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The role of herbivores as ecosystem engineers in Great Barrier Reef seagrass meadows

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The role of herbivores as ecosystem engineers in Great Barrier Reef seagrass meadows

Thesis submitted by

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This thesis is dedicated to my Gran, who always believed in my Australian PhD dream, but never saw it come true.

Abstract

The Great Barrier Reef (GBR) contains extensive, diverse seagrass meadows that are an important food source for a range of herbivores. These herbivores can act as ecosystem engineers and cause structural changes in the seagrass meadows where they graze. Such structural modifications to seagrasses can also alter the other important ecosystem functions and services that the meadows provide. Although we know there are large populations of herbivores in the GBR, and particularly megaherbivores who can have the biggest impact on meadow structure, there is limited research into how herbivory can act to modify seagrass meadows in the GBR. Understanding how the top-down pressure of herbivory modifies GBR seagrasses is essential to inform management measures that rely on aboveground seagrass properties to assess meadow health.

I advance this area of research by investigating the impact of herbivory in GBR seagrass meadows using exclusion treatments to understand the role of each herbivore group, megaherbivores (turtles and dugongs), macroherbivores (fish and urchins) and mesoherbivores (amphipods and isopods), individually and interactively in structuring GBR seagrasses. I also investigate how the structuring impact of herbivory varies over space and time. My studies then focussed on the largest and most significant herbivore group – the megaherbivores, and I also used seagrass tethering to quantify rates of herbivory by fish and urchins in seagrass meadows. My studies focussed on two locations in the GBR; a multi-species assemblage in a marine national park around Green Island in the northern GBR, and a coastal estuarine region around Gladstone in the southern GBR with large areas of intertidal seagrass meadows.

I found that megaherbivore grazing can significantly reduce aboveground seagrass biomass and shoot heights in GBR seagrass meadows, although megaherbivore feeding differed between the meadows that I studied, which changed the scale of the impact. At Green Island I observed the formation of grazing plots for the first time in the GBR, where green turtles reduced aboveground biomass and shoot heights by forming distinct grazing plots within the meadow. I also observed green turtles feeding on seagrass rhizomes and roots, which caused reductions in belowground biomass. This feeding behaviour may have been motivated by dietary requirements of the green turtles, which targeted leaf tissue nutrients or the higher carbohydrate content belowground material, and was the first time this behaviour had been recorded in the GBR and only the second time documented globally.

In Gladstone, megaherbivores had an overwhelming impact on meadow structure compared to macro- and mesoherbivores. Here they grazed broadly across the whole meadow, causing large-scale reductions in aboveground biomass and shoot height. Excluding other herbivore groups did not result in further structural changes to the meadow or the epiphyte load, and they did not interact with megaherbivores to produce overall structuring impacts. Megaherbivore exclusion experiments in multiple meadows in the Gladstone region showed that the structuring impact of megaherbivory varied between different meadows and over time.

Herbivory by fish and urchins also varied over space and time. Rates of macroherbivory at Green Island were low compared to other tropical locations and for most of the year macroherbivores consumed a small percentage of seagrass productivity, however this varied between meadows and throughout the year. The observed low levels of macroherbivory may be due to the area at Green Island being afforded the highest level of marine spatial protection, where both the herbivores themselves and their predators are protected. This dynamic may maintain a relatively intact food chain and prevent large increases in macroherbivore populations that can cause overgrazing events.

I developed a conceptual model which predicts how changes in seagrass meadow structure caused by herbivory would modify the ecosystem services delivered by a seagrass meadow. This model is a continuum with a seagrass dominated system at one end, where grazing is limited and a high biomass meadow is present, and a herbivore dominated system at the other end where grazing reduces seagrass meadow structure. I predict that the greatest range of ecosystem services would be delivered in the middle of this continuum in a balanced system. My research shows that the sites I studied differ in their position on this continuum: Green Island represents a balanced system where a moderate level of grazing takes place but seagrass biomass remains high and provides a range of ecosystem services. Gladstone represents a herbivore dominated system where high levels of grazing, particularly by megaherbivores, maintains the seagrass meadows here in a lower biomass state.

