# THE UNIVERSITY OF QUEENSLAND

### AUSTRALIA

**The grazing impact of common surgeonfish on algal dynamics of the Great Barrier Reef**

Alyssa Louise Marshell

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School of Biological Sciences

## Thesis Abstract

Herbivory is a key ecological process that structures coral reef benthic communities, and consequently is important for ecosystem resilience. Most species of the family Acanthuridae (surgeonfish, unicornfish and tangs) are herbivores, and are widespread, abundant members of Indo-Pacific coral reef fish assemblages. Despite the prevalence of acanthurids on coral reefs, there are few investigations of their feeding ecology and functional role as herbivores. This lack of knowledge limits predictions of the impacts of acanthurid exploitation, which is important because many acanthurids are heavily targeted by coral reef fisheries and the aquarium trade. Therefore, the overall objective of this thesis was to investigate the ecological role of herbivorous acanthurids on coral reefs.

Chapter 2 examines the grazing impact of herbivorous fishes on macroalgal dynamics (*Sargassum* spp.) amongst coral reef zones (inner, mid and outer reef flat, and at 4 m deep on the reef slope). Settlement tiles were deployed for five weeks within three treatments (caged, partially-caged, and open plots). Grazing reduced the abundance of *Sargassum* recruits on partially-caged and open tiles, and patterns of *Sargassum* recruitment reflected adult distribution (e.g., most *Sargassum* zygotes settled in the inner reef flat zone where adult plants proliferate). Settlement tiles were then used in aquarium experiments to quantify the removal of *Sargassum* recruits by key herbivorous fish species from three functional groups ('scraping' parrotfish, 'cropping' surgeonfish, blennies and surgeonfish that 'comb' the substrate). All fishes, except blennies, removed *Sargassum* recruits through their foraging activity, highlighting their role in mitigating macroalgal blooms through their impact on developmental stages of macroalgae. Importantly, this is the first documentation of this functional role by acanthurids.

Chapter 3 investigates the grazing impact of the most abundant and common surgeonfishes, *Acanthurus nigrofuscus* and *Ctenochaetus striatus*, on algal turf dynamics. *A. nigrofuscus* is a grazer that crops algal turfs, while *C. striatus* is detritivorous and was thought to 'brush' detritus from the surface of algal turfs, causing little damage. In experimental aquaria trials, both surgeonfish fed more intensively upon sparse/short algal turfs even though the yield of algae per bite was greater for dense/long algal turfs. Surprisingly, *C. striatus* removed significantly more algal turf per hour than *A. nigrofuscus*, irrespective of canopy height. The capability of *C. striatus* to remove significant quantities of algal turf through their foraging activity implies that this abundant

and widespread species needs to be considered as a potentially important influence on reef algal turf dynamics.

Chapter 4 explores spatial variability in algal turf dynamics (productivity and grazed standing crop biomass), herbivorous fish biomass (Acanthuridae, Labridae, and Siganidae), and grazing intensity at different depths and exposures of reef slope habitats. This aim was achieved through controlled field experiments, fish visual censuses, and *in situ* video surveys of fish grazing intensity. Algal turf productivity was highest in windward and shallow sites, and herbivorous fish biomass mirrored this pattern. However, there was no difference in the algal turf standing crop biomass or total number of bites taken daily among habitats. To identify the daily grazing impact of surgeonfish species on algal turfs, data on total surgeonfish biomass and grazing intensity were combined with algal turf productivity estimates. In the most productive reef slope habitat (windward-shallow), surgeonfishes accounted for 74% of the total herbivore biomass, took 51% of the total bites and removed 73% of daily turf productivity. This study highlights the critical functional role of surgeonfishes in algal turf dynamics on reef slopes, and hence maintaining benthic community structure.

In Chapter 5, a grazing simulation model was developed to investigate the interactions between fish grazing intensity and algal turf dynamics at different depths (shallow, deep) and exposures (leeward, windward) on reef slope habitats. The model predicts turf biomass that closely matches the observed turf biomass in three of four reef slope habitats. However, the model output currently underestimates the amount of observed turf biomass in the most productive habitat (windward-shallow), suggesting that there are gaps in our knowledge of turf dynamics in this zone. The model provides new insights into the fine spatial and temporal scales of algal turf dynamics on reefs, and enhances our knowledge of processes involved these dynamics. Furthermore, the grazing model is an adaptive tool that will be developed further as additional empirical data become available, facilitating investigations into the potential outcomes of different management scenarios, and adding to our understanding of complex processes that prevent or reverse coral-algal shifts following large-scale reef disturbances.

In summary, this thesis fills critical knowledge gaps in acanthurid feeding ecology by quantifying acanthurid grazing impact, identifying the role of key species, and examining the influence of acanthurids on algal community dynamics. These data clearly demonstrate the importance of acanthurids to reefs. This research also provides insights into the implications of acanthurid exploitation and provides a clear rationale for their protection.

**<u>Declaration by author</u>**

This thesis is composed of my original work, and contains no material previously published or written by another person except where due reference has been made in the text. I have clearly stated the contribution by others to jointly-authored works that I have included in my thesis.

I have clearly stated the contribution of others to my thesis as a whole, including statistical assistance, survey design, data analysis, significant technical procedures, professional editorial advice, and any other original research work used or reported in my thesis. The content of my thesis is the result of work I have carried out since the commencement of my research higher degree candidature and does not include a substantial part of work that has been submitted to qualify for the award of any other degree or diploma in any university or other tertiary institution. I have clearly stated which parts of my thesis, if any, have been submitted to qualify for another award.

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## Publications during candidature

Rogers A, Harborne AR, Brown CJ, Bozec Y-M, Castro C, Chollett I, Hock K, Knowland C, **Marshell A**, Ortiz JC, Razak T, Roff G, Samper-Villarreal J, Saunders M, Wolff N, Mumby PJ (2014) Anticipative management for coral reef ecosystem services in the 21st century. Global Change Biology (doi: 10.1111/gcb.12725)

Taylor, BM, Rhodes KL, **Marshell A**, McIlwain JL (2014) Age-based demographic and reproductive assessment of orangespine, *Naso lituratus*, and bluespine, *Naso unicornis*, unicornfishes. Journal of Fish Biology 85:901-916

Hartup JA, **Marshell A**, Stevens G, Kottermair M, Carlson P (2013) *Manta alfredi* target multispecies surgeonfish spawning aggregations. Coral Reefs Reef Site 32:367

**Marshell A**, Mumby PJ (2012) Revisiting the functional roles of the surgeonfish *Acanthurus nigrofuscus* and *Ctenochaetus striatus*. Coral Reefs 31:1093-1101

Doropoulos C, Ward S, **Marshell A**, Diaz-Pulido G, Mumby PJ (2012) Interactions among chronic and acute impacts on coral recruits: the importance of size-escape thresholds. Ecology 93:2131-2138

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## Publications included in this thesis

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| Contributor | Statement of contribution |
|---|---|
| Alyssa Marshell | Designed and analysed experiments (70%) <br> Wrote the paper (80%) |
| Peter J. Mumby | Designed experiments (30%) <br> Wrote and edited paper (20%) |

**Contributions by others to the thesis**

Peter J Mumby contributed to the thesis funding, conception, design, conduct, data analysis, interpretation, and editing of all Chapters.

Alastair Harborne contributed to the design, data analysis, interpretation, and editing of Chapters 1 and 2.

Christopher Doropoulos contributed to the design, data analysis, interpretation and editing of Chapter 2.

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**Statement of parts of the thesis submitted to qualify for the award of another degree**

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FoR code: 0501, Ecological Applications, 20%

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**<u>Abbreviations</u>**

AFDW: ash free dry weight

AIC: Akaike Information Criteria

ANOVA: analysis of variance

ARC: Australian Research Council

CCA: crustose coralline algae

EAM: epilithic algal matric

FL: fork length

GBR: Great Barrier Reef

GBRMPA: Great Barrier Reef Marine Park Authority

GLM: generalised linear model

GLMM: generalised linear mixed model

GPS: global positioning system

HD: high definition

HIRS: Heron Island Research Station

MSEL: Marine Spatial Ecology Lab

SD: standard deviation

SE: standard error

TL: total length

TN: total nitrogen

TOC: total organic carbon

Tukey's HSD: honestly significant differences

Turf: filamentous algal turf

UQ: University of Queensland

UVC: underwater visual census

# Chapter 1. General Introduction

**Herbivory, coral-algal phase shifts, and coral reef resilience**

Coral reef ecosystems are important economic, social and environmental assets (Hughes et al. 2010) that provide ecosystem goods and services to nearly 500 million people that live within 100 kilometres of a coral reef (Bryant et al. 1998). The U.S. commission on Ocean Policy estimated that coral reefs provide goods and services of $375 billion per year (Hay and Rasher 2010). However, coral reefs are in crisis worldwide (Hay and Rasher 2010), and the decline of coral reef health is due to increasing and interacting stresses on global and local scales. On a global scale, climate change is affecting coral reef ecosystems by increasing temperature stress, disease outbreaks, ocean acidification and the frequency and intensity of natural disturbances, such as storms. While local threats include increasing levels of coastal pollution and runoff, and overfishing (Hughes et al. 2003; Hoegh-Guldberg et al. 2007). Combinations of these stressors can lead to ecosystem phase shifts on reefs with low resilience (Hughes et al. 2007; Mumby 2009; Cheal et al. 2010). Phase shifts from coral-dominated to algal-dominated reefs are an indication of coral reef degradation (Hughes 1994; McCook 1999), and reversal back to coral dominance is challenging (Mumby 2009). Algal-dominated reefs lose key ecological functions and processes provided by coral-dominated reefs, and consequently have decreased ecological, social, and economic value (Scheffer et al. 2001; Nyström et al. 2008).

Resilience is defined as either 'ecological' or 'engineering' in the ecological literature (Mumby et al. 2014). Ecological resilience applies to ecosystems that move towards different community types even in the absence of acute disturbance events. This can be an issue for some coral reefs (particularly in the Caribbean) where the natural reef trajectory is either one of coral recovery or decline. In this sense, ecological resilience is the system's ability to display recovery trajectories even though disturbances push the reef closer to thresholds where coral mortality outweighs recovery (Mumby et al. 2014). Alternatively, engineering resilience refers to ecosystems that always recover towards the same long-term state, and measures the rate of recovery to an equilibrial state after a disturbance event (Mumby et al. 2014). However, there are practical limitations to this form of resilience, as some systems may have multiple community trajectories, or suffer periodic disturbances (e.g., storms) that inhibit reaching equilibrium. Furthermore, equilibria of systems may be difficult to define due to processes such as shifting baselines and climate change that may continually change the potential equilibrial ecosystem state (Mumby et al. 2014). Managers are

increasingly focused on supporting the natural resilience of coral reefs, and require the ability to identify resilient reefs and regions to concentrate management efforts (Maynard et al. 2010; Mumby et al. 2013). Currently, this is achieved through monitoring of measurable resilience indicators. However, there has been minimal testing of the relative importance of different resilience indicators, and our knowledge of measurable indicators of resilience is still developing (Maynard et al. 2010).

Herbivory is widely acknowledged as a key ecological process that structures benthic communities, and is important for coral reef resilience (Obura and Grimsdith 2009). Therefore, coral reef herbivore abundance is considered an important resilience indicator, with large numbers of herbivores indicative of a resilient reef (Maynard et al. 2010). Herbivory is probably more intense on some coral reefs than in any other terrestrial or marine habitat (Hatcher and Larkum 1983; Carpenter 1986; Lewis 1986; Choat 1991). Herbivorous fishes exert top-down controls on algal biomass (Lewis and Wainwright 1985), productivity (Russ 2003), and succession (Hixon and Brostoff 1996). Through their foraging activity, herbivores reduce the establishment and growth of algal communities that compete with coral for space and inhibit coral recruitment, especially post-disturbance events (Hughes et al. 2007; Ledlie et al. 2007). As the main consumers of primary production, herbivorous fishes consume 50–100% of total algal production on pristine reefs (Carpenter 1986). A strong relationship between the grazing intensity of herbivorous fishes and macroalgal cover has been demonstrated (e.g., Williams and Polunin 2001; Mumby et al. 2006; 2007; Wismer et al. 2009), with insufficient grazing by herbivorous fishes accepted as a major driver of phase shifts on Caribbean coral reefs with lowered resilience (Hughes 1994; Mumby et al. 2006). While nutrification may enhance algal growth, reduced herbivore populations (usually through overfishing) seem more important than eutrophication in driving many coral-macroalgal phase shifts (Diaz-Pulido and McCook 2003; Burkepile and Hay 2006; Mumby 2006).

There are marked differences in the relative abundance of algal turfs and macroalgae among habitats within a reef and across the continental shelf of the Great Barrier Reef (GBR) (Wismer et al. 2009). Within a reef, canopy forming and foliose forms of macroalgae are characteristic of shallow reef flats (McCook 1996, 1997), while crustose coralline algae is typically common in fore reef slopes and crests (Hay 1981). Large, erect and foliose brown macroalgae (Phaeophyta), in particular *Sargassum* spp., are common and abundant on coral reefs worldwide, and are often linked with phase-shifts and reef degradation (Hughes 1994; Lapointe 1997, Hughes et al. 2007). On the GBR, macroalgae can form dense stands on inshore, coastal reefs, covering > 50% of the substrate,

but are generally present in low densities on mid- and outer-shelf reefs, with possible drivers of these patterns including grazing intensity, wave energy and sedimentation (Wismer et al. 2009). On the mid- and outer-shelf GBR, the epilithic algal matrix (EAM) dominates the substrate, covering 50 to 80 % of reef flats and back reefs and 30 to 70 % of reef slopes (Hatcher and Larkum 1983; Klumpp and McKinnon 1992; Purcell and Bellwood 2001; Wismer et al. 2009). The EAM is a major source of primary production, and is the predominant grazing surface for many herbivorous fishes (Hatcher 1997; Wilson et al. 2003). The EAM is a complex assemblage consisting of microalgae, filamentous algal turfs < 1 cm high, juvenile stages of macroalgae, crustose algae, and detrital material (dead organic matter, inorganic material, microbes, meiofauna) (Steneck 1988; Choat 1991). The EAM primarily forms short, sparse mats of algal turfs < 1 cm high that have a high turnover rate because of intense grazing (Hatcher and Larkum 1983; Carpenter 1986). Macroalgal recruits are known to settle amongst algal turfs within the EAM, with a positive relationship between algal turf cover and recruit density that is potentially facilitated by the refugia provided by turfs against grazing and dislodgment (Santelices 1990; Diaz-Pulido and McCook 2004).

The most abundant and ecologically important herbivorous fishes on tropical coral reefs are the families Acanthuridae (surgeonfishes), Labridae (parrotfishes), Siganidae (rabbitfishes), and Pomacentridae (damselfishes). In addition, Kyphosidae (rudderfishes) are abundant and important in both tropical and temperate waters (Horn 1989). To monitor and use these diverse families as resilience indicators, they are categorised into functional groups depending on how they feed, what they consume, and how they affect the structure of benthic communities (Green and Bellwood 2009). The four functional groups that are important for coral reef resilience in different and complementary ways are: small excavators/scrapers, large excavators/bioeroders, grazers/detritivores, and browsers (Green and Bellwood 2009). Most small (< 35 cm) parrotfishes are scrapers/excavators that intensely graze epilithic algal turf, limit the establishment and growth of macroalgae, and create exposed areas of substrate for coral recruitment. The majority of large (> 35 cm) parrotfishes are excavators/bioeroders that play a similar role to small scrapers/excavators, but expose large areas for coral recruitment (Bruggemann 1995; Green and Bellwood 2009). Rabbitfishes and surgeonfishes are generally grazers/detritivores that limit the establishment and growth of macroalgae while intensely grazing epilithic algal turfs. Unlike parrotfishes, grazers/detritivores generally do not scrape or excavate the reef substratum as they feed (Green and Bellwood 2009). The majority of unicornfishes and rudderfishes are browsers that selectively feed on fleshy macroalgae, and therefore reduce coral overgrowth and shading by macroalgae.

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Damselfishes are not included in resilience monitoring because they are small (contribute less to ecosystem resilience), hard to identify, and have a wide variety of diets (herbivores, detritivores, and planktivores) that makes it complex to assign them to functional groups. Additionally, herbivorous damselfish species are often territorial and farm algae for their own consumption, with mixed implications for reef resilience (e.g., negative influence: reduce coral recruitment through fouling vs. positive influence: increase coral recruitment by providing refuge from other grazers). Detritivores and planktivores are not considered for resilience monitoring, as they typically do not impact algae dynamics (Green and Bellwood 2009).

Studies of the functional role of large herbivorous fishes in the Indo-Pacific have focused largely on scarids (parrotfish) (e.g., Bonaldo and Bellwood 2008) and siganids (rabbitfish) (e.g., Fox et al. 2009). Since the late 1970s it has been recognised that few investigations have been undertaken on the ecology of surgeonfishes (Robertson et al. 1979), which is surprising as acanthurids are a dominant group of herbivorous fishes on reefs (Hobson 1974; Bouchon-Navaro and Harmelin-Vivien 1981; Russ 1984a; Fishelson et al. 1987; Cheal et al. 2012). Acanthurids affect the structure of reef substrate by influencing algal competition, abundance, and dynamics (Lewis 1986; Hixon and Brostoff 1996; McClanahan 1997; Burkepile and Hay 2010). Due to their large abundance and biomass in most reef fish communities, acanthurids are likely to fulfil critical ecological roles (Green and Bellwood 2009; Hoey and Bellwood 2009), but there is still a paucity of quantitative information on the feeding ecology and functional role of the diverse Acanthuridae, especially in the Indo-Pacific region. An analysis of coral reef publications worldwide revealed that 13% of studies related to herbivory (Cvitanovic et al. 2007). However, studies of herbivory on the GBR were only 2.7% of these publications, with the majority (~ 60%) conducted in the central (Orpheus Island) and northern (Lizard Island) GBR regions. Therefore, our knowledge of herbivory processes across the vast expanse of the GBR is still very limited (Cvitanovic et al. 2007). Investigating the different ecological roles of key herbivorous fish species could potentially be important for understanding coral reef resilience; therefore, we need to improve our knowledge of the functional role played by key species of herbivores (Fox et al. 2009). Evidence of the ecosystem impact of individual herbivorous fish species will help with the development of future management plans for the GBR (Cvitanovic et al. 2007).

**Family Acanthuridae**

Surgeonfishes were probably the most important fish herbivores on Eocene (50 Ma) coral reefs, shaping the evolution of modern coral reefs by playing a central role in mediating coral–algal interactions (Bellwood et al. 2014a). Today acanthurids are a large and diverse family of reef fishes, comprised of 83 species that have a widespread, tropical to subtropical range (Froese and Pauly 2012; Randall 2001). Acanthurids are among the dominant families of fishes on tropical coral reefs, both in terms of numbers of individuals and biomass (Russ 1984a, 1984b; Randall 2001; Cheal et al. 2012). Some acanthurid species are important in commercial and subsistence coral reef fisheries (Hensley and Sherwood 1993; Rhodes et al. 2008; Houk et al. 2012; Bejarano et al. 2013), and many of the colourful species are of considerable value to the aquarium fish trade (Randall 2001). Acanthurinae is the largest subfamily with four genera that include 56 species: *Acanthurus* (surgeonfishes), *Zebrasoma* (tangs), *Ctenochaetus* (bristletooths), and the monotypic *Paracanthurus* (palette tang) (Randall 1955; Kuiter and Debelius 2001). However, it has recently been recommended that the genus *Ctenochaetus* should be dissolved into the genus *Acanthurus* based on molecular analyses and in conjunction with a large body of morphological evidence (Sorenson et al. 2013). The Nasinae are represented by the single genus *Naso* (unicornfishes) encompassing nearly 20 species, and the Prionurinae are represented by the single genus *Prionurus* (sawtails) containing seven species (Randall 1955; Kuiter and Debelius 2001).

**Acanthurid feeding ecology**

Acanthurids are generally herbivores that feed on benthic algae (Randall 2001). Of the 41 acanthurid species found on the Great Barrier Reef, 27 are herbivorous; the third most speciose herbivorous reef fish family behind only damselfishes (Pomacentridae) ($n = 61$) and blennies (Blenniidae) ($n = 47$) (Cvitanovic et al. 2007). Although most species are herbivores, there are diverse feeding habits within acanthurids (Table 1; Choat 1991), including diets of planktonic animal matter, organic detritus (Choat et al. 2002), and invertebrates (Klanten et al. 2004). Acanthurid foraging and diet diversity is strongly related to highly varied dentition within and across genera (Fishelson and Delarea 2014; Bellwood et al. 2014b). *Acanthurus* and *Zebrasoma* species (algal turf grazers) tend to have spatulate tooth morphologies, while *Naso* species (browsers/planktivores) have pointy, serrated teeth (Purcell and Bellwood 1993; Fishelson and Delarea 2014; Bellwood et al. 2014b). Foraging behaviour is also varied, with species that form pairs or feeding aggregations, while others individually defend territories (Randall 2001).

The majority of surgeonfishes (*Acanthurus* and *Zebrasoma* species) are algal turf grazers, feeding upon the EAM. The remainder of *Acanthurus* species are either planktivores or graze over sand, feeding on both algae and detritus (Table 1). All species of the genus *Ctenochaetus* are primarily detritivores (Choat 1991; Choat et al. 2002; Bellwood et al. 2014b), and play an important role in sediment dynamics on coral reefs (Goatley and Bellwood 2010; Krone et al. 2011). Most unicornfishes are planktivores (Table 1, Choat 1991; Choat and Clements 1998; Choat et al. 2002), with the largest species (*N. annulatus*, *N. hexacanthus* and *N. lopezi*) feeding on macroplankton in open water (Table 1, Choat 1991). A second group of unicornfishes are browsers, feeding on large macroscopic algal species (Table 1; Choat and Clements 1998; Hoey and Bellwood 2009). All *Prionurus* species are considered browsers (Randall 2001).

Table 1. Functional groups of the family Acanthuridae (modified from Green and Bellwood 2009).

| Common name (sub-family) | Functional Group | Genera and Species | Reference |
|---|---|---|---|
| **Surgeonfishes (Acanthurinae)** | Grazers | All species of *Acanthurus* and *Zebrasoma*, except those that are detritivores or planktivores | Choat 1991, Choat et al 2002 |
| | Detritivores | All *Ctenochaetus* species | Choat 1991 |
| | Planktivores | *A albipectoralis, A. mata, A. nubilus, A. thompsoni* and *Paracanthurus hepatus* | Choat 1991, Choat et al 2002 |
| **Unicornfishes (Nasinae)** | Planktivores | All species except those that are browsers | Choat 1991, Choat and Clements 1998, Choat et al 2002 |
| | Browsers | All: *N. tuberosus, N. brachycentron, N. elegans, N.lituratus, N. tonganus* and *N.unicornis* | Choat and Clements 1998 |
| | Browsers | Juveniles (< 20 cm) of: *N. annulatus, N. brevirostris, N. maculatus, N. mcdadei*, and *N. vlamingii* | Choat 1991, Choat and Clements 1998, Choat et al 2002 |
| **Sawtails (Prionurinae)** | Browsers | All species | Randall 2001 |

**Acanthurid research**

A search of the 'Web of Science' database (January, 2014) resulted in 341 publications directly related to 'coral reef Acanthuridae/surgeonfish'. Of those 341 publications, the majority (16.6%) related to herbivory, diet, or feeding ecology. The remainder of publications were divided between subjects such as population dynamics, recruitment, biogeography, parasitology, reproduction, and population connectivity (using genetics). Most studies of acanthurids have been conducted in the Caribbean (25.1%), followed by the South Pacific (20%) and the Great Barrier Reef (16.2%) (Figure 1).
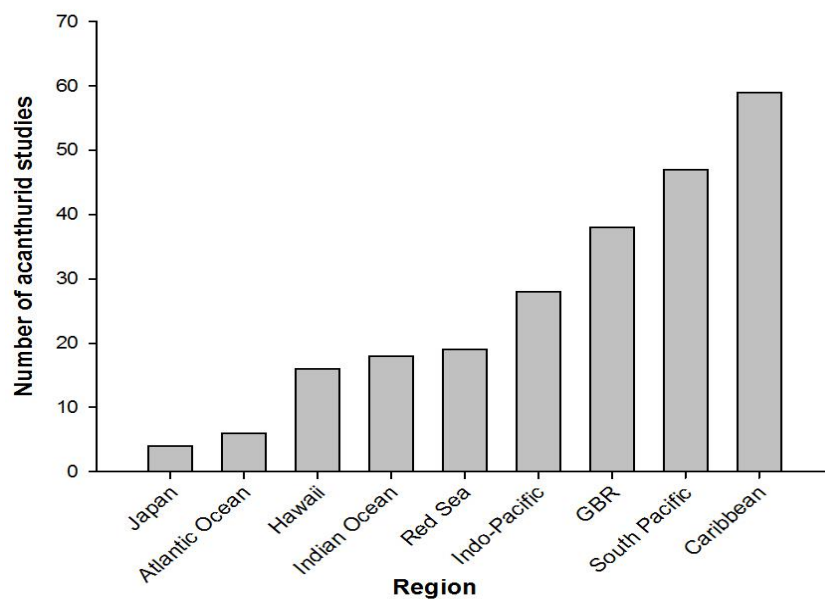


Figure 1. The number of acanthurid studies conducted in various broad regions, as determined through a search of the Web of Science database (GBR = Great Barrier Reef).

Surprisingly few investigations of acanthurid feeding ecology exist (Robertson et al. 1979). To date, acanthurids have continued to receive much less attention than other major herbivorous families (Robertson et al. 1979; Montgomery et al. 1989). The studies that have examined acanthurid feeding ecology have focused on aspects of: morphology (e.g., Purcell and Bellwood 1993); behaviours such as territoriality (e.g., Choat and Bellwood 1985); algal palatability (e.g., Wylie and Paul 1988; Meyer et al. 1994; Cronin et al. 1997); feeding strategies, interspecific relationships and social/mating systems (e.g., Robertson et al. 1979; Fishelson et al. 1987; Montgomery et al. 1989; Fouda and El-Sayed 1994; Polunin et al. 1995); and specific dietary and trophodynamic analyses (e.g., Choat 1991; Choat et al. 2002; Choat et al. 2004). Very few studies have examined the ecological role of herbivorous surgeonfish on coral reefs, or their specific grazing impact on the

benthic community (but see Montgomery et al. 1980; Hoey and Bellwood 2009; Burkepile and Hay 2010).

**Acanthurid species-specific research**

Grazer/detritivore species from *Acanthurus, Zebrasoma* and *Ctenochaetus* genera that feed upon the EAM are widespread and abundant members of coral reef fish communities throughout the Indo-Pacific. Two of the most abundant acanthurids are the brown surgeonfish *Acanthurus nigrofuscus* (Forsskal, 1775) and the lined bristletooth *Ctenochaetus striatus* (Quoy & Gaimard, 1825). These species are often amongst the numerically dominant fish species throughout Indo-Pacific coral reefs (Choat & Bellwood 1985; Robertson & Gaines 1986; Fishelson et al. 1987; Montgomery et al. 1989, Cheal et al. 2012), and are among the best studied Indo-Pacific acanthurid species (Figure 2). *C. striatus* is the most studied Indo-Pacific acanthurid (Figure 2), and its roles in sediment dynamics and as an important detritivore have been well established (e.g., Nelson and Wilkins 1988; Fouda and El-Sayed 1994; Krone et al. 2008, 2011; Schuhmacher et al. 2008; Goatley and Bellwood 2010). However, the most studied acanthurids overall are the common western Atlantic (Caribbean) species: *Acanthurus bahianus*, *A. coeruleus* and *A. chirurgus* (Figure 2; e.g., Reinthal and Lewis 1986; Burkepile and Hay 2010; Francini-Filho et al. 2010; Kopp et al. 2010; Vermeij et al. 2010).
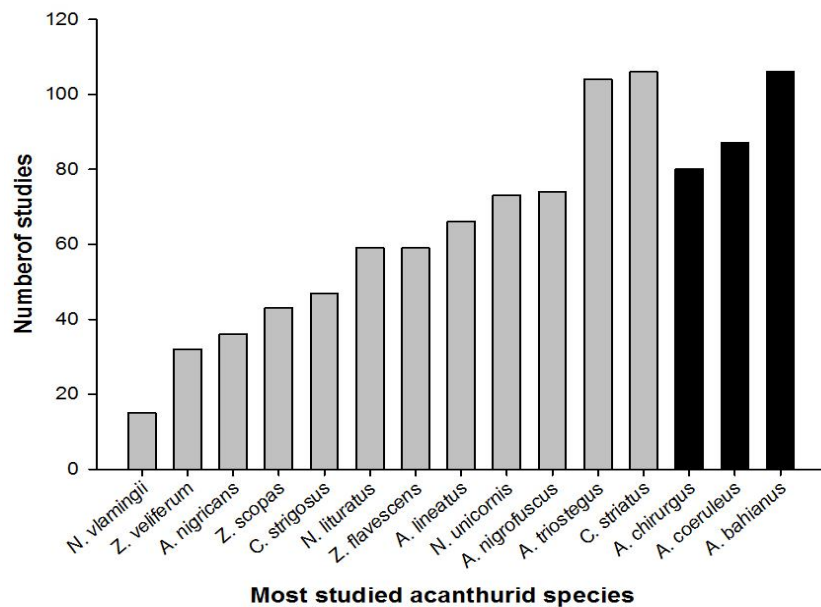


Figure 2. The number of studies conducted per species of the top fifteen most commonly studied acanthurids, as determined by a search of the Web of Science database. Black bars indicate western Atlantic (Caribbean) species.

The most conspicuous acanthurid browsers that consume fleshy macroalgae on coral reefs throughout the Indo-Pacific are *Naso unicornis* and *Naso lituratus* (Russ 1984a; Hoey and Bellwood 2009), and these species are the most studied of the acanthurid browsers (Figure 2). Most studies of *N. lituratus* and *N. unicornis* have examined disease/parasite prevalence, distribution, demography, and observed behaviours such as social interactions and competition. *N. unicornis,* the bluespine unicornfish, often dominates macroalgal herbivory and likely plays a key ecological role on some coral reefs (Hoey and Bellwood 2009; Rasher et al. 2013). Although both of these species have widespread distributions, are predominant on coral reefs, and are important in many Pacific Island nations' coral reef fisheries (Rhodes et al. 2008, Houk et al 2012, Bejarano et al. 2013), very little is known about their feeding ecology and the functional role they play in the reef ecosystem as dominant browsers. Species-specific management is severely lacking, especially in regions where they are heavily targeted in local fisheries (Rhodes et al. 2008, Houk et al 2012, Bejarano et al. 2013). Therefore, there are major knowledge gaps in the ecology of both acanthurids overall and also individual species, particularly in examining the functional role of key herbivorous species.

**Thesis Aims**

Acanthurids are widespread and abundant members of coral reef fish communities that are heavily targeted in coral reef fisheries and the aquarium trade. However, there are few investigations of acanthurid feeding ecology and their important roles as herbivores on Indo-Pacific coral reefs. Therefore, this thesis examines the ecological role of key acanthurid species in driving algal dynamics in coral reef ecosystems. Knowledge gaps are filled by quantifying the grazing impact of key acanthurids on algal turf dynamics, determining their influence on macroalgal population dynamics, and finally building a grazing simulation model of algal turf dynamics in different reef slope habitats that incorporates algal turf growth dynamics and species- and size-specific bite rates and sizes of herbivorous fishes. In addition to adding to our knowledge of the ecology and functional role of acanthurids, the information collected is anticipated to help to protect, conserve, and manage acanthurids in areas where they are heavily targeted within coral reef fisheries and aquarium trades.

By using a combination of field observations, manipulative field and aquarium experiments, and empirical modelling, the overall aim of this thesis was to investigate the ecological role of key herbivorous surgeonfish on coral reefs. Specifically, the aims were to determine:

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1. The impact of grazing fishes on patterns of macroalgal recruitment and adult distribution in different coral reef zones (Ch. 2).
2. The functional roles of the common surgeonfish *Acanthurus nigrofuscus* and *Ctenochaetus striatus*, and their grazing impact on algal turfs (Ch. 3).
3. The ecological role of grazing surgeonfish in different habitats of coral reef slopes (Ch. 4).
4. The balance between herbivorous fish grazing and algal turf dynamics in different coral reef slope habitats using a grazing simulation model (Ch. 5).

