal turf height in the three cleared plots grazed by turtles in just three hours (Fig. 2c; $F_{1,\ 232} = 6.47$, $p = 0.01$). Grazing by both herbivorous fishes and green turtles will have contributed to this reduction and it is impossible to attribute the cause of the reduction to either group, in fact, the reduction observed did not differ from that seen in plots without turtles (21.4%). Herbivorous reef fish, however, appeared to be deterred by the presence of turtles, and as such, the presence of a single turtle appeared to have comparable effects to multiple reef fishes. The large size and large number of bites made by turtles might indicate a possibly important role.

Analysis of 288 hours of video footage of the *S. swartzii* assays across the six habitats revealed that while most browsing was by fishes, two turtles were recorded feeding on the *Sargassum*. Both were hawksbill turtles, *E. imbricata*, (approx. 58 cm SCL), with one being recorded to feed on *Sargassum* in the back reef habitat, and the other in the sheltered reef base (Figs. 1, 3; videos S2 and S3). On each occasion the turtles took three bites from the *Sargassum*.

Discussion

Our results provide observational evidence that marine turtles may function as both grazing and browsing herbivores on coral reefs. Collectively, green and hawksbills turtles displayed responses to sediment reductions of algal turfs and macroalgal assays that were remarkably similar to those of herbivorous fishes. While we were unable to isolate the effects of turtles from those of fishes in reducing the algal biomass, our observations clearly show that marine turtles are actively targeting and removing both algal turfs and leathery macroalgae from coral reef habitats. We postulate that, in doing so, turtles may potentially play a role in important ecological processes on coral reefs.

Numerous studies have advocated the importance of herbivory to reef health and resilience, focusing on the roles performed by herbivorous fishes [2–4,9,12,36]. Fishes, while undoubtedly playing a key role in reef processes, lack some important morphological and behavioural traits of larger organisms. Larger animals, having larger mouths, usually take larger, more forceful, bites, and as such may be expected to have greater functional impacts [43,44]. While the general scarcity of macroherbivores reduces the net benefits of size, larger individuals can offer greater

Figure 3. A hawksbill turtle (*Eretmochelys imbricata*) feeding on a transplanted thallus of the brown macroalga *Sargassum swartzii*.
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ecological benefits in terms of mobility and may complement the roles of herbivorous fishes and urchins on coral reefs.

Ecological resilience may derive from overlapping function within scales, and reinforcement across scales [45]. Within coral reef systems, even some of the largest herbivorous reef fishes have relatively small home ranges. For example, the grazing steephead parrotfish, *Chlorurus microrhinos* (maximum length 80 cm) has a home range of less than 1 ha [40] and large browsing herbivores, such as the bluespine unicornfish, *Naso unicornis* (maximum length 70 cm) maintain home ranges well under 10 ha [37,39]. As such, the ability of herbivorous reef fishes to respond to phase shifts appears somewhat limited by their spatial distribution; truly wide-ranging or roving reef herbivores may be rarer than previously assumed. Marine turtles, however, have far larger home ranges (over 3900 ha [46]) and often undergo large migrations [47–49]. We suggest that, regardless of phylogeny, large mobile herbivores with large home ranges could play any ecological roles on reefs at a broad scale, providing a function not yet observed on reefs.

Grazing by Green Turtles, *Chelonia Mydas* on Coral Reefs

Green turtles made over forty times more bites on plots of algal turfs (EAMs) that had been subject to artificial sediment reduction than those with natural sediment loads. The observed behaviour of green turtles mirrors that seen by fishes in the only other study using sediment reductions on coral reefs [42]. Why sediment suppresses herbivory is unclear, but is likely to be associated with diminished accessibility of resources and reduced energy uptake per bite [50,51]. Regardless of the cause, it appears that natural sediment loads in coral reef EAMs are enough to suppress herbivory on coral reefs across multiple herbivorous taxa.

The large size of green turtles compared to herbivorous reef fishes suggests they could play a greater functional role per-individual than herbivorous fishes. However, as turtles were not observed to respond differently to fishes, well-grazed reefs may not gain any potential benefits from increased turtle grazing. Larger turtle populations might not act as an alternative to current management techniques, only to supplement them.

Green turtles are well known as herbivores (Table S1), however most studies have used gut contents data to determine what algae the turtles have consumed. While analysis of gut contents clearly indicates what the study animal has ingested, it provides no indication of the source of the prey. As such, the propensity of green turtles to feed on coral reefs has remained unclear. The source of ingested algae could have been non-reefal hard substrates or flotsam. Furthermore, grazing of algal turfs is likely to be under-reported in gut contents analyses, as algal filaments are small and difficult to identify. Our observations demonstrate that green turtles do actively consume turf algae from coral reef environments. Furthermore they respond to turf-associated sediment in a manner comparable to fishes [42].