My research shows that megaherbivores can act as ecosystem engineers in GBR seagrass meadows and can cause significant reductions in shoot heights and losses in aboveground biomass. However, these impacts are not constant between meadows or over time. These changes in meadow structure caused by herbivory will change the ecosystem services provided by the meadow, and a more valuable feeding ground would result in trade-offs with the delivery of other ecosystem services. Seagrass management and monitoring programs in

the GBR currently do not include an assessment of grazing pressure, however an understanding of the impact of herbivory would help to give an overall picture of meadow health. My research shows that seagrasses should ideally be managed as a coupled plant-herbivore system in the GBR to achieve the best outcomes for seagrasses, the herbivores that rely on them, and to maintain the delivery of seagrass ecosystem services.

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Publications produced during my candidature

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Scott, A. L., York, P. H., Duncan, C., Macreadie, P. I., Connolly, R. M., Ellis, M. T., Jarvis, J. C., Jinks, K. I., Marsh, H. and Rasheed, M. A. 2018. The role of herbivory in structuring tropical seagrass ecosystem service delivery. *Frontiers in Plant Sciences.* 9, 1–10. https://doi.org/10.3389/fpls.2018.00127. (Chapter 2)

Scott, A. L., York, P. H. and Rasheed, M. A. 2021a. Herbivory has a major influence on structure and condition of a Great Barrier Reef subtropical seagrass meadow. *Estuaries and Coasts*. 44, 506 – 521. https://doi.org/10.1007/s12237-020-00868-0. (Chapter 3)

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Scott, A. L., York, P. H. and Rasheed, M. A. 2018. Keep off the grass: Using herbivore exclusion cages to understand herbivory in seagrass meadows. World Seagrass Conference, Singapore.

Scott, A. L., York, P. H. and Rasheed, M. A. 2018. Keep off the grass: Using herbivore exclusion cages to understand herbivore feeding on GBR seagrass meadows. Australian Turtle Symposium, Bundaberg

Scott, A. L., York, P. H. and Rasheed, M. A. 2019. Exclusion studies reveal the interactions between herbivores in structuring seagrass meadows their ecosystem services and the implications for effective management. Australian Marine Sciences Association Conference, Perth, Australia

Scott, A. L., York, P. H. and Rasheed, M. A. 2019. Exclusion studies reveal the interactions between herbivores in structuring seagrass meadows. Coastal and Estuarine Research Federation Conference, Mobile, Alabama

Chapter 1

General introduction

The Great Barrier Reef (GBR) contains extensive and diverse seagrass meadows that are grazed by a range of herbivore groups, from small invertebrates, to large marine reptiles and mammals. Despite the diversity of both grazer and seagrass populations, the role of herbivores in structuring seagrass meadows in the GBR is not well understood. This chapter summarises the current understanding of plant-herbivore interactions in seagrass meadows and identifies the knowledge gaps which my research will address. This chapter leads into a more detailed review of the impact of herbivory on seagrass ecosystems in Chapter 2. I also outline the objectives and chapters that make up the thesis.

Introduction

Herbivores can act as ecosystem engineers, modifying the habitats that they graze on as they feed (Bakker *et al.*, 2016a: Jones *et al.*, 1994). The structuring impacts of herbivory and plant responses to grazing pressure create complex plant-herbivore interactions in grazing ecosystems. In terrestrial grasslands, the plant-herbivore interactions taking place are well established (McNaughton, 1984, 1990). Grasslands have coevolved with herbivores and both grazers and grasslands have adaptations to each other (McNaughton *et al.*, 1989). For example, herbivores feed to maximise their intake of energy or nutrients (e.g. McNaughton, 1984, 1990). In these terrestrial grazing systems, herbivores can export significant amounts of plant biomass and their grazing can control primary productivity, species diversity and nutritional content of the ecosystems where they graze (Asner *et al.*, 2009; Díaz *et al.*, 2007b).