**Chapter Outlines**

*Chapter 2. The impact of grazing fishes on macroalgal recruitment and adult distribution patterns.*

Macroalgal blooms require the establishment of new recruits, and it is a long-held, but untested assumption that grazing fish remove early post-settlement macroalgal recruits from within the algal turfs. Chapter 2 examines the grazing impact of herbivorous fishes on macroalgal dynamics (*Sargassum* spp.) amongst coral reef zones (inner, mid and outer reef flat, and at 4 m deep on the reef slope). Settlement tiles were deployed within three treatments (caged, partially-caged, and open plots) for five weeks, and then used in aquarium experiments to quantify the removal of *Sargassum* recruits by key herbivorous fish species from three functional groups ('scraping' parrotfish, 'cropping' surgeonfish, blennies and surgeonfish that 'comb' the substrate). The results highlight the role of grazing fish in mitigating macroalgal blooms through their impact on developmental stages of macroalgae.

*Chapter 3. Revisiting the functional roles of the surgeonfish Acanthurus nigrofuscus and Ctenochaetus striatus*

The grazing impact on algal turfs of the most abundant and common surgeonfish, *Acanthurus nigrofuscus* and *Ctenochaetus striatus*, was quantified in experimental aquaria trials. *A. nigrofuscus* is a grazer that crops algal turfs, while *C. striatus* is detritivorous and was thought to 'brush' detritus from the surface of algal turfs, causing little damage. Surprisingly, *C. striatus* removed significantly more algal turf biomass than *A. nigrofuscus*. The capability of *C. striatus* to remove significant quantities of algal turf through their foraging activity implies that this abundant and widespread species may substantially affect algal turf dynamics on reefs.

*Chapter 4. Spatial variation in the grazing impact of surgeonfish on epilithic algal turfs.*

Chapter 4 explores spatial variability in algal turf dynamics, and fish herbivore biomass and grazing intensitys in different depths and exposures of coral reef slope habitats. This was achieved through controlled field experiments, herbivorous fish visual census surveys, and remote video *in situ* grazing intensity surveys. To identify the daily grazing impact of surgeonfish species on algal turfs, data on total surgeonfish biomass and grazing intensity were combined with algal turf productivity estimates. This study improves our understanding of the ecological role that surgeonfish play in maintaining algal turf biomass.

*Chapter 5. The balance between fish grazing and algal turf dynamics on coral reefs: a grazing simulation model*

In Chapter 5, a grazing simulation model was developed to investigate the balance between fish grazing intensity and algal turf dynamics in different depths and exposures of coral reef slope habitats. The model provides insight into our understanding of fine spatial and temporal scales of algal turf growth on coral reefs, and enhances our knowledge of processes involved in algal turf dynamics. The grazing model is an adaptive tool that will be developed further to enable investigation into potential outcomes of different management scenarios, adding to our understanding of complex processes that may prevent or reverse coral-algal shifts following large-scale reef disturbances.

*Chapter 6. General Discussion*

In Chapter 6, the ecological roles of grazing surgeonfish and *Ctenochaetus striatus* in particular, are discussed. The challenges in estimating the bite size of grazing surgeonfish and rabbitfish and the seasonality of herbivory and algal dynamics are then explored, followed by the overall conclusions of the thesis.

# Chapter 2. The impact of grazing fish on *Sargassum* recruitment and adult distribution patterns

## Abstract

Coral reef deterioration is often associated with blooms of benthic algae that can lead to a phase-shift from a coral-dominated to an algal-dominated ecosystem state. Most studies have focused on the top-down control of adult macroalgae, while the impact of grazing fishes on the earliest stages of macroalgal recruitment are less understood. However, algal blooms require the establishment of new recruits, and it is a long-held, but fundamentally untested assumption that algal turf grazing fish remove settled macroalgal recruits from within the epilithic algal matrix. Here, we tested the grazing impact of herbivorous fish on the recruitment dynamics of a large foliose macroalgae commonly associated with reef degradation, *Sargassum* spp., using a series of field and laboratory experiments. *Sargassum* recruitment patterns were investigated in four reef zones (inner, mid and outer reef flat, and at 4 m deep on the reef slope) in the southern Great Barrier Reef (Heron Island), by deploying settlement tiles for five weeks within three treatments (caged, partially-caged, and open plots) during the annual *Sargassum* peak. Grazing reduced the abundance of *Sargassum* recruits, and *Sargassum* recruitment reflected adult distribution patterns, with most zygotes settled in the inner reef flat zone where adult plants proliferate. Most *Sargassum* recruits (~ 98%) generally settle within 1 m of their adult source. Therefore, it was interesting that despite the absence of adult *Sargassum* plants at 4 m deep on the reef slope, *Sargassum* zygotes had settled there, with the greatest abundance of recruits within caged treatment plots. Settlement tiles were then used in aquarium experiments to quantify the removal of *Sargassum* recruits by key herbivorous fish species from three functional groups ('scraping' parrotfish, 'cropping' surgeonfish, blennies and surgeonfish that 'comb' the substrate). All fish, except blennies, removed *Sargassum* recruits through their foraging activity, highlighting their role in mitigating macroalgal blooms through their impact on the earliest macroalgal life-stage. Collectively, our study demonstrates the influence of fish herbivory on *Sargassum* recruitment dynamics across different reef zones and how this contributes towards controlling adult macroalgal distribution.

## Keywords

## Introduction

Coral reef deterioration is often associated with blooms of benthic algae that can lead to phase-shifts from a coral-dominated to an algal-dominated ecosystem state (Hughes 1994; McCook 1999). Reversal back to coral-dominance is challenging due to positive feedbacks that stabilize phase shifts (Mumby 2009; Hoey and Bellwood 2011). Algal-dominated reefs lose key ecological functions and processes provided by coral-dominated reefs, and therefore have decreased ecological, social, and economic value (Scheffer et al. 2001; Nyström et al. 2008).

On coral reefs, there is a strong relationship between the grazing intensity of herbivorous fishes and macroalgal cover (e.g., Williams and Polunin 2001; Mumby et al. 2006; 2007), with insufficient grazing accepted as a major driver of coral-algal phase-shifts on Caribbean coral reefs (Mumby 2006). Herbivorous fish consume most of the total daily algal production on coral reefs (Hatcher 1981; Carpenter 1986), and through their grazing activity, affect algal biomass (Lewis 1986; Hughes et al. 2007a; Burkepile and Hay 2008), productivity (Russ 2003), and succession (Hixon and Brostoff 1996). Herbivorous fish exert top-down control of algal communities by reducing the establishment and growth of algae that compete with corals for space, and inhibit coral recruitment (Carpenter 1986; Hughes et al. 2007a). Consequently, herbivory is considered a key ecological process that structures benthic communities and is important for the resilience of coral reefs (Steneck 1988; Bellwood et al. 2004; Mumby and Steneck 2008). While the relative importance of 'bottom-up' (factors within basal trophic levels that move up the food web; e.g., nutrification) versus 'top-down' (factors within higher trophic levels that move down the food web; e.g., herbivory) controls of benthic algal blooms have been widely debated (e.g., Lapointe 1997; Hughes et al. 1999; McCook 1999), the reduction of herbivore populations and grazing intensity (usually through overfishing) seems more important than eutrophication in driving coral-algal phase-shifts (Diaz-Pulido and McCook 2003; Burkepile and Hay 2006; Mumby 2006).

Investigations of the herbivorous control of macroalgal populations or blooms have largely focused on the top-down control of adult macroalgal plants (e.g., McCook 1997; Hoey and Bellwood 2010; Bennett and Bellwood 2011; Hoey and Bellwood 2011), however, adult macroalgal populations are also controlled by processes occurring at the recruitment stage (settlement and post-settlement survival and growth) (Diaz-Pulido and McCook 2003; Doropoulos et al. 2013). Macroalgal blooms require the establishment of new recruits, and it is a long-held, but untested assumption that algal turf grazing fish remove early post-settlement macroalgal recruits from within the epilithic algal matrix (EAM). Diaz-Pulido and McCook (2003) showed that herbivores reduced macroalgal recruit

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(> 40 d old, settled in aquaria on bare terracotta plates) density and growth on an offshore coral reef (reef slope 6–9 m depth), and concluded that the relative importance of bottom-up and top-down processes influencing macroalgal recruitment was dependent on the species, life-history and circumstances under consideration. However, they did not identify the herbivores responsible for reducing macroalgal recruitment, or investigate any differences among reef zones. Therefore, there are still large gaps in our knowledge of the impact of grazers on macroalgal early post-settlement processes, and in order to better understand herbivore control of macroalgal populations, it is important to quantify the grazing impact of herbivores on macroalgal recruit early post-settlement survival, and identify the role played by different herbivore species.

The large, foliose, brown macroalga, *Sargassum* spp. (Phaeophyta), was chosen as our focal species for this study, as these seaweeds are common and abundant on coral reefs worldwide, and are often linked with phase-shifts and reef degradation (Hughes 1994; Lapointe 1997, Hughes et al. 2007b). *Sargassum* recruits are known to settle amongst algal turfs, with a positive relationship between algal turf cover and recruit density that is potentially facilitated by the refugia provided by turfs against grazing and dislodgment (Santelices 1990; Diaz-Pulido and McCook 2004). In sub-tropical rocky reefs, dispersal of *Sargassum* propagules is highly-localized, with most (~ 98%) propagules settling within their bed of origin, less than 1 m from their original adult source (Kendrick and Walker 1995; Deysher and Norton 1981).

Here, we quantify the effect of herbivorous fish on *Sargassum* recruitment and adult distribution. The aim of this study was to investigate: (1) patterns of *Sargassum* recruitment dynamics within the context of corresponding adult *Sargassum* distribution patterns; (2) how herbivores impact *Sargassum* recruitment and adult dynamics; and (3) how different functional groups of herbivorous fish impact the abundance of *Sargassum* recruits settled within algal turfs. The grazing impact of herbivorous fish on *Sargassum* dynamics was examined in four zones of Indo-Pacific reefs (inner, mid and outer reef flat, and the shallow reef slope) at Heron Reef during the peak annual *Sargassum* bloom (April-May). Field observations and tethering experiments were used to quantify adult *Sargassum* patterns and rates of herbivory; and settlement tiles were deployed within three treatments (caged, partially-caged, and open plots) to quantify natural recruitment in the presence and absence of herbivory. Complementary aquarium experiments were conducted to obtain a mechanistic understanding of how different herbivore functional groups impact *Sargassum* recruit (< 2 mm height) survival when they are at their earliest post-settlement life-stage in the EAM. Four common EAM grazing fish species were chosen to represent different herbivorous fish functional groups: grazers that 'crop', 'comb', and 'scrape' the EAM. *Acanthurus nigrofuscus* and

*Ctenochaetus striatus* are abundant and widespread surgeonfish throughout Indo-Pacific coral reefs (Choat and Bellwood 1985; Trip et al. 2008; Cheal et al. 2012). *A. nigrofuscus* is functionally classified as a grazer that feeds upon the EAM, 'cropping' microalgal turf filaments from the substrate (Horn 1989; Purcell and Bellwood 1993; Polunin et al. 1995; Green and Bellwood 2009). *C. striatus* is classified as a detritivore that feeds upon sparse algal turfs and calcareous algae, 'combing' detritus from the EAM surface causing little damage to algal turfs (Choat 1991; Purcell and Bellwood 1993; Polunin et al. 1995; Choat et al. 2002, 2004; Goatley and Bellwood 2010; but see Marshell and Mumby 2012). *Salarius fasciatus*, a grazer/detritivore that also 'combs' the EAM, was chosen as it is abundant in reef flat habitats (Townsend and Tibbetts 2000), and has an important ecological role (Townsend and Tibbetts 2004). Finally, initial-phase parrotfish (*Scarus* and *Chlorurus* spp.) were chosen as they are abundant and intense grazers of the EAM, and are one of the main herbivorous fish families. Most parrotfish species 'scrape' the EAM from the surface of hard substrates (Hoey and Bellwood 2008, Green and Bellwood 2009). Our results demonstrate natural patterns of *Sargassum* population dynamics across different reef zones and indicate how different groups of herbivorous fish influence macroalgal abundance at different life stages, highlighting their role in providing an important mitigation service against macroalgal blooms on coral reefs.

## Methods

### Study site

Heron Reef is a lagoonal platform reef 11 km long x 5 km wide (~ 27 km$^2$) located approximately 70 km from the mainland coast of Queensland, Australia in the southern Great Barrier Reef (Fig. 1, 23°26' S, 151°55' E). The study site was located on the southern side of Heron Island, a small coral cay (~ 800 x 300 m) situated near the western end of Heron Reef, where the reef flat is ~ 400 m wide (Fig. 1d). The reef flat has a tidal range of 1–3 m and is divided into distinct zones: an inshore gutter (~ 20 m wide and ~ 50 cm deep at low tide), and a broad reef flat (~ 15–30 cm deep at low tide) that is scattered with emergent coral rubble, micro-atoll remains, and has a fine sandy substrate inshore increasing to gravels towards the reef crest (Figs. 1, 3c; Rogers 1997). Approximately 340 m from shore the reef flat deepens to 50–100 cm at low tide, live coral cover increases, and ~ 380 m from shore is the reef crest. Beyond the reef crest is a gentle slope that is exposed at low tide and dominated by encrusting coralline algae, gradually dropping off into a live coral dominated zone of the reef slope (Rogers 1996, Fig. 3c). This study investigates the macroalgal and herbivorous fish

dynamics among four zones that run parallel to Heron Island shore: the inner, mid, and outer reef flat zones, and at 4 m deep on the reef slope, just below the reef crest (Fig.1e). Each zone is separated by approximately 120 m.

**Roving herbivore and adult *Sargassum* distribution and abundance patterns**

Roving herbivore distribution and biomass were estimated by conducting underwater visual census (UVC) surveys within ± 2 h of the afternoon high tide to minimise tide or time effects. Six 5 min timed-swim surveys were conducted parallel to shore within each of the four zones, with a minimum of ~ 30 m separating each survey. An individual GPS track was recorded for each transect to allow the distance of each survey to be calibrated. All herbivore species encountered within a 5 m wide transect were recorded into 3 cm size classes. As it is difficult to identify juvenile parrotfish to species in the field, all individuals less than 10 cm were placed in the category '*Scarus*' (with the exception of *Chlorurus sordidus* and *Chlorurus microrhinos* which are readily identifiable as juveniles). Herbivore abundance was converted to biomass estimates using published length-weight relationships (Kulbicki et al. 2005), with recorded fish length converted to the midpoint of the respective size class.

To examine adult *Sargassum* distribution patterns, benthic surveys were conducted at high tide in each of the zones of the reef flat (inner, mid, outer) and at 4 m deep on the reef slope. Six 40 m belt transects were conducted parallel to shore in each of the zones, and each consecutive transect was separated by ~ 30 m. A 1 x 1 m quadrat was photographed every 5 m of each 40 m transect, (for a total of eight photo-quadrats per transect, and 48 photo-quadrats per zone). The photo-quadrats were analysed using Vidana software (available from www.marinespatialecologylab.org), with substratum percent cover classified into the following categories: live coral (functional groups: branching, tabular, massive, submassive etc.), dead coral, soft coral, macroalgae genera (> 10 mm), crustose coralline algae, pavement, rubble and sand. In addition, to find the average *Sargassum* adult height (as a proxy for biomass) per zone, the maximum height of *Sargassum* thalli was measured to the nearest cm in each quadrat, using a 1 m ruler.

The average abundance (individuals m$^{-2}$) and biomass (g m$^{-2}$) of roving herbivorous fish, and average percent cover and height (cm) of adult *Sargassum* (primarily *S. polycystum*), was calculated for each zone, and comparisons among zones (fixed, 4 levels) were conducted using separate one-way ANOVAs. The fish data were transformed (abundance data: square-root, biomass data:

log(x+1)) to meet parametric assumptions of normality and homoscedasticity, whereas the raw algal data met model assumptions. Differences in abundance or biomass among zones were investigated using a Tukey's HSD post-hoc test.

**Daily removal rates of adult *Sargassum polycystum***

To examine the removal of adult *S. polycystum* among the four zones, bioassays were conducted at two sites within each zone. *S. polycystum* was collected from the inner zone of the Heron reef flat, where it was most abundant. Individual thalli were removed carefully from the substrate at the holdfast and kept for less than 24 h in flow-through seawater aquaria at Heron Island Research Station (HIRS). Thalli were spun in a salad spinner for 20 seconds to remove excess water, and combined with elastic-bands into standardised assays, using small coloured cable ties secured through the elastic-bands to mark and identify individual assays. The assays were wet-weighed (to the nearest 0.1 g) and measured (maximum height) to the nearest mm (Bennett and Bellwood 2011). Six *S. polycystum* assays were randomly secured to dead coral substrate (~ 2 m apart) using cable ties at two sites within each zone (inner, middle, outer reef flat, 4 m deep reef slope). One assay in each group of six was caged to exclude herbivores and control for biomass loss due to handling (Hoey and Bellwood 2010). The macroalgal assays were left for approximately six hours, within ± three hours of the maximum midday high tide, then collected and reweighed/measured using the same methods. This procedure was repeated at the same sites over three days (for a total of 30 grazed replicates and 6 control replicates per zone) (Bennett and Bellwood 2011). To identify browsing herbivorous fishes responsible for removal of *S. polycystum*, one assay from each group of six was filmed using a stationary GoPro HD video camera for four hours. A scale bar was held next to the assay during initial recording to allow estimation of fish sizes when analysing the footage. The fish species, size (total length, cm), and number of bites taken from the assay was recorded from the video footage.

Assay removal estimates were compared using a mixed-effects ANOVA with zone as a fixed factor, and site and day as random factors. There was no effect of site or day on removal rates, and no significant interaction between factors ($P > 0.25$); therefore, the random effects were pooled and all subsequent comparisons were conducted at the reef zone level (Underwood 1997). The daily removal of adult *S. polycystum* biomass was compared among the zones (4 levels) using a one-way ANOVA, with Tukey's HSD post-hoc test to identify different homogenous groups. The analysis was conducted on the proportion of the initial biomass lost from *S. polycystum* assays ($n = 30$ per

zone), which was logit-transformed (Warton and Hui 2011) to meet normality and homoscedasticity ANOVA assumptions. A Tukey's HSD post-hoc test was used to identify homogenous groups.

### *Sargassum* recruitment patterns and impact of herbivores

To investigate macroalgal recruitment patterns and dynamics, settlement tiles were deployed in the four zones of Heron's southern reef flat during the peak biomass and reproductive period of dominant brown macroalga *Sargassum polycystum* (April–May 2013). Settlement tiles were rough-textured, limestone outdoor pavers (13 x 13 x 1.5 cm) that were preconditioned on the reef flat for over 12 months. Prior to deployment in experimental treatments, the preconditioned tiles were scrubbed to begin with an algal biomass of zero, while maintaining a live cover of encrusting benthic organisms. It was not possible to differentiate between different individual *Sargassum* species as < 5 mm recruits, therefore *Sargassum* recruits refers to all species found on Heron Reef hereafter (although *S. polycystum* was the most abundant and conspicuous species).

Settlement tiles were deployed in four zones parallel to shore (inner, mid and outer reef flat, and at 4 m deep on the reef slope) across the southern reef flat (Fig. 1). To investigate the impact of grazers on macroalgal recruitment patterns, the tiles were deployed in plots of three, which were randomly assigned to experimental exclusion treatments (caged, partially caged, and open tiles; ~ 1 m apart). In each zone there were ten replicates plots that were each separated by ~ 25 m (for a total of 30 tiles per zone, and 120 overall). Ten tiles per zone were protected from grazing fish (> 5 cm total length) by black plastic exclusion cages (22 x 22 x 18 cm) with a mesh size of 2.5 x 2.5 cm. Partial cages ($n = 10$ per zone) were identical, but were open on two sides to create a 'tunnel' that allowed grazing, while controlling for any cage effects. The tiles were mounted horizontally inside the cages and partial cages, secured to a 30 cm long half-piece of PVC pipe with a cable tie. To prevent sedimentation, the PVC pipe was secured through the cage walls, so that the tile was raised ~ 10 cm above the substrate. The remaining ten tiles were open and exposed to natural grazing levels, secured to substrate such as dead coral heads that were at approximately the same height as the tiles within cage treatments. Cages and partial cages were secured with cable ties to two pieces of rebar that had been hammered into the substrate, while open tiles were secured directly to the substrate using a cable tie, and also between two pieces of rebar. Tiles were deployed for five weeks (12 April – 19 May 2013) and caged and partial treatments regularly maintained. Additionally during this period: (1) Hobo™ data loggers were deployed for seven days to measure and compare light (lux, SI) and temperature (°C) among treatments (caged, partially caged and open tiles) and

zones; (2) water flow was measured by deploying plaster-of-paris clod cards ($n = 5$ per treatment, per zone, $n = 60$ in total) simultaneously for a 24-hour period, and comparing their dissolution among treatments and zones (Fulton and Bellwood 2005); and (3) a tile within each treatment (cage, partial cage, open) in each zone ($n = 4$) was filmed using a GoPro HD video camera for ~ 4 h over high-tide and repeated over three days (for ~ 12 h total of video footage recorded per treatment, per zone). Subsequent video analysis was conducted to identify grazers and quantify average grazing rates on tiles within each treatment and zone. After five weeks the tiles were collected and transported with minimal disturbance to shaded HIRS holding aquaria with a low-flow of filtered seawater.

To quantify the number of *Sargassum* recruits on each tile, settlement tiles were removed from aquaria within 48 h of collection and individually photographed for percent cover calculations. The average height of algal turfs was then recorded by taking five random measurements across each tile. The tiles were washed very gently with running seawater to reduce sediment load and allow the *Sargassum* recruits to be more visible amongst the algal turfs. A black plastic mesh 12.5 x 12.5 cm quadrat divided into 2.5 x 2.5 cm squares was used as a guide to examine each settlement tile sequentially. To enable the number of recruits to be counted, each 2.5 cm$^2$ was searched using fine forceps and probes to scrutinize amongst algal turfs thoroughly under a stereomicroscope (1.2 x 40 zoom). The position of *Sargassum* recruits was mapped on a datasheet and the total number of recruits per tile recorded. Subsequent blind reads were conducted randomly and regularly to ensure accuracy. After the recruits were counted and mapped, the tile was returned to the holding aquarium for subsequent use in experimental grazing trials.

The number of *Sargassum* recruits on settlement tiles after five weeks was compared among zones and treatments using a generalised linear model (GLM) with negative binomial distribution, in the "glmmADMB" package (Bolker et al. 2013) of R (R Development Core Team 2013). A negative binomial variance structure was used because the mean variance was highly inflated (Crawley 2007). Zone (inner, mid, outer, slope) and treatment (cage, partial cage, open) were considered categorical fixed effects. Plot was initially incorporated as a random effect (in a GLMM), but was removed from the final model during step-wise model simplification because it was highly non-significant ($P > 0.25$) and did not add to the best fit model using Akaike Criterion Information (AIC).

**Aquarium grazing trials**

To quantify fish grazing impacts on *Sargassum* recruit (< 2 mm height) abundance, controlled experimental trials were conducted in aquaria. The trials were conducted with different functional groups of common EAM grazers: blennies (*Salarius fasciatus*), parrotfish (initial-phase *Scarus* and *Chlorurus* spp.), and two species of surgeonfish with different jaw morphologies and feeding strategies (*Acanthurus nigrofuscus* and *Ctenochaetus striatus*). The parrotfish and surgeonfish were captured from the reef slope of northern Heron Reef, in shallow spur-and-groove habitat, using a barrier net herding technique, while blennies were captured on the southern reef flat using small hand nets and diluted clove oil solution if necessary. Captured fish were transported to HIRS, where they were kept in outdoor, partly-shaded aquaria with a continuous supply of flow-through seawater. The fish were well-fed on a natural diet of turf-covered coral rubble collected daily from the nearby reef flat. Experimental trials began after a 48 hour acclimatisation period and were conducted between 07:00–16:00.

To quantify the grazing impact of different herbivorous fish functional groups, settlement tiles with > 30 mapped *Sargassum* recruits growing within the EAM were chosen randomly to be subjected to grazing in experimental trials. Tiles were reprocessed as described previously for tiles retrieved from experimental treatments in the field, to recount recruits and remap each tile immediately before and after its use in a grazing trial. Each experimental grazing trial consisted of placing one photographed and processed settlement plate into the tank to be subjected to grazing by *A. nigrofuscus* (17.3 ± 1.69 cm, $n = 5$), *C. striatus* (20 ± 1.26 cm, $n = 6$), *S. fasciatus* (9.2 ± 1.12 cm, $n = 6$), and initial-phase parrotfish (17.7 ± 1.94 cm, $n = 6$) (mean fork length ± SD) for approximately three hours. Control settlement tiles ($n = 6$) were treated identically to experimental tiles, but were placed within a plastic mesh cage that excluded fish and prevented grazing.

To allow grazing intensity on each tile to be calculated, each trial was filmed for its total duration using a GoPro HD Hero placed within the experimental tank. To investigate if the grazing intensity on settlement tiles differed between species, the mean number of bites per minute taken by each fish per settlement plate was calculated by counting the number of bites taken in recorded video footage over the experimental trial duration (~ 3 h per trial). A one-way ANOVA was used to determine if the grazing intensity/bite-rate (bites min$^{-1}$) differed between settlement plates of each experimental trial, after testing that the data met assumptions of normality and equal variances. Homogenous groups were identified using Tukey's HSD post-hoc analysis.

The number of *Sargassum* recruits removed by herbivorous fish grazing was quantified by measuring recruit survivorship as either removed (dead = 0), or still attached (alive = 1) to the settlement tile. To analyse survivorship in the original model, we used fish species as a fixed factor, while the number of recruits per tile (initial density), and fish fork length (cm) were continuous predictors. Fish bite rate (bites min$^{-1}$) was not included in the model as initial ANOVA analysis showed that there was no significant difference in bite rates among treatments (fish species). The final model was determined with step-wise model simplification that identified the model with the lowest AIC from these possible explanatory variables and their interactions. Fish fork length was removed from the final model as this predictor had no significant effect on recruit survivorship. The final model used a GLMM to analyse the binomial response of the number of *Sargassum* recruits removed, with a fixed factor of fish species (*A. nigrofuscus, C. striatus, S. fasciatus* and parrotfish), continuous predictor of initial number of recruits per tile (density), and tile as a random factor, using the "lme4" package (Bates et al. 2013) in R (R Development Core Team 2013).

## Results

**Roving herbivore and adult *Sargassum* distribution and abundance patterns**

A total of 24 herbivore species were recorded on the visual census surveys (Table S1). The abundance of herbivores varied significantly among zones (ANOVA, $F_{3,20} = 5.121$, $P = 0.009$), with a greater abundance of herbivores on the outer reef flat than the mid reef flat, while herbivore abundance did not differ significantly among the remaining zones (Fig. 2a). Although the abundance of herbivores on the outer reef flat was similar to that observed on the inner flat, the inner zone assemblage was composed predominantly of juvenile initial-phase parrotfish schools with individuals that were 5–10 cm in length. While abundant, these groups contributed little in terms of biomass, and resulted in the outer reef flat zone having a much higher total biomass (Fig. 2b).

The distribution of herbivore biomass also varied significantly among reef zones ($F_{3,20} = 18.004$, $P < 0.001$, Fig. 2b). There was a significantly greater biomass of herbivores on the outer reef flat and reef slope than the inner and mid reef flat zones; while there was no difference in herbivore biomass between the outer reef flat and reef slope, or between the inner and mid reef flat (Fig. 2b). Roving

herbivore biomass was approximately 20-fold higher in the outer compared to inner reef flat (Fig. 2b).

The average percent cover of adult *Sargassum* (primarily *S. polycystum*) was significantly greatest in the inner zone decreasing towards the outer reef flat, with no adult *Sargassum* plants found on the reef slope ($F_{3,116} = 29.19$, $P < 0.001$; Fig. 3a). Average *Sargassum* height showed a similar pattern, with the tallest adult plants (and largest biomass) found in the inner zone, and significantly decreased in height towards the outer reef flat ($F_{3,86} = 126.03$, $P < 0.001$; Fig. 3b). The majority of *Sargassum* plants found in the outer zone of the reef flat were only remaining holdfasts and thalli 'stumps' (< 10 cm), with little-to-no leaf biomass (Marshell, pers. obs). The percentage of grazeable substrate (pavement + dead coral + rubble benthic categories) was significantly greater in the reef slope (27.2%) and outer reef flat (19.3%), compared to the inner (0.3%) and mid (2.7%) reef flat zones ($F_3 = 69.59$, $P < 0.001$; Fig. 3c).

**Removal rates of adult *Sargassum polycystum***

There were pronounced differences in the removal rates of adult *S. polycystum* across the four zones ($F_{3,116} = 29.19$, $P < 0.001$; Fig. 4). The removal rate of *S. polycystum* was greatest on the reef slope compared to the reef flat zones, with the majority (94.9% ± 0.58 SE) of the *S. polycystum* assay biomass on the slope removed (Fig. 4). *Sargassum* removal rates were equivalent in the mid and outer zones, and differed significantly from the inner reef flat (Fig. 4). There was no difference in *Sargassum* removal between experimental and caged assays in the inner reef flat, suggesting that there was minimal grazing in this zone (subsequent video analysis will quantify and confirm this). On the reef slope, preliminary video analysis revealed that *Naso unicornis* was the main roving herbivore species responsible for the rapid removal of *S. polycystum* (subsequent video analysis will quantify and confirm this). Most assays on the reef slope were almost completely removed within ~ 30 min after deployment, as the assays were a novelty in an area where normally no adult *Sargassum* is found (Fig. 3).

***Sargassum* recruitment patterns and impact of herbivores**

Five weeks following settlement tile deployment, the newly settled *Sargassum* recruits were < 2 mm high. There was no difference in water flow among exclusion treatments ($P = 0.834$), confirming that flow was not altered by the caging artefacts. However, water flow was different

among zones ($P < 0.05$), driven by greater flow on the reef slope than in the inner reef flat zone (Table S2, Fig. S1).

There was a highly significant effect of zone (fixed, 4 levels, $P < 0.001$) on *Sargassum* recruit abundance, while treatment was marginally non-significant (fixed, 3 levels, $P = 0.062$), and there was no interaction between these factors. There were significantly less *Sargassum* recruits at 4 m deep on the reef slope in comparison to all three reef flat zones (Fig. 5, $P < 0.001$). On the reef flat, the number of *Sargassum* recruits settled in the inner zone was similar to the mid zone ($P = 0.1695$), but much greater than the outer zone ($P < 0.01$), while the number of recruits in the mid zone did not differ from the outer zone ($P = 0.11$). To test if the non-significant ($P = 0.062$) treatment effect was driven by the anomalous result of more *Sargassum* recruits settled on tiles in open vs. caged plots in the outer reef flat zone (Fig. 5), we removed the outer zone and re-ran our model. When the outer reef flat zone was removed, the number of *Sargassum* recruits in caged treatments was significantly greater than open and partially-caged plots ($P = 0.004$).

**Aquaria experimental grazing trials**

Grazing intensity was similar on settlement tiles across experimental trials, as the number of bites per minute taken on each settlement plate did not significantly differ between fish species (bites min$^{-1}$ ± SE: *C. striatus*: 2.8 ± 0.98, *S. fasciatus* 2.8 ± 0.42, *A. nigrofuscus* 3.96 ± 0.64, initial-phase parrotfish 5.7 ± 1.08; $F = 2.710$, $df = 22$ $P = 0.09$).

The removal of *Sargassum* recruits differed significantly among fish species ($P < 0.001$, Fig. 6), while initial density of recruits had no effect on survivorship ($P = 0.6212$). The number of recruits removed by *A. nigrofuscus, C. striatus* and parrotfish grazing differed significantly from the control treatment ($P < 0.001$); however, *S. fasciatus* grazing did not differ from controls ($P = 0.5984$), suggesting that blennies had no significant grazing impact on *Sargassum* recruit survivorship (13% mortality). *Sargassum* recruits subjected to grazing by *C. striatus* suffered the highest mortality (59%) in comparison to all other fish species ($P < 0.001$, Fig. 6). *A. nigrofuscus* and parrotfish grazing had similar impact on *Sargassum* recruit mortality (32 and 30%, respectively; $P = 0.8145$), which was significantly more than blennies and significantly less than *C. striatus* ($P < 0.01$).