Browsing by Hawksbill Turtles, *Eretmochelys Imbricata* on Coral Reefs

Although few bites were videoed, the evidence presented herein supports previous observations by the authors of turtles feeding on leathery macroalgae on both algal dominated inshore reefs and offshore coral dominated reefs on the GBR. Previous studies using gastric lavages or dissections have demonstrated that sponges and other sessile invertebrates account for over 95% of the diet of *E. imbricata*, with macroalgae only representing a very minor component (Table S2). However, similarly to those for green turtles, these studies do not provide information on the source of the small proportions of macroalgae ingested by hawksbill turtles, which could have been ingested incidentally when feeding on sponges or from floating algal mats. Our observations indicate that adult hawksbill turtles may be actively targeting and ingesting leathery macroalgae when available on coral reefs.

Historical Roles, Shifting Baselines and Generalist Herbivory

The concept of shifting baselines on reefs [52,53] is of particular relevance when considering macroherbivores as they show some of the quickest declines after human exploitation [54]. Marine turtles, along with most marine macrofauna have been hunted for considerably longer than their populations have been monitored; as such, estimates of historical populations are hard to derive and highly variable [14,15,55].

Regardless of the actual figures, turtle populations have suffered considerable depletion worldwide [56–58]. Only after the depletion of Caribbean green turtle populations did their role as the principal grazer of seagrass communities become apparent (cf. [23]). Some modern populations of turtles can control and even overgraze some marine habitats [22], further highlighting that even at low densities turtles have the potential to play significant roles in marine ecosystems.

We speculate that, although each species was only seen to feed on one functional group of algae (green turtles on EAMs and hawksbills on leathery macroalgae), and in combination with previous reports of the diets of marine turtles (Tables S1 and S2), contrary to most fish taxa, marine turtles might represent a trophically flexible group of herbivores on coral reefs. As the resilience of coral reefs is often reliant on numerous roles provided by individual species or small functional groups [10,36,59], large generalist herbivores would be particularly valuable, as they would provide a measure of redundancy across a wide array of functions. Reported dietary shifts with changes in prey abundances by turtles highlight their potential as ecological stand-ins [60]. At current population densities, however, the scarcity of turtles means that, even if turtles were generalist herbivores they would be unlikely to be able to replace any lost ecosystem function. Furthermore, the capacity for fishes to take over the roles of turtles is limited [35]. Of the 60–70 species of nominally herbivorous fishes found on the Great Barrier Reef less than 10 have been found to feed on leathery macroalgae, and in each case they have highly restricted diets [35,61]. Turtles may, therefore, provide a unique combination of size, mobility and dietary flexibility that is unlikely to be matched by fishes.

While recent conservation efforts have yielded encouraging results [57], threats to turtles are not restricted to hunting and bycatch. Changing environmental conditions and sea level rise are a particular threat to turtles, which are reliant on specific nesting beaches and have temperature dependent sex ratios [62–64]. These threats are far more challenging to manage than those from exploitation and the future for turtle populations remains uncertain. The population declines and continuing threats to marine turtles may, therefore, mean that coral reefs might have lost, what may be, their largest generalist macroherbivores before their role was fully understood.

Supporting Information

Video S1 Green turtle (*Chelonia mydas*) feeding on algal turfs. The darker area to the left of the frame is cleared of sediment.
(MOV)

Video S2 Hawksbill turtle (*Eretmochelys* imbricata), feeding on *Sargassum swartzii* assay at the back reef (see Fig. 1).
(MOV)

Video S3 Hawksbill turtle (*Eretmochelys* imbricata), feeding on *Sargassum swartzii* assay at the sheltered reef base (see Fig. 1).
(MOV)

Table S1 Summary of previous dietary studies of the green turtle, *Chelonia mydas*. Values represent percent volume of each dietary category. Where quantitative estimates were not available †† indicates the dominant component, and * indicates presence as a minor component. Literature cited referenced in Appendix S1.
(PDF)

Table S2 Summary of previous dietary studies of the hawksbill turtle, *Eretmochelys imbricata*. Values represent percent volume of each dietary category. Where quantitative estimates were not available †† indicates the dominant component, and * indicates presence as a minor component. Literature cited referenced in Appendix S1.
(PDF)

Appendix S1 References cited in tables S1 and S2.
(DOC)

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Author Contributions

Conceived and designed the experiments: CHRG ASH DRB. Performed the experiments: CHRG ASH. Analyzed the data: CHRG ASH. Contributed reagents/materials/analysis tools: CHRG ASH DRB. Wrote the paper: CHRG ASH DRB.