These complex plant-herbivore interactions also operate in marine ecosystems. Similar to terrestrial grasslands, seagrasses are flowering plants living in the shallow (<100m) marine environment that can form extensive, diverse meadows across the globe (Short *et al.*, 2007). These meadows are important for marine organisms. By providing a structured, complex habitat where a diverse range of animals live, breed and hunt, seagrasses act as biodiversity hotspots (Heck *et al.*, 2003; Hughes *et al.*, 2009). Seagrass meadows also benefit people by providing ecosystem services such as fisheries habitat provision, coastal protection and cultural values (Nordlund *et al.*, 2016). One of the most important ecosystem services provided by seagrasses is the provision of food for herbivores (Nordlund *et al.*, 2016). Like their terrestrial counterparts, seagrasses are grazed by a diverse group of herbivores that act to structure meadows and modify the other ecosystem services they provide (see Chapter 2 – Scott *et al.*, 2018). However, the complex plant-herbivore interactions that act to modify seagrass meadows and their ecosystem services are not well understood in many seagrass meadows (Heck and Valentine, 2006; Valentine and Heck, 2020).

Our understanding of the fundamental role of seagrasses as a food source for herbivores is relatively recent. The presence of extensive, lush meadows that appeared undisturbed by grazing, and the apparent poor nutritional value of seagrass material, suggested that seagrasses were not extensively grazed (e.g. Bjorndal, 1980; Thayer *et al.*, 1984). However, we now know that the top-down pressure of herbivory, and the trophic cascades it causes, can be equally or more important in determining seagrass meadow structure and function than

bottom-up drivers (Heck and Valentine, 2007). The role of herbivory in structuring seagrass meadows has been demonstrated for meadows worldwide and all grazer groups can play a role in structuring meadows, particularly for seagrasses in the tropics and subtropics (Valentine and Heck, 1999, 2020). While these structuring impacts can be significant and dramatic, seagrasses are well adapted to cope with herbivory having evolved with large populations of diverse megaherbivores (Jackson *et al.*, 2001). So although herbivory can have negative impacts on seagrass meadow structure, some level of herbivory may actually benefit seagrass meadows (see Chapter 2 - Scott *et al.*, 2018).

Herbivory in seagrasses also has broader seascape level benefits and creates trophic links to other coastal ecosystems. Export of primary productivity from seagrass meadows via herbivores and drift detritus subsidises other marine ecosystems, from adjacent coral reefs and mangroves to distant deep sea habitats (Heck *et al.*, 2008; Hyndes *et al.*, 2014). Large herbivores can also ingest and transport viable seagrass seeds long distances to form new meadows and contribute to genetic diversity of existing meadows (Tol *et al.*, 2017).

Seagrass meadows globally are threatened and declining, and recent conservation measures that protect large herbivores may be contributing to these declines and exacerbating existing anthropogenic pressures on meadows (Arthur *et al.*, 2013; Fourqurean *et al.*, 2019; Orth *et al.*, 2006). Where seagrass consumption by herbivores exceeds daily seagrass productivity, especially where large herbivores are present or herbivores aggregate in groups, overgrazing and seagrass loss can occur (e.g. Eklöf *et al.*, 2008; Heithaus *et al.*, 2014). Therefore, to effectively manage both seagrass meadows and the herbivores that rely on them, the plant-herbivore system as a whole should be considered (see Chapter 2 - Scott *et al.*, 2018).