# Discussion

Here, we have characterised the top-down influence of roving herbivorous fish on multiple life-stages of *Sargassum*, a large foliose brown macroalga often associated with coral reef degradation and phase-shifts. Using field observations and field and laboratory experiments, we provide a mechanistic understanding of how the three major functional groups of roving herbivorous fish impact components of *Sargassum* population dynamics in multiple coral reef zones. Firstly, a gradient of grazing pressure increasing in intensity from the inner reef flat to the reef slope has been characterized on adult *Sargassum*. Similar to other studies from the region (e.g., Hoey and Bellwood 2011, Fox and Bellwood 2007), this is related to the inverse abundance of the macroalgae found in each of four main zones. Secondly, *Sargassum* recruitment (incorporating settlement and very early post-settlement survival) followed adult distribution patterns, with most recruits settling in the inner and mid reef flat zones, where adult plants were most prolific. Previously it has been demonstrated that ~ 98% of *Sargassum* propagules settle within 1 m from a single source (Kendrick and Walker 1995), but here we show that recruits settled on the reef slope, > 100 m away from adult plants. Finally, the post-settlement survival of *Sargassum* recruits in the EAM was significantly affected by herbivory, and our laboratory experiments revealed that the magnitude of pressure differs among fish functional groups. Importantly, the grazing impact of *C. striatus,* one of the most abundant EAM grazers on Indo-Pacific reefs, exerted the strongest top-down forcing on the post-settlement survival of *Sargassum* recruits.

There was a strong negative relationship between adult macroalgal abundance and herbivore biomass from the inner to outer zone of Heron reef flat. This pattern has been well documented in many other reef systems, both in the Pacific (e.g., Fox and Bellwood 2007) and Caribbean (e.g., Hay et al. 1983). However, we have demonstrated for the first time that this relationship also occurs at the earliest post-settlement stages of macroalgal recruitment. On average, there were over twice as many *Sargassum* recruits when grazing was prevented, with the exception of the outer reef flat zone. Recruitment on tiles where grazers were not excluded in the outer reef flat may have been reduced as this zone had the highest percentage of grazeable substrate (19.3%, Fig. 5) of the three reef flat zones, possibly reducing the novelty of the tiles and the likelihood that they were grazed upon. Additionally, the increased abundance and biomass of fish in the outer zone potentially increased grazing of tiles inside cages by small-bodied grazers, as the cages provided convenient shelter from predators (Marshell, pers. obs). Both of these hypotheses will be investigated through subsequent analysis of *in situ* treatment videos.

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Daily removal of adult *Sargassum* was limited (< 20% per day) across the reef flat, while 95% of adult *Sargassum* biomass was removed on the reef slope; a pattern similar to studies in the northern Great Barrier Reef (e.g., Hoey and Bellwood 2010 and Fox and Bellwood 2008). The limited removal of *Sargassum* in the inner reef flat zone contributed to a dense canopy-forming bed of adult plants. Although canopy-forming brown macroalgae (such as *Sargassum* or *Turbinaria* spp.) compete with corals for space, they also enhance habitat complexity and may provide shelter from predation for small fish in back reef areas (Hoey and Bellwood 2011). Interestingly, the abundance of herbivorous fish in the inner zone was equivalent to the abundance of fish in the outer zone, although the biomass and size structure differed greatly. The inner zone assemblage was composed predominantly of schools of juvenile scarid and siganid fishes of 5 - 10 cm in size. Therefore, the *Sargassum* beds of the inner and mid reef flat areas are likely to be providing nursery habitat for juvenile fish during the seasonal bloom of *Sargassum* (Wilson et al 2010, Evans et al 2014).

Dispersal of *Sargassum* spp. propagules is highly-localized, with most propagules settling within their bed of origin, less than 1 m from their original adult source (Kendrick and Walker 1995; Deysher and Norton 1981). These localized recruitment dynamics result in heterogenous distributions of *Sargassum* recruits in these areas (Kendrick and Walker 1995). Mortality of locally-settled propagules is high, with only 0.0001% of recruits surviving for 12 months, yet the causes of high density-independent mortality is not resolved (Kendrick and Walker 1995). Here, we show that *Sargassum* dispersal is also highly-localized on coral reefs, with the largest number of recruits found in the inner and mid reef flat zones, where adult *Sargassum* dominated the substrate. However, there were *Sargassum* recruits found within the EAM at 4 m in the reef slope zone (which were twice as abundant inside caged treatments), despite the absence of adult *Sargassum* plants, suggesting the lack of adult *Sargassum* in the reef slope is due to grazing and not recruitment limitation (although physical limitations such as wave exposure were not investigated). Thus, our results have important implications when considering the top-down control of macroalgae communities by grazers: i.e. herbivorous fish can limit macroalgal blooms and coral-algal phase shifts by limiting the post-settlement survival of macroalgae at the earliest stage of recruitment.

*Sargassum* is common and abundant on coral reefs worldwide, and is often proposed as a genus responsible for macroalgal blooms and reef deterioration (Hughes 1994; Diaz-Pulido and McCook 2004; Hughes et al. 2007b). Following disturbances on coral reefs, the occurrence of macroalgal blooms will likely depend on the interaction between major benthic groups (corals, CCAs, algal turfs), and macroalgal settlement, recruitment and survival (Diaz-Pulido and McCook 2002).

*Sargassum* invasion of new areas requires propagule dispersal and recruitment, processes that initially seem limited outside established adult *Sargassum* bed populations, as the majority of germlings arise within 2–3 m of parent plants (Deysher and Norton 1981; Kendrick and Walker 1995; McCook 1999). Yet, *Sargassum* propagules have the ability to disperse further from established adult populations through local environmental processes such as tide-, wave- and wind-driven currents (Stimson 2013), or regional processes such as surface ocean currents that carry floating mats of detached adult *Sargassum* (Deysher and Norton 1981; Wells and Rooker 2004). The occurrence of *Sargassum* recruits on Heron reef slope could be due to the large tidal range (1 - 3 m) and strong currents experienced on Heron Reef, with maximum tidal current velocities reaching 0.3 m/s under mild conditions on the reef flat, and the occurrence of large off-reef waves causing maximum velocities of 0.5 to 0.7 m/s (Gourlay and Colleter 2005; Gourlay and Hacker 2008). Therefore, despite generally having limited dispersal ability, it is possible that *Sargassum* blooms could still occur on coral reefs that lack established adult populations. The likelihood of a bloom would increase if macroalgal recruits settled within the EAM are freed from herbivory (e.g., due to overfishing) and able to develop into dominant macroalgal beds (Hatcher 1990, McCook 1999). However, the potential for macroalgal dominance will be dependent on species-specific recruitment dynamics and local environmental factors (McCook 1999; Cheal et al. 2013).

The survival of *Sargassum* recruits (< 2 mm) settled within the EAM differed among fish types in our aquarium trials. Over the experiment duration, *Ctenochaetus striatus* induced the highest mortality (59%), followed by *A. nigrofuscus* and parrotfish species (~30%). This is noteworthy as *C. striatus* is: (1) a dominant species on Indo-Pacific coral reefs in terms of density and biomass (e.g., Sabater and Tofaeono 2007, Cheal et al. 2012), (2) constitutes a significant part of some Pacific coral reef fisheries (e.g., American Samoa, Ochavillo et al. 2011), and (3) currently classified as a detritivore that 'combs' detritus from the EAM surface, causing little damage to algal turfs (Purcell and Bellwood 1993; Green and Bellwood 2009). However, we have demonstrated that *C. striatus* is capable of removing significant quantities of macroalgal recruits and algal turfs in aquarium experiments (Marshell and Mumby 2012). Therefore, due to the capability of *C. striatus* to significantly impact algal dynamics, its detritivorous classification may need to be reconsidered, especially when considering its current exclusion from reef resilience monitoring (Green and Bellwood 2009). The capability of *C. striatus*, *A. nigrofuscus* and parrotfish species to remove significant numbers of macroalgal recruits from within the EAM is of significant ecological importance, as these species intensely graze the EAM with fast average bite rates, and are very abundant and widespread on most reefs throughout the Indo-Pacific (Choat and Bellwood 1985;

Polunin et al. 1995; Trip et al. 2008; Cheal et al. 2012). Thus, the recovery of coral reefs following large disturbances may be influenced by these fish through their limiting effects on macroalgal recruitment, aiding in the prevention of macroalgal phase-shifts through ecosystem resilience (Graham et al. 2013).

The actual grazing impact that herbivorous fish collectively have on macroalgal recruits within the EAM will depend on what natural densities of recruits are found within the EAM across different reef habitats; data that is currently not available for most areas. The limited information on *Sargassum* recruitment dynamics is mostly from sub-tropical/temperate regions, and knowledge of early post-settlement recruitment dynamics in different habitats is lacking (i.e. Kendrick and Walker 1995). There is one coral reef study of *Sargassum* recruitment, that found approximately 100 *Sargassum* recruits per 100 cm$^{-2}$ on dead coral settlement plates within an inshore reef-flat *Sargassum* bed (Diaz-Pulido and McCook 2004). Studies are probably limited because it is difficult to measure the natural densities of early-stage seaweed recruits across habitats, as the recruits are often too small to be counted and may settle in cryptic habitats to avoid grazing (Santelices 1990; Brandl et al. 2013; Poray & Carpenter 2014). Consequently, there is a paucity of studies investigating early stage *Sargassum* recruitment dynamics across coral reef habitats, and rates of recruit dispersal, post-settlement growth and mortality are largely unknown. However, it is widely accepted that grazing is the most important cause of macroalgal recruit mortality, and likely responsible for regulating recruit distribution patterns (Santelices 1990). Our results quantify the grazing impact on macroalgal recruits across reef zones, identify the role of different functional groups of herbivorous fish, and provide an important insight into the patterns occurring at this early recruitment post-settlement stage on coral reefs.

In summary, it is likely that common parrotfish (*Scarus* and *Chlorurus* spp.) and surgeonfish species (*A. nigrofuscus* and *C. striatus*) contribute significantly towards reducing overall macroalgal cover on reefs and have important ecological roles, potentially providing a mitigation service against macroalgal blooms on coral reefs. However, it is not yet known whether 'prevention' is better than 'cure'. While prevention of macroalgal blooms by EAM grazers is undoubtedly important, the role of browsing herbivores that can possibly reverse phase shifts is certainly equally important and protecting a combination of these key species is likely to be the best management policy. Therefore, it is important to determine the nature of the top-down control of grazers upon algae as part of a complete investigation of all the drivers that might promote or mitigate a macroalgal bloom on reefs, and examining the specific ecological role of key herbivorous fish

species is essential to understand reef resilience (Graham et al. 2013). Protecting key herbivore species with 'prevention' or 'reversal' capabilities in some disturbed coral reef areas may prove vital to reducing algal overgrowth and coral reef degradation through macroalgal blooms.

## Acknowledgements
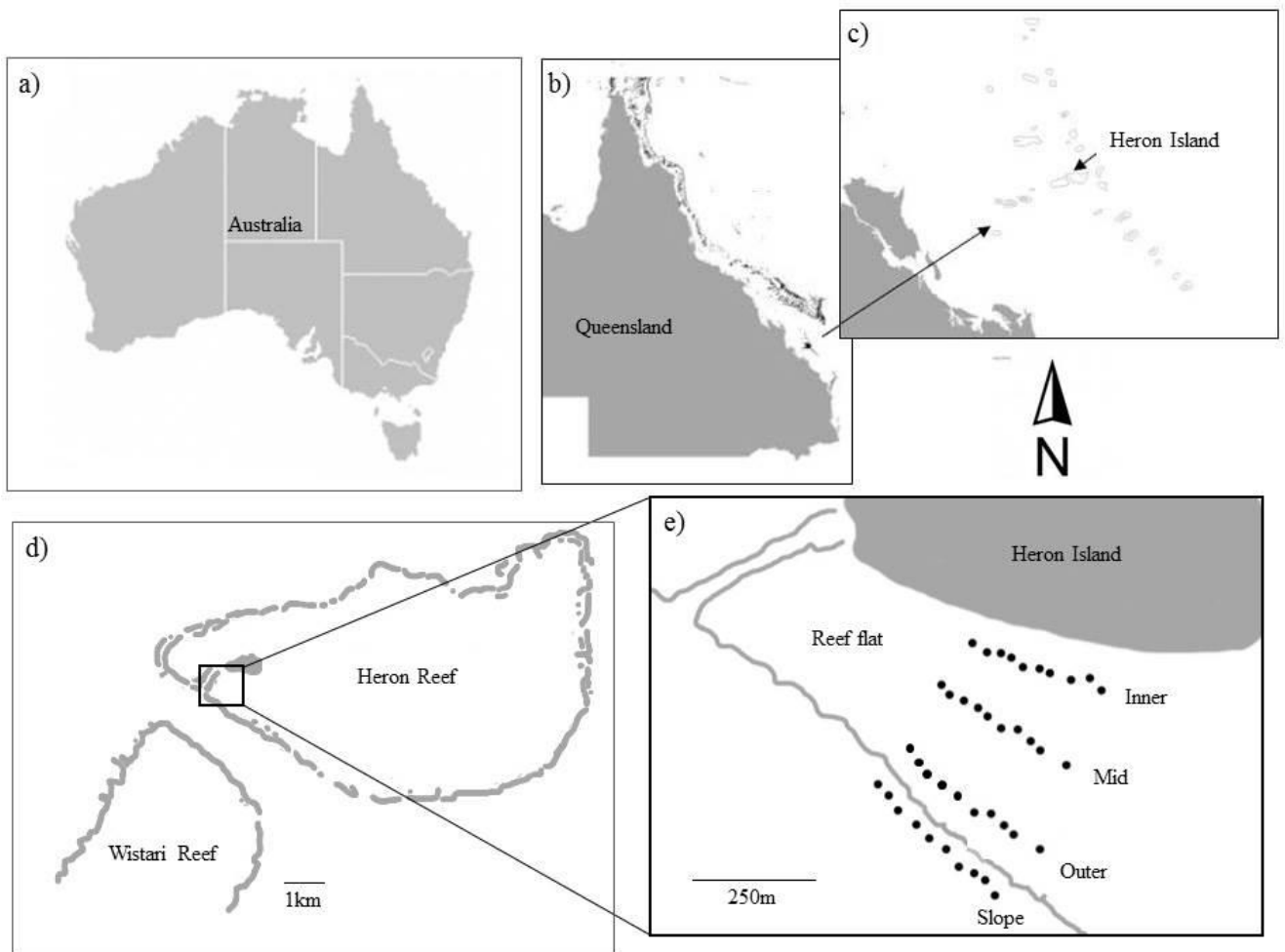
Figure 1. Heron Reef is located ~ 70kms off (a) Australia's Queensland coast, in the (b) southern Great Barrier Reef, and within the (c) Capricorn Bunker Group. The study site was located on (d) the southern side of Heron Island, (e) across four zones parallel to shore: the inner, mid, and outer reef flat, and at 4 m deep on the reef slope. Black circles indicate the positions of the settlement tile plot groups ($n = 10$ replicates per zone, each ~ 30m apart). Each circle represents a plot group of three treatments (~ 1 m apart): a caged, partially-caged and open tile ($n = 30$ tiles per zone and 120 tiles overall).
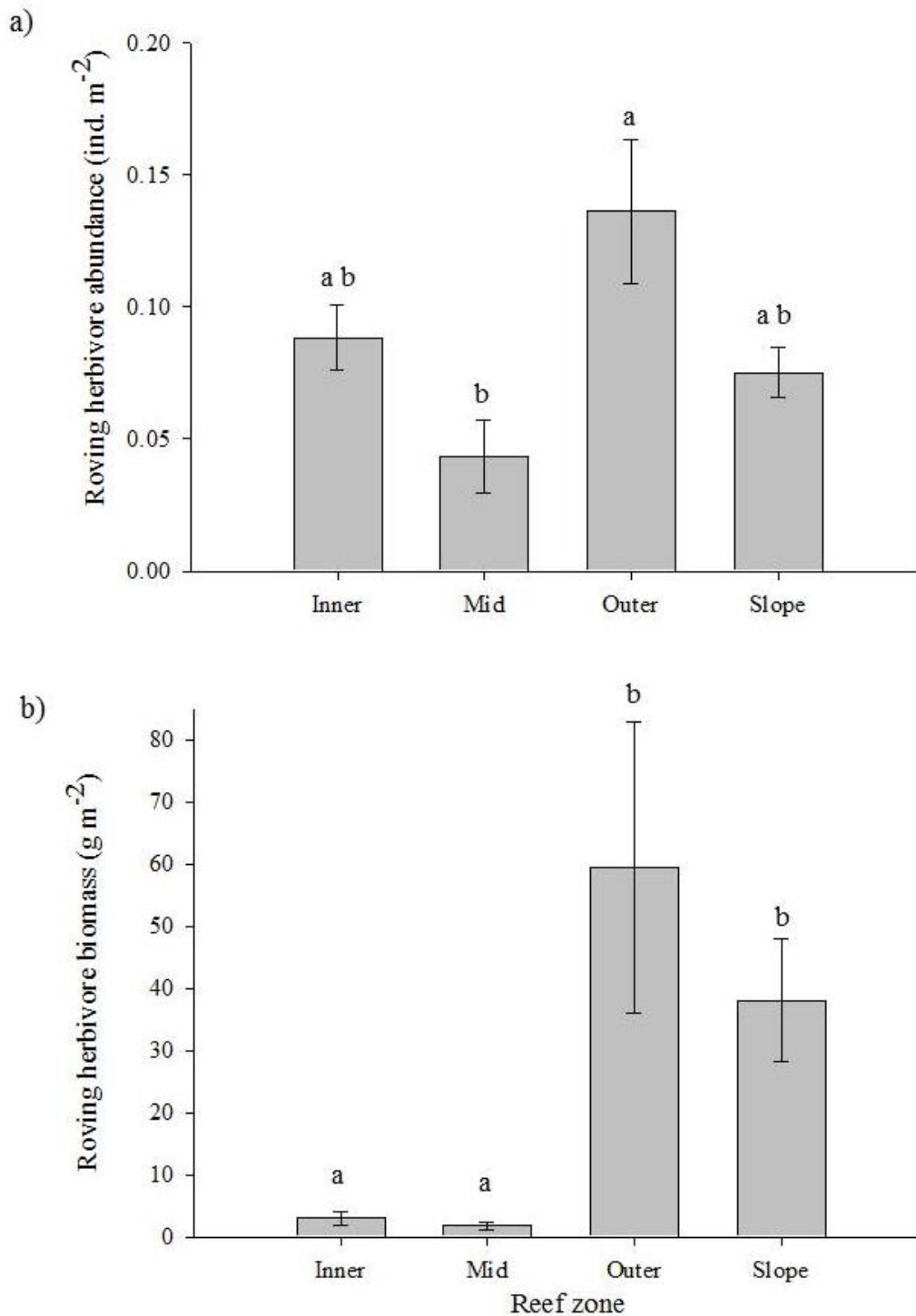
Figure 2. High-tide distribution of total roving herbivore a) abundance (ind.m$^{-2}$ ± SE), and b) biomass (g m$^{-2}$ ± SE) across the southern Heron reef flat zones (inner, mid and outer), and at 4 m deep on the reef slope. The letters above each bar indicate homogenous groups as identified by a Student-Newman-Keuls (SNK) post-hoc test.
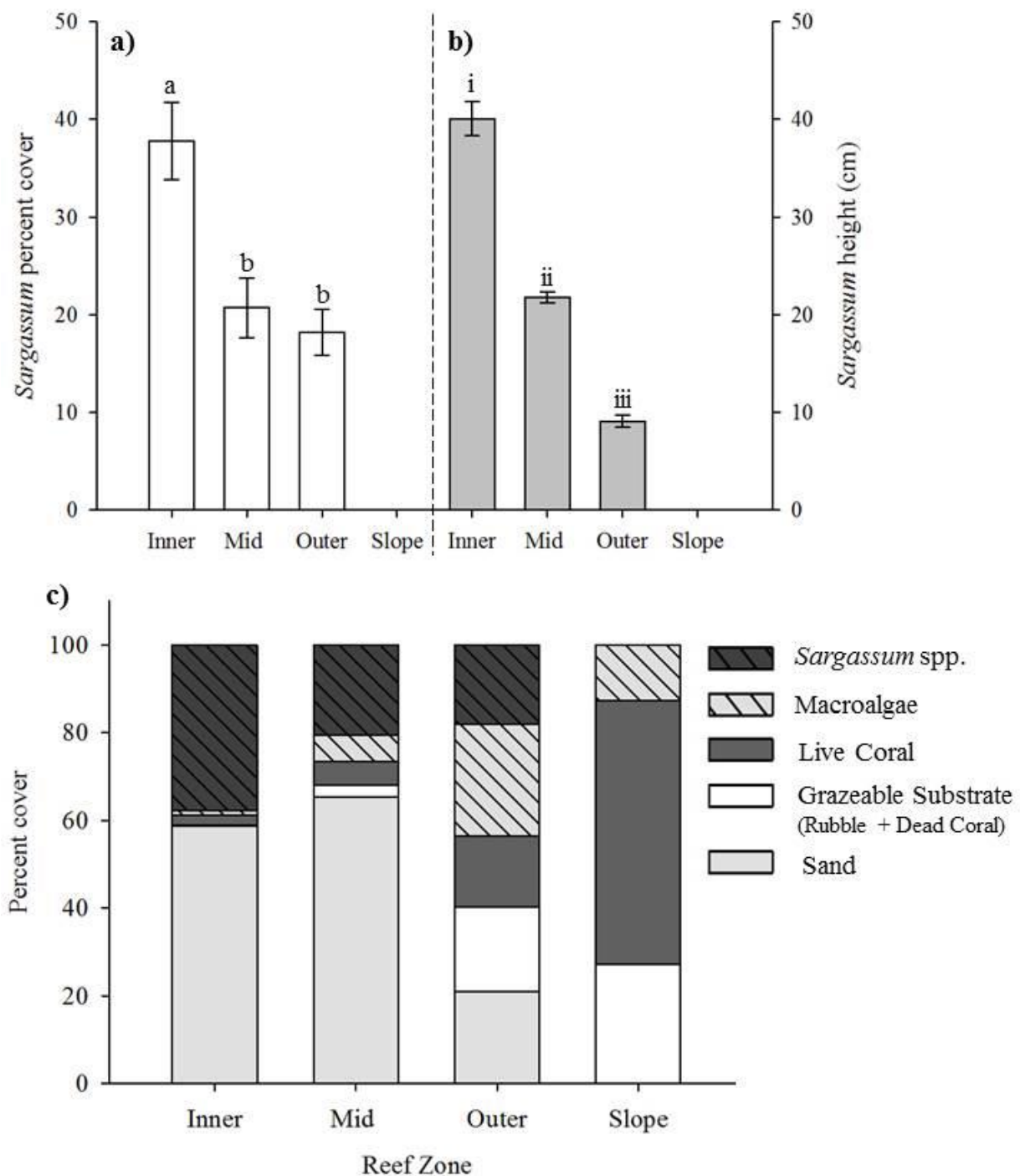
Figure 3. a) The average adult *Sargassum* spp. percent cover (% ± SE), and b) height (cm ± SE) in the inner, mid, outer reef flat, and reef slope (4 m) zones of Heron Island, April 2013 (N.B., there was no adult *Sargassum* found on the reef slope). The letters above each bar indicate homogeneous zones within each category as identified by Tukey's HSD post-hoc analyses. c) The average percent cover of substrate in the inner, mid, outer reef flat, and reef slope (4m) zones (see Figure 1e for zone locations). N.B., macroalgae in the slope zone was primarily the rhodophyta *Amansia glomerata* growing amongst the branching live and dead coral.
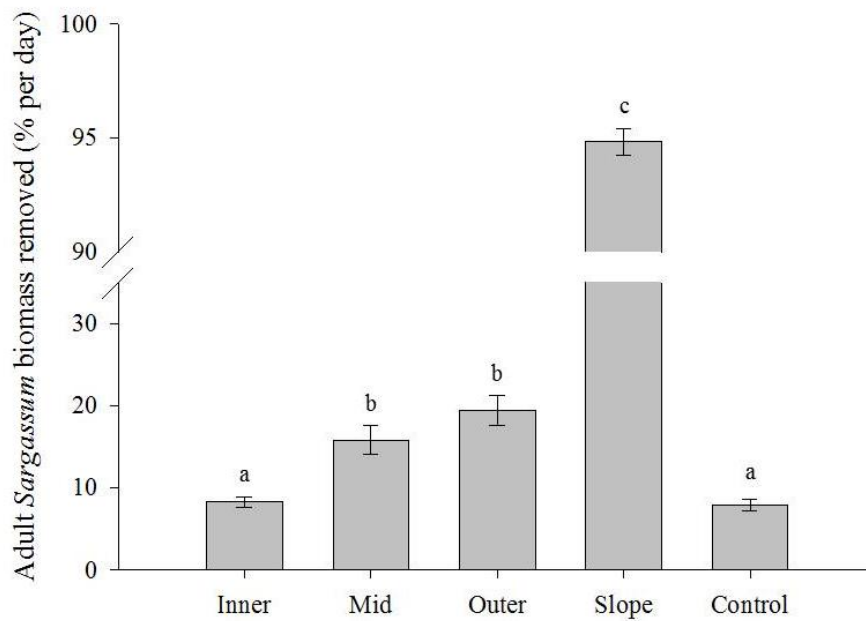
Figure 4. The average (± SE) percentage of adult *Sargassum polycystum* assays removal rates per day in different zones of the southern Heron Island reef flat and slope (4 m depth). The letters above each bar indicate homogeneous *Sargassum* removal rates among zones, as identified by Tukey's HSD post-hoc analyses.
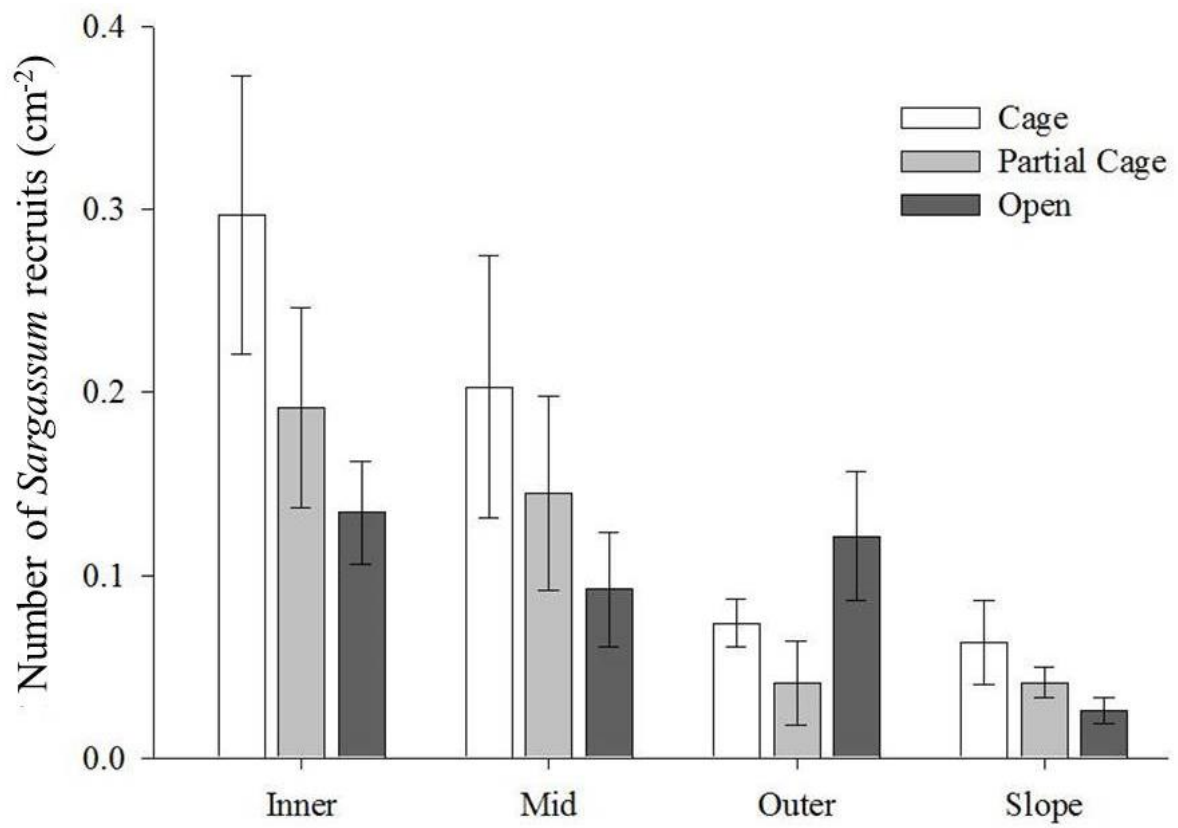
Figure 5. The average (± SE) number of *Sargassum* recruits (< 2mm) per cm$^{-2}$ in different zones of the southern Heron Island reef flat (inner, mid, outer) and slope (4 m deep).
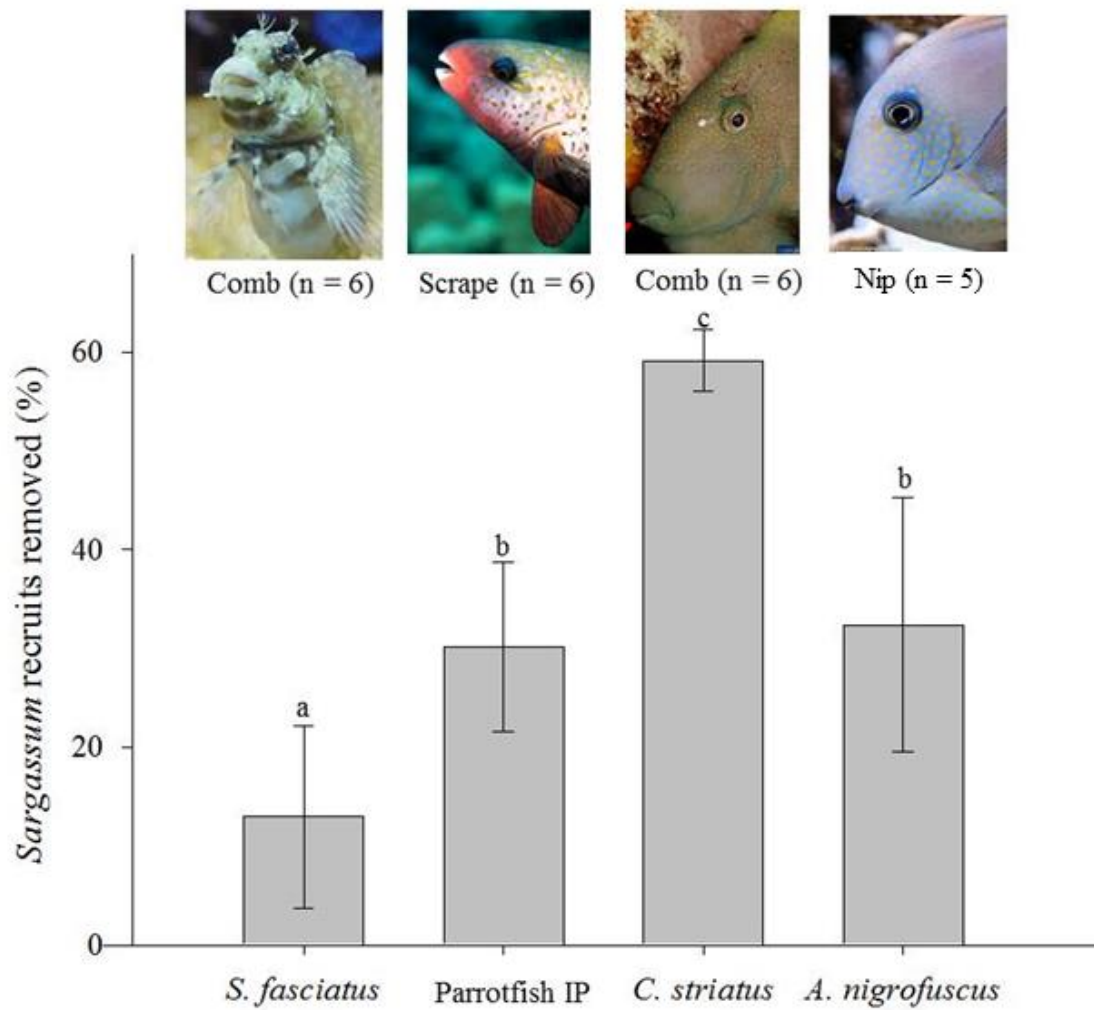
Figure 6. The average (± SE) percentage of *Sargassum* recruits removed, per herbivorous fish species, per experimental grazing trial (t = ~ 3 hours). The letters above each bar indicate homogeneous *Sargassum* removal rates among species, as identified by GLMM analyses.