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Appendix 3.2.2. Green turtle (*Chelonia mydas*) feeding on algal turfs. The darker area to the left of the frame is cleared of sediment. See video at: http://www.plosone.org/article/fetchSingleRepresentation.action?uri=info:doi/10.1371/journal.pone.0039979.s001

Appendix S3.2.3: Hawksbill turtle (*Eretmochelys* imbricata), feeding on *Sargassum swartzii* assay at the back reef (see Fig. 3.2.1). See video at: http://www.plosone.org/article/fetchSingleRepresentation.action?uri=info:doi/10.1371/journal.pone.0039979.s002

Appendix 3.2.4: Hawksbill turtle (*Eretmochelys imbricata*), feeding on *Sargassum swartzii* assay at the sheltered reef base (see Fig. 3.2.1). See video at: http://www.plosone.org/article/fetchSingleRepresentation.action?uri=info:doi/10.1371/journal.pone.0039979.s003

Appendix 4.1: Ecological consequences of sediment on high-energy coral reefs. Available at: http://www.plosone.org/article/info:doi/10.1371/journal.pone.0077737

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Ecological Consequences of Sediment on High-Energy Coral Reefs

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Abstract

Sediments are widely accepted as a threat to coral reefs but our understanding of their ecological impacts is limited. Evidence has suggested that benthic sediments bound within the epilithic algal matrix (EAM) suppress reef fish herbivory, a key ecological process maintaining reef resilience. An experimental combination of caging and sediment addition treatments were used to investigate the effects of sediment pulses on herbivory and EAMs and to determine whether sediment addition could trigger a positive-feedback loop, leading to deep, sediment-rich turfs. A 1-week pulsed sediment addition resulted in rapid increases in algal turf length with effects comparable to those seen in herbivore exclusion cages. Contrary to the hypothesised positive-feedback mechanism, benthic sediment loads returned to natural levels within 3 weeks, however, the EAM turfs remained almost 60% longer for at least 3 months. While reduced herbivore density is widely understood to be a major threat to reefs, we show that acute disturbances to reef sediments elicit similar ecological responses in the EAM. With reefs increasingly threatened by both reductions in herbivore biomass and altered sediment fluxes, the development of longer turfs may become more common on coral reefs.

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Introduction

Coral reefs are among the most biodiverse ecosystems on the planet. Despite the ecological and physical complexity associated with this biodiversity, they are remarkably fragile. The increasing rate of disturbances associated with climate change and other anthropogenically induced stressors has repeatedly highlighted that acute stressors can have long lasting impacts [1,2]. For example, temperature anomalies lasting for very short periods can result in bleaching events, which have long-term effects at reef-wide scales [3]. While temperature anomalies might be the best understood, there are many other acute threats to coral reefs. These include storms, freshwater inundation and, potentially, sediments.

The source of sediment on coral reefs affects its physical and chemical properties. Fine marine (primarily carbonate) and terrigenous (primarily silicate) sediments can be transported long distances in suspension and/or driven by hydrodynamic activity [4]. While these sediments can be particularly deleterious to coral reefs, blocking light penetration and, upon settling, producing blankets of smothering silt [5], their affects tend to be best-documented on near-shore reefs [6]. The proximity to the sources of terrigenous sediments and shallow waters allow sediments to be effectively resuspended and transported to these reefs [4]. On reefs further from shore, however, most sediment is produced *in situ* as the reef matrix is eroded into sediments by physical, biological and, chemical processes [7].

While benthic sediments are highly dynamic on offshore coral reefs [8,9]. The continual production of sediments through erosion is often balanced by hydrodynamically driven losses to deep water or accretion into cays or beaches [8]. As such, although the sediment is constantly moving, the system remains in a state of dynamic stability [10,11], with all but the most severe perturbations being short lived [12].

On hard coral reef substrata some sediment exists in sand patches, but a large proportion of the benthic sediment is bound within algal turfs [13–16]. The turfs also trap detritus and provide habitat for infaunal organisms [17,18]. Together, these components form an epilithic algal matrix (EAM; [19]); a ubiquitous feature of coral reefs, often occupying more benthic space than corals [16,20]. On the Great Barrier Reef, EAMs

cover between 18 and 59% of the reef surface [21]. While EAMs can play positive roles on coral reefs, with some components providing settlement cues for corals [22] and others directly adding to carbonate accretion [23], they also have several deleterious impacts. Algae within the EAMs can compete with corals for space [24,25], increase sediment deposition [26,27] and reduce the settlement success and survivorship of juvenile corals [28,29]. The algal turfs in EAMs can also represent an early stage in successional growth of macroalgae on reefs [30,31].