The Great Barrier Reef (GBR) has some of the most extensive and diverse seagrass meadows in the world which are grazed by a diverse herbivore community (Coles *et al.*, 2015). The meadows in the GBR cover tropical and subtropical environments and are made up of fifteen species of seagrass (Coles *et al.*, 2015). These seagrass meadows are a food source for a diverse community of herbivores, from mesoherbivores such as small amphipods, isopods and gastropods (Hoffmann *et al.*, 2020), to macroherbivores such as fish and urchins (Fox and Bellwood, 2008), to megaherbivores such as green turtles and dugongs (Aragones *et al.*, 2006; Fuentes *et al.*, 2006). The diversity of both seagrasses and their herbivores in the GBR, along with the significant populations of large bodied herbivores, mean this is an environment likely to be similar to that under which seagrasses evolved and adapted, making this an interesting place to study plant-herbivore interactions. Despite the possible significant

impacts of herbivory on seagrasses of the GBR, we currently have a limited understanding of how the herbivores here structure the meadows they feed on (York *et al.*, 2017).

Knowledge gaps and rationale for thesis

Research has highlighted the function of herbivory as a top-down structuring force that modifies seagrass characteristics, particularly in tropical and subtropical meadows where megaherbivores are present. However, the impacts of herbivory depend on the characteristics of each seagrass-herbivore system, and these will vary between locations and over time. Current knowledge of plant-herbivore interactions in GBR seagrass meadows is limited, and my research establishes whether the patterns of herbivory seen in other locations are also applicable here.

York *et al.,* (2017) identify key knowledge gaps for Australian seagrass research. Two key questions identified as priorities for further study are addressed by my research. These are: How does herbivory influence the structure and function of seagrass? And how do different factors (scaled from gene to landscape) influence the functional processes involved in ecosystem service delivery? I address these by using field exclusion studies to understand the impact of herbivory on seagrass meadow structure and link this to ecosystem service provision.

Nordlund *et al*., (2017) identify three key themes for future seagrass ecosystem service research. My thesis addresses the first of these; to investigate variability in ecosystem service delivery within and between seagrass meadows, due to differing meadow characteristics. I address this in terms of the variability in the provision of food for herbivores and understanding the possible trade-offs with the delivery of other ecosystem services that occur as a result of herbivore mediated structuring of seagrass meadows.

My work adds to the published body of seagrass herbivory research by understanding plant-herbivore interactions and the interactions between herbivore groups that structure seagrass meadows in the GBR. My research will allow managers to understand more about the seagrass-herbivore system as a whole in the GBR, to inform monitoring and management. This will assist in conservation efforts for herbivores, seagrass meadows and their associated ecosystem services.

Thesis aims and objectives

My research investigates how feeding by herbivores structures seagrass meadows in the GBR. The goal of this research was to understand how grazing by all herbivore groups in GBR seagrasses acts to structure meadows, identify the important herbivores and understand how the pressure of herbivory varies over space and time.

My thesis has the following specific objectives:

Objective 1: **Produce a conceptual model which shows how herbivores can modify ecosystem service delivery in tropical seagrass meadows and identifies where data gaps exist**

Although the role of herbivores in modifying seagrass meadow structure and function in tropical environments is known to be important, few studies have linked these herbivore driven changes to the delivery of ecosystem services. By bringing together a group of experts and current research, I produced a conceptual model in Chapter 2 to understand how herbivores may modify ecosystem service delivery in tropical seagrass meadows, and what the management implications of this are. This provides the framework around which my following data chapters are based.

Objective 2: **Understand the individual effects of, and interactions between, different herbivore groups in structuring GBR seagrass meadows**

Understanding how the herbivore community as a whole can impact seagrass meadows and how different herbivore groups can interact with each other to structure seagrass meadows, is essential to quantifying plant-herbivore interactions in seagrass meadows. However, few subtropical or tropical studies have attempted to assess herbivory by different grazer groups, and no such interactive studies have been carried out in the GBR. I address this objective in Chapter 3 with a multi-grazer exclusion study.