## Supplementary Material

Table S1. Summary of the species composition (*n* = 24) of herbivorous fish observed during underwater visual census surveys of Heron Island reef flat (inner, mid and outer) and slope (~ 4 m deep) during April 2013.

| Acanthuridae | Scaridae | Signaidae |
|---|---|---|
| *Acanthurus nigrofuscus* | *Chlorurus microrhinus* | *Siganus argenteus* |
| *Ctenochaetus binotatus* | *Chlorurus sordidus* | *Siganus canaliculatus* |
| *Ctenochaetus striatus* | *Scarus chameleon* | *Siganus corallinus* |
| *Naso annulatus (juvenile < 20 cm)* | *Scarus ghobban* | *Siganus doliatus* |
| *Naso unicornis* | *Scarus niger* | *Siganus puellus* |
| *Naso lituratus* | *Scarus rivulatus* | *Siganus punctatissimus* |
| *Zebrasoma scopas* | *Scarus shlegeli* | *Siganus spinus* |
| *Zebrasoma veliferum* | *Scarus spinus* | *Siganus vulpinus* |

Table S2. Summary of a two-way ANOVA comparing the percent dissolution of plaster-of-paris clod cards deployed simultaneously over 24 hours within different treatments (cages, partial cages, and open) and zones (inner, mid, outer reef flat and reef slope at 4 m deep).

| Source of Variation | DF | SS | MS | F | *P* |
|---|---|---|---|---|---|
| Zone | 3 | 334.6 | 111.5 | 2.81 | 0.050* |
| Treatment | 2 | 14.5 | 7.3 | 0.18 | 0.834 |
| Zone x Treatment | 6 | 80.1 | 13.3 | 0.34 | 0.915 |
| Residual | 48 | 1908.3 | 39.8 | | |
| Total | 59 | 2337.42 | 39.62 | | |
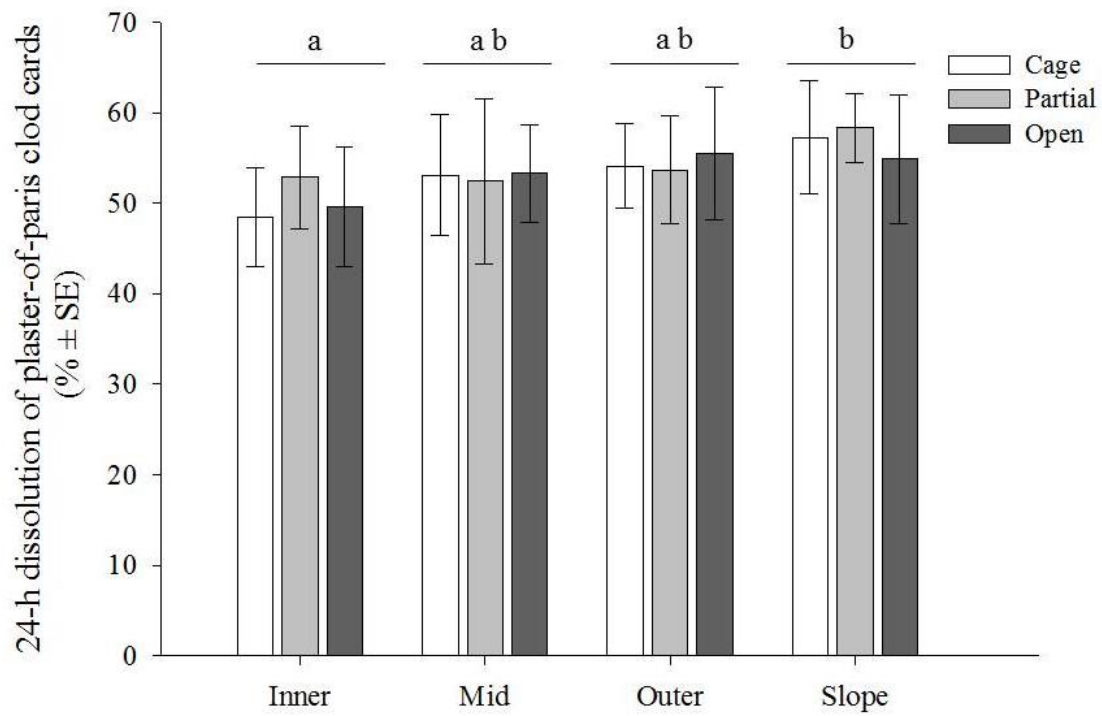
Figure S1. The average percent dissolution (± SE) of plaster-of-paris clod cards deployed simultaneously over 24 hours within different treatments (cages, partial cages, and open) and zones (inner, mid, outer reef flat and reef slope at 4 m). The letters above each zone indicate homogeneous groups as identified by Tukey's HSD post-hoc analyses.

# Chapter 3. Revisiting the functional roles of the surgeonfish *Acanthurus nigrofuscus* and *Ctenochaetus striatus*

## Abstract

Investigating the functional role of herbivorous fish species is important for understanding reef resilience and developing targeted management plans. Amongst the most abundant fish species on Indo-Pacific coral reefs are the surgeonfishes *Acanthurus nigrofuscus* and *Ctenochaetus striatus*. *A. nigrofuscus* is an herbivorous grazer that crops filamentous algae from the epilithic algal matrix (EAM), while *C. striatus* is detritivorous and was thought to 'brush' detritus from the surface of filamentous algae, causing little damage to algal strands. Although the foraging mechanisms and general diet of these surgeonfishes have been established, their grazing impact on epilithic algal turfs has been unclear. This is the first study to quantify directly the grazing impact of *A. nigrofuscus* and *C. striatus* on algal turfs. Through aquaria trials using epilithic algal turf grown on experimental tiles, we found that both *A. nigrofuscus* and *C. striatus* consistently fed more intensively upon sparse/short algal turfs even though the yield of algae per bite was greater for dense/long algal turfs. As there was no difference in the nutritional value of sparse and dense algal turfs, we hypothesise that *A. nigrofuscus* avoided dense turf due to its significantly greater sediment-load than sparse turf, while *C. striatus* likely avoided dense turf as it would become entangled in their bristle-like teeth. Unexpectedly, despite its dental morphology, *C. striatus* removed significantly more algal turf per hour than *A. nigrofuscus*, irrespective of canopy height. The capability of *C. striatus* to remove significant quantities of algal turf through their foraging activity implies that this abundant and widespread species may substantially affect algal turf dynamics. If this is the case, the exclusion of detritivorous *Ctenochaetus* species from herbivorous fish functional groups used in resilience monitoring will need to be re-evaluated.

## Keywords

# Introduction

Herbivory can be more intense on coral reefs than in any other marine or terrestrial habitat (Hatcher and Larkum 1983; Carpenter 1986; Lewis 1986; Choat 1991). Herbivorous fishes generally consume the majority of daily coral reef primary production, although invertebrate grazers are also important on some reefs (Hatcher 1981; Carpenter 1986). Herbivorous fish exert top-down controls on algal biomass (Lewis 1986; Hughes et al. 2007; Burkepile and Hay 2008), productivity (Russ 2003), and succession (Hixon and Brostoff 1996), thus reducing the establishment and growth of algal communities that compete with coral for space and inhibit coral recruitment, especially post-disturbance (Carpenter 1986; Hughes et al. 2007). Disturbances such as cyclones, bleaching, and outbreaks of crown of thorns starfish often lead to the loss of coral cover and increase of algae on coral reefs. Following disturbances, herbivorous fish play an important role in removing algae and promoting reef resilience and recovery (Nyström and Folke 2001; Bellwood et al. 2004; Ledlie et al. 2007). Therefore, herbivory is widely acknowledged as a key ecological process that structures benthic communities, and is important for the resilience of coral reefs (Steneck 1988; Bellwood et al. 2004; Mumby and Steneck 2008).

Determining the nature of top down controls of grazers upon algae is important as part of a holistic analysis of all the drivers that might promote or mitigate an algal bloom on reefs (Russ 2003). On coral reefs across the mid and outer Great Barrier Reef, the epilithic algal matrix (EAM) covers 50 to 80 % of reef flats and back reefs and 30 to 70 % of reef slopes (Hatcher and Larkum 1983; Klumpp and McKinnon 1992; Wismer et al. 2009). The EAM is a major source of primary production, and is the predominant grazing surface for many herbivorous fishes (Hatcher 1997; Wilson et al. 2003). The EAM is a complex assemblage consisting of microalgae (e.g., diatoms, cyanobacteria), filamentous algal turfs < 1 cm high, juvenile stages of macroalgae, crustose algae, and detrital material (dead organic matter, inorganic material, microbes, meiofauna) (Steneck 1988; Choat 1991). More than 70% of the detrital component of the EAM is derived from decaying filamentous algae, which is more nutritious than live algal turf because of the addition of bacteria and microalgae, and this dissolved organic matter is also more palatable and easier to digest (Wilson et al. 2003). The EAM primarily forms short, sparse mats of algal turfs < 1 cm high that have a high turnover rate because of intense grazing (Hatcher and Larkum 1983; Carpenter 1986). Long, dense mats of algal turfs > 1 cm high are generally only found within damselfish territories (Wilson and Bellwood 1997), or areas with heavy sediment-load. Long, dense algal turfs trap more

sediment than short, sparse algal turfs, resulting in a relatively stable, sediment-rich algal turf mat (Bellwood and Fulton 2008).

Herbivorous fish are a diverse ecological group (Choat 1991) and broad functional categories were established to aid development of general models of plant-herbivore interactions (Steneck 1988). Functional groups are formed based on species roles in ecosystem processes (Bellwood et al. 2004; Green and Bellwood 2009), and species are assigned to functional groups based on their ability to carry out similar ecosystem functions, regardless of their taxonomic classification (Steneck and Dethier 1994). Fish species are categorised into functional groups depending on how they feed, what they consume, and how they affect the structure of benthic communities (Green and Bellwood 2009). The most widely-recognised functional groups of herbivorous fish are: small excavators/scrapers, large excavators/bioeroders, grazers/detritivores, and browsers (Green and Bellwood 2009). Herbivorous fishes that feed on the EAM are an important trophic link between algal primary production and secondary consumers (Horn 1989; Choat 1991). However, it is often difficult to determine the trophic class or functional group of fishes that feed upon the EAM because of its complex species assemblage and physical structure. Consequently, EAM grazing fishes are classified into the single functional group of grazers/detritivores. Yet, species that are considered exclusively detritivorous, causing little damage to algae through their grazing (e.g., *Ctenochaetus* species), are recommended to be excluded from resilience monitoring, as they are thought to not limit the establishment and growth of algal communities (Green and Bellwood 2009).

Inevitably, the categorisation of organisms into functional groups requires a compromise between highlighting major differences among groups and recognising the existence of heterogeneity within individual groups. Unfortunately, the functional role of some herbivorous fish species remains somewhat obscure (Fox et al. 2009), which prevents the adequacy of some functional classes from being evaluated. A case in point are the numerically-dominant herbivores on many Indo-Pacific reefs, the surgeonfishes (Acanthuridae) that feed upon the EAM (Steneck 1988). Recent work has highlighted the ecological importance of acanthurid browsers in macroalgal dynamics (Hoey and Bellwood 2009), and acanthurid detritivores in sediment dynamics (Goatley and Bellwood 2010), but the functional role of highly-abundant, diminutive acanthurid grazing species in algal turf dynamics is less understood.

Throughout the Indo-Pacific, two of the most abundant reef fishes that feed upon the EAM are the brown surgeonfish, *Acanthurus nigrofuscus*, and the lined bristletooth, *Ctenochaetus striatus* (Russ

1984; Choat and Bellwood 1985; Trip et al. 2008; Cheal et al. 2012). *A. nigrofuscus* is classified as a grazer that feeds upon sparse algal turfs, nipping epilithic microalgal turf filaments from the substratum (Horn 1989; Purcell and Bellwood 1993; Polunin et al. 1995). *C. striatus* is classified as a detritivore that feeds upon sparse algal turfs and calcareous algae, 'brushing' detritus off the substratum surface and causing little damage to algal turfs (Choat 1991; Purcell and Bellwood 1993; Polunin et al. 1995; Choat et al. 2002; Choat et al. 2004; Goatley and Bellwood 2010). Given the abundance of *C. striatus* and *A. nigrofuscus*, which can dominate fish communities and attain average densities on sheltered reefs of up to 33 and 13 individuals per 300m$^{-2}$ respectively (Choat and Bellwood 1985), it is important to establish the foraging impact of these species on algal turf communities. A key functional question, from an ecosystem perspective, is whether these species can physically remove algal turfs from the EAM. If a species simply 'brushes' the algal turf surface for detritus, then it may have little or no direct impact on algal dynamics. However, should the action of their foraging effectively remove significant algal turf biomass – even if targeting detritus rather than living algal turf, then the functional impact on algal dynamics will be very different.

Here we study the grazing impact of *A. nigrofuscus* and *C. striatus* on algal turfs. Through experimental trials we aim to: (1) investigate the potential grazing impact of acanthurid grazer *A. nigrofuscus* and detritivore *C. striatus* on epilithic algal turfs, (2) establish whether these species prefer to feed upon different stages (sparse/short: 2-week growth, or dense/long: 6-week growth) of algal turfs, and examine whether this is correlated with differing algal nutritional value or sediment load, and (3) determine the average amount of algal turfs ingested per bite by these fishes.

## Methods

### Fish capture and husbandry

This study was undertaken at Heron Island Research Station (HIRS), southern Great Barrier Reef, Queensland, Australia (23.44°S, 151.91°E). Individuals of *Acanthurus nigrofuscus* ($n = 10$) and *Ctenochaetus striatus* ($n = 8$) were captured from northern Heron reef slope, in shallow spur-and-groove habitat (23°26'23"S, 151°58'37.2"E), using a barrier net (25 x 1.5 m) herding technique. The average fork length (cm ± S.D.) of captured *A. nigrofuscus* and *C. striatus* was 16.7 ± 1.4 and 19.7 ± 1.6, respectively. Captured fish were transported to the HIRS laboratory where they were kept in outdoor, partly-shaded aquariums for a maximum of 3–5 days before the trials commenced. *C. striatus* individuals were kept in a large circular aquarium (2.05 m diameter x 0.6 m deep, 1980

l), while *A. nigrofuscus* individuals were kept in an oval aquarium (2.15 m long x 1 m wide x 0.5 m deep, 878 l), both with a continuous supply of unfiltered flow-through seawater pumped directly from the reef. Both species were kept well-fed on a natural diet of dead massive coral pieces that were covered with algal turfs and sediment collected daily from the nearby reef flat. Rectangular aquariums for experimental trials (1.85 m long x 0.7 m wide x 0.25 m deep, 324 l) were divided in half using black plastic 2.5 cm$^2$ mesh, to create two experimental areas per aquarium. Each experimental area had a concrete block housing and was partly-covered with shade-cloth. Individual fish were removed from the holding aquaria on the evening prior to their experimental trials and placed into the experimental aquariums. Experimental trials were conducted the following day between 08:00–12:00 hrs. If the fish fed and there was a noticeable reduction in algal turf biomass, they were released post-trial, otherwise, on rare occasions, the trial was cancelled and the fish were returned to holding aquaria to be retried on another day. If the fish did not feed on a second attempt, they were released without being used in trials. There were a maximum of 2–3 fish per species that were released because they were not behaving normally in the trials.

**Feeding preference aquaria experimental trials**

To develop epilithic algal turf growth on experimental tiles, limestone tiles (13 x 13 x 1.5 cm) with a rough textured surface were preconditioned on the reef for four months prior to the experiments and then scrubbed gently to begin with an algal biomass of zero, while maintaining turf holdfasts and live cover of encrusting benthic organisms, before being placed in aquarium troughs (1.85 m long x 0.7 m wide x 0.25 m deep, 324 l) with continuous flow-through unfiltered seawater pumped directly from the reef flat. To determine whether *A. nigrofuscus* and *C. striatus* prefer to feed upon different stages of algal turf growth, we allowed different stages of algal turfs to develop, by placing the preconditioned tiles into troughs in phases, resulting in tiles with sparse (< 1 cm, 2-week growth) and dense (> 1 cm, 6-week growth) algal turf growth.

To determine the average algal turf biomass (g C cm$^{-2}$) and sediment/inorganic biomass (g cm$^{-2}$) on each tile before and after each experimental trial, eight random 2.5 x 2.5 cm squares were scraped, dried to constant weight at 60°C and weighed to the nearest 0.0001 g. The random squares were scraped using a razor blade to remove all algal biomass within the 2.5 cm$^2$ square of a plastic mesh quadrat placed gently on the tile surface. The organic weight (or ash free dry weight – AFDW) of each scraped algal turf sample was determined by reweighing the sample after ashing at 500°C for at least 6 h (Paine and Vadas 1969), and subtracting the weight of the remaining ash from the

constant dry weight. The inorganic weight of each scraped sample was determined by subtracting the remaining ash after the trial, from the ash before the trial to give an indication of the average sediment (inorganic remaining ash) removed during the trial. The surface area ($cm^2$) was determined by measuring the length and width of each tile.

Each experimental trial consisted of two experimental tiles (one with sparse/short and one with dense/long algal turf growth) offered to an individual fish (*A. nigrofuscus*: $n = 9$; *C. striatus*: $n = 8$) by randomly placing them in the experimental tank a few centimetres apart. Experimental tiles were left in the tank for 60 min, or until there was a noticeable reduction in algal biomass. Each feeding trial was filmed using a Sanyo Xacti HD2000 camcorder and subsequent video analysis permitted the number of bites taken to be counted. To control for loss of algal turf biomass due to handling during each experimental trial, control sparse ($n = 11$) and dense ($n = 11$) tiles were scraped and kept under identical conditions as experimental tiles, but without fish present. Experimental tiles were also individually photographed before and after each trial.

To investigate the nutritional quality of the algal turf growth on experimental tiles, ten samples of both sparse and dense algal turfs were scraped from random tiles, frozen immediately, and their energy contents determined from C and N mass fraction analysis. Nitrogen is a limiting nutrient for the growth of herbivores (Choat 1991). Therefore, C:N ratios of food sources have been extensively used as an indicator of nutritional quality to consumers and provide a useful measure for comparing the potential nutritional significance of food sources (Purcell and Bellwood 2001).

For C and N mass fraction analysis, each dried algal turf sample was weighed and then ground up with a mortar and pestle. A portion of this was run through a LECO TruSpec CHN analyser, at the University of Queensland School of Agriculture and Food Science, to combust a known quantity of sample wrapped in tin foil with pure oxygen at 950°C which volatilizes all forms of nitrogen and carbon into a gaseous state. The various nitrogen oxides (NO, NO2) are reduced to nitrogen ($N_2$) gas which is then quantitatively determined, while the carbon is converted to carbon dioxide ($CO_2$) which is measured with an infrared detector cell to determine total C and total N. The instrument calculates the results and provides them in a weight percent (Wt %) format, and to convert the Wt % results to milligrams per kilogram (mg/kg), the Wt % result was multiplied by 10,000. The leftover sample was treated with acid and the inorganic carbonate loss was measured gravimetrically, to obtain organic carbon estimates. The inorganic carbon is a background level and

is not related to the organic carbon of organisms. As there was not a lot of leftover sample to work with, there is ~ 2% error in the organic carbon estimates.

**Data analysis**

The potential grazing intensity ($m^{-2}$ $h^{-1}$) of *A. nigrofuscus* and *C. striatus* was calculated for both sparse and dense algal turf treatments by:

$$\text{mean number of bites (h}^{-1}) \times \text{mean bite size (cm}^{-2}).$$

The mean bite size of each species was calculated by measuring the area ($cm^2$) of grazing scars left on experimental tiles using freeware image analysis program 'Image J', and then scaling up the mean grazing scar area to $m^2$. Combined error terms were calculated using Goodman's estimator (Travis 1982; Marnane and Bellwood 2002):

$$\text{SE } (\bar{x} \times \bar{y})^2 = \bar{x}^2 \times \text{SE}_{\bar{y}}^2 + \bar{y}^2 \times \text{SE}_{\bar{x}}^2 + \text{SE}_{\bar{x}}^2 \times \text{SE}_{\bar{y}}^2$$

where $\bar{x}$ = mean number of bites; $\bar{y}$ = mean bite size; $\text{SE}_{\bar{x}}$ = standard error of mean number of bites; $\text{SE}_{\bar{y}}^2$ = standard error of mean bite size.

The average amount of algal turf removed per bite by *A. nigrofuscus* and *C. striatus*, was determined by calculating the average decrease in algal turf biomass after a known number of bites on experimental tiles with epilithic algal turf growth (Bruggemann et al. 1994b). Food intake per bite was calculated as (g algal AFDW):

$$\text{mean algal biomass}_{\text{before}} - \text{mean algal biomass}_{\text{after}}/\text{no. of bites cm}^{-2}.$$

All results are presented as mean ± standard error, unless stated otherwise. To investigate whether differences existed between sparse and dense turf tile treatments, normal distribution of the data was established using a Shapiro-Wilk test, and paired t-tests were used to compare between the two treatments. Log-transformation of samples achieved normal distributions and/or obtained equal variances when required.

# Results

Both *Acanthurus nigrofuscus* (grazer) and *Ctenochaetus striatus* (detritivore) preferred sparse/short algal turf to dense/long algal turf growth, with 88% of *A. nigrofuscus* bites ($n = 5648/6430$), and 74% of *C. striatus* bites ($n = 1734/2351$) taken on sparse algal turfs.

On average, *A. nigrofuscus* took significantly more bites on sparse than dense algal turfs (Fig. 1a-i; $t_8 = 4.782$, $P = 0.001$), and removed more algal turf per bite when feeding on dense algal turf (Fig. 1b-i; $t_8 = -3.761$, $P = 0.006$). Although *A. nigrofuscus* removed more algal turf per bite when feeding on dense algal turf, the fish consistently invested a greater proportion of their time (> 80%) and effort feeding upon sparse algal turf throughout the experimental trial (Fig. 1c).

The results from *C. striatus* were qualitatively similar to *A. nigrofuscus* in that (i) their grazing rate was higher on sparse algal turf than dense algal turf (Fig. 1a-ii; $t_7 = 3.529$, $P = 0.01$), (ii) they removed more algal turf per bite when feeding on dense algal turf (Fig. 1b-ii; $t_7 = -3.463$, $P = 0.01$), and (iii) the investment of time feeding on sparse algal turfs was consistently greater (> 70%) over the duration of the trial despite a larger harvest per bite on dense algal turfs (Fig. 1d). The data in Figures 1a and 1c/d are directly related (number of bites = time/effort spent on a treatment); however, Figures 1c/d display how the fish behaved over the duration of the trial, with both species preferring to feed consistently upon the sparse turf treatment.

*A. nigrofuscus* was observed to remove turf and leave sediment behind, whereas *C. striatus* removed both turf and sediment indiscriminately from the experimental tiles (Fig. 2 a, b). *C. striatus* removed more inorganic sediment biomass (g cm$^{-2}$ h$^{-1}$) per trial than *A. nigrofuscus* for both sparse ($t_{15} = -4.531$, $P = < 0.001$) and dense ($t_{15} = -3.435$, $P = 0.004$) algal turf treatments (Fig. 2c). On average, the detritivorous species *C. striatus* also removed significantly more algal turf biomass (g C cm$^{-2}$ h$^{-1}$) than the grazing species *A. nigrofuscus,* for both sparse (Fig. 3; $t_{15} = -5.171$ , $P = < 0.001$) and dense (Fig. 3; $t_{15} = -4.226$ , $P = < 0.001$) algal turf treatments.

Although both species preferred sparse algal turfs, the higher yield of algae per bite from dense algal turfs meant that the total amount of turf removed over time did not differ between turf classes (Fig. 3; *A. nigrofuscus*: $t_8 = -1.237$, $P = 0.251$; *C. striatus*: $t_7 = 0.495$, $P = 0.636$).

From the functional perspective of grazing intensity, calculated as the product of grazing rate per treatment and mean bite area, it is clear that the grazing intensity (m$^{-2}$ h$^{-1}$) is greater for sparse turf algae than dense turf algae for both species (Fig. 4). Although the differences in grazing intensity between algal turf classes are similar to the proportions in Figures 1a-i and 1a-ii, the grazing intensity plotted in Figure 4 allows a clearer comparison of the 2-dimensional grazing intensity by both algal density and fish species.

Prior to experimental trials, dense algal turf contained a significantly greater average sediment load (0.19 ± 0.018 g cm$^{-2}$, ± S.E.) than sparse algal turf (0.09 ± 0.008 g cm$^{-2}$, ± S.E.; $t_{32}$ = -4.658, $P$ = < 0.001). However, there was no difference in the average nutritional value of sparse (7.8:1 ± 0.23, mean ± S.E.) and dense (7.4:1 ± 0.28) algal turfs, as evidenced by statistically indistinguishable ratios of total organic carbon (TOC) to total nitrogen (TN) ($t_{19}$ = -1.326, $P$ = 0.201). Control tiles (controlling for experimental handling effects) showed that there was no significant difference in algal turf biomass before and after experimental trials in the absence of herbivorous fish ($t_{20}$ = 1.536, $P$ = 0.140).

## Discussion

This is the first study to quantify directly the grazing impact of *A. nigrofuscus* and *C. striatus* on algal turfs. Both *Acanthurus nigrofuscus* and *Ctenochaetus striatus* fed more intensively on sparse/short algal turfs even though the yield of algae per bite was greater for dense/long algal turfs. Unexpectedly, the detritivorous species, *C. striatus*, removed significantly more algal turf per hour than the grazing species, *A. nigrofuscus*, irrespective of canopy height.

The ecological importance of *C. striatus* in reef sediment dynamics has been investigated extensively (e.g., Nelson and Wilkins 1988; Krone et al. 2008; Goatley and Bellwood 2010). However, its impact on epilithic algal turf dynamics had previously not been studied. Given their elongate, flexible teeth with incurved tips, it was thought that *C. striatus* were limited to 'brushing' loose particulate matter off the substratum surface and unable to crop attached algal turfs, thereby causing little damage to the epilithic algal turf community overall (Robertson 1982; Purcell and Bellwood 1993). However, here we show that *C. striatus* are capable of removing significant quantities of epilithic algal turf through their foraging activity. Being one of the most abundant fishes on Indo-Pacific reefs and having one of the highest maximum bite rates (30 bites min$^{-1}$; Polunin et al. 1995) of detritivorous fishes (Wilson et al. 2003), their ability to remove significant quantities of algal turfs has important implications for their functional role in driving EAM dynamics, and potentially in driving interspecific interactions among herbivores.

In this study, detritivorous *C. striatus* removed significantly more epilithic algal turf per hour than the grazing species *A. nigrofuscus*. *C. striatus* individuals were 3 cm bigger (on average) than *A. nigrofuscus* in this study, and their larger body size and bite size likely contributed to this result. However, it remained surprising to observe such a strong impact of *C. striatus* on turfs given that it

was expected to cause little damage to algal turfs. Although we did not test whether *C. striatus* ingested or assimilated the algal turf, it is functionally important that they have the capability to remove significant quantities of it through their foraging activity. On outer reef flats, *C. striatus* have been observed foraging across sparse filamentous algal turf covered rocks and crustose coralline algal surfaces (Polunin and Klumpp 1989). Algal filaments represented ~ 20 % of the dietary items found in organic matter in *C. striatus* gizzards from the northern Great Barrier Reef (Choat et al. 2002). However, it was unclear whether these filaments were 'grazed from the substratum or represented detrital elements', and most studies of *C. striatus* stomach contents show that they ingest calcareous sediments and organic detritus with little evidence of algal consumption (Robertson and Gaines 1986; Nelson and Wilkins 1988; Montgomery et al. 1989; Choat et al. 2002). Therefore, if they are not ingesting and assimilating the algae that they possibly remove, it is likely that they are major contributors to the production of organic detritus by dislodging living turfs. Previous studies have found that a substantial amount of the algal material removed by reef herbivores is not digested (Purcell and Bellwood 2001) and fishes assimilate only between 20 - 70% of algae consumed (Horn 1989; Galetto and Bellwood 1994; Bruggemann et al. 1994b). We hypothesize, therefore, that *C. striatus* may contribute to the detrital pool (> 70% derived from filamentous algae, Wilson et al. 2003) by harvesting and depositing large amounts of turf. Moreover, it is possible that *C. striatus* is effectively contributing to the creation of their own detrital pool within their relatively small (average: 12.1 m$^2$) home range (Krone et al. 2008).

*A. nigrofuscus* and *C. striatus* are thought to coexist in 'synergistic cohabitation' because of their ability to exploit different resources (filamentous algae and detritus, respectively) from the EAM, given major differences in their jaw morphologies (jaw bones, gape, tooth structure) and foraging actions (Purcell and Bellwood 1993). Additionally, *C. striatus* generally exhibit weak territorial aggression (Polunin and Klumpp 1989), and their distributions commonly overlap spatially with territorial surgeonfish and parrotfish, while *A. nigrofuscus* are often aggressively excluded from herbivorous fish territories (Choat and Bellwood 1985; Robertson and Gaines 1986). Future studies will need to manipulate turf composition and substrate type simultaneously to investigate any partitioning that may occur among species. Prior studies have suggested that the relationship between *C. striatus* and territorial fishes (e.g., *Acanthurus lineatus*) could be mutually advantageous in that *C. striatus* removes sediments from algal turfs for territorial fish and in return is permitted access to actively defended territories with a large algal standing crop (Purcell and Bellwood 1993). However, in some regions, cohabitation between *Ctenochaetus* species and territorial herbivorous fishes is rare and habitat specific (Robertson and Gaines 1986). Therefore, if *C. striatus* are

removing significant quantities of algal turfs, then their interspecific relationships may be more complex than has previously been proposed. Future studies are needed to establish whether interspecific relationships between *Ctenochaetus* species and herbivorous fishes are region and/or habitat specific.

Algae are generally low in protein and energy. Therefore, herbivorous fish may spend time and effort to select algae with the highest nutritional quality and obtain the best diet available (Lobel and Ogden 1981; Horn 1989; Choat 1991; Bruggemann et al. 1994a), or alternatively may be less selective and consume greater quantities of algae with lower nutritional quality. Although new algal growth is generally more nutritious and palatable than older growth (Cronin and Hay 1996), we found no difference in TOC:N ratios among our two classes of algal growth. The TOC:N ratios of algal turfs in this study (6:1–9:1) were comparable to field ratios of Lizard Island epilithic filamentous algae within lagoonal damselfish (*Stegastes nigricans* and *Hemiglyhidodon plagiometopon*) territories (6:1–9:1, Wilson and Bellwood 1997), and windward, sub-tidal reef zones (8:1–10:1, Purcell and Bellwood 2001). Therefore, as there were no differences in nutritional content of the algal turf classes, *A. nigrofuscus* likely preferred sparse/short turf because of its relatively low sediment content. Grazers are deterred by inorganic sediments that accumulate in the EAM (Choat 1991), and inorganic sediment loads are directly related to canopy height (Purcell 2000). Although the dense/long algal turf had a greater sediment load, it is also likely that *C. striatus* fed less frequently on this substratum because the elongated filaments would become entangled in their teeth and they would often forcefully reject it (Marshell, *pers. obs.*). *C. striatus* has previously been observed to avoid areas with long filamentous algae (> 5 mm) and reject long filaments which became entangled in their teeth when feeding on algae-covered substratum in aquaria (Purcell and Bellwood 1993). The inorganic sediment load of algal turfs in this study (sparse 0.09 and dense 0.19 g cm$^{-2}$) were within the lower range of sediment loads found across natural reef zones (0.1 - 0.56 g cm$^{-2}$), excluding the low values of the reef crest (0.01 - 0.02 g cm$^{-2}$; Purcell 2000).

Herbivory is inversely related to sediment-load of the EAM (Steneck et al. 1997; Purcell and Bellwood 2001), with increased sediment having a direct negative effect on grazing activity (Bellwood and Fulton 2008). By finding both a grazer and detritivore preference for sparse algal turfs with significantly less sediment-load, our data support an earlier hypothesis that fishes contribute to the development and maintenance of a sediment-dominated substrate by avoiding such areas while foraging. Bellwood and Fulton (2008) proposed that positive feedbacks between

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increased sediment load and decreased grazing lead to a grazing-resistant, sediment-laden algal mat. The overwhelming surgeonfish preference for sparse/short algal turfs with reduced sediment load provides further evidence for this potential mechanism for the development and maintenance of these stable sediment-rich algal turf mats, that likely limit both coral and macroalgal colonisation and may represent an alternative degraded stable state to macroalgal-dominance on coral reefs (Bellwood and Fulton 2008). Future studies could manipulate sediment load within the same algal canopy to determine whether this affects surgeonfish preference.