On 'healthy' coral reefs, EAMs are maintained as well-cropped productive turfs by herbivores, usually reef fishes [32]. The intensity of herbivory by fishes on these reefs can control the growth of algae [33–35]. While herbivory is clearly a vital function on coral reefs, recent evidence suggests that sediments may affect reef fish communities [36,37], and furthermore, sediments trapped in the EAM can deter herbivores from feeding [10,11]. Sediment reductions result in almost instantaneous increases in rates of reef fish herbivory and measurable declines in algal turf length in less than four hours [10]. The increased herbivory with reduced sediment loads indicates that trapped sediments actively deter herbivores, however, evidence for sediment suppression of herbivory remains almost entirely based on sediment removal experiments, which report increasing herbivory following sediment reductions [10,11]. Yet questions remain: a) will an increase in sediments produce similar changes in herbivory? And b) are these effects long-lasting or temporary? This is particularly interesting as increased sediments are believed to pose an ongoing threat to coral reefs [5,38].

The interactions between benthic sediment and herbivory suggest the possibility of a positive feedback loop. Any disturbance leading to increased EAM sediment load, such as exposure to a sediment plume from storms, flooding or dredging could deter herbivores. The reduced top down pressure on the EAM is likely to result in an increase in EAM length [10], allowing further sediment trapping [27,35]. The potential result is a self-sustaining, long, sediment-rich EAM, unpalatable to herbivores. Using a combination of herbivore exclusion cages and pulsed sediment additions we attempt to initiate this positive feedback and generate a deep, sediment-rich EAM. In doing so, we will provide information on the relative impacts of sediment pulses and herbivore removal on coral reef resilience.

Materials and Methods

Ethics statement

All procedures were conducted according to the ethics guidelines of James Cook University, Townsville (ethics approval A1522), and permitting requirements of the Great Barrier Reef Marine Parks Authority (permit number: G10/33755.1). Data are available in the supplementary material (Table S1).

Experimental procedures

Experimental manipulations were conducted at two sites on the exposed reef crest southeast of Lizard Island in the northern section of the Great Barrier Reef, Australia. The experiment was conducted between December and March, in the southern hemisphere summer. The sites had similar topographies, were at a depth of 2-4 m, and separated by over 800 m. Sites were characterised by sparse coral colonies, separated by expanses of short well-cropped EAMs on a flat, low-complexity reef matrix. At each site, six fully caged, six open (uncaged) and six partially caged 1 m^2 plots were haphazardly delineated on the flat EAM. Full cages were constructed of a steel bar frame, 25 cm high, enclosing the 1 m^2 plot, attached to the reef using epoxy putty and enclosed with galvanised 4 cm wire mesh. Partial cages were constructed of vertical panels identical to those used in the fully caged treatments and were deployed to control for any effect of the cage treatments on the EAM or sediment, while allowing herbivores access to graze the EAM.

Half of the plots in each cage treatment were subjected to an experimental sediment addition. In these addition plots, a sediment load of 8.6 kg m^{-2} was maintained for one week. This sediment load was equivalent to that on the adjacent reef flat (approximately 40 m leeward of the crest), which was determined by weighing dried sediment samples collected using an electric vacuum sampler from 20 replicate 5.8×10^{-3} m^2 rings (see [39]). The sediment for treatments was collected from a reef-margin sand apron and had a similar particle size profile to that found on the reef flat. When evenly spread, the 8.6 kg of sediment covered the 1 m^2 plot to a depth of 15 mm. Sediment was added daily to each plot to maintain this depth for one week, simulating an acute sedimentation event. Then the plots were left undisturbed for the remainder of the three-month experimental period.

The sediment depth and EAM turf length in each plot were recorded using the depth probe of vernier calipers (n = 20 reps for each plot). Measurements were made as sediment was initially manipulated (T_0), then at weekly intervals for 6 weeks post-manipulation ($T_{1\text{-}6}$), and again after three months (T_7).

EAM turf length data were standardised to percent increase over initial turf length (at T_0) correcting for initial variation among plots. The data were then analysed using 2- and 3-way analyses of variances (ANOVAs) of the T_7 data. Site was categorised as a random factor and was found to have no significant effect or interaction. It was therefore pooled to increase the power of the analysis [40,41]. Data normality was assessed using residuals plots and square-root transformations were applied where necessary. To allow data transformation for statistical analyses, negative percent EAM turf length values were removed by the addition of a constant to all data. Time series data were analysed using 2- and 3-way repeated measures ANOVAs (RM ANOVAs). Multivariate comparisons (Pillai's Trace; RM MANOVAs) were used if assumptions of sphericity were violated.