Objective 3: **Understand the role of megaherbivore grazing in structuring GBR seagrass meadows and how this varies over space and time**

Although there are large megaherbivore populations in the GBR that graze on seagrass meadows, we know little about the impact that these herbivores have on different GBR seagrass meadows. Seagrasses are dynamic systems so the megaherbivore-seagrass interactions are likely to have high spatial and temporal variability between and within

meadows. I address this objective in Chapters 4 and 6 with experiments at two different locations within the GBR World Heritage Area.

Objective 4: **Quantify the level of seagrass herbivory by fish and urchins, investigate feeding preference and understand how macroherbivory varies spatially and temporally**

Fish and urchins are important herbivores in seagrass meadows, however we know little about herbivory by fish and urchins on tropical seagrass meadows, especially within the GBR. In Chapter 5, I used a range of techniques to quantify macroherbivory, identify the macroherbivores present and understand the impact of their grazing in a GBR seagrass meadow with a range of macroherbivores present.

Thesis outline

My thesis is presented as a series of scientific publications. Authorship on these publications is shared with my supervisors and some of the larger project team. However, I am the lead author on all chapter publications and conducted all fieldwork and lab work with assistance from Seagrass Ecology Lab staff and volunteers. I carried out all data analysis and produced first drafts for input from all authors. The structure of my thesis is detailed below and outlined in Figure 1.1.

Chapter 1: Provides an introduction to the current knowledge of seagrass-herbivore interactions in tropical seagrass meadows.

Chapter 2: Brings together scientists from the Australian Research Council project which my work is a part of, to discuss the role of herbivory in structuring tropical seagrass meadows and modifying the ecosystem services they deliver. This chapter is published in *Frontiers in Plant Science* as part of a multi-author paper based on a workshop which I developed and led. I wrote the manuscript with edits from co-authors.

Chapter 3: This chapter focusses on Gladstone Harbour as a study site to quantify the impact of all three size classes of herbivore group (mesoherbivores, macroherbivores and megaherbivores) in structuring a subtropical seagrass meadow. Experimental work investigates the interaction between herbivore groups in structuring this seagrass meadow, which exists in an environment containing high levels of industrial activity and large megaherbivore populations. This chapter is published in *Estuaries and Coasts*, I conceived the study with advice from my supervisors, carried out all field work and lab work with help

from the TropWATER Seagrass Ecology Lab, conducted all of the data analysis and wrote this publication with input on data interpretation and manuscript edits from my supervisors.

Chapter 4: Investigates the impact and feeding behaviour of megaherbivores at Green Island, by using exclusion cages to understand how green turtles can structure a tropical seagrass meadow, within a Marine Protected Area that has a high tourism value. This chapter is published in *Marine Environmental Research*, I conceived the study with advice from my supervisors, carried out all field work and lab work for this chapter with help from the TropWATER Seagrass Ecology Lab team, conducted all of the data analysis and wrote this publication with input on data interpretation and manuscript edits from my supervisors.

Chapter 5: Uses a combination of methods to quantify grazing by fish and urchins on seagrass meadows at Green Island, identify these grazers, understand their feeding preferences and how their grazing structures the meadow. This chapter is currently under review in *Diversity*, I conceived the study with advice from my supervisors, carried out all field work and lab work with help from the TropWATER Seagrass Ecology Lab team, conducted all of the data analysis and wrote this publication with input on data interpretation and manuscript edits from my supervisors.

Chapter 6: Focusses on how megaherbivory can vary on regional spatial scales over tens of kms and over time, by carrying out a multi-site megaherbivore exclusion experiment within a 50km stretch of coastline in the southern GBR near Gladstone. This publication is currently under review in *Marine Ecology Progress Series*, I conceived the study with advice from my supervisors, carried out all field work for this chapter with help from the TropWATER Seagrass Ecology Lab team, conducted all of the data analysis and wrote this publication with input on data interpretation and manuscript edits from my supervisors.

Chapter 7: Summarises the key knowledge gaps that have been addressed by this thesis, the management implications for these findings and how my data chapters relate to the theoretical model of herbivore and seagrass interactions detailed in Chapter 2.