As recent carbonates of tropical reefs can be thermally unstable at ashing temperatures, the 'loss after combustion' method can produce an error of approximately 3–4% of the dry weight of carbonate sediments at the ashing temperatures used in this study (e.g., Purcell 1997). In other words, some carbon can be lost from the mineral component in addition to the oxidative decomposition of organic matter, leading to a possible overestimation of organic matter. This error in determination of organic matter will vary among samples collected from different areas and depending on the proportional weight of sediments in the samples. However, as the algal turfs on the experimental tiles were all developed in shallow aquaria with filtered seawater, the samples were very similar to each other and consisted mostly of turfs with relatively small amounts of fine associated sediments. Therefore the vast majority of the sample weight was algal turfs, not sand or carbonate particles, which likely reduced the overall associated error. Furthermore, a recent study by Fang et al. (2013) compared the loss after combustion (LAC) and acid decalcification (ADC) methods to quantify different components (organic matter, siliceous spicules, calcareous substrate, and salts) of entire coral skeleton samples of a reef excavating sponge. They found that the LAC and ADC methods gave very similar results of the dry weight of organic matter, siliceous spicules, calcareous substrate and salts in the samples, but overall recommended the use of the LAC method as it had low variability, and was fast and simple (Fang et al. 2013).

The results of this study only represent surgeonfish grazing on algal turfs grown on limestone tiles in aquaria, and further work is needed to investigate the removal rates and preference for algal turfs on the reef. However, a similar experimental study to this study was conducted by Axe (1990), where controlled aquarium experiments examined the grazing impact of juvenile *C. striatus* and *A. nigrofuscus* on natural substrata collected from the reef. The juvenile fish were allowed to acclimatise in aquaria for several days while being fed on natural substrata, and then starved for 24 h prior to the experiments to empty their stomachs. Axe (1990) found that algal turf biomass decreased overall on the natural substrates exposed to feeding by juvenile *C. striatus* and *A.*

*nigrofuscus*. Although, that the "decreases in algal biomass were small and did not differ greatly between treatments." Therefore, the aquarium experiments by Axe (1990) support our findings here, and suggest that even small, juvenile *C. striatus* were able to remove algal biomass from natural substrate in quantities equal to *A. nigrofuscus*. Other studies have also provided evidence that *C. striatus* are capable of denuding the substrate (Krone et al. 2006; Krone et al. 2011; Schuhmacher et al. 2008). In these studies, the authors describe a compact palate structure found in *C. striatus* jaws that sometimes contacts the substrate while grazing. They observed two different *C. striatus* grazing techniques: (1) brushing the substrate surface with their bristleteeth, exerting only slight pressure to ingest detritus and fine algae, and (2) chafing the substrate with energetic grasping bites with contact pressure being generated by a shaking of the whole body. During the second feeding mode the jaws are wide open, allowing the palate dentation to rasp and erode the reef substrate (Krone et al. 2006). Therefore, these studies also provide substantial evidence of the ability of *C. striatus* to remove algal turfs from the natural reef substrate. Exploring long-term trophodynamics of *C. striatus* using stable isotopes techniques may determine whether *C. striatus* is ingesting/assimilating live algal turfs in significant quantities on the reef, as it has been difficult to determine this unequivocally using 'snapshot' stomach content analyses where algal turfs are often only a minor component. Regardless of whether *C. striatus* is ingesting and assimilating live algal turfs in significant quantities, it is important to recognise that this widespread and abundant detritivore, previously thought to cause little damage to algal turfs, is capable of removing significant quantities of algal turf through their foraging activities. Consequently, despite their detritivorous diet, *C. striatus* may play an important functional role in grazing pressure on Indo-Pacific reefs and their grazing impact would need to be considered when assessing the consequences of grazing fishes on EAM dynamics. If this is the case, the exclusion of detritivorous *Ctenochaetus* species from herbivorous fish functional groups used in resilience monitoring would also need to be re-evaluated.

## Acknowledgements

Figure 1. **a)** (i) The mean number of bites taken on sparse (white bar) and dense (grey bar) algal turf by *Acanthurus nigrofuscus* ($n = 9$) per hour experimental trial. (ii) The mean number of bites taken on sparse (white bar) and dense (grey bar) algal turf by *Ctenochaetus striatus* ($n = 8$). Error bars indicate standard error. **b)** (i) The mean algal turf biomass per bite (g C = grams of organic carbon, or ash free dry weight) taken by *A. nigrofuscus* ($n = 9$). (ii) The mean algal turf biomass per bite (g C) taken by *C. striatus* ($n = 8$). Error bars indicate standard error. **c)** The proportion of total *Acanthurus nigrofuscus* ($n = 9$) bites taken on sparse (white) and dense (grey) algal turf, per 5-minute time period of the trials. **d)** The proportion of total *Ctenochaetus striatus* ($n = 8$) bites taken on sparse (white) and dense (grey) algal turf, per 5-minute time period of the trials.
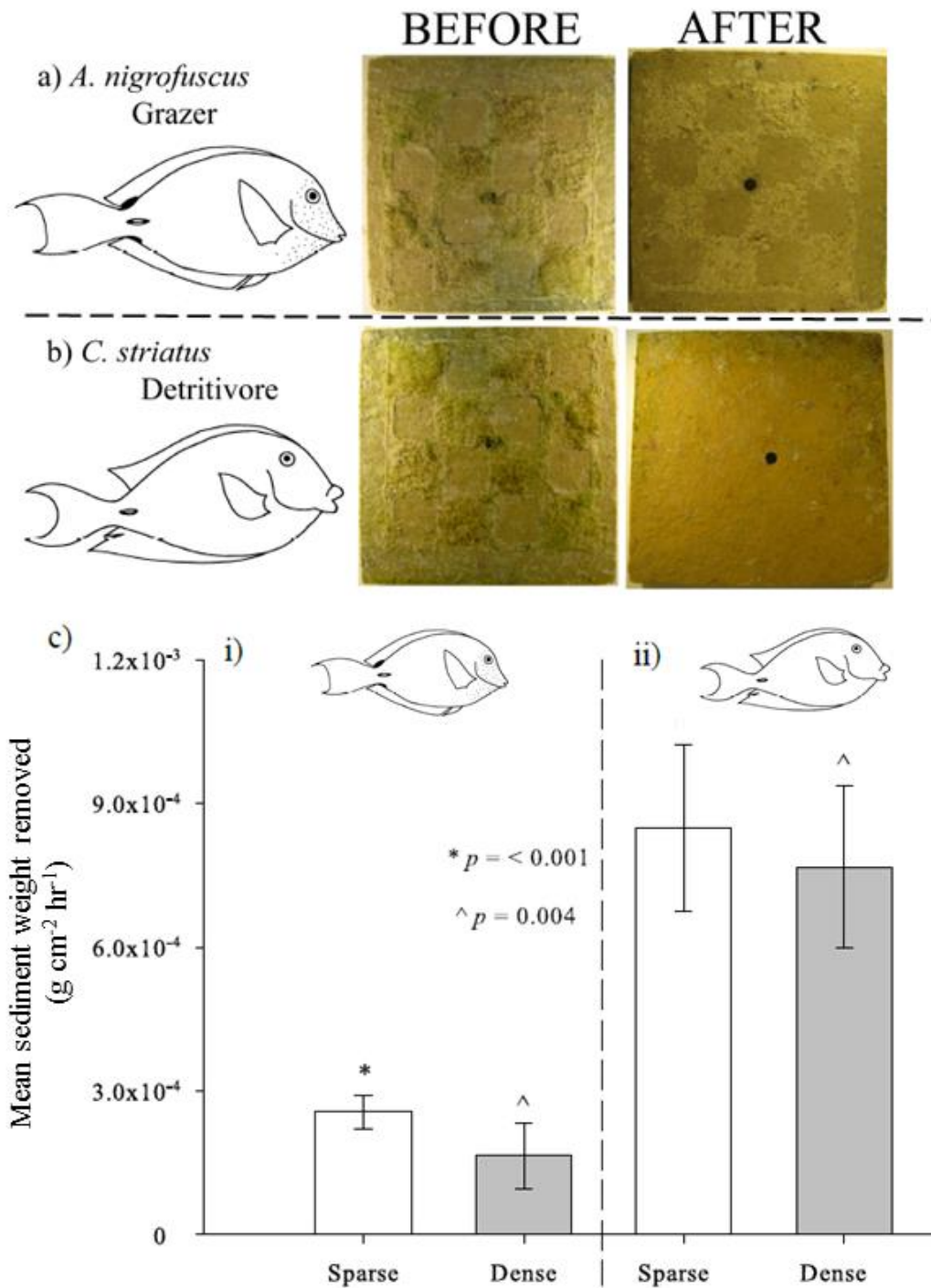
Figure 2. Examples of sparse algal turf experimental tiles before and after an experimental trial for a) grazer *Acanthurus nigrofuscus* and b) detritivore *Ctenochaetus striatus*. *A. nigrofuscus* generally removed turf and left sediment behind, while *C. striatus* generally removed both turf and sediment. c) The mean inorganic sediment biomass (g cm$^{-2}$ h$^{-1}$) removed per sparse and dense treatment by (i) *Acanthurus nigrofuscus* and (ii) *Ctenochaetus striatus*. Error bars indicate standard error.
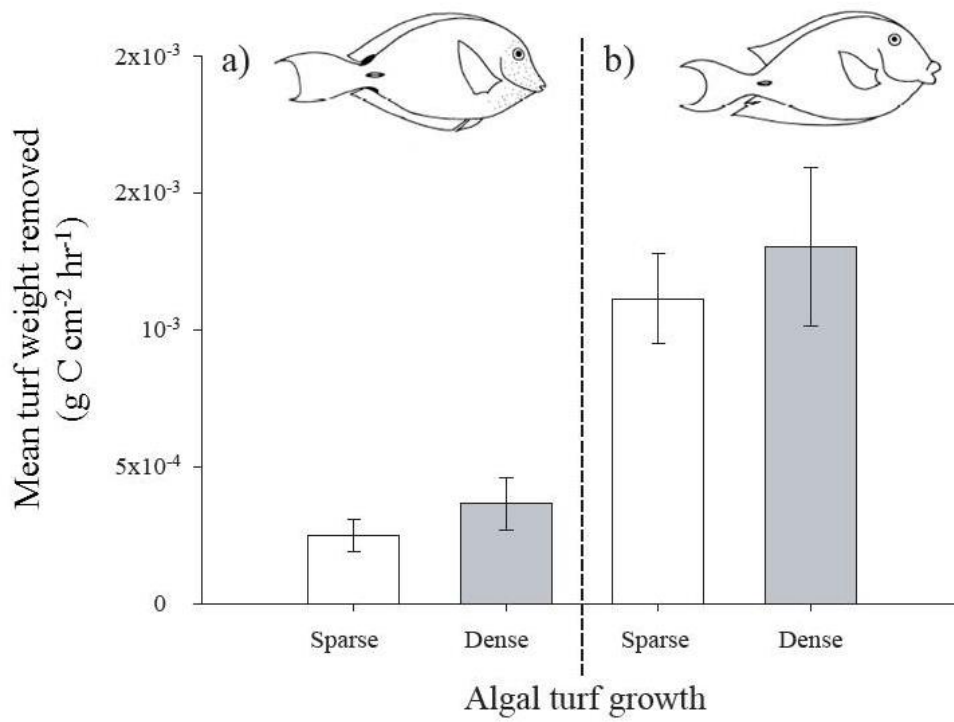
Figure 3. The mean sparse and dense algal turf biomass removed per trial (g C cm$^{-2}$ h$^{-1}$) by a) *Acanthurus nigrofuscus* and b) *Ctenochaetus striatus*. Error bars indicate standard error.
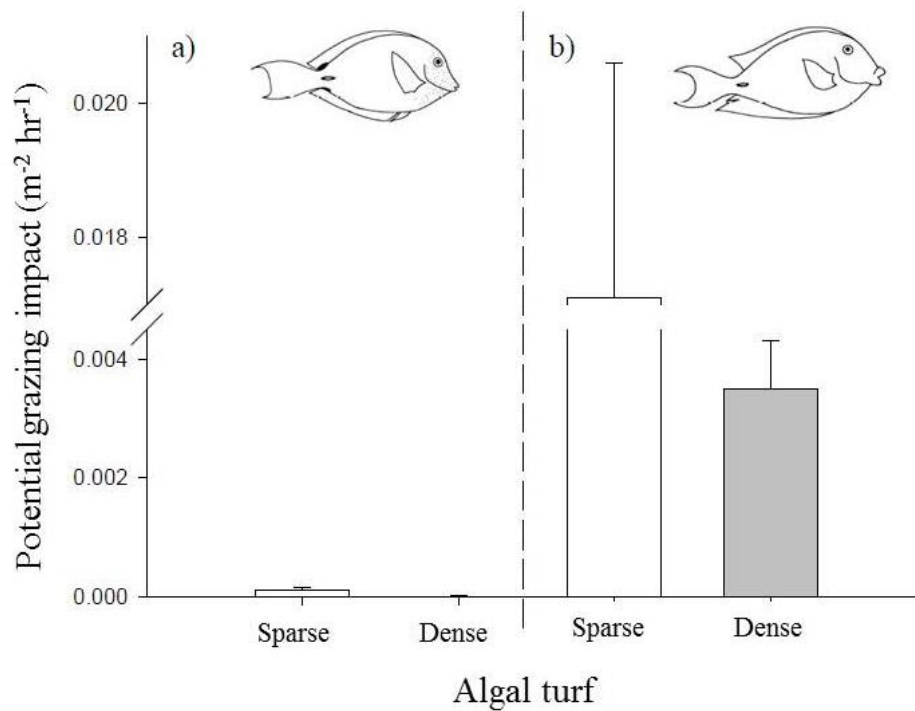


Figure 4. The potential grazing intensity (m$^{-2}$ h$^{-1}$) upon sparse and dense algal turf by: a) *Acanthurus nigrofuscus* and b) *Ctenochaetus striatus*. Potential area grazed = mean number of bites per hour × mean bite size (measured from grazing scar area). Error bars indicate combined error using Goodman's estimator (Travis 1982, Marnane and Bellwood 2002).

# Chapter 4. Spatial variation in the grazing impact of surgeonfish on epilithic algal turfs.

## Abstract

Coral reefs are one of the most highly productive ecosystems, with the largest trophic exchange attributed to the interaction between herbivores and algae. The epilithic algal matrix (EAM) is a major source of primary productivity, and represents up to 80% of the total surface area of coral reef microhabitats. Most relatively undisturbed reefs support a high biomass of herbivorous grazing fish, but a comparatively low biomass of their EAM food source. Grazing disturbance enhances productivity, and it is the high productivity of algal turfs rather than their standing crop that maintains high grazer biomass. This study quantifies and compares: (1) algal turf dynamics (productivity and biomass of grazed standing crop), (2) the biomass of herbivorous fishes (families: Acanthuridae, Labridae, and Siganidae), and (3) family-specific grazing intensity in different habitats (two levels of exposure and depth) of Heron Island reef slope. This was achieved through controlled field experiments, herbivorous fish visual census surveys, and remote video *in situ* grazing intensity surveys. Algal turf productivity was highest in windward and shallow sites, and herbivorous fish biomass mirrored this pattern. However, there was no difference in the algal turf standing crop biomass or total number of bites taken daily among habitats. Acanthurid (surgeonfish) EAM grazers are dominant members of most reef fish communities, and are likely to fulfil critical functional roles. Yet, there is a paucity of quantitative information on their feeding ecology and functional role, especially in the Indo-Pacific region. To identify the daily grazing impact of observed surgeonfish species on the EAM, data on their biomass and grazing intensity were combined with algal turf productivity estimates. In the most productive habitat (windward-shallow), EAM grazing surgeonfish accounted for 74% of the total herbivore biomass, took 51% of the total bites ($m^{-2}$ $day^{-1}$) and removed 73% of daily turf productivity. Quantifying the grazing impact of surgeonfish significantly improves our understanding of herbivory processes on coral reefs and the role that this key functional group plays in maintaining algal turfs, and possibly preventing shifts from coral- to algal-dominance.

# Introduction

Coral reefs are one of the most highly productive marine ecosystems, with the largest trophic exchange attributed to the interaction between herbivores and algae (Carpenter 1986; Hatcher 1988, 1990). The epilithic algal matrix (EAM) is a major source of coral reef primary productivity, and is one of the dominant benthic microhabitats (Klumpp and McKinnon 1992; Wilson et al. 2003; Wismer et al. 2009; Vermeij et al. 2010). On mid- and outer-shelf Great Barrier Reef (GBR) sites, the EAM dominates the substrate, covering 50 to 80 % of reef flats and back reefs and 30 to 70 % of reef slopes (Hatcher and Larkum 1983; Klumpp and McKinnon 1992; Wismer et al. 2009). The EAM consists of short, sparse mats that are dominated by densely-packed filamentous algal turfs, and also contain loose detritus and inorganic sediments (Carpenter 1986; Wilson et al. 2003; Kramer et al. 2013). The morphology and species composition of the EAM can vary due to stresses such as grazing, desiccation (intertidal zones) (Hay 1981), sedimentation (Airoldi 1998), and physical disturbance (Sousa 1980). The EAM is one of the most nutritious food resources on coral reefs (Wilson et al. 2003), with high productivity rates (highest in shallow water) that support a diverse and abundant assemblage of grazers (Adey and Goertemiller 1987; Steneck 1988; Choat 1991; Miller et al. 2009).

Coral reefs have distinguishable zones (e.g., reef flat, crest, slope, lagoon) that differ markedly in their physical and biological characteristics, including depth, water movement, light levels and faunal composition (Hay 1981; Lewis and Wainwright 1985; Steneck 1988; Bellwood and Wainwright 2001; Paddack et al. 2006; Fox and Bellwood 2007). This zonation also applies to the EAM, in that there are distinct differences in the relative amount of particulate inorganic (sediment) and organic matter (detritus) in different zones, which directly affects the nutritional quality. Herbivores usually target algal turfs with a higher detrital component, which are most nutritious and abundant on the reef crest and shallow reef slope (Purcell and Bellwood 2001; Wilson et al. 2003). Productivity also differs between zones and is influenced by local environmental factors such as light, nutrients, desiccation, biotic composition, substrate availability and water motion (Hatcher and Larkum 1983; Carpenter 1986; Steneck and Dethier 1994; Schaffelke and Klumpp 1997). Of these, light (drives photosynthesis) and water flow (delivery rate of nutrients) are probably the most important factors (Adey and Steneck 1985). Light decreases with depth and turbidity, while water flow is influenced by oceanic currents, depth, microhabitat topographic complexity and wave/wind surge. Exposed areas subjected to high wave energy are usually dominated by algae that can endure scouring, such as crustose coralline algae and short, sparse algal turfs (Adey and Steneck 1985;

Littler and Littler 1988; Cheroske et al. 2000). In addition to environmental factors, grazing disturbance also shapes EAM morphology and enhances productivity (Carpenter 1986).

Herbivorous fishes play a key role in controlling the standing crop of algae (Hatcher and Larkum 1983; Klumpp and Polunin 1989; Russ 2003), and determining benthic community succession patterns (Hay 1981; Hixon and Brostoff 1996). It is estimated that herbivorous fishes remove between 20 and 90% of the net daily production of algae (Hatcher and Larkum 1983; Polunin and Klumpp 1992), and can completely turn over algal biomass every 4 to 25 d (Klumpp and Polunin 1989). Most relatively undisturbed reefs support a high biomass of herbivorous grazing fish, but a low biomass of their algal turf food source and it is the high productivity of algal turfs rather than their standing crop that maintains a high standing stock of grazers (Hatcher 1988, 1990; Hatcher and Larkum 1983; McCook 1999; Russ 2003). The distribution of herbivore biomass is thought to generally be influenced by the rate of algal turf production rather than standing crop biomass, although only a few studies have tested this (Hatcher 1988, 1990; Russ 2003).

Grazing is important to maintain the balance between corals and algae, and prevent phase-shifts from coral to algal dominance (Hughes 1994; Mumby et al. 2006). Quantifying the functional grazing impact of key herbivorous fish species is important to understand the ecosystem function of herbivory on coral reefs, and the current knowledge of quantitative ecosystem impacts of individual taxa are limited (McManus and Polsenberg 2004; Fox and Bellwood 2008). Indo-Pacific examples of investigations into the functional roles of species are largely restricted to parrotfish (e.g., Bonaldo and Bellwood 2008) or rabbitfish (e.g., Fox et al. 2009). However, different functional groups of fishes have different effects on algal communities (Hixon and Brostoff 1996; Green and Bellwood 2009; Burkepile and Hay 2010).

In terms of abundance and species richness, herbivory on Indo-Pacific coral reefs is dominated by a single lineage of Acanthuridae: the genus *Acanthurus* (surgeonfish), which has recently been updated to also include *Ctenochaetus* species (Sorenson et al. 2013; Bellwood et al. 2014). In the Indo-Pacific, *Acanthurus* species occupy more reef habitats and are more abundant than any other genus (Russ 1984a,b; Choat and Bellwood 1985; Randall et al. 1997; Cheal et al. 2012; Bellwood et al. 2014). Acanthurids affect the structure of the reef substrate by influencing algal competition, abundance, and dynamics (Lewis 1986; Hixon and Brostoff 1996; McClanahan 1997; Burkepile and Hay 2010), and due to their dominance in most reef fish communities are likely to fulfil critical functional roles (Green and Bellwood 2009; Hoey and Bellwood 2009), However, since the late

1970s it has been recognised that few investigations are undertaken on the feeding ecology of surgeonfishes (Robertson et al. 1979), and there is still a paucity of quantitative information on the feeding ecology and functional role of acanthurids, especially in the Indo-Pacific region.

Therefore, the aim of this study was to quantify the functional role of EAM grazing surgeonfish in different reef slope habitats of varying depths and exposure, by combining species- and size-specific bite rates and sizes with algal turf productivity estimates to calculate the total daily surgeonfish grazing impact on algal turfs. Additionally, this study quantifies and compares the algal turf dynamics (grazed standing crop and maximum ungrazed productivity) and patterns of biomass and grazing intensity of herbivorous fishes among different reef slope habitats.

## Methods

### Study site

Heron Reef is a lagoonal platform reef 11 km long x 5 km wide (~ 27 $km^{-2}$) located approximately 70 km from the mainland coast of Queensland, Australia in the southern Great Barrier Reef (Fig. 1a, 23°26' S, 151°55' E). The predominant wind on Heron Reef is from the southeast, therefore the southern-side of Heron Reef is generally exposed (windward), while the northern side of the reef is relatively sheltered (leeward) (Fig. 1b; Gourlay and Hacker 2008). This study was conducted in different habitats of the reef slope, with six study sites divided between the windward ($n = 3$) and leeward ($n = 3$) sides of Heron reef (Fig. 1a). At each site all methods were replicated at two depths: shallow (2–4 m) and deep (9–12 m). Therefore, the four reef slope habitats investigated were: windward-shallow, windward-deep, leeward-shallow, and leeward-deep. After ensuring that there were no significant differences among sites within each exposure, the site data was pooled to investigate the overall effect of habitat (exposure and depth) on algal turf productivity, standing crop biomass, and herbivorous fish community spatial patterns.

### Algal turf spatial patterns

Algal turf standing crop biomass (g C $m^{-2}$) and productivity (g C $m^{-2}$ $day^{-1}$) was measured at 2–4 m (shallow) and 9–12 m (deep) depths at each of the study sites on Heron reef slope (Fig. 1a). At each site and depth, twelve preconditioned (> 12 months) limestone tiles (13 x 13 x 1.5 cm; $n = 144$) with a rough textured surface were secured to the substrate (dead coral or pavement crevices and

holes) with cable ties. Prior to deployment, the tiles were gently scrubbed to begin with a null algal biomass, while maintaining a base of live encrusting benthic organisms and algal turf holdfasts. The twelve tiles at each site and depth were randomly assigned to two treatment groups: caged and open. Six caged tiles were protected from grazing fish (> 5 cm total length) by black plastic exclusion cages (22 x 22 x 18 cm; $n = 72$) with a mesh size of 2.5 x 2.5 cm. The remaining six tiles were open and exposed to natural grazing levels. The cages were secured to dead reef substrate using cable ties and were maintained regularly throughout the study. All tiles and cages were recovered and no replicates were lost. All twelve tiles and six cages at each site and depth were deployed within a few meters of each other and left for 28 d during the Austral summer months of January–February 2012. Hobo™ data loggers were deployed to measure light (lux, SI) and temperature (°C) inside and outside cages and each location. Water flow was measured simultaneously amongst sites and treatments by deploying plaster-of-paris clod cards for 24 h and measuring the percentage dissolution rate (% weight loss) (Jokiel and Morrissey 1993; Fulton and Bellwood 2005).

At the end of the experimental period, tiles were photographed and assessed for micro-herbivore abundance (although their effect on algal biomass is small - Carpenter 1986), before being carefully placed into individual, zip-lock plastic bags. The tiles were then frozen to prevent decay before processing in the laboratory, where they were thawed and the developed algal turf biomass was scraped thoroughly from the flat, upper surface. Each sample was dried to a constant weight at 60°C for 24 h, and then weighed to the nearest 0.0001g. The organic weight (or ash free dry weight – AFDW) of each scraped algal turf sample was determined by reweighing the sample after ashing at 500°C for at least 6 h (Paine and Vadas 1969; Fang et al 2013), and subtracting the weight of the remaining ash from the constant dry weight to calculate the algal turf biomass as grams of organic carbon (g C cm$^{-2}$ day$^{-1}$). This method determines the grams of total organic material, including associated microfauna and organic detritus, which have been shown not to bias results (Paine and Vadas 1969; Hatcher and Larkum 1983).

The mean algal turf productivity (g C m$^{-2}$ day$^{-1}$, caged tiles), maximum final biomass (g C m$^{-2}$, caged tiles), standing crop (g C m$^{-2}$, open tiles), and relative water flow (% weight loss) was calculated for each of the four habitats: windward-shallow, windward-deep, leeward-shallow, and leeward-deep. Comparisons among habitats (exposure = fixed, 2 levels: windward, leeward; depth = fixed 2 levels: deep, shallow) were made using two-way ANOVA for each variable. The data were transformed (log(x + 1)) when necessary to meet parametric assumptions of normality and

homoscedasticity, and differences among habitats were investigated using Tukey's HSD post-hoc test.

**Herbivorous fish community spatial patterns**

Underwater visual census (UVC) surveys were conducted to compare the distribution, abundance and biomass of key herbivorous fish families (acanthurids, siganids and labrids; see Table S1 for a species list per habitat) at windward and leeward sites of Heron reef slope in shallow (2–4 m) and deep (9–12 m) zones (six sites, Fig. 1a). At each site, eight 30 x 5 m transects ($n = 24$ per exposure-depth) were surveyed consecutively within ± two hours of the daytime high tide. Prior to commencing the surveys at each site, divers were trained in visually estimating the 5 m width of each transect by laying a 5 m length of transect tape across the beginning of the transect for calibration. The transect tapes were laid as the survey was being conducted, in order to minimize disturbance and increase the probability of encountering larger roving herbivores that are wary of diver activity. Transects were laid parallel to the reef slope wall along the desired depth contour, and each was separated by at least 20 m. The abundance (number of individuals) and size (total length, cm) of each species was recorded. For analysis, individual fish larger than 5 cm in length were assigned to 3 cm size categories. All eight transects were completed by the same observers (Marshell: surgeonfish and rabbitfish counts, Doropoulos: parrotfish counts) during a single dive (~ 75 min). All observers were trained in estimating fish size underwater using fish models (Bell et al. 1985). Due to the difficulty of identifying juvenile parrotfish species in the field, individuals less than 10 cm were recorded as '*Scarus*', with the exception of *Chlorurus sordidus* and *Chlorurus microrhinos* which are readily identifiable.

Herbivore abundance was converted to biomass using published length-weight relationships (Kulbicki et al. 2005), with fish length taken as the midpoint of the size class. The formula used for the conversion was: $W = a\,L^b$, where $W$ = fish weight in grams (g); $L$ = total length (TL) of the fish (cm); and $a$ and $b$ are constants calculated for each species or genus (Kulbicki et al. 2005). The mean biomass (g m$^{-2}$) of herbivorous fish families was then calculated for each habitat. Comparisons among habitats (exposure = fixed, 2 levels: windward, leeward; depth = fixed 2 levels: deep, shallow) were made using two-way ANOVA with data transformed ($\log(x + 1)$) when necessary to meet parametric assumptions of normality and homoscedasticity. Differences in fish biomass between habitats were investigated using a Tukey's HSD post-hoc test.

After the fish surveys were completed, benthic cover of each transect was assessed using 50 x 50 cm photo-quadrats ($n = 6$ per 30 m transect, $n = 48$ per site/depth). In addition to a photograph, measurements of rugosity (maximum height, cm), algal turfs (height, mm; $n = 5$ per quadrat) and upright macroalgae (height, mm; $n = 5$ per quadrat) were also recorded in each quadrat. The high-resolution photographs were analysed using Vidana software (available from www.marinespatialecologylab.org). Organisms were classified into the following categories: algal turfs, upright fleshy macroalgae genera (> 10 mm), calcareous macroalgae, crustose coralline algae (CCA), live coral (functional groups: branching, tabular, massive etc.), dead coral, soft coral, sand, pavement, and coral rubble. Algal categories were further identified to functional groups and genera where possible.

**Field surveys of grazing intensity**

Grazing intensity was calculated as the total number of bites taken by herbivorous fish (m$^{-2}$ day$^{-1}$). It was quantified using GoPro HD video cameras deployed in each habitat type: deep and shallow zones of each of the windward ($n = 3$) and leeward ($n = 3$) sites. Four cameras were deployed to film a randomly chosen 1 m$^2$ patch of > 70% grazeable substrate with relatively low structural complexity (to minimise blind-spots and standardise area). The cameras were left for a minimum of 70 minutes during the morning (~0800–1100), and then deployed again in the afternoon (~1300–1600). This was to allow for any diurnal differences in feeding rates and give a realistic average daily bite rate. Therefore, the overall bite rate data comes from a total of 24 replicates of 1 m$^2$ video surveys per habitat type (3 sites × 4 AM + 4 PM surveys). The cameras were attached to dive weights, and positioned in relatively high and stable places pointing down towards the substrate, at a minimum of 10 m apart. A 1 m$^2$ quadrat was briefly placed in front of the camera on the substrate after filming commenced, to allow subsequent grazing analysis to be based on a calibrated 1 m$^2$ area. The 10 x 10 cm grid lines of the quadrat enabled fish size estimation in subsequent video analyses. Divers would surface and leave the area once all cameras were recording, and return > 70 minutes later to retrieve the cameras.

*Video analysis of grazing intensity*

To minimise any diver disturbance to grazing, video analysis began 10 minutes after initial recording commenced. While the quadrat was in view at the start of the video, the percentage of grazeable substrate per quadrat (camera replicate) was estimated and recorded, and the quadrat grid

area was drawn onto a plastic sheet attached to the monitor to mark out the 1 m² survey area. Each 60 min video was divided into consecutive 3 min segments, and grazing intensity was quantified for ten alternating 3 min segments (50% of total footage). The videos were played at double-time until a grazing fish (surgeonfish, parrotfish or rabbitfish) entered the quadrat area and took a bite of the substrate. The video was then paused, slowed-down, and replayed to count and record the total number of bites taken, the fish species (and parrotfish life-phase), and estimated size (cm, fork length). To calculate the foray time of each individual fish, the quadrat area entry and exit time was also recorded. If there was more than one fish feeding at a time, the information for each fish was recorded separately by rewinding and replaying the video as necessary. Distinguishing individual fish that may have fed multiple times during these surveys was not possible; however, the aim was to measure the average grazing intensity exerted over a 1 m² reef area, rather than an individual's bite rates. The video analysis allowed the average bite rate per species, per size class, per 1 m² (standardised to 100% grazeable substrate), per day (bite rate per minute × 600 minutes to represent a conservative 10 h grazing day) to be calculated for each habitat (bites m⁻² day⁻¹).

**The grazing impact of EAM grazing surgeonfish species**

Total surgeonfish grazing intensity, expressed as grams of algal turfs removed per day (g C m⁻² day⁻¹), was calculated as a function of size- and species-specific bite rates and bite sizes (Mumby et al. 2006). Grazer/detritivore surgeonfish species intensely graze the epilithic algal matrix (EAM), but do not scrape or excavate the substrate as they feed (Green and Bellwood 2009). Therefore, it is not possible to calculate a size-specific bite area as there are no grazing scars left by these species. Consequently, to quantify the daily grazing impact of EAM grazing surgeonfish species observed on Heron reef slope in UVC and video surveys, the average species- and size-specific daily bite rate observed in video surveys was multiplied by the corresponding estimated bite size. It was assumed that *Ctenochaetus* species are able to remove algal turfs through their foraging activity (Marshell and Mumby 2012). Bite size for each size class was determined by using the relationship between carbon (C, organic biomass) intake (g C day⁻¹) and fish body mass ($W$ = Wet body mass in grams) for herbivorous fish daily consumption (Table 3; g C intake day⁻¹ = $0.0342 \times W^{0.816}$; Van Rooij et al. 1998). To convert the daily total carbon intake to the amount of algal biomass removed per bite, the total carbon intake per day was divided by the average daily total bites taken by each species (Marshell, unpublished data; Polunin et al. 1995). Species-specific length-weight relationships were used to calculate the wet biomass (g) of different size classes (Kulbicki et al. 2005).