Results

After three months (T_7) the greatest increase in the length of algae in the EAM was seen in the caged plots and a significant difference in turf length was observed between the caged and open plots (Figure 1; 3-way ANOVA on square root

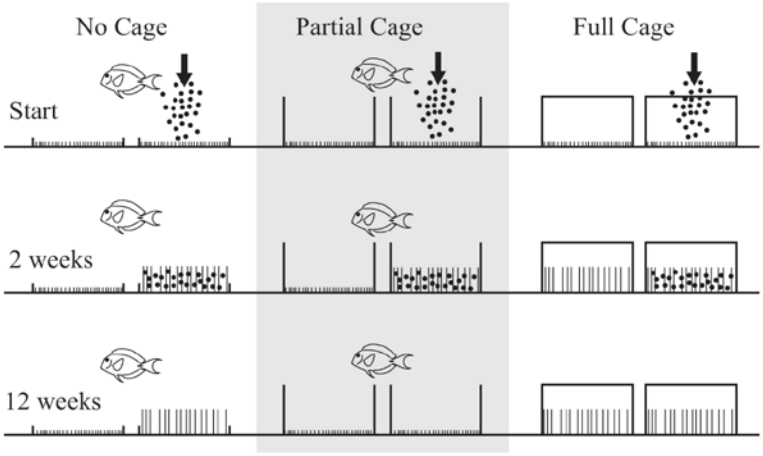

Figure 1. The effects of the experimental manipulations, at sediment addition, 2 and 12 weeks. Black circles represent added sediment and vertical lines the relative length of turfs in the EAM. Fishes indicate where herbivores had access to the plots.
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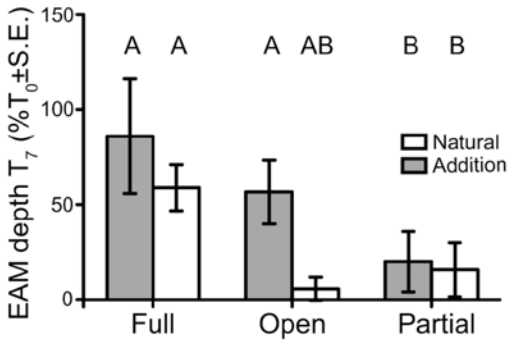

Figure 2. EAM turf lengths at T_7 (3 months post sediment addition). Filled bars represent sediment addition treatments and open bars natural sediment treatments. A and B denote significant groupings (Fisher's LSD). Data are shown as percentage of T_0 ± standard error, sites are pooled, therefore n = 6 replicates for each.
doi: 10.1371/journal.pone.0077737.g002

transformed data: $F_{2,24}$ = 7.32, P = 0.003). While no other factors or interactions were significant (Table S2), a Fisher's least significant difference (LSD) post-hoc test revealed two groupings in the caging × sediment treatment interaction (Figure 2). Without sediments, a clear cage effect was observed. Algal length increased by 58.9%; no response was seen in the open or partial cages.

Sediment additions to caged and partially caged plots resulted in no observable differences to the EAM when compared to the corresponding natural sediment plots. Sediment additions to the open plots, however, resulted in remarkable EAM turf algae growth, i.e., over 435% greater than observed on open, natural sediment treatment plots (Figure 2).

The time series data showed an initial rapid increase in turf length followed by an apparent asymptote after approximately three weeks (Figure 3). Data differed significantly over time (RM MANOVA; Pillai's Trace = 0.647, $F_{6,25}$ = 7.639, P <0.0001) and in the time × caging interaction (Pillai's Trace = 0.636, $F_{12,52}$ = 2.022, P = 0.041). No other factors showed significant interactions (Table S3).

Direct measurements of the sediment loads in the EAMs were conducted alongside measurements of the EAM turf length. Unlike the turf length, sediment rapidly declined in all treatments to levels indistinguishable from natural sediment loads within three weeks (Figure 4; Table S4).

Discussion

We found that a one-week pulsed increase in sediment loads resulted in significant and sustained (3-month) increases in the length of turfs in EAMs on a coral reef (Figure 1). However, our results provide only limited support for the existence of the proposed positive feedback loop. Although the length of turfs increased, high hydrodynamic activity on the crest (e.g. [42]) quickly removed sediment from the turfs and the predicted deep, sediment-rich turfs were not formed. Increased EAM turf length did not appear to require high sediment loads.

The EAMs on the exposed crest used in this study are heavily grazed by coral reef fishes, which maintain short, productive algal turfs [43]. Previous studies have demonstrated that when EAM with long turfs are transplanted from the reef flat (low herbivore pressure) to the crest (high herbivore pressure) they are rapidly consumed by fishes [13,35]. It was,