Chapter 1:
Introduction

Chapter 2:
The role of herbivory in structuring tropical seagrass ecosystem service delivery

Chapter 3:
Herbivory has a major influence on structure and condition of a Great Barrier Reef subtropical seagrass meadow

Chapter 4:
Green turtle grazing plot formation creates structural changes in a multi-species GBR seagrass meadow

Chapter 5:
Spatial and temporal patterns in macroherbivore grazing in a multi-species GBR seagrass meadow

Chapter 6:
Spatial and temporal variability of green turtle and dugong herbivory in seagrass meadows of the southern GBR

Chapter 7:
General discussion

Figure 1.1: Overall structure of the thesis

Chapter 2

The role of herbivory in structuring tropical seagrass ecosystem service delivery

Chapter 1:
Introduction

Chapter 2:
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Chapter 3:
Herbivory has a major influence on structure and condition of a Great Barrier Reef subtropical seagrass meadow

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Green turtle grazing plot formation creates structural changes in a multi-species GBR seagrass meadow

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Chapter 6:
Spatial and temporal variability of green turtle and dugong herbivory in seagrass meadows of the southern GBR

Chapter 7:
General discussion

Chapter 2

The role of herbivory in structuring tropical seagrass ecosystem service delivery

Chapter 2 is a perspective article that summarises current knowledge of how herbivory can structure tropical seagrass meadows and impact ecosystem service delivery in seagrass meadows. This chapter sets the scene for my experimental work which investigates the structuring impact that herbivores can have on tropical seagrass meadows and links this to the ecosystem services that they deliver.

This chapter has been published in Frontiers in Marine Science as part of the Conservation Ecology of Aquatic Plants research topic:

Scott, A. L., York, P. H., Duncan, C., Macreadie, P. I., Connolly, R. M., Ellis, M. T., Jarvis, J. C., Jinks, K. I., Marsh, H. and Rasheed, M. A. 2018. The Role of Herbivory in Structuring Tropical Seagrass Ecosystem Service Delivery. *Frontiers in Plant Science.* 9. doi:10.3389/fpls.2018.00127.

Author Contributions

ALS, PHY, MAR, PIM and CD conceived the main concept of the manuscript. All authors participated in a workshop led by ALS to discuss and develop the themes of the perspective article. ALS prepared the manuscript. All authors reviewed, revised and approved the final manuscript.

Abstract

Seagrass meadows support key ecosystem services, via provision of food directly for herbivores, and indirectly to their predators. The importance of herbivores in seagrass meadows has been well-documented, but the links between food webs and ecosystem services in seagrass meadows have not previously been made explicit. Herbivores interact with ecosystem services – including carbon sequestration, cultural values, and coastal protection. Interactions can be positive or negative and depend on a range of factors including the herbivore identity and the grazing type and intensity. There can be unintended consequences from management actions based on a poor understanding of trade-offs that occur with complex seagrass-herbivore interactions. Tropical seagrass meadows support a diversity of grazers spanning the meso-, macro-, and megaherbivore scales. I present a conceptual model to describe how multiple ecosystem services are influenced by herbivore pressure in tropical seagrass meadows. My model suggests that a balanced system, incorporating both seagrass and herbivore diversity, is likely to sustain the broadest range of ecosystem services. My framework suggests the pathway to achieve desired ecosystem service outcomes requires knowledge on four key areas: (1) how size classes of herbivores interact to structure seagrass; (2) desired community and management values; (3) seagrass responses to top–down and bottom–up controls; (4) the pathway from intermediate to final ecosystem services and human benefits. I suggest research should be directed to these areas. Herbivory is a major structuring influence in tropical seagrass systems and needs to be considered for effective management of these critical habitats and their services.