# Results

## Algal turf spatial patterns

Algal turf production rates (g C m$^{-2}$ day$^{-1}$) were significantly influenced by exposure ($F_{1,68} = 7.84$, $P = 0.007$) and depth ($F_{1,68} = 9.86$, $P = 0.002$), while there was no interaction between these factors ($P = 0.963$). Overall, algal turf productivity was significantly greater in shallow vs. deep sites (Tables 1 and 2, Fig. 2a). At deep sites (9–12 m), algal productivity was significantly greater in windward than leeward habitats, while at shallow sites (2–4 m) there was marginally no difference in productivity between windward and leeward habitats ($P = 0.056$, Tables 1 and 2, Fig. 2a). After 28 d, the maximum biomass (28 d carrying capacity) reached when grazers were excluded was significantly greater in windward than leeward habitats ($F_{1,68} = 9.49$, $P = 0.003$, Tables 1 and 2), and in shallow than deep sites ($F_{1,68} = 10.69$, $P = 0.002$, Tables 1 and 2). However, there was no difference in the standing crop algal turf biomass (g C cm$^{-2}$) of open tiles exposed to grazing in different exposures ($P = 0.249$) or depths ($P = 0.599$) (Tables 1 and 2, Fig. 2b).

Over a 24 h period, water flow was significantly influenced by exposure ($F_{1,88} = 15.93$, $P = < 0.001$, Table 2, Fig. 2c), and depth ($F_{1,88} = 12.534$, $P = < 0.001$, Table 2, Fig. 2c). The cages did not reduce water flow, as there was no difference in water flow between caged and open treatments ($P = 0.112$). Water flow was significantly greater in shallow depths of both windward and leeward habitats (Fig. 2c). In the deep zone, windward sites had significantly less flow than leeward sites. However, there was no difference between windward and leeward shallow sites ($P = 0.05$, Fig. 2c).

## Herbivorous fish community spatial and grazing patterns

Herbivorous fish biomass (g m$^{-2}$) was significantly greater at shallow depths in both windward and leeward habitats ($F_{1,92} = 13.99$, $P < 0.001$; Table 2, Fig. 3a). When compared to deep sites, the herbivorous fish biomass was 3.72 times greater in the shallow zone of windward sites, and there was 2.33 times the biomass of herbivorous fish in the shallow zone of leeward sites (Fig. 3a). Exposure had no effect on herbivorous fish biomass, with no overall difference between windward and leeward sites ($F_{1,92} = 0.49$, $P = 0.488$; Table 2, Fig. 3a). Grazing intensity on Heron reef slope was high, with up to ~ 7000 bites taken (m$^{-2}$ day$^{-1}$). On average, there were more bites taken per day in shallow than deep habitats, however there was no significant difference in the total number of bites (m$^{-2}$ day$^{-1}$) taken in each habitat (Table 2, Fig. 4a).

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**The grazing impact of EAM grazing surgeonfish species**

There were six species of EAM grazing acanthurid species present in the grazing intensity video and UVC surveys of Heron reef slope: *Acanthurus blochii, Acanthurus nigrofuscus, Ctenochaetus striatus, Ctenochaetus binotatus, Zebrasoma scopas* and *Zebrasoma veliferum*. The two *Ctenochaetus* species were the most abundant grazing surgeonfish species on Heron reef slope, with *C. binotatus* the most abundant species in deep habitats, while *C. striatus* was most abundant in shallow habitats (Fig. 5). Surgeonfish represented the greatest biomass (g m$^{-2}$) of herbivorous fish species in the most productive habitats: windward-shallow (74%), and leeward-shallow (56%) (Fig. 3b); and were responsible for 51% of the total bites (m$^{-2}$ day$^{-1}$) taken in the most productive habitat (windward-shallow), 32% of the total bites taken in the windward-deep habitat, 40% of bites in the leeward-shallow habitat, and 42% of bites in the windward-deep habitat (Fig. 4b). The six surgeonfish species were estimated to remove up to 73% of the daily productivity (g C m$^{-2}$ day$^{-1}$) in the most productive habitat (windward-shallow), and 41% of the daily productivity in the leeward-shallow habitat (Table 4). In the leeward-deep habitat, surgeonfish species removed an estimated 47% of the daily productivity, and were responsible for removing 30% of the daily productivity in the windward-deep habitat (Table 4).

## Discussion

This study highlights the critical functional role of epilithic algal matrix (EAM) grazing surgeonfish, which represented 74% of the herbivore biomass, took 51% of the total bites and removed 73% of daily turf productivity in the most productive habitat of Heron reef slope (windward-shallow). Algal turf productivity was highest in shallow zones, and herbivorous fish biomass mirrored this pattern. There was no difference in standing crop biomass of grazed algal turf or the daily grazing intensity among habitats. Quantifying the grazing impact of surgeonfish significantly improves our understanding of herbivory processes on coral reefs and the role that this key functional group plays in maintaining algal turfs, and possibly preventing shifts from coral- to algal-dominance.

The results of this study are limited to the summer months, although algal turf productivity and grazing intensity are known to fluctuate seasonally (Hatcher and Larkum 1983; Klumpp and McKinnon 1989; Hatcher 1990; Polunin and Klumpp 1992; Afeworki et al. 2011; 2013a; 2013b). Grazing intensity and productivity generally peak in summer (Klumpp and McKinnon 1989;

Polunin and Klumpp 1992), therefore, the results of this study are likely to represent the maximum values for Heron reef slope. On a neighbouring reef (One Tree Island), the standing crops of algal turfs varied spatially and were three to five times higher in shallow and intertidal habitats than in deeper areas and showed seasonal variation (Hatcher and Larkum 1983). At Heron Reef however, the standing crop of algal turfs did not vary spatially during the summer months. The EAM standing crop of reefs is largely thought to be controlled by grazing, while productivity rates are influenced by light and nutrient supply (Hatcher and Larkum 1983; Carpenter 1986; Hatcher 1988; McCook 1999). Water flow and turbulence determine the rate of nutrient supply to algae and are major drivers of productivity, whereas nutrient concentration by itself has a relatively minor influence (Williams and Carpenter 1998). Therefore, large variations in productivity are expected along a wave exposure (water turbulence) gradient. In theory, reducing herbivory (e.g., overfishing) on a windward reef with high productivity is more likely to cause an algal phase shift than on a leeward reef with low productivity and algal growth rates. Thus, for a given level of herbivore biomass, leeward reefs with lower production may have a higher surplus grazing capacity (Mumby and Steneck 2008). This suggests that management efforts to maintain the process of herbivory should focus on windward sites with high productivity, although this remains to be tested (Mumby and Steneck 2008).

Algal turf productivity is generally two to three times higher on the reef crest than the reef flat (Klumpp and McKinnon 1989), while studies of productivity on reef slopes are rare (Hatcher 1990; Russ 2003). This study is one of only a few that has measured productivity on reef slopes along a depth gradient (Caribbean studies: Adey and Steneck 1985; Adey and Goertemiller 1987). Hatcher and Larkum (1983) investigated algal turf dynamics at One Tree Island reef, but their sites were in the lagoon and emergent, intertidal windward reef crest, so are not comparable to the reef slope zone studied here. Russ (2003) measured algal turf productivity at an outer shelf reef in the central Great Barrier Reef, where the mean summer productivity ($0.25$ g C cm$^{-2}$ day$^{-1}$) of the deep (15 m) leeward reef slope was similar to this study ($0.24$ g C cm$^{-2}$ day$^{-1}$). In contrast, the productivity of the leeward reef crest (2–3 m; $1.1$ g C cm$^{-2}$ day$^{-1}$) was more than double the leeward reef crest productivity in this study (2–4 m; $0.53$ g C cm$^{-2}$ day$^{-1}$). However, it is problematic to compare rates of productivity among studies due to large variability in methodologies and local environmental conditions. Also, the cage exclusion method may actually underestimate production rates because it does not account for biomass losses due to small grazers, fragmentation, detachment, reproduction, or self-shading as biomass accumulates over time (Russ 2003). Although these factors may vary

between zones and were not measured here, the differences are unlikely to change the general patterns observed.

The interaction between primary productivity and herbivory regimes may alter the successional trajectory of the reef benthic community and determine what community (turfs, macroalgae, coralline algae etc.) will dominate (Carpenter 1986; Burkepile and Hay 2010). On Heron reef slope, herbivorous grazing fish biomass was highest in the shallow zone, mirroring patterns of algal turf productivity, but unrelated to grazed algal turf standing crop biomass. Herbivorous fish abundance is consistently higher on shallow reef crests/slopes than in other coral reef zones (Hatcher 1981; Russ 1984a, 1984b; Fox and Bellwood 2007; Afeworki et al. 2013a). Higher grazing intensities in shallow relative to deeper zones have also previously been demonstrated (Hatcher 1981; Hay 1981; Fox and Bellwood 2007). In this study, there was no difference between the bite rates of herbivorous fishes between depths, and this may be due to variability in the grazing rate determined by remote video surveys. Grazing activity is thought to stimulate epilithic algal productivity by selecting for fast-growing species and growth forms, removing senescent material, reducing self-shading effects, and enhancing availability of nutrients (Carpenter 1986; Hatcher 1988; Klumpp and McKinnon 1992). Due to the low standing crop biomass and height of algal turfs in all habitats of Heron reef slope, it is unlikely that grazers are selectively targeting different turf species compositions between zones, and it is more likely that grazers are aggregating in shallow zones due to their high food availability (Russ 2003). Differences in habitat complexity and predation or recruitment rates between zones are also likely to influence the distribution and abundance of coral reef fish. However, this study is consistent with other studies, where grazers concentrate in the shallow zone of the reef slope with higher rates of algal turf productivity (Russ 2003).

Acanthurids are widespread and among the dominant families of fishes on tropical coral reefs, both in terms of numbers of individuals and biomass (Russ 1984a, 1984b; Randall 2001; Cheal et al. 2012). Some acanthurid species are important in commercial and subsistence coral reef fisheries (Rhodes et al. 2008; Houk et al. 2012; Bejarano et al. 2013; Bejarano et al. 2014), and many of the colourful species are of considerable value to the aquarium fish trade (Randall 2001). The high removal rates of daily algal turf productivity by surgeonfishes in this study suggests that their feeding activity may be important in maintaining algal turf biomass and preventing coral-algal phase shifts on coral reefs. Although coral reef degradation is usually characterised by macroalgal outbreaks, coral decline may also be facilitated or accompanied by a detrimental increase in algal turf biomass (Diaz-Pulido and McCook 2004; McManus and Polsenberg 2004; Birrell et al. 2005;

Hughes et al. 2007; Vermeij et al. 2010). The high consumption of algal turfs by abundant surgeonfishes is likely to be important in maintaining algal turfs in a closely cropped state, which enhances reef resilience. Additionally, surgeonfishes and other EAM grazers remove significant quantities of macroalgal recruits settled within the EAM (Chapter 2); consequently reducing the potential for macroalgal outbreaks. Overharvesting of grazing surgeonfish will reduce their grazing impact and may change the dynamics of the EAM, a dominant substrate of most coral reef ecosystems that is maintained by grazing fish. Therefore, the important ecosystem functional role of surgeonfish should be taken into account when considering ecosystem-based management of surgeonfish fisheries and aquarium trades.

**Acknowledgements**

Table 1. The range (minimum, median, maximum) and average (± S.D.) final biomass (caged tiles, g C m$^{-2}$), and standing crop biomass (open tiles, g C m$^{-2}$) of algal turfs (g m$^{-2}$) in different habitats of Heron Island reef slope.

| Habitat | 28 d | Ungrazed Final Biomass (caged tiles, g C m$^{-2}$, ± S.D.) | Grazed Standing Biomass (open tiles, g C m$^{-2}$, ± S.D.) | Productivity (g C m$^{-2}$ day$^{-1}$, ± S.E.) |
|---|---|---|---|---|
| *Windward, Shallow* | Minimum | 3.85 | 1.11 | |
| | Median | 16.5 | 6.79 | |
| | Maximum | 102 | 24.9 | |
| | Average | 24.2 ± 24.5 | 8.16 ± 6.61 | 0.865 ± 0.21 |
| *Windward, Deep* | Minimum | 1.54 | 1.11 | |
| | Median | 9.49 | 7.38 | |
| | Maximum | 30.1 | 17.5 | |
| | Average | 1.38 ± 9.44 | 7.11 ± 3.56 | 0.483 ± 0.08 |
| *Leeward, Shallow* | Minimum | 0.466 | 0.805 | |
| | Median | 12.1 | 5.57 | |
| | Maximum | 52.6 | 13.2 | |
| | Average | 14.8 ± 12.2 | 6.55 ± 3.39 | 0.527 ± 0.102 |
| *Leeward, Deep* | Minimum | 1.27 | 1.51 | |
| | Median | 5.72 | 4.79 | |
| | Maximum | 15.6 | 10.1 | |
| | Average | 6.61 ± 4.45 | 5.39 ± 2.67 | 0.236 ± 0.04 |

Table 2. ANOVA results comparing: (a) algal turf productivity (g C m$^{-2}$ day$^{-1}$, caged tiles final biomass/28), (b) algal turf maximum biomass (g C m$^{-2}$, caged tiles), and (c) algal turf standing biomass (g C m$^{-2}$, open tiles) after 28 d in experimental plots; d) relative water flow (% weight loss); e) herbivorous fish biomass (g m$^{-2}$), and f) herbivorous fish bite rate (bites m$^{-2}$ day$^{-1}$) in different habitats of Heron Island reef slope. Conclusions of post-hoc tests (Tukey) are summarised.

| Source of variation | df | MS | $F$ | $P$ | Conclusions: Tukey |
|---|---|---|---|---|---|
| a.  Productivity | | | | | |
| Exposure | 1 | 0.09 | 7.84 | 0.007* | Windward: Shallow > Deep |
| Depth | 1 | 0.12 | 9.86 | 0.002* | Leeward: Shallow > Deep |
| Exposure x Depth | 1 | 0.00003 | 0.0022 | 0.963 | Deep: Windward > Leeward |
| Residual | 68 | 0.012 | | | Shallow: Windward = Leeward ($P = 0.056$) |
| b.  Maximum Biomass | | | | | |
| Exposure | 1 | 0.95 | 9.49 | 0.003* | Windward: Shallow > Deep |
| Depth | 1 | 1.07 | 10.69 | 0.002* | Leeward: Shallow > Deep |
| Exposure x Depth | 1 | 0.016 | 0.163 | 0.688 | Deep: Windward > Leeward |
| Residual | 68 | 6.79 | | | Shallow: Windward = Leeward   ($P = 0.063$) |
| c.  Standing Biomass | | | | | |
| Exposure | 1 | 0.0754 | 1.351 | 0.249 | No difference in standing |
| Depth | 1 | 0.0156 | 0.279 | 0.599 | biomass among habitats |
| Exposure x Depth | 1 | 0.0222 | 0.398 | 0.530 | |
| Residual | 68 | 3.796 | | | |
| | | | | | |
| d.  Flow | | | | | |
| Exposure | 1 | 920.84 | 15.93 | <0.001* | Windward: Shallow > Deep |
| Depth | 1 | 724.37 | 12.53 | <0.001* | Leeward: Shallow > Deep |
| Treatment | 1 | 148.52 | 2.57 | 0.112 | |
| Exposure x Depth | 1 | 22.23 | 0.39 | 0.537 | Deep: Windward < Leeward |
| Residual | 88 | 57.79 | | | Shallow: Windward = Leeward ($P = 0.05$) |
| | | | | | Treatment: Open = Cage |
| e.  Fish Biomass | | | | | |
| Exposure | 1 | 0.07 | 0.49 | 0.488 | Windward = Leeward |
| Depth | 1 | 1.99 | 13.99 | <0.001* | Shallow > Deep |
| Exposure x Depth | 1 | 0.007 | 0.05 | 0.823 | Leeward: Shallow > Deep |
| Residual | 92 | 0.14 | | | Windward: Shallow > Deep |
| | | | | | |
| f.  Fish Bites | | | | | |
| Exposure | 1 | 0.069 | 0.55 | 0.461 | No difference in bite rates |
| Depth | 1 | 1.99 | 2.34 | 0.129 | among habitats |
| Exposure x Depth | 1 | 0.0072 | 0.062 | 0.804 | |
| Residual | 92 | 0.14 | | | |

Table 3. The algal turf biomass taken per bite (g) of surgeonfish species by size class (cm, mid-point) present in Heron grazing intensity video and UVC surveys. Fish biomass is determined from length-weight relationship parameters (Kulbicki 2005).

| Species | Size Class Mid-point (cm) | Algal turf biomass per bite (g) | Fish Wet Weight ($W$) biomass (g) | Reference |
|---|---|---|---|---|
| *Acanthurus nigrofuscus* | 14 | $9.5 \times 10^{-5}$ | 77.9 | VanRooij et al 1998 |
| | 17 | $1.53 \times 10^{-4}$ | 140.4 | C intake (day$^{-1}$) = $0.0342 \times W^{0.816}$ |
| | 20 | $2.29 \times 10^{-4}$ | 229.7 | |
| *Acanthurus blochii* | 14 | $9.19 \times 10^{-5}$ | 74.94 | VanRooij et al 1998 |
| | 17 | $1.49 \times 10^{-4}$ | 135.02 | C intake (day$^{-1}$) = $0.0342 \times W^{0.816}$ |
| | 20 | $2.22 \times 10^{-4}$ | 221 | |
| | 23 | $3.14 \times 10^{-4}$ | 337.62 | |
| | 26 | $4.25 \times 10^{-4}$ | 489.64 | |
| | 29 | $5.57 \times 10^{-4}$ | 681.81 | |
| *Ctenochaetus striatus* | 11 | $5.62 \times 10^{-5}$ | 35.8 | VanRooij et al 1998 |
| | 14 | $1.03 \times 10^{-4}$ | 74.9 | C intake (day$^{-1}$) = $0.0342 \times W^{0.816}$ |
| | 17 | $1.69 \times 10^{-4}$ | 135.9 | |
| | 20 | $2.5 \times 10^{-4}$ | 223.5 | |
| *Ctenochaetus binotatus* | 8 | $2.63 \times 10^{-5}$ | 15.5 | VanRooij et al 1998 |
| | 11 | $5.54 \times 10^{-5}$ | 38.7 | C intake (day$^{-1}$) = $0.0342 \times W^{0.816}$ |
| | 14 | $9.76 \times 10^{-5}$ | 77.3 | |
| | 17 | $1.54 \times 10^{-4}$ | 135.1 | |
| *Zebrasoma scopas* | 11 | $6.32 \times 10^{-5}$ | 38.1 | VanRooij et al 1998 |
| | 14 | $1.14 \times 10^{-4}$ | 78.4 | C intake (day$^{-1}$) = $0.0342 \times W^{0.816}$ |
| | 17 | $1.83 \times 10^{-4}$ | 140.2 | |
| *Zebrasoma veliferum* | 17 | $1.56 \times 10^{-4}$ | 115.2 | VanRooij et al 1998 |
| | 20 | $2.28 \times 10^{-4}$ | 183.6 | C intake (day$^{-1}$) = $0.0342 \times W^{0.816}$ |

Table 4. The amount of algal turf biomass (g C m$^{-2}$ day$^{-1}$), and percentage of the mean daily productivity (g C m$^{-2}$ day$^{-1}$) removed per day by grazing surgeonfish species on Heron reef slope.

| Species | Reef slope habitat type | Total amount of algal turf biomass removed per day (g C m$^{-2}$ day$^{-1}$) | % of mean productivity removed per day (g C m$^{-2}$ day$^{-1}$) |
|---|---|---|---|
| *All grazing surgeonfish species (combined total)* | Leeward-Deep | 0.111 | 47% |
| | Leeward-Shallow | 0.216 | 41% |
| | Windward-Deep | 0.145 | 30% |
| | Windward-Shallow | 0.629 | 73% |
| *A. blochhi* | Leeward-Deep | N/A | N/A |
| | Leeward-Shallow | N/A | N/A |
| | Windward-Deep | N/A | N/A |
| | Windward-Shallow | 0.415 | 48% |
| *A. nigrofuscus* | Leeward-Deep | 0.017 | 7.4% |
| | Leeward-Shallow | 0.014 | 3% |
| | Windward-Deep | 0.017 | 3% |
| | Windward-Shallow | 0.14 | 16.2% |
| *C. striatus* | Leeward-Deep | N/A | N/A |
| | Leeward-Shallow | 0.072 | 13% |
| | Windward-Deep | N/A | N/A |
| | Windward-Shallow | 0.004 | 0.4% |
| *C. binotatus* | Leeward-Deep | 0.091 | 38.3% |
| | Leeward-Shallow | 0.072 | 13.6% |
| | Windward-Deep | 0.085 | 17.5% |
| | Windward-Shallow | 0.018 | 2.1% |
| *Z. scopas* | Leeward-Deep | 0.003 | 1.3% |
| | Leeward-Shallow | 0.058 | 10.9% |
| | Windward-Deep | 0.033 | 6.8% |
| | Windward-Shallow | 0.033 | 3.8% |
| *Z. veliferum* | Leeward-Deep | N/A | N/A |
| | Leeward-Shallow | 0.001 | 0.2% |
| | Windward-Deep | 0.011 | 2.2% |
| | Windward-Shallow | 0.019 | 2.1% |

Figure 1. a) Location of study sites (white circles) on the leeward (north-side; $n = 3$) and windward (south-side; $n = 3$) zones of Heron reef slope (shallow = 2–4 m; deep = 9–12 m). b) Map of average wind speed from Heron Island Research Station 2010–2012 meteorological data. Legend and shading indicates wind speed in knots.

Figure 2. The mean (± S.E.) algal turf: a) productivity (g C m$^{-2}$ day$^{-1}$ = caged tiles final biomass/28), and (b) standing crop biomass (g C m$^{-2}$, open tiles final biomass), after 28 d in experimental plots on Heron Island reef slope. c) The mean percentage (± S.E.) loss of the initial weight of plaster-of-paris clod-cards ($n$ = 24 per habitat) deployed simultaneously over 24 h. Deep = 9–12 m and Shallow = 3–6 m at pooled leeward (left-side, $n$ = 3) and windward sites (right-side, $n$ = 3). Conclusions of post-hoc tests (Tukey) are displayed as letters above the graphs to highlight significant differences.

Figure 3. a) The mean (± S.E.) herbivorous fish biomass observed in underwater visual census surveys ($n = 24$ per habitat-type). b) The percentage of the total biomass (g m$^{-2}$) of the three main herbivorous fish families (rabbitfish – dark grey, parrotfish – light grey, surgeonfish - white).

Figure 4. a) The mean (± S.E.) number of bites (m$^{-2}$ day$^{-1}$) observed in remote video surveys ($n$ = 24 cameras: 3 sites x 8 replicates). b) The percentage of total bites taken (m$^{-2}$ day$^{-1}$) by the three major herbivorous fish families (Siganidae – dark grey, Labridae – light grey, Acanthuridae - white).

Figure 5. The relative abundance (%) of epilithic algal matrix grazing surgeonfish species on Heron reef slope in different habitats: leeward-deep, leeward-shallow, windward-deep, windward-shallow.

# Supplementary Material

Table S1. Summary of the species composition of epilithic algal matrix grazing herbivorous fish communities observed during surveys of Heron Island reef slope habitats (Windward, *n* = 3 sites; Leeward, *n* = 3 sites; Shallow = 2–4 m; Deep = 9–12 m deep) during February 2012.

| Genera | Leeward, Deep | Leeward, Shallow | Windward, Deep | Windward, Shallow |
|---|---|---|---|---|
| **Acanthuridae** | • *Acanthurus nigrofuscus*<br>• *A. blochii*<br>• *Ctenochaetus binotatus*<br>• *C. striatus*<br>• *Zebrasoma scopas* | • *Acanthurus nigrofuscus*<br>• *A.blochii*<br>• *Ctenochaetus binotatus*<br>• *C. striatus*<br>• *Zebrasoma scopas*<br>• *Z. veliferum* | • *Acanthurus nigrofuscus*<br>• *Ctenochaetus binotatus*<br>• *C. striatus*<br>• *Zebrasoma scopas*<br>• *Z. veliferum* | • *Acanthurus nigrofuscus*<br>• *A. blochii*<br>• *Ctenochaetus binotatus*<br>• *C. striatus*<br>• *Zebrasoma scopas*<br>• *Z. veliferum* |
| **Scaridae** | • *Chlorurus microrhinus*<br>• *C. sordidus*<br>• *Scarus chameleon*<br>• *S. frenatus*<br>• *S. ghobban*<br>• *S. globiceps*<br>• *H. longiceps*<br>• *S. longipinnis*<br>• *S. niger*<br>• *S. psittacus*<br>• *S. rivulatus*<br>• *S. shlegeli*<br>• *S. spinus* | • *Chlorurus microrhinus*<br>• *C. sordidus*<br>• *Scarus chameleon*<br>• *S. frenatus*<br>• *S. globiceps*<br>• *H. longiceps*<br>• *S. longipinnis*<br>• *S. niger*<br>• *S. psittacus*<br>• *S. rivulatus*<br>• *S. shlegeli*<br>• *S. spinus* | • *Chlorurus sordidus*<br>• *Scarus flavipectoralis*<br>• *S. forsteni*<br>• *S. frenatus*<br>• *S. ghobban*<br>• *S. globiceps*<br>• *S. longipinnis*<br>• *S. niger*<br>• *S. psittacus*<br>• *S. rivulatus*<br>• *S. shlegeli*<br>• *S. spinus* | • *Cetoscarus bicolor*<br>• *Chlorurus sordidus*<br>• *Scarus chameleon*<br>• *S. dimidiatus*<br>• *S. flavipectoralis*<br>• *S. forsteni*<br>• *S. frenatus*<br>• *S. ghobban*<br>• *S. globiceps*<br>• *S. longipinnis*<br>• *S. niger*<br>• *S. oviceps*<br>• *S. psittacus*<br>• *S. rivulatus*<br>• *S. shlegeli*<br>• *S. spinus* |
| **Signaidae** | • *Siganus corallinus*<br>• *S. doliatus*<br>• *S. puellus*<br>• *S. punctatissimus* | • *Siganus canaliculatus*<br>• *S. corallinus*<br>• *S. doliatus*<br>• *S. punctatissimus* | • *Siganus corallinus*<br>• *S. doliatus*<br>• *S. lineatus*<br>• *S. puellus*<br>• *S. punctatissimus*<br>• *S. vulpinus* | • *Siganus corallinus*<br>• *S. doliatus*<br>• *S. puellus*<br>• *S. punctatissimus*<br>• *S. vulpinus* |

# Chapter 5. The balance between fish grazing and algal turf dynamics on coral reefs: a grazing simulation model

## Abstract

On coral reefs, herbivory is critical to maintain the balance between corals and algae, and prevent shifts from coral to macroalgal dominance. Macroalgae comprises large (> 1 cm), rigid, and structurally complex algal forms, while epilithic algal turfs are a multi-species assemblage of diminutive (< 1 cm) and primarily filamentous algae, which can include developmental stages of macroalgae that may emerge if not grazed. Therefore, it is important to better understand the interaction and balance between grazing and algal turf dynamics. A grazing simulation model was developed to investigate the interactions between species- and size-specific fish grazing intensity and algal turf dynamics at different depths (shallow, deep) and exposures (leeward, windward) of reef slope habitats. The model explores the impact of grazing on algal turf dynamics and produces a predicted turf biomass that closely matches the observed turf biomass in three of four reef slope habitats. The model currently underestimates the amount of observed turf biomass in the most productive habitat (windward-shallow). This suggests that our knowledge of turf dynamics in this zone in lacking and needs further field investigation to better parameterise highly productive turf growth. The model output is most sensitive to an increase in the maximum growth rate of turfs, which has the largest influence of all of the parameters in increasing turf biomass. The grazing model developed here provides new insights into the fine spatial and temporal scales of algal turf dynamics on reefs, and enhances our knowledge of processes involved in these dynamics.

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# Introduction

On coral reefs, herbivory is critical to maintain the balance between corals and algae, and prevent shifts from coral to macroalgal dominance (Hughes 1994; Mumby et al. 2006). Herbivores can also play a role in reversing macroalgal dominance, although this process is rare and not well understood (Bellwood et al. 2006; Fox and Bellwood 2008). Macroalgae refers to large (> 1 cm), rigid, and structurally complex algal forms, while epilithic algal turfs (hereafter, turf) are a multi-species assemblage of diminutive (< 1 cm) and primarily filamentous algae, which can include developmental stages of macroalgae that may emerge if not grazed (Steneck 1988). Turfs are one of the dominant benthic microhabitats and major sources of primary productivity on coral reefs, supporting a diverse and abundant assemblage of grazers (Wilson et al. 2003; Wismer et al. 2009; Cheal et al. 2012). Hence, the reasons for modelling turf dynamics were threefold. Firstly, turfs are abundant, support highly productive food webs, and any change in turf productivity or dynamics could have important consequences at higher trophic levels, with most food web models assuming a certain base-level of productivity (Christensen and Pauly 1992; Van Rooij et al 1998; Rogers et al 2014). Secondly, if the balance of bottom-up and top-down forces that control turf biomass shift, then the standing crop could increase, with possible detrimental effects. For example, a number of studies have found that long turfs (> 4 mm) trap sediment, deter herbivores, and vastly reduce coral recruitment (e.g., Purcell and Bellwood 2001; Birrell et al. 2005; Bellwood and Fulton 2008; Arnold et al. 2010). Thirdly, protracted reductions in grazing could allow developmental stages of fleshy macroalgae to escape from turfs and form erect macrophytes that are less palatable and become dominant (Diaz-Pulido and McCook 2003). Macroalgal dynamics are of great interest because of their strong competitive interactions with corals and subsequent degradation of the reef ecosystem following a shift from coral to algal dominance (McCook et al. 2001).

Herbivorous fishes play a key role in controlling turf biomass, and therefore preventing macroalgal emergence (Hatcher and Larkum 1983; Klumpp and Polunin 1989; Van Rooij et al. 1998; Russ 2003). In addition to shaping turf morphology, grazing disturbance also enhances turf productivity (Carpenter 1986). It is estimated that herbivorous fishes remove between 20 and 90% of the net daily primary production (Hatcher and Larkum 1983; Polunin and Klumpp 1992), and can completely turn over turf biomass every 4 to 25 d (Klumpp and Polunin 1989). Therefore, herbivory is considered a key ecological process that contributes to coral reef resilience, and there is an urgent need to manage human activities (e.g., overfishing) that threaten this process (Green and Bellwood 2009). However, there are large gaps in our understanding of the relationship between grazing and

turf dynamics in different coral reef zones and at fine spatial and temporal scales, and we need to expand our knowledge of the processes and interactions involved in order to be able to apply ecosystem-based management strategies that boost coral reef resilience.

Herbivorous fishes inhabit most coral reef zones, and the assemblages that occur are usually characteristic of each zone (Russ 1984a). The variability in the distribution and abundance of herbivorous fishes among zones within a reef is largely associated with depth and productivity (Russ 1984b; Russ 2003; Fox and Bellwood 2007). Most relatively undisturbed reefs support a high biomass of herbivorous grazing fish, but a low biomass of their turf food source and it is the high productivity of turfs rather than their standing crop that maintains a high standing stock of grazers (Hatcher 1988, 1990; Hatcher and Larkum 1983; McCook 1999; Russ 2003). The distribution of herbivore biomass is thought to generally be influenced by the rate of turf production rather than standing crop biomass, although only a few studies have tested this (Hatcher 1988, 1990; Steneck 1983; Russ 2003). Observations of grazing do not predict algal biomass directly as turf biomass is the result of a dynamic balance between algal production (area for colonisation, recruitment rate and growth) and algal removal through grazing (Mumby 2006). There is a paucity of data on turf growth at fine temporal and spatial scales (but see, Bonaldo and Bellwood 2009). However, we do know that turf photosynthesis rates are related positively to flow, while mass transfer to turfs is negatively influenced by an increase turf biomass (Carpenter and Williams 2007). Also, that flow speeds over turfs vary temporally due to changing ambient conditions (e.g., tides), and over small spatial scales in relation to turf height and substrate complexity (Carpenter and Williams 1993).