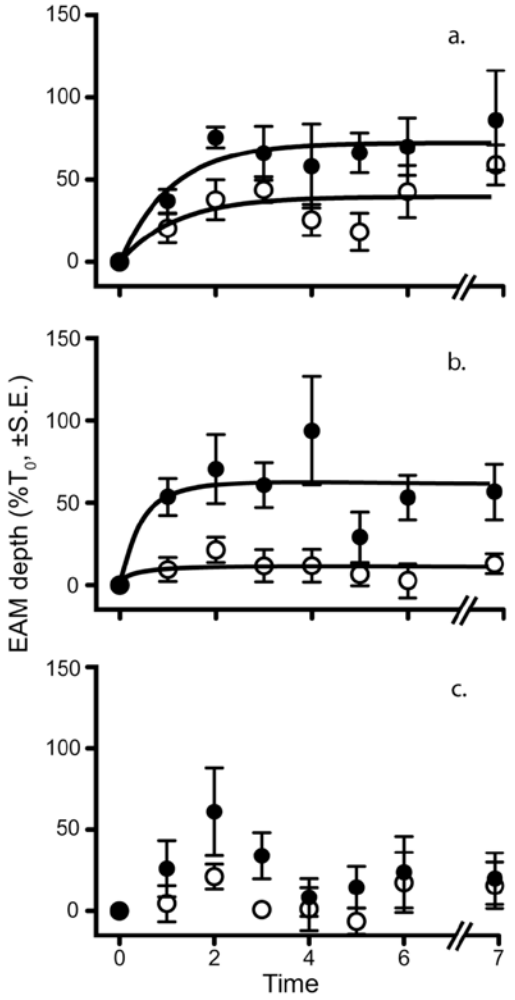

Figure 3. EAM turf length over time. Data are pooled between sites and standardized as percentage of T_0. Filled circles represent sediment addition, open circles represent natural sediment loads. Time is measured in weeks except T_7, which is three months after T_0. a. shows the responses of the caged plots, b. the open plots, and c. the partially caged plots. Data are shown as percentage of T_0 ± standard error, with sites pooled, n = 6 replicates for each point. The lines fitted follow a one-phase decay model where appropriate.

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therefore, expected that any sediment-induced increase in the length of EAM turfs would be rapidly reversed as sediments returned to normal levels, as a result of hydrodynamic activity,

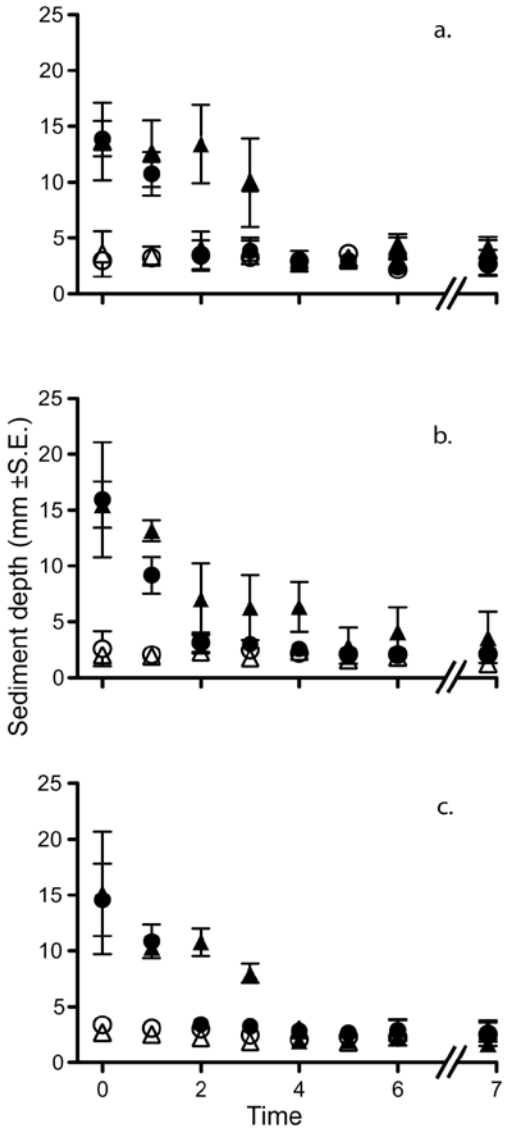

Figure 4. Sediment depth over time. Filled points represent sediment addition treatments, open points represent natural sediment treatments. Circles represent data from site 1, and triangles site 2. Time is measured in weeks except T_7, which is three months after T_0. a. shows data from the caged plots, b. the open plots, and c. the partially caged plots. Data are shown as mean depth in mm ± standard error, n = 3 replicates for each.

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releasing the algae from any sediment-induced suppression of herbivory (e.g. [10,11]). This was not the case.

The EAMs in the present study grew in response to reduced herbivory (cages), increased sediments, or a combination of these factors. Growth in the cages was probably a result of the reduction in grazing [33,35]. While sediment addition may increase algal turf length as a result of the algae investing greater energy resources in linear extension to reach light [44] and/or increased availability of nutrients desorbed from the sediment [13,45]. In both cage and sediment treatments the algal growth was rapid and occurred soon after the initial manipulations were made, while any added sediment was still present. The growth of the EAMs slowed rapidly as sediment loads diminished. Notably, there was no growth of macroalgae, only an increase in turf length. Whether the time for macroalgal development was insufficient, if propagules or juveniles were absent or if the high hydrodynamic activity at this site limited development of macroalgae [10,42], the key result is that responses of algal turfs with artificially reduced herbivory (cages) were comparable to those with increased sediment loads.