Introduction

Herbivores can dramatically influence primary production through top-down regulation in global ecosystems, including seagrass meadows. Seagrasses are well adapted to cope with grazing pressure (Heck and Valentine, 2006); however, plant-herbivore interactions can modify characteristics such as biomass, productivity and species diversity. There are 31 tropical seagrass species, approximately half of the global total, grazed by a broad suite of herbivores (Carruthers *et al.*, 2002; Short *et al.*, 2007). This diversity leads to complex interactions among plants and herbivores. In the tropics, how these interactions shape seagrass meadow properties is not fully understood (York *et al.*, 2017). Such grazer-mediated changes in meadow structure can also influence the ecosystem services provided by seagrass, an area that has received little research focus (Bakker *et al.*, 2016b).

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The Millennium Ecosystem Assessment outlined four categories of ecosystem services: provisioning, regulating, cultural and supporting (MEA, 2005). These categories have been refined to better reflect how humans use ecosystems and to distinguish between intermediate ecosystem services, final ecosystem services, and benefits (Mace *et al.*, 2012). This new classification prevents double-counting of services in management or economic valuations (Boyd and Banzhaf, 2007; Fisher *et al.*, 2008). Final ecosystem services are 'aspects of ecosystems utilised (actively or passively) to produce human well-being', whereas intermediate services are not used by humanity, either directly or indirectly (Fisher *et al.*, 2008). Benefits are the ways human well-being is enhanced through ecosystem services (Mace *et al.*, 2012), and sometimes require human inputs such as people, knowledge or equipment (Fisher *et al.*, 2008). Seagrass meadows provide numerous intermediate and final ecosystem services (Nordlund *et al.*, 2016). For example, nutrient cycling in seagrass meadows is an intermediate service, which produces the final ecosystem service of improved water quality, with the benefit of improved human health. Herbivory has the potential to modify these seagrass ecosystem services by reducing biomass, changing productivity, or altering species assemblages within meadows.

The multiple ecosystem services provided by seagrass meadows respond to environmental pressure and interact in complex ways, presenting challenges for managers. Science-based management requires knowledge of the trade-offs that arise from antagonistic interactions between ecosystem services. Trade-offs occur when one service is enhanced at a cost to another, and are a common outcome of management decisions, often unrecognised (Bas Ventin *et al.*, 2015; Raudsepp-Hearne *et al.*, 2010). Synergistic interactions occur when the combined effect of ecosystem service responses is greater than the sum of the individual effects, positive and negative (Côté *et al.*, 2016). I contend that an understanding of how herbivores can structure tropical seagrass meadows (see Figure 2.1) is essential for effective management and conservation.

In this chapter, I review the current literature and identify the plant-herbivore interactions that structure tropical seagrass meadows. I synthesise this information to develop a conceptual model of how seagrass and herbivory interact to deliver ecosystem services. I suggest a management framework to ensure a holistic approach to achieve desired community and management outcomes for seagrasses, herbivores and the ecosystem services they deliver.

Plant-herbivore interactions structuring tropical seagrass meadows

Herbivores in tropical seagrass meadows are diverse, with a range of feeding strategies, each influencing meadows differently. I classify them into three groups based on size: mesoherbivores, macroherbivores and megaherbivores. Mesoherbivores (e.g. amphipods, isopods and gastropods) live on seagrass blades, and mainly consume epiphytes (Duffy *et al.*, 2003), although they can also consume seagrass (e.g. Rossini *et al.*, 2014). Macroherbivores (e.g. sea urchins and fish) shred or take bites out of the seagrass blades (Alcoverro and Mariani, 2004). In contrast, megaherbivores, green turtles and dugongs, crop leaves. Dugongs also excavate whole seagrass plants (turtles only excavate in extreme cases) (Christianen *et al.*, 2014; Marsh *et al.*, 1982, 2011). Each herbivore group contributes to structuring seagrass meadows in different ways, influencing biomass, productivity, leaf nutritional quality, species assemblage structure and meadow extent.