*Ctenochaetus* species graze upon turfs intensively, but are considered exclusively detritivorous and were thought to cause little damage to turfs through their grazing activity of 'combing' detritus from turf strands (Purcell and Bellwood 1993). However, recently *Ctenochaetus striatus* have been shown to be capable of removing significant quantities of algal turfs in lab experiments (Marshell and Mumby 2012). As *Ctenochaetus* species are one of the most abundant fishes on Indo-Pacific coral reefs and have one of the highest maximum bite rates of grazing fishes (Polunin et al. 1995; Wilson et al. 2003), their ability to remove significant quantities of turfs has potentially important implications for their functional role in driving turf dynamics. However, the grazing impact of *C. striatus* on turf biomass in the field remains to be tested.

Grazing intensity, grazed turf biomass (uncaged tiles), and ungrazed turf biomass (caged tiles) were quantified at leeward and windward sites of the reef slope in shallow (2–4 m) and deep (9–12 m)

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zones of Heron Island Reef, an outer-shelf reef located in the southern Great Barrier Reef (see Chapter 4). The reef slope zone is defined as the steeply inclined area on the seaward side of reefs, immediately below the reef crest and with depth ranges of approximately 5–50m (Bellwood and Wainwright 2001). Here, the first objective was to use these field data to parameterise and develop a comprehensive grazing model that equilibrates and predicts grazed turf biomass close to the observed grazed turf biomass. A second objective was to use the model to investigate the impact of *Ctenochaetus* species on turf dynamics. To do this it was assumed that *Ctenochaetus* species are able to remove turfs through their grazing activity for initial model runs (Marshell and Mumby 2012), and then a scenario where *Ctenochaetus* species were removed from grazing intensity estimates was run to investigate the effect on predicted turf biomass. Developing a model system of turf dynamics enables investigation into the effect of grazing intensity and turf growth parameters on observed turf biomass on coral reefs, and enhances our understanding of the processes and interactions involved in maintaining a balanced ecosystem.

## Methods

### Model overview

A spatially explicit simulation model was developed to examine the balance between turf growth, and the impact of turf grazing fish in different habitats of Heron Island reef slope (Fig. 1). The model was parameterised to represent four Heron reef slope habitats: (1) windward-shallow; (2) windward-deep, (3) leeward-shallow; and (4) leeward-deep (shallow = 2–4 m, deep = 9–12 m; for study site description, see Chapter 4). The model includes the habitat-specific observed grazing intensity (bite rates) and estimated bite sizes (g C) of specific species and size classes from the three main herbivorous fish families (Acanthuridae, Labridae, Siganidae), and accounts for daily turf growth assuming a logistic growth model, that comprises the turf parameters: observed grazed biomass, modelled initial 'time-zero' biomass, modelled maximum growth rate and modelled 28 d carrying capacity (Fig. 1, Table 1).

The model is a square lattice of 10,000 cells, with each originally occupied by the habitat-specific, average observed grazed turf biomass (g C cm$^{-2}$). The model simulates a flat planar area of 100 × 100 cm$^{-2}$ grazeable cells. Turf biomass in individual cells is updated on a daily basis after being fed-upon by fish in a random sequence. The use of spatially random grazing is motivated by future applications of the model where we plan to introduce spatial grazing behaviour and micro-

complexity, which are not currently incorporated in this first version of the model. The model output is the mean daily grazed turf biomass (g C cm$^{-2}$) remaining after 50 simulations which accounts for highly variable grazing intensity. The model was run for 90 days (time-steps), which is an appropriate maximum time interval, given that the empirical data used to parameterise the model are only from a single summer field season, and empirical studies from the same region found seasonal differences in grazing and algal patch dynamics (Hatcher and Larkum 1983). Nevertheless, the model was found to equilibrate within this time period. Coding was accomplished using Matlab (The Mathworks, Natick, Massachusetts, USA) and each reef habitat was run separately.

**Modelling the process of grazing**

The model includes the daily average grazing intensity of the three most significant grazing fish families on Indo-Pacific reefs: the acanthurids (surgeonfish), labrids (parrotfish), and siganids (rabbitfish) (Green and Bellwood 2009; Cheal et al. 2012). Herbivorous fish species from these families target a wide variety of food sources and reef substrates, feeding almost continuously during the day, but exhibiting a diurnal pattern of slow feeding during the morning, that gradually increases throughout the day (Horn 1989; Polunin and Klumpp 1989; Choat 1991; Zoufal and Taborsky 1991; Ferreira et al. 1998; Choat et al. 2002; Zemke-White et al. 2002; Brandl et al. 2013; Hoey et al. 2013; Khait et al. 2013).

*Field surveys of grazing intensity*

Grazing intensity was calculated as the total number of bites taken by herbivorous fishes (m$^{-2}$ day$^{-1}$), and was quantified using GoPro HD video cameras ($n = 4$) deployed for one hour during both the morning and afternoon in each habitat type: deep and shallow zones of each of the windward ($n = 3$) and leeward ($n = 3$) sites (for a detailed study site and methods description, please see Chapter 4 methods). Therefore, the overall grazing intensity data comes from a total of 24 replicates of 1 m$^2$ video surveys per habitat type (3 sites × 4 AM + 4 PM surveys).

*Video analysis of grazing intensity*

Subsequent video analysis of the field surveys of grazing intensity allowed the average bite rate per species, per size class, per 1 m$^2$ (standardised to 100% grazeable substrate), per day (bite rate min$^{-1}$

× 600 min to represent a conservative 10 h grazing day) to be calculated for each habitat (bites m$^{-2}$ day$^{-1}$) (for a detailed video analysis methods description, please see Chapter 4 methods).

*Algal turf grazing fish bite size estimation*

Herbivorous fishes are diverse and comprised of several functional groups that differ in how they feed, what they consume and their impact on the substrate. Most parrotfishes (*Scarus* and *Hipposcarus* species) are scrapers, feeding on epilithic algal turfs by scraping the reef surface, leaving behind a shallow grazing scar. This is in contrast to excavating parrotfish species (all *Chlorurus* species, *Cetoscarus bicolor*, *Bolbometopon muricatum*) which leave deeper grazing scars and remove significant quantities of substrate with each bite (Green and Bellwood 2009). Therefore, the bite area was calculated in various ways using available data from the literature for different species and size classes of parrotfish observed in the grazing intensity video surveys. The relationship between parrotfish species total length (TL, cm) and bite area (cm$^2$) was used to calculate size-specific (3 cm size class midpoint) bite areas for: *Chlorurus sordidus* (√BiteArea = -0.34 + 0.04 × TL cm), *Chlorurus microrhinos* (√BiteArea = -0.29 + 0.02 × TL cm), *Cetoscarus bicolor* (√BiteArea = -0.14 + 0.02 × TL cm) and *Scarus psittacus* (√BiteArea = -0.06 + 0.02 × TL) (Table 2; Bejarano 2009). Due to a lack of species-specific data, the relationship between body length and bite area for *S. psittacus* was also used to calculate bite areas for similar *Scarus* species: *S. chameleon, S. flavipectoralis, S. longipinnis, S. frenatus, S. spinus, S. globiceps, S. niger, S. schlegeli* (Table 2) (Bellwood and Choat 1990). The bite areas of *S. rivulatus* size classes were calculated from data on the relationship between this species total length and bite area in Bonaldo and Bellwood (2008). To convert the bite areas (cm$^2$) into algal biomass removed per bite (g C), the species- and size-specific bite area was multiplied by the habitat-specific mean grazed turf biomass (Table 2).

In contrast to parrotfishes, grazers/detritivores that intensely graze epilithic algal turfs (most rabbitfishes, and surgeonfishes species from the genera: *Acanthurus, Ctenochaetus* and *Zebrasoma*) do not scrape or excavate the substrate as they feed (Green and Bellwood 2009). Therefore, it is not possible to calculate a size-specific bite area as there are no grazing scars left by these species. Consequently, the relationship between algal carbon (C, organic biomass) intake (g C day$^{-1}$) and fish body mass (*W* = Wet body mass in grams) for herbivorous fish consumption was used to calculate species- and size-specific bite sizes of relevant rabbitfish and surgeonfish species from the genera *Acanthurus, Ctenochaetus* and *Zebrasoma* (Table 3; C intake (day$^{-1}$) = 0.0342 × $W^{0.816}$;

Bruggemann 1995; Van Rooij et al. 1998). This general relationship was determined by fitting a regression to quantitative estimates of daily food intake by a range of herbivorous reef fishes (parrotfish, surgeonfish, damselfish) available in the literature from a wide variety of locations, such as the Caribbean, Red Sea, Great Barrier Reef, and Papua New Guinea (Van Rooij et al. 1998). It was assumed that *Ctenochaetus* species are able to remove turfs through their foraging activity (Marshell and Mumby 2012). Species-specific length-weight relationships were used to calculate the wet biomass (g) of different size classes (Kulbicki et al. 2005). To convert the daily total carbon intake to the amount of algal biomass removed per bite per bite, the total carbon intake per day was divided by the average daily total bites taken by each species (Marshell, unpublished data; Polunin et al. 1995; Fox and Bellwood 2007).

*Modelling the daily grazing intensity*

For every habitat, and at each time step (one day), all observed size classes of fish species have a total 'food demand' that is estimated from a random distribution of their observed bite rates (bites $m^{-2}$ $day^{-1}$ ± S.D.) multiplied by the fixed bite size (g) estimated for each specific size class and species (Tables 2 and 3). The model simulates grazing in a random sequence among individual cells (10,000 cells, each 1 x 1 cm) of the square lattice 1 $m^2$ 'reef' area. The model removes algal biomass from randomly chosen reef cells, until the total 'food demand' of that size class and species has been met, and then the process is repeated for all size classes and species, until all simulated 'fish' have fed, and their total 'food demand' has been met for that day. If the total overall food demand is greater than the food available on the simulated reef, then the total amount of negative turf biomass or 'food debt' is recorded for that day as a model output.

**Modelling algal turf dynamics**

*Algal turf dynamics parameterisation – field observations*

Parameters of turf dynamics were measured in each reef slope habitat (shallow and deep zones of the same windward and leeward sites as the grazing intensity video surveys). The grazed turf biomass (g C $cm^{-2}$), and ungrazed turf biomass (g C $cm^{-2}$) were quantified after 28 d. At each site, twelve preconditioned (> 12 months) limestone tiles (13 x 13 x 1.5 cm) with a rough textured surface were secured to dead reef substrate. The tiles were gently scrubbed to begin with a null algal biomass prior to deployment in experimental treatments, while maintaining a base of live encrusting

benthic organisms and turf holdfasts. The tiles were randomly assigned to two treatment groups: caged and open. Six caged tiles were protected from grazing fish (> 5 cm total length) by exclusion cages (22 x 22 x 18 cm) with a mesh size of 2.5 x 2.5 cm. The remaining six tiles were open and exposed to natural grazing levels. Exclusion cages were secured to dead substrate and maintained regularly throughout the study. The grazed turf biomass was determined from the tiles that were exposed to grazing, representing the grazed turf standing crop of the surrounding reef substrate. Tiles were placed within a few meters of each other at the same depth and left for 28 d during the austral summer months of January–February 2012 (for detailed methods of lab sample processing of the tiles please see Chapter 4 Methods).

*Algal turf dynamics parameterisation – modelled estimates*

As the turf biomass field data was limited to one time-point (28 d), the initial turf biomass at 'time-zero' ($B_0$), maximum growth rate (r) and carrying capacity (K) for each habitat was modelled by applying a nonlinear least squares best fit of the logistic growth model to available data (Fig. 2, Table 1). The Heron reef slope habitat-specific observed ungrazed turf biomass (g C cm$^{-2}$) was used as an estimated 28 d maximum carrying capacity. Logistic growth was used because sigmoid theory makes simple reasonable assumptions about the dynamics of a population and is a valuable means of obtaining a rough appreciation from minimal data when detailed information does not exist (Haddon 2001). Logistic growth is widely used to describe density-dependent population growth, where there is accelerating growth with a rapid increase in population size, until the maximum rate of increase is reached at half the population size. After that the growth rate decelerates in a symmetric way to the way it accelerated, and the asymptotic population size is eventually reached. Therefore, implicit assumptions are made in relation to density-dependent population regulation, in that the maximum growth rate occurs at 50% of the population size (Haddon 2001).

Information on initial (0–7 days) turf growth was estimated from the dynamics of parrotfish grazing scar recovery (Bonaldo and Bellwood 2009), where the daily reduction (%) in *Scarus rivulatus* grazing scar area was measured over seven consecutive days in leeward-shallow habitat. To estimate the turf biomass at time steps 1–7, the daily recovery of grazing scars (percent reduction in grazing scar area) through turf growth was multiplied by the mean observed Heron reef slope habitat-specific grazed turf biomass (g C cm$^{-2}$). This gave the initial data points of daily turf biomass to define the logistic growth curve for days 1–7, with the assumption that the percent

reduction in grazing scar area was the same in each habitat due to a lack of available data in different habitats (Fig. 2).

To estimate a 'mid-point' of turf biomass between the observed 28 d biomass and estimated biomass during days 1–7, data from a similar turf biomass study in Palau (unpublished, Mumby) were used to determine logistic growth curves for leeward-shallow and windward-shallow habitats (Fig. 2). A range of 11 d turf biomass (maximum = 0.0022, media$n$ = 0.0017, and minimum = 0.0011 g C cm$^{-2}$) values were estimated from 18 Palau sites of varying exposure (Fig. 2). These data points (estimated turf biomass at days 1–7, 11 and 28) were then used to find the best fit of the logistic growth curve and estimate the growth parameters ($B_0$, r, K) for each habitat (Fig. 2).

*Modelling algal turf dynamics*

The model was run for 50 replicate simulations at each time-step (day) to obtain a mean modelled output of daily net turf biomass (g C cm$^{-2}$) and account for the large daily variability in grazing intensity. The turf biomass in every cell (1 cm$^2$) of the simulated reef begins at the habitat-specific observed average grazed turf biomass (g C cm$^{-2}$). Daily turf growth follows the general logistic growth model equation (1):

$$(1) \qquad \frac{dB(t)}{dt} = rB(t)\left(1 - \frac{B(t)}{K}\right)$$

where (B) = turf biomass, (t) = time, (r) = maximum growth rate, and (K) = carrying capacity.
At every model iteration, fish feed across the reef randomly until their total food demand has been met for the day. If the turf biomass of a cell ($B_{x,y}$) at each time step is greater than zero ($B_{x,y} > 0$), i.e., it is not grazed (or only partially grazed) that day (t), then at the next time step (t + 1) the turf biomass of that cell ($B_{x,y}(t + 1)$) is determined using the equations (2a) and (2b):

$$(2a) \quad t_{eq} = \frac{-\log\left(-B_0\left(B_{x,y} - K\right)\right)}{r \times B_{x,y}\left(K - B_0\right)}$$

$$(2b) \qquad B_{x,y}(t + 1) = \frac{K \times B_0}{B_0 + (K - B_0)e^{(-r(t_{eq}+1))}}$$

where $t_{eq}$ is the time equivalent turf biomass on the scale of the logistic growth curve, and the modelled fixed turf growth parameter values are: initial biomass at 'time-zero' ($B_0$), maximum growth rate (r) and carrying capacity (K).

If turf biomass of a cell is equal to zero ($B_{x,y} = 0$), i.e., it is fully grazed that day (t), then at the next time step (t + 1) the turf biomass of that cell ($B_{x,y}(t + 1)$) is determined using the equation (3):

$$(3) \qquad B_{x,y}(t+1) = \frac{K \times B_0}{(B_0 + (K - B_0)e^{-r}}$$

The model output for each day/time step is the mean ($n = 50$ simulations) turf biomass (g C m$^{-2}$) remaining on the simulated reef following fish grazing and turf growth. This represents the daily predicted grazed turf biomass, which is then compared to the observed grazed turf biomass to investigate if the predicted model values are close to balancing with the observed values.

**Sensitivity analysis**

Sensitivity analyses were carried out to investigate the sensitivity of the grazing model to simulated changes in turf dynamics parameters: mean grazed turf biomass (g C cm$^{-2}$), growth rate (r), carrying capacity (K, g C cm$^{-2}$), initial biomass ($B_0$, g C cm$^{-2}$); and herbivorous fish grazing impact (bite rates and bite sizes), using the modelled mean net turf biomass after 90 d as a response variable. The sensitivity analyses calculated the absolute difference in mean net turf biomass output associated with a fixed change (± 10%) in the value of each of the input parameters individually, while the other parameters remained fixed. This highlights the influence of the respective parameters on the model performance, indicating which parameter had the largest effect on model output.

## Results and Discussion

The predicted net turf biomass after 90 d was compared to the observed grazed turf biomass of each habitat (Figs. 3 and 4). The predicted turf biomass was closely matched the observed grazed turf biomass in all habitats, except the windward-shallow habitat, which is the most productive and has the highest variability of grazing and turf dynamics (Figs. 3 and 4). The predicted turf biomass was not only within the observed turf biomass variability, but also very close to the observed mean for three of four reef slope habitats (Fig. 4). Currently, the level of grazing intensity in the windward-

shallow habitat, exceeds modelled turf growth, with the model output of estimated mean net turf biomass (0.0212 g C m$^{-2}$) approximately four-fold less than the observed average grazed turf biomass (0.0816 g C m$^{-2}$). This suggests that the balance between high grazing intensity and enhanced turf productivity is not captured by current model parameterisation, and that data at finer spatial and temporal scales are needed to better parameterise the model for this habitat to reach equilibrium.

*Ctenochaetus* species are currently functionally classified as detritivores, and were thought to not impact turfs through their grazing activity (Purcell and Bellwood 1993; Green and Bellwood 2009). However, it was assumed that *Ctenochaetus* grazing removes algal turf biomass when quantifying and incorporating grazing intensity into the model, as *Ctenochaetus* feed intensively upon the epilithic algal matrix (Polunin et al. 1995; Wilson et al. 2003), are able to remove turfs through their foraging activity (Marshell and Mumby 2012), and algal turf filaments represent ~ 20% of the organic matter in their diets (Choat et al. 2002). To investigate whether removing *Ctenochaetus striatus* and *Ctenochaetus binotatus* grazing impact influenced the model output, their bites were removed from the grazing intensity data in the leeward-shallow habitat, and the model was re-run. The leeward-shallow habitat was chosen as an example case study, as grazing intensity was highest in shallow habitats, and the variability was less in this habitat compared to the windward-shallow habitat (Chapter 4, Fig. 5a). When *Ctenochaetus* grazing impact was removed from the leeward-shallow habitat, the modelled output of turf biomass was 2.76 times greater, and went from a near-balanced system, to a system with turf biomass surplus (Fig. 5). Therefore, based on these assumptions, the model suggests that *Ctenochaetus* species are potentially important in removing and maintaining turf biomass, although this will need to be investigated further in the field.

Algal turfs are intensively grazed (Hatcher and Larkum 1983; Carpenter 1986; Russ 1987; Klumpp and Polunin 1989), and maintained in a state of low biomass, but rapid turnover (Hatcher and Larkum 1983; Carpenter 1985). However, the dynamic interaction and balance between high grazing intensity and enhanced turf productivity is a complex relationship that needs to be investigated and understood further. The disparity between the predicted vs observed turf biomass in the windward-shallow habitat highlights our current lack of understanding of the processes occurring at the early stages of turf growth in response to high grazing intensity. One reason that the model does not balance in this habitat could be because the grazer-exclusion technique used to estimate net accumulation of turf biomass actually underestimates absolute net production, due to unknown amounts of biomass lost through fragmentation and sloughing (Klumpp and McKinnon

1989). However, while the model-predicted turf biomass of the windward-shallow habitat is currently a four-fold underestimation of the mean observed turf biomass, it is still within the lower range of the observed standard deviation (Fig. 4). This is currently a limitation of the model as the simulated reef begins with a habitat-specific, fixed, mean observed grazed turf biomass value; but in reality, there is variability in the grazed turf biomass actually found within each habitat (Fig. 4). Therefore, this suggests that the collection of field data at finer temporal and spatial scales is needed to better parameterise turf growth dynamics in the highly productive and variable windward-shallow habitat, before we can fully understand the interaction and processes occurring between grazers and turf dynamics in this zone.

A major assumption of the model involved estimating the turf growth parameters during the first seven days of growth, when starting from an initial turf biomass of theoretically zero, at 'time-zero' following grazing disturbance ($B_0$; Fig. 2). Data from leeward-shallow habitat on parrotfish grazing scar recovery was used to estimate this relationship, and likely underestimates the actual levels of parrotfish grazing scar recovery and the early stages of turf growth in the more productive windward-shallow habitat, and overestimates turf growth in the less productive deeper habitats. However, data on daily turf growth rates from an initial biomass of zero are currently not available from different habitats and will need to be investigated further in future field studies. Information on turf productivity (g C cm$^{-2}$ day$^{-1}$) in the literature is usually estimated by dividing the total final ungrazed turf biomass by the number of experimental days, and provides no insight into the shape of the growth curve (logistic, linear etc.). Further field experiments are necessary to determine the actual shape of the turf growth curve in different reef slope habitats, where daily measurements are taken, instead of measurements at only one final end point.

The behaviour of the model depends on the shape of the relationship incorporated in the growth equations. The shape of the response is partly determined by the value of the 50% mid-point of turf biomass between the initial biomass ($B_0$) and carrying capacity (K). Therefore, an assumption was made when estimating the turf growth parameters by estimating the turf biomass mid-point between the early stages of turf growth and the maximum carrying capacity at 28 d. This was done by using an observed 11 d mean turf biomass from a similar study in Palau of a range of exposed and sheltered sites (unpublished, Mumby). To examine the effect that the estimated mid-point turf biomass level had on the modelled output of the turf growth parameters (initial biomass at time zero - $B_0$, maximum growth rate - r, and carrying capacity - K), a range of 11 d mid-point turf biomass levels (maximum = 0.0022, median = 0.0017, and minimum = 0.0011 g C cm$^{-2}$) were used to

determine the shape of the logistic model growth curve and corresponding model output (Fig. 6). The maximum growth rate varied greatly in response to different mid-point turf biomass levels, with the maximum 11 d midpoint corresponding to the fastest growth rate (Fig. 6a). Somewhat counterintuitively, the fastest growth rate and maximum turf biomass mid-point corresponded with the worst model output fit for windward-shallow habitat, and an overall net turf biomass 'food-debt', where the grazing intensity exceeded turf growth (Fig. 6d). The best fit model output corresponded to the lowest modelled maximum growth rate and minimum turf biomass mid-point (Fig. 6c, f). However, as the best fit modelled turf parameters for the windward-shallow habitat still produce a four-fold underestimation of the observed grazed turf biomass. The first objective of the model was to subject current understanding of the process of herbivory on turfs to a test – if the model balances then we might understand it well (although that is not a given, as it is possible to fit a model for the wrong reasons). But, perhaps more importantly, if the model does not fit then clearly there is something missing in our current understanding.

The dynamics of parrotfish grazing scar recovery was used to estimate turf growth parameters, including the initial biomass at 'time-zero' ($B_0$) following grazing (Fig. 2). The actual initial turf biomass at 'time-zero' following grazing would be virtually impossible to actually measure in the field, as it would depend on the species and size class of fish that grazed a particular area of reef substrate. For example, the diverse grazing impact of different functional groups of parrotfish (small scrapers vs. large excavators), results in different dynamics of initial grazing scar size and recovery (Bellwood and Choat 1990; Bonaldo and Bellwood 2009; Green and Bellwood 2009). This presents an interesting challenge for modelling turf growth, as in the field, some excavating parrotfish species grazing scar recovery ($cm^{-2}$) actually begins from a turf biomass of zero due to the way that these larger parrotfish scrape the substrate (for a list of species that excavate see Table 1 in Bellwood and Choat 1990). However, when modelling turf growth, it is not possible to begin from zero, due to the inherent computation of the logistic growth curve, where the initial biomass must begin at some point greater than zero. Additionally, the grazing impact of small parrotfish scrapers, rabbitfish and surgeonfish differs from the grazing impact of excavating parrotfish. Whereas excavating parrotfish remove some component of the reef substrate, leaving behind a scar and null algal biomass, the smaller scraping parrotfish, surgeonfish and rabbitfish crop turfs and leave behind holdfasts and an unknown cropped biomass of basal portions (Choat et al. 2002). This level of fine scale detail is currently not able to be incorporated into the model, but is nevertheless interesting to consider. Therefore, the actual initial turf biomass ($B_0$) of a particular reef substrate

area would be dependent on species- and size-specific grazing impact, and is virtually impossible to measure directly in the field and incorporate into the model at this stage.

Sensitivity analyses highlighted that of all of the model input parameters, a 10% increase in the maximum growth rate changed the model output the most, causing a disproportionately large increase in the modelled mean net turf biomass (g C cm$^{-2}$; Fig. 7). As expected, increasing or decreasing fish bite rates or bite sizes, had a corresponding increase or decrease in modelled turf biomass (Fig. 7). Increasing the modelled turf parameters of initial biomass at time-zero ($B_0$), and carrying capacity (K) by 10% resulted in a slight increase in net turf biomass, while decreasing the values by 10% had the opposite effect. Altering the observed mean grazed turf biomass of the simulated reef by ± 10% had the least overall impact on modelled net turf biomass (Fig. 7). Therefore, these results show that the model is currently most sensitive to increases in the maximum growth rate of turfs, suggesting that turf dynamics is most sensitive to increases in algal growth rates, which drives the system towards surplus and overestimates grazed turf biomass.

The grazing simulation model development enhances our understanding of the interactions and balance between grazing fish and turf dynamics in different exposures and depths of reef slopes. The model assumptions highlight parameters and processes that will require further investigation and better parameterisation. Once better parameterised with more comprehensive field data on algal turf parameters, the grazing simulation model will be used to explore different scenarios, such as examining the effects of overfishing (e.g., adding/removing specific grazing species or size classes) or nutrification (increasing/decreasing productivity) on overall algal turf dynamics in different habitats of the reef ecosystem. Furthermore, the grazing model is an adaptive tool that will be developed further as additional empirical data become available, facilitating investigations into the potential outcomes of different management scenarios, and adding to our understanding of complex processes that prevent or reverse coral-algal shifts following large-scale reef disturbances.

**Acknowledgements**

Table 1. The modelled algal turf: (1) initial biomass at time-zero ($B_0$), (2) maximum logistic growth rate (r), and (3) carrying capacity biomass (K); and the observed 28 d: (4) ungrazed mean final biomass (caged tiles, g cm$^{-2}$), and (5) grazed mean standing crop biomass in different habitats of Heron Reef slope. The corresponding coefficient of variation (C.V.) is shown for observed ($n$ = 18 tiles per habitat) and modelled ($n$ = 6 models) data. The C.V. of modelled data comes from the average of parameter values derived from six models run for the observed maximum and average ungrazed final biomass of each habitat, each with varying estimated 11 d algal turf biomass: maximum = 0.0022, median = 0.0017, minimum = 0.0011 (g C cm$^{-2}$) from Palau data (unpublished, Mumby). The C.V. of Leeward, Deep habitat could not be estimated due to a limited number of possible models from low observed algal turf values.

| Habitat | Modelled 'time-zero' initial biomass ($B_0$) | | Modelled maximum logistic growth rate (r) | | Modelled carrying capacity (K) | | Observed 28 d ungrazed mean final biomass (caged tiles, g C cm$^{-2}$ ± SD) | | Observed 28 d grazed mean turf biomass (open tiles, g C cm$^{-2}$ ± SD) | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Mean | C.V. | Mean | C.V. | Mean | C.V. | Mean | C.V. | Mean | C.V. |
| *Windward, Shallow* | 0.0004 | 44% | 0.1485 | 22% | 0.0025 | 69% | 0.00242 ± 0.000245 | 101% | 0.000816 ± 0.000661 | 81% |
| *Windward, Deep* | 0.0004 | 22% | 0.1777 | 33% | 0.0014 | 40% | 0.00138 ± 0.000944 | 68% | 0.000711 ± 0.000356 | 50% |
| *Leeward, Shallow* | 0.0003 | 32% | 0.2019 | 31% | 0.0015 | 61% | 0.00148 ± 0.00122 | 82% | 0.000655 ± 0.000339 | 52% |
| *Leeward, Deep* | 0.0002 | N/A | 0.3739 | N/A | 0.0007 | N/A | 0.000661 ± 0.000445 | 67% | 0.000539 ± 0.000267 | 50% |

Table 2. The algal biomass per bite (g) of turf grazing labrid fish species and size classes present in Heron grazing intensity video surveys. Algal biomass per bite (g C) is calculated by: habitat-specific (Exposure, Depth) grazed turf biomass (g cm$^{-2}$) × bite area (cm$^2$).

| Species | Size Class (TL, cm) | Bite Area (cm$^{-2}$) | Algal Biomass per bite (g C) Leeward-Deep (Grazed turf biomass: 0.000539 g C cm$^{-2}$) | Algal Biomass per bite (g C) Leeward-Shallow (Grazed turf biomass: 0.000655 g C cm$^{-2}$) | Algal Biomass per bite (g C) Windward-Deep (Grazed turf biomass: 0.000711 g C cm$^{-2}$) | Algal Biomass per bite (g C) Windward-Shallow (Grazed turf Biomass: 0.000816 g C cm$^{-2}$) | Bite Area Reference |
|---|---|---|---|---|---|---|---|
| *Scarus psittacus* + *S. chameleon* + *S. flavipectoralis* + *S. longipinnis* + *S. frenatus* + *S. spinus* + *S. globiceps* + *S. niger* + *S. schlegeli* | 8 | 0.01 | $5.39 \times 10^{-6}$ | $6.55 \times 10^{-6}$ | $7.11 \times 10^{-6}$ | $8.16 \times 10^{-6}$ | Bejarano 2009 $\sqrt{\text{BiteArea}} = -0.06 + 0.02 \times$ TL(cm)  Bellwood & Choat 1990 - Similar *Scarus* species that do not leave a significant grazing mark/scar. |
| | 11 | 0.03 | $1.38 \times 10^{-5}$ | $1.68 \times 10^{-5}$ | $1.82 \times 10^{-5}$ | $2.09 \times 10^{-5}$ | |
| | 14 | 0.05 | $2.61 \times 10^{-5}$ | $3.17 \times 10^{-5}$ | $3.44 \times 10^{-5}$ | $3.95 \times 10^{-5}$ | |
| | 17 | 0.08 | $4.23 \times 10^{-5}$ | $5.14 \times 10^{-5}$ | $5.57 \times 10^{-5}$ | $6.4 \times 10^{-5}$ | |
| | 20 | 0.12 | $6.23 \times 10^{-5}$ | $7.57 \times 10^{-5}$ | $8.22 \times 10^{-5}$ | $9.43 \times 10^{-5}$ | |
| | 23 | 0.16 | $8.62 \times 10^{-5}$ | $1.05 \times 10^{-4}$ | $1.14 \times 10^{-3}$ | $1.31 \times 10^{-4}$ | |
| | 26 | 0.21 | $1.14 \times 10^{-4}$ | $1.39 \times 10^{-4}$ | $1.5 \times 10^{-4}$ | $1.73 \times 10^{-4}$ | |
| | 29 | 0.27 | $1.46 \times 10^{-4}$ | $1.77 \times 10^{-4}$ | $1.92 \times 10^{-4}$ | $2.21 \times 10^{-4}$ | |
| *Chlorurus microrhinus* | 20 | 0.48 | $2.57 \times 10^{-4}$ | $3.12 \times 10^{-4}$ | $3.39 \times 10^{-4}$ | $3.89 \times 10^{-4}$ | Bejarano 2009 $\sqrt{\text{BiteArea}} = 0.29 + 0.02 \times$ TL(cm) |
| | 23 | 0.56 | $3.03 \times 10^{-4}$ | $3.68 \times 10^{-4}$ | $3.99 \times 10^{-4}$ | $4.59 \times 10^{-4}$ | |
| | 26 | 0.66 | $3.54 \times 10^{-4}$ | $4.3 \times 10^{-4}$ | $4.67 \times 10^{-4}$ | $5.35 \times 10^{-4}$ | |
| | 29 | 0.76 | $4.08 \times 10^{-4}$ | $4.96 \times 10^{-4}$ | $5.38 \times 10^{-4}$ | $6.18 \times 10^{-4}$ | |
| | 32 | 0.87 | $4.66 \times 10^{-4}$ | $5.67 \times 10^{-4}$ | $6.15 \times 10^{-4}$ | $7.06 \times 10^{-4}$ | |
| *Cetoscarus bicolor* | 20 | 0.29 | $1.57 \times 10^{-4}$ | $1.91 \times 10^{-4}$ | $2.07 \times 10^{-4}$ | $2.38 \times 10^{-4}$ | Bejarano 2009 $\sqrt{\text{BiteArea}} = 0.14 + 0.02 \times$ TL(cm) |
| | 23 | 0.36 | $1.94 \times 10^{-4}$ | $2.36 \times 10^{-4}$ | $2.56 \times 10^{-4}$ | $2.94 \times 10^{-4}$ | |
| | 26 | 0.44 | $2.35 \times 10^{-4}$ | $2.85 \times 10^{-4}$ | $3.1 \times 10^{-4}$ | $3.55 \times 10^{-4}$ | |
| | 29 | 0.52 | $2.79 \times 10^{-4}$ | $3.4 \times 10^{-4}$ | $3.69 \times 10^{-4}$ | $4.23 \times 10^{-4}$ | |

| Species | TL (cm) | col3 | col4 | col5 | col6 | col7 | Reference |
|---|---|---|---|---|---|---|---|
| *Scarus rivulatus* | 8 | 0.05 | $2.7 \times 10^{-5}$ | $3.28 \times 10^{-5}$ | $3.56 \times 10^{-5}$ | $4.08 \times 10^{-5}$ | Bonaldo & Bellwood 2008 (Bite Area from Fig. 3) |
| | 11 | 0.09 | $4.85 \times 10^{-5}$ | $5.9 \times 10^{-5}$ | $6.4 \times 10^{-5}$ | $7.34 \times 10^{-5}$ | |
| | 14 | 0.2 | $1.08 \times 10^{-4}$ | $1.31 \times 10^{-4}$ | $1.42 \times 10^{-4}$ | $1.63 \times 10^{-4}$ | |
| | 17 | 0.35 | $1.89 \times 10^{-4}$ | $2.29 \times 10^{-4}$ | $2.49 \times 10^{-4}$ | $2.86 \times 10^{-4}$ | |
| | 20 | 0.4 | $2.16 \times 10^{-4}$ | $2.62 \times 10^{-4}$ | $2.84 \times 10^{-4}$ | $3.26 \times 10^{-4}$ | |
| | 23 | 0.45 | $2.43 \times 10^{-4}$ | $2.95 \times 10^{-4}$ | $3.2 \times 10^{-4}$ | $3.67 \times 10^{-4}$ | |
| | 26 | 0.55 | $2.97 \times 10^{-4}$ | $3.6 \times 10^{-4}$ | $3.91 \times 10^{-4}$ | $4.49 \times 10^{-4}$ | |
| | 29 | 0.75 | $4.04 \times 10^{-4}$ | $4.91 \times 10^{-4}$ | $5.33 \times 10^{-4}$ | $6.12 \times 10^{-4}$ | |
| *Chlorurus sordidus (spirulus)* | 8 | 0.004 | $2.16 \times 10^{-7}$ | $2.62 \times 10^{-7}$ | $2.84 \times 10^{-7}$ | $3.26 \times 10^{-7}$ | Bejarano 2009 $\sqrt{BiteArea} = -0.34 + 0.04 \times$ TL(cm) |
| | 11 | 0.01 | $5.39 \times 10^{-6}$ | $6.55 \times 10^{-6}$ | $7.11 \times 10^{-6}$ | $8.16 \times 10^{-6}$ | |
| | 14 | 0.05 | $2.61 \times 10^{-5}$ | $3.17 \times 10^{-5}$ | $3.44 \times 10^{-5}$ | $3.95 \times 10^{-5}$ | |
| | 17 | 0.12 | $6.23 \times 10^{-5}$ | $7.57 \times 10^{-5}$ | $8.21 \times 10^{-5}$ | $9.43 \times 10^{-5}$ | |
| | 20 | 0.21 | $1.14 \times 10^{-4}$ | $1.39 \times 10^{-4}$ | $1.5 \times 10^{-4}$ | $1.73 \times 10^{-4}$ | |
| | 23 | 0.34 | $1.81 \times 10^{-4}$ | $2.2 \times 10^{-4}$ | $2.39 \times 10^{-4}$ | $2.75 \times 10^{-4}$ | |
| | 26 | 0.49 | $2.64 \times 10^{-4}$ | $3.21 \times 10^{-4}$ | $3.48 \times 10^{-4}$ | $3.99 \times 10^{-4}$ | |