Remarkably, after the initial growth of the algal filaments the new, longer, EAMs remained for at least three months in both caged and open plots. The three treatments followed different trajectories: (1) by reducing herbivory, cages maintained a long EAM regardless of sediments (as in previous studies, e.g. [31,34]). (2) In open plots, EAMs likewise remained long, but only if exposed to sediment. This was particularly striking given the rapid loss of sediment. It may be that the vertical distribution of the remaining sediments through the EAM plays an important role in deterring herbivores, or that changes in the microbial community [46,47] or detrital load of the turfs [48] made them less palatable to herbivores. The methods used in this study, however, could not detect any of these factors and, as such, further study is necessary to determine what is underpinning this stability. However, the lack of recovery is worrying as it highlights that reefs are slow to recover from sediment-induced disturbances, even short, 'pulsed' events. (3) The partially caged plots followed similar initial growth trajectories to their equivalent open plots, however, the longer EAMs appeared to 'recover' (i.e. reduce in length) as sediment was removed. The apparent 'recovery' of the EAM in the partial cages was unexpected. It was expected that, as herbivores had access to the benthos, the EAMs would follow the responses seen in the open plots. However, this difference appears to be a result of increased herbivory in the partial cages. The partial cages increased topographic complexity, and provided shelter for a range of reef herbivores allowing localised increases in grazing (cf. [49–52]).

We found that the growth of EAMs after a one-week sediment pulse was equivalent to, or greater than, that seen in simulated herbivore removals using cages. While increased sediment is often considered deleterious to reefs, most information pertaining to its effects are at a physiological scale, considering the impact on individual organisms [53]; little is known about how sediments affect the broader ecosystem functions on which coral reefs rely [54]. At physiological scales, sediments have deleterious impacts on almost all benthic reef taxa [53], however the role of sediments in mediating reef processes is currently limited to studies addressing the impact of sediment laden EAMs in driving settlement and survivorship of corals. While some algae within EAMs may induce settlement [22] increased sediments result in reduced settlement of reef corals as they create a mobile substrate, preventing access to the consolidated reef matrix [14,29]. Furthermore, benthic sediments reduce survival of post-settlement corals particularly during their early development presumably due to abrasion and shading [29,55]. In addition to affecting benthic coral reef organisms, our findings suggest that increased sediments might suppress herbivory resulting in the development and persistence of longer EAMs driving further implications for reef ecosystems. Reduced herbivory through increased fishing pressure is widely publicised as a major threat to coral reefs on a global scale [56], but it appears that short-term increases in sediment release or resuspension through anthropogenic activities (e.g. [5,38,57]) have the potential to have similar effects at localised scales.

The manipulation used in this study is comparable to that of other short-term (acute) perturbations caused by natural or anthropogenic disturbances. Storms and cyclones can move sediment from areas with high natural loads, such as lagoons or reef flats, which, as with this study site, may be only a few tens of meters away [58]. Storms can also increase runoff to inner and mid-shelf reefs [8,9,59]. Similarly, anthropogenic sediment perturbations caused by dredging and other shallow-water maritime activities can resuspend sediments [5,60,61]. These events may all generate long EAMs similar to those seen after the experimental sediment manipulation. An even greater impact may be observed if these events happen in succession, without sufficient recovery time. The longer EAMs generated in this study persisted for at least 3 months, with no obvious sign of recovery. If disturbances increasing sediment loads occurred more often than this, there is the risk that the turfs may grow longer still and persist for longer periods. An assessment of the recovery time is necessary to assess whether such a ratchet effect (*sensu* [62]) is likely to lead to the disruption of ecological processes on reefs.

It is essential to note that our observations are of the effects of 'natural' carbonate dominated sediments, which characterise offshore coral reefs. The disturbance induced by this study, therefore, represents the best-case scenario for the effects of sediments on reefs. Terrigenous sediments, with higher silicate and nutrient loads alongside a high likelihood of associated pollutants (e.g. from metals, chemical fertilisers and pesticides), are likely to have even greater impacts [38,63].

Although our study did not find evidence to support the existence of a positive feedback leading to sediment-laden turfs, a clear and lasting effect was observed following an acute disturbance, with the development of a long-turfed EAM. Longer EAMs on reefs have the potential to reduce coral settlement [29], provide inferior grazing surfaces for fishes [10,11], and present an ecologically and economically less-desirable state [2]. The development of these long EAMs appears to be driven by increases in both benthic sediments and reductions in herbivory. In a world where reefs are affected by increasingly unpredictable climatic conditions and chronic

reductions in herbivore abundances, these longer EAMs are likely to become an increasingly common feature on coral reefs.