Table 3. The estimated algal turf biomass taken per bite (g C), by size classes (mid-point) of herbivorous acanthurid and siganid species present in Heron grazing intensity video surveys. Fish biomass is determined from length-weight parameters (Kulbicki 2005).

| Species | Size Class (cm) | Algal turf (C) biomass per bite (g) | Fish Wet (W) biomass (g) | Reference |
|---|---|---|---|---|
| *Acanthurus nigrofuscus* | 14 | $9.5 \times 10^{-5}$ | 77.9 | VanRooij et al 1998 |
| | 17 | $1.53 \times 10^{-4}$ | 140.4 | C intake $(\text{day}^{-1}) = 0.0342 \times W^{0.816}$ |
| | 20 | $2.29 \times 10^{-4}$ | 229.7 | |
| *Acanthurus blochii* | 14 | $9.19 \times 10^{-5}$ | 74.94 | VanRooij et al 1998 |
| | 17 | $1.49 \times 10^{-4}$ | 135.02 | C intake $(\text{day}^{-1}) = 0.0342 \times W^{0.816}$ |
| | 20 | $2.22 \times 10^{-4}$ | 221 | |
| | 23 | $3.14 \times 10^{-4}$ | 337.62 | |
| | 26 | $4.25 \times 10^{-4}$ | 489.64 | |
| | 29 | $5.57 \times 10^{-4}$ | 681.81 | |
| *Ctenochaetus striatus* | 11 | $5.62 \times 10^{-5}$ | 35.8 | VanRooij et al 1998 |
| | 14 | $1.03 \times 10^{-4}$ | 74.9 | C intake $(\text{day}^{-1}) = 0.0342 \times W^{0.816}$ |
| | 17 | $1.69 \times 10^{-4}$ | 135.9 | |
| | 20 | $2.5 \times 10^{-4}$ | 223.5 | |
| *Ctenochaetus binotatus* | 8 | $2.63 \times 10^{-5}$ | 15.5 | VanRooij et al 1998 |
| | 11 | $5.54 \times 10^{-5}$ | 38.7 | C intake $(\text{day}^{-1}) = 0.0342 \times W^{0.816}$ |
| | 14 | $9.76 \times 10^{-5}$ | 77.3 | |
| | 17 | $1.54 \times 10^{-4}$ | 135.1 | |
| *Zebrasoma scopas* | 11 | $6.32 \times 10^{-5}$ | 38.1 | VanRooij et al 1998 |
| | 14 | $1.14 \times 10^{-4}$ | 78.4 | C intake $(\text{day}^{-1}) = 0.0342 \times W^{0.816}$ |
| | 17 | $1.83 \times 10^{-4}$ | 140.2 | |
| *Zebrasoma veliferum* | 17 | $1.56 \times 10^{-4}$ | 115.2 | VanRooij et al 1998 |
| | 20 | $2.28 \times 10^{-4}$ | 183.6 | C intake $(\text{day}^{-1}) = 0.0342 \times W^{0.816}$ |
| *Siganus doliatus* | 17 | $1.56 \times 10^{-4}$ | 93.9 | VanRooij et al 1998 |
| | 20 | $2.34 \times 10^{-4}$ | 154.6 | C intake $(\text{day}^{-1}) = 0.0342 \times W^{0.816}$ |
| | 23 | $3.32 \times 10^{-4}$ | 237.2 | |
| *Siganus punctatus* | 17 | $1.5 \times 10^{-4}$ | 89.9 | VanRooij et al 1998 |
| | 20 | $2.24 \times 10^{-4}$ | 146.6 | C intake $(\text{day}^{-1}) = 0.0342 \times W^{0.816}$ |
| | 23 | $3.16 \times 10^{-4}$ | 223.2 | |
| | 26 | $4.26 \times 10^{-4}$ | 322.6 | |
| | 29 | $5.57 \times 10^{-4}$ | 447.9 | |
| *Siganus corallinus* | 14 | $1.02 \times 10^{-4}$ | 55.7 | VanRooij et al 1998 |
| | 17 | $1.59 \times 10^{-4}$ | 96.3 | C intake $(\text{day}^{-1}) = 0.0342 \times W^{0.816}$ |
| | 20 | $2.31 \times 10^{-4}$ | 152.1 | |
| | 23 | $3.18 \times 10^{-4}$ | 225.5 | |
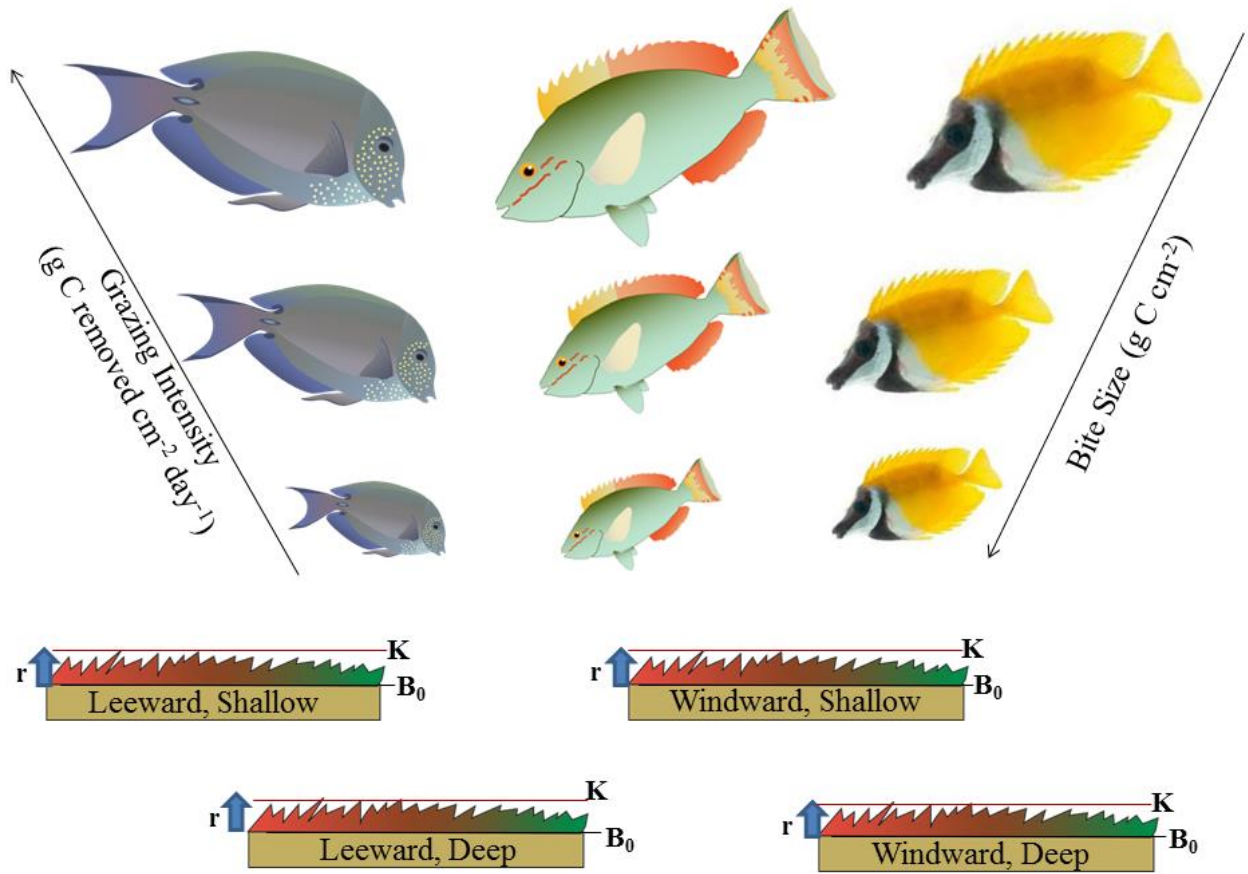
Figure 1. A representation of the model implementation, which includes four habitats of different exposures and depths on Heron reef slope. Each simulation models 100 x 100 cm cells to represent a planar 1 m$^2$ reef area of 100% grazeable substrate. Each modelled reef cell (1 x 1 cm) begins with a habitat-specific, observed mean grazed turf biomass (g C cm$^{-2}$), with 50 model simulations run per time step (day). Each simulation uses a modelled initial biomass at time-zero (B$_0$) growth rate (r), and carrying capacity (K) based on field data observations from each habitat. Algal turf grazing fish (surgeonfish, parrotfish and rabbitfish) bite rates (grazing intensity) are habitat-, species- and size-class-specific taken from a random distribution for each simulation (mean ± S.D., removed g C cm$^{-2}$ day$^{-1}$), and multiplied by the corresponding fixed habitat-, species- and size-class-specific bite sizes (g C cm$^{-2}$).

Figure 2. The modelled logistic growth curve (black line) and data points (blue squares) used to model the growth curve for the: a) windward, shallow, b) windward, deep, c) leeward, shallow, and d) leeward, deep habitats, with an estimated initial biomass at time-zero ($B_0$; g C cm$^{-2}$) maximum growth rate (r), and carrying capacity (K; g C cm$^{-2}$), based on field data observations from each habitat.

Figure 3. The mean net algal turf biomass (g C cm$^{-2}$ day$^{-1}$ ± 95% C.I.) modelled per time step (day) of 50 simulations for each habitat: a) Windward, Shallow, b) Windward, Deep, c) Leeward, Shallow, and d) Leeward, Deep. The dashed green line shows the average observed grazed turf biomass in each habitat (g C cm$^{-2}$).

Figure 4. The overall mean net algal turf biomass (g C cm$^{-2}$ ± S.D.; black circles, left y-axis) modelled after 90 d of 50 simulations per day, and the mean initial algal turf biomass (g C cm$^{-2}$ ± S.D.; grey triangles, right y-axis) for each habitat: windward – shallow and deep (left); and leeward - shallow and deep (right).

## a) Leeward, Shallow
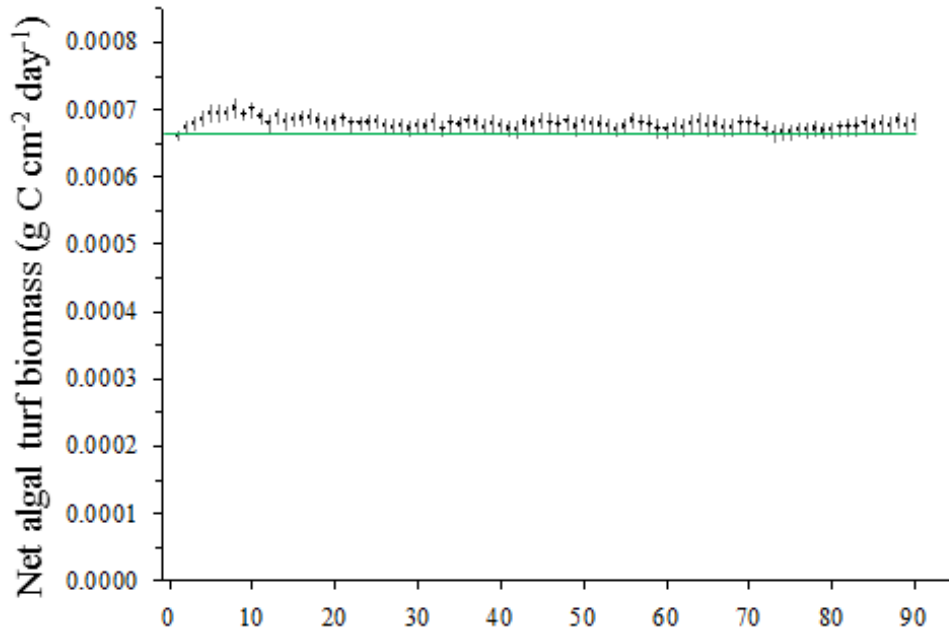


## b) Leeward, Shallow (No *Ctenochaetus*)



Time Steps

Figure 5. The net algal turf biomass (g C cm$^{-2}$ day$^{-1}$) model output for leeward-shallow habitat when *Ctenochaetus striatus* and *Ctenochaetus binotatus* grazing impact is (a) included or (b) removed from the grazing intensity data.

Figure 6. A comparison of different modelled logistic growth curves, using the fixed observed average final biomass of Heron reef slope windward-shallow habitat caged tiles after 28-d, and assuming an estimated mid-point from 11 d Palau field data (unpublished, Mumby) of either: a) maximum = 0.0022, b) median = 0.0017, and c) minimum = 0.0011 (g C cm$^{-2}$). Figures d, e, and f show the corresponding model output using each combination of the different model parameters in a–c. Note that Figure 6d scale begins at -0.0001, and the negative model output values represent the average daily 'food-debt' of grazing fish.

Figure 7. The sensitivity of the grazing model to simulated changes in algal turf dynamics parameters: mean grazed turf biomass (g C cm$^{-2}$), growth rate (r), carrying capacity (K, g C cm$^{-2}$), initial biomass (B$_0$, g C cm$^{-2}$); and herbivorous fish grazing impact (bite rates and bite sizes). The x-axis shows the absolute change in net turf biomass output, brought about by a ± 10% change in the selected model parameter (y-axis). The observed variability (coefficient of variation) of each parameter is given in Table 1.

# Chapter 6. General Discussion

Understanding the functional role of species that support key ecosystem processes is central to our understanding of the structure and functioning of ecological systems. Herbivory is a critical ecological process on coral reefs that maintains the balance between corals and algae, and prevents ecosystem degradation due to shifts from coral- to algal-dominance. Acanthurids (surgeonfish) occupy a wide range of coral reef habitats and are dominant herbivores of most Indo-Pacific reef fish communities that are likely to fulfil critical ecological roles. However, there has been a paucity of quantitative information on the feeding ecology and functional role of acanthurids, especially in the Indo-Pacific region. Collectively, this thesis adds to our understanding of the grazing impact of common herbivorous surgeonfish in different habitats of coral reefs, by quantifying their grazing impact on both algal turf and macroalgal dynamics. The studies in this thesis were conducted at Heron Island, in the southern Great Barrier Reef (23°26' S), and therefore the results of these studies may, or may not be typical on reefs at lower latitudes. However, the species studied are very common and have broad distributions throughout the Indo-Pacific and there is no evidence that their diet or feeding behaviour would change substantially with latitude.

## The ecological role of common grazing surgeonfish

The most abundant and common surgeonfish species on Indo-Pacific coral reefs are *Ctenochaetus striatus* and *Acanthurus nigrofuscus* (Russ 1984; Choat and Bellwood 1985; Trip et al. 2008; Cheal et al. 2012). Both species removed significant numbers of macroalgal recruits through their grazing activity (Chapter 2), indicating that they play an important role in preventing the emergence of macroalgae from developmental stages settled within the algal turf matrix. These common surgeonfish species preferred grazing on sparse rather than dense algal turfs, and the amount of algal turfs they remove per bite was quantified, which assists in assessing their role in controlling turf biomass (Chapter 3). Additionally, *Acanthurus* and *Ctenochaetus* species dominated the herbivore community biomass of shallow reef slope sites and removed significant amounts of the total daily turf productivity in different reef slope habitats, with their largest impact (removal of 73% of the daily productivity) in the highly productive windward-shallow reef slope habitat (Chapter 4). Furthermore, removing *Ctenochaetus* species from the grazing fish community resulted in a ~ 30% increase of predicted turf biomass in a simulated grazing model system, suggesting that these species do potentially play a role in maintaining turf biomass (Chapter 5). Overall, this thesis

quantifies and highlights the critical ecological role that surgeonfish species fulfil through their daily grazing activity, which significantly impacts algal turf and macroalgal dynamics.

**The ecological role of *Ctenochaetus striatus***

The role of *Ctenochaetus striatus* in sediment dynamics on coral reefs has been well established (e.g., Nelson and Wilkins 1988; Fouda and El-Sayed 1994; Schuhmacher et al. 2008; Goatley and Bellwood 2010; Krone et al. 2011). *Ctenochaetus* species are considered exclusively detritivorous, and were thought to cause little damage to algal turfs through their grazing activity (Purcell and Bellwood 1993). Therefore, it is currently recommended that this genus is excluded from resilience monitoring, as they are thought to not limit the establishment and growth of algal communities (Green and Bellwood 2009). However, this thesis demonstrates that *C. striatus* have the ability to remove algal turfs and macroalgal recruits settled within algal turfs through their grazing activity in lab experiments (Chapters 2 and 3). As *Ctenochaetus* species are one of the most abundant fishes on Indo-Pacific reefs and have one of the highest maximum bite rates of grazing fishes (Polunin et al. 1995; Wilson et al. 2003), their potential ability to remove algal turfs and macroalgal recruits has important implications for their functional role in possibly influencing reef algal dynamics (Chapter 5). The next step for future research is to quantify the grazing impact of *Ctenochaetus* species on algal turf biomass and macroalgal recruits in the field to resolve their role in algal dynamics on reefs, and then perhaps to formally reassess their classification as strict detritivores excluded from resilience monitoring. Latest assessments of herbivorous fishes have included *Ctenochaetus* species as grazer/detritivores (Cheal et al. 2012; Edwards et al. 2014), and it has recently been recommended that the genus *Ctenochaetus* should be dissolved into the genus *Acanthurus* based on molecular analyses and in conjunction with a large body of morphological evidence (Sorenson et al. 2013). Although *Ctenochaetus* are not targeted in fisheries on the Great Barrier Reef where this thesis was conducted, they are caught in some Pacific Island fisheries (e.g., Ochavillo et al. 2010). Therefore, it is important to resolve the potential functional role of *Ctenochaetus* species in algal dynamics on reefs. Protecting key species with critical functional roles could possibly prevent coral-algal shifts in some disturbed coral reef areas, and may prove vital to reducing algal overgrowth and ecosystem degradation through algal blooms (Green and Bellwood 2009).

**Challenges in estimating the bite size of grazing surgeonfish and rabbitfish**

Herbivorous fishes are diverse and comprised of several functional groups that differ in how they feed, what they consume and their impact on the substrate (Green and Bellwood 2009). Most parrotfishes (*Scarus* and *Hipposcarus* species) are scrapers, feeding on epilithic algal turfs by scraping the reef surface, leaving behind a shallow grazing scar. This is in contrast to excavating parrotfish species (all *Chlorurus* species*, Cetoscarus bicolor, Bolbometopon muricatum*) which leave deeper grazing scars and remove significant quantities of substrate with each bite (Green and Bellwood 2009). Because parrotfish leave behind a grazing scar, it is relatively straightforward to calculate their bite area and grazing impact on the substrate (e.g., Bruggemann 1995; Bonaldo and Bellwood 2008).

For surgeonfish and rabbitfish, the task of calculating their bite size is much more complex. In contrast to parrotfishes, grazers/detritivores that intensely graze epilithic algal turfs (most rabbitfishes, and surgeonfishes species from the genera: *Acanthurus, Ctenochaetus* and *Zebrasoma*) do not scrape or excavate the substrate as they feed (Green and Bellwood 2009). Therefore, it is not possible to calculate a size-specific bite area, as there are generally no grazing scars left by these species. Consequently, in Chapters 4 and 5, a general relationship between algal carbon (organic biomass) intake and fish body mass for herbivorous fish consumption was used to calculate species- and size-specific bite sizes of relevant rabbitfish and surgeonfish species from the genera *Acanthurus, Ctenochaetus* and *Zebrasoma* (Bruggemann 1995; Van Rooij et al. 1998). This general relationship was determined by fitting a highly correlated regression ($r^2 = 94.6\%$) to quantitative estimates of daily food intake by a range ($n = 13$) of herbivorous reef fishes (parrotfish, surgeonfish, damselfish) available in the literature from a wide variety of locations, such as the Caribbean, Red Sea, Great Barrier Reef, and Papua New Guinea (Van Rooij et al. 1998).

An alternative method used to estimate the bite sizes of some of these species has been conducted by dividing the mean gut contents mass at the point of fullness by the mean number of bites taken up to that point (e.g., Polunin et al. 1995; Ferreira et al. 1998; Townsend and Tibbetts 2004; Fox et al. 2009). However, when using data from these studies to calculate species- and size-specific bite sizes of surgeonfish and rabbitfish, generally the estimates notably differed to the estimates from the general relationship of Van Rooij et al. (1998). This discrepancy is likely due to large variability between the different methods used to estimate bite sizes of different species across the literature. However, it was considered that using the general relationship between algal intake and fish body

mass was the most suitable standardised method for estimating the species- and size-specific bite sizes of surgeonfish and rabbitfish. Another reason for the discrepancy between methods for estimating bite size could be due to the wide-range of assumptions used when using the general relationship. For example, there are large differences in parameters used to calculate fish species length-weight relationships from different regions (Froese and Pauly 2014). For this reason, parameters from the general approach to length-weight relationships of Kulbicki et al. (2005) were used consistently where possible throughout the thesis to calculate the size class biomass of species, for use in the general relationship (daily C intake $= 0{\cdot}0342 \times W^{0{\cdot}816}$; wet body mass $W$ in g). However, these parameters are specific to New Caledonia and could be a potential source of error that causes differences in the bite size estimates. Another source of error could be due to the estimation of total number of bites taken per day by fish species. In actual fact, the daily number of bites of an individual fish would vary between locations, seasons, fish size, and has an error associated with it. But to be able to calculate the biomass of algal carbon (C) per bite the relationship estimate (daily C intake $= 0{\cdot}0342 \times W^{0{\cdot}816}$) had to be divided by the 'average' number of bites taken by that particular species. This was sourced from Heron Island data collected during the same study where possible or the literature if bite rates for a particular species were not available from Heron Island. Obviously, this is a large assumption that could potentially be a source of error in the bite size estimates. Although using the general relationship from Van Rooij et al (1998) involved numerous assumptions and sources of potential error, it was still deemed the most appropriate method to achieve the studies objectives and provided a standardised way to estimate size- and species-specific rabbitfish and surgeonfish bite sizes.

Comparing these different methods of estimating bite size for surgeonfish and rabbitfish was an interesting exercise that highlighted the difficulties in accurately calculating the bite sizes of these families, and extrapolating these estimates to predict ecosystem function. Thus, the method chosen to estimate bite size can vastly influence the predicted ecosystem function of a species. Future research would ideally quantify habitat-, species- and size-specific amounts of algal turfs removed per bite by grazing surgeonfish and rabbitfish using comparable methods. Although, this would be a vast undertaking and is likely to only be possible for a selected suite of key species with critical functional roles that are intensively studied.

**Herbivory and algal dynamics**

This thesis has quantified the ecological role of algal turf grazing fish in maintaining algal turf biomass and preventing the emergence of macroalgal recruits in different coral reef habitats. The objective of the grazing simulation model (Chapter 5) was to combine collected field data to build a model system that subjects our current understanding of the process of herbivory on algal turfs to a test – if the model balanced (i.e., in three of four reef slope habitats tested), then we can assume that we understand it well in these habitats. However, the model did not balance in the most productive and variable windward-shallow reef slope habitat, which suggests that there is something missing in our understanding of the dynamics and processes controlling algal turf biomass in this habitat. Therefore, the model summarises and enhances our understanding of the processes involved in the interactions between grazing fish and algal turf dynamics, and parameterisation of the turf dynamics of the model highlighted that there was a lack of data on algal turf growth dynamics at fine spatial and temporal scales in different reef habitats. There are also the challenges of estimating the species- and size-specific bite sizes of herbivorous fishes, as discussed previously. Although, when testing the model sensitivity to parameter changes, a slight change (± 10%) in bite size did not influence the model output significantly. Future research will focus on developing the grazing simulation model to be able to determine what the critical level of herbivore grazing is that causes a shift towards detrimental amounts of algal turf biomass as a function of both grazing intensity and productivity. Once the model is refined further, it will then be used as a tool to explore different management scenarios and ideally incorporated it into larger food web models (e.g., Rogers et al. 2014).

**Seasonality of herbivory and algal dynamics**

Annual, predictable patterns of seasonal variations in environmental conditions may cause temporary shifts in coral reef benthic community structure (Schaffelke and Klumpp 1997). For example, algal distributions often exhibit seasonal fluctuations, with seasonal development driven by temperature, which affects algal growth, reproduction and survival (Ateweberhan et al. 2005, 2006; Ferrari et al. 2012). In the southern Red Sea, there are strong seasonal shifts in the relative biomass of canopy, foliose, turf and crustose algae. The shallow reef flat algal turf biomass increases with seawater temperature, whereas canopy, foliose and crustose algal biomass decreases in the warmer months (Ateweberhan et al. 2005, 2006).

Herbivores respond significantly in numerous ways to seasonal changes in algal biomass. The abundance of herbivorous fishes can vary seasonally, and generally peaks in summer months (e.g., Carpenter 1986). In areas with extreme seasonal variations in water temperature, the distinct community structure of herbivore distribution among reef zones is lost in summer as species move to exploit changes in algal biomass (Afeworki et al. 2013a). Furthermore, overall decreases in herbivory on macroalgae in winter have been observed, due to seasonal variation in the condition of macroalgae (Lefevre and Bellwood 2010). Corresponding to the decrease in algal condition and availability, resource use and feeding preferences of herbivores also vary seasonally in shallow reef zones, although not in deeper areas of the fore reef, and some species are likely to be energetically limited in winter (Afeworki et al. 2011). Bite rates have also been shown to increase in summer for small (< 25 cm) herbivorous fish, although, the yield per bite does not differ seasonally (Afeworki et al. 2013b). Therefore, seasonality greatly influences algal turf dynamics and herbivory on coral reefs that experience significant seawater temperature changes throughout the year. However, due to logistical constraints, the data on grazing intensity and algal turf dynamics in Chapter 4 are limited to the austral summer months, and further long-term research is needed in order to be able to examine seasonal patterns of Heron Island Reef and incorporate seasonal fluctuations of both grazing intensity and algal turf dynamics into the grazing simulation model. Nevertheless, grazing intensity and productivity generally peak in the summer months (Klumpp and McKinnon 1989; Polunin and Klumpp 1992; Afeworki et al. 2011), and therefore, the results of this study (Chapter 4) are likely to represent the maximum values for Heron Reef.

**Conclusions**

Coral reef health is declining rapidly worldwide due to unprecedented and increasing local (overfishing, pollution, disease, crown of thorns starfish) and global (bleaching, storms) disturbances (Hughes et al. 2007). In coral reef ecosystems, fast-growing algae compete with corals for space by smothering adult coral and preventing juvenile replenishment (McCook et al. 2001; Birrell et al. 2005; Arnold et al. 2010). Herbivorous fishes remove algae through their grazing activity, and therefore play an important role in reducing algal biomass and facilitating coral recovery following disturbance. However, overfishing has caused major declines of herbivorous fish populations on many reefs worldwide, contributing to algal blooms and shifts from coral to algal dominated reefs (Mumby et al. 2006).

Herbivory is widely acknowledged as a key ecological process that structures benthic communities, and is important for coral reef resilience (Obura and Grimsdith 2009). Therefore, herbivore abundance is considered an important resilience indicator, with large numbers of herbivores indicative of a resilient reef (Maynard et al. 2010). Consequently, effective management of herbivore fisheries is a critical part of maintaining coral reef resilience and local ecosystem conservation in some reef systems, and should be a high priority for reef managers in these areas. Yet, determining ecologically-sustainable levels of herbivore harvest remains elusive (Mumby 2014). Throughout the Indo-Pacific, one of the many challenges of fisheries management is the lack of reliable data that is essential for the evaluation of exploitation status and policy implementation. Other challenges include the lack of political-will, effective enforcement and management capacity. Consequently, reef fisheries catches remain mostly unrestrained by catch-control policies, and there is a current increasing and worrying unregulated shift to open access resource exploitation and commercialization (Houk et al. 2012).

Acanthurids are often the main components of Indo-Pacific artisanal and commercial fisheries catches (Gillett and Moy 2006; Rhodes et al. 2008; Ochavillo et al. 2010; Houk et al. 2012; Bejarano et al. 2013; Lindfield et al. 2014), and are also heavily targeted in the aquarium trade (Williams et al. 2009). However, acanthurids are rarely protected by species-specific fisheries policies and targeted fisheries management strategies are urgently required in some regions (Rhodes et al. 2008; Ochavillo et al. 2010; Houk et al. 2012; Bejarano et al. 2013). The important ecological role of parrotfish on coral reefs has been well established (e.g., Bellwood and Choat 1990; Bruggemann 1995; Bonaldo 2010), and has led to effective protection measures such as complete parrotfish fisheries bans in the Caribbean (e.g., Belize and Turks and Caicos Islands) in order to protect their ecosystem functional role. The overall aim of this thesis was to quantify the potential ecological impact of grazing surgeonfish, in order to improve our knowledge of the critical role of surgeonfishes in controlling algal dynamics and highlight their functional role in coral reef ecosystems. It is hoped that the information in this thesis will encourage the development of effective acanthurid species-specific fisheries management plans that enhance reef resilience and ecosystem conservation in areas of the Indo-Pacific region where they are heavily targeted.

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