Supporting Information

Table S1. Raw data. 'Time' column is measured in weeks. Plots 1-9 are site 1 and 10-18 site 2. 'Turf/Sed' column indicates what is being measured.
(PDF)

Table S2. 2-way ANOVA of T7 turf length data (square root x + 21.0633 transformed data, sites pooled).
(PDF)

Table S3. RM MANOVA results of EAM depth over time, across caging and sediment treatments, pooled between sites (Figure 3). Assumptions of sphericity were violated by univariate tests, as such multivariate tests (Pillai's Trace) were used.
(PDF)

Table S4. RM MANOVA results of sediment depth over time, across caging and sediment treatments, pooled between sites (Figure 4). Assumptions of sphericity were violated by univariate tests, as such multivariate tests (Pillai's Trace) were used.
(PDF)

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Author Contributions

Conceived and designed the experiments: CHRG DRB. Performed the experiments: CHRG. Analyzed the data: CHRG DRB. Contributed reagents/materials/analysis tools: CHRG DRB. Wrote the manuscript: CHRG DRB.

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Appendix 4.2: 2-way ANOVA of T7 turf length data (square root x + 21.0633 transformed data, sites pooled).

	SS	df	MS	*F*	*P*
Cage	82.595	2	41.298	6.309	0.005
Sediment	16.180	1	16.180	2.472	0.126
Cage × Sediment	12.300	2	6.150	0.940	0.402
Error	196.368	30	6.546		

Appendix 4.3: RM MANOVA results of EAM depth over time, across caging and sediment treatments, pooled between sites (Figure 4.3). Assumptions of sphericity were violated by univariate tests, as such multivariate tests (Pillai's Trace) were used.

Sphericity				
	W	χ^2	df	*P*
Time	0.31	32.54	20	0.038

Multivariate RM ANOVA					
	Pillai's trace	*F*	Effect	Error	*P*
Time	0.65	7.64	6	25	<0.0001
Time × Cage	0.64	2.02	12	52	0.041
Time × Sed	0.08	0.36	6	25	0.900
Time × Cage × Sed	0.46	1.31	12	52	0.243

Appendix 4.4: RM MANOVA results of sediment depth over time, across caging and sediment treatments, pooled between sites (Figure 4.4). Assumptions of sphericity were violated by univariate tests, as such multivariate tests (Pillai's Trace) were used.

Sphericity				
	W	χ^2	df	*P*
Time	0.01	92.45	27	0.000

Multivariate RM ANOVA					
	Pillai's trace	*F*	Effect	Error	*P*
Time	0.97	82.01	7	18	<0.0001
Time × Site	0.90	24.16	7	18	<0.0001
Time × Cage	0.92	2.33	14	38	0.020
Time × Sed	0.95	51.59	7	18	0.000
Time × Site × Cage	1.02	2.84	14	38	0.005
Time × Site × Sed	0.84	13.90	7	18	<0.0001
Time × Cage × Sed	0.87	2.09	14	38	0.036
Time × Site × Cage × Sed	0.87	2.11	14	38	0.035

Appendix 5.1: Chapter 5: Biologically mediated sediment fluxes on coral reefs: sediment removal and off-reef transportation by the surgeonfish *Ctenochaetus striatus*. Available at: http://www.int-res.com.elibrary.jcu.edu.au/abstracts/meps/v415/p237-245/

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Biologically mediated sediment fluxes on coral reefs: sediment removal and off-reef transportation by the surgeonfish *Ctenochaetus striatus*

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ABSTRACT: Off-reef sediment transport by the surgeonfish *Ctenochaetus striatus* (Acanthuridae) was quantified on the reef crest at Lizard Island, Great Barrier Reef. Three independent methods were implemented to estimate sediment ingestion rates. These considered (1) the bite rate and bite volume, (2) the defecation rate and faecal pellet size, and (3) the average gut contents and throughput rate. The 3 methods provided a broad range of estimates of sediment ingestion from 8.8 ± 2.4, to 66.1 ± 14.4 g fish^{-1} d^{-1} (mean ± SE). Nevertheless, these estimates were comparable to rates of sediment ingestion by parrotfishes (Labridae), the other major sediment-moving group on reefs. Overall, 36.5% of all sediment ingested was transported from the upper reef crest into deeper water, equating to a removal rate of 28.6 ± 6.2 kg 100 m^{-2} yr^{-1} at the study site. By brushing the reef, *C. striatus* reduces the sediment loading in the epilithic algal matrix (EAM) while causing little damage to the algal turf. Reducing sediments in EAMs provides favourable settlement surfaces for benthic organisms and increases the palatability of the EAM to herbivorous reef fishes, thus supporting reef resilience. The ecological importance of *C. striatus*, which is abundant on reefs throughout the Indo-Pacific, appears to have been underestimated, particularly when considering reef sediment dynamics.

KEY WORDS: *Ctenochaetus striatus* · Sediment transport · Coral reef · Reef fish

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