The impact of herbivory on seagrass biomass changes with herbivore size and density. Megaherbivores and macroherbivores can consume significant amounts of seagrass, resulting in biomass declines, particularly when they are present in large numbers (Fourqurean *et al.*, 2010; Lal *et al.*, 2010; Masini *et al.*, 2001; Vonk *et al.*, 2015). In multi-species tropical meadows, biomass declines may only be observed in some seagrass species (Armitage and Fourqurean, 2006). Grazing by fish can result in bare strips, or halos, around reefs (Randall, 1965), and can outstrip production in tropical meadows (Unsworth *et al.*, 2007). Biomass losses from increased megaherbivore and macroherbivore grazing, or high numbers of herbivores, are often accompanied by reductions in shoot density (Bessey *et al.*, 2016; Burkholder *et al.*, 2013; Lal *et al.*, 2010; Preen, 1995), although not always (Moran and Bjorndal, 2005; Mutchler and Hoffman, 2017). Other structural properties including canopy height, leaf width and area, might decrease due to megaherbivore and macroherbivore grazing (Ebrahim *et al.*, 2014; Kuiper-Linley *et al.*, 2007; Lal *et al.*, 2010; Moran and Bjorndal, 2005). In contrast, mesoherbivores can have positive effects on seagrass biomass. These animals feed on leaf epiphytes, which benefit seagrasses by reducing shading (Orth and Van Montfrans, 1984; Reynolds *et al.*, 2014). Experiments show that mesoherbivores substantially reduce seagrass epiphytes in temperate and subtropical systems (Cook *et al.*, 2011; McSkimming *et al.*, 2015; Whalen *et al.*, 2013) and their presence can increase seagrass biomass (Myers and Heck, 2013).

Herbivory directly affects seagrass productivity, with impacts caused by grazing intensity and the size class of herbivores. Increased productivity has been recorded in response to grazing

by megaherbivores (Aragones and Marsh, 2000; Christianen *et al.*, 2012), but when grazing reaches high levels, productivity declines (Fourqurean *et al.*, 2010; Kelkar *et al.*, 2013b). We know less about smaller herbivores in tropical meadows, but temperate studies have shown that macroherbivore grazing increases seagrass growth up to a certain point, after which it declines (Vergés *et al.*, 2008) and mesoherbivore studies show seagrass productivity increases with increasing grazing on epiphytes (Jaschinski and Sommer, 2008). Megaherbivore grazing can also cause the redistribution of productivity within tropical seagrasses, leading to higher leaf growth relative to rhizome growth (Aragones and Marsh, 2000).

Grazing activity can also affect the seagrass species assemblage. Megaherbivore grazing disturbance creates an environment that favours colonising seagrass species (sensu Kilminster *et al.*, 2015), causing the seagrass meadow to shift towards a grazing-tolerant, early successional stage community (Aragones and Marsh, 2000; Kelkar *et al.*, 2013b; Kuiper-Linley *et al.*, 2007; Preen, 1995). The opposite pattern has also been observed where urchins prefer colonising species, and their grazing maintains the climax community (Vonk *et al.*, 2008). Seagrass diversity increases as meadows recover from disturbance because a mix of climax and coloniser species are present (Rasheed, 2004). Recovery from grazing can take less than a month, to years, depending on the grazing intensity and the life history traits of the seagrass species (Aragones and Marsh, 2000; Kilminster *et al.*, 2015; Lefebvre *et al.*, 2017). High herbivore diversity can enhance secondary production in temperate seagrass meadows (Duffy *et al.*, 2003), however these relationships require more investigation in diverse tropical systems (Clarke *et al.*, 2017).

Herbivores can also have large-scale positive impacts on seagrass meadows: by dispersing seagrass propagules and seeds up to hundreds of kilometres, they provide a mechanism for meadow recovery (Tol *et al.*, 2017). Herbivores reduce the accumulation of organic matter and nutrients by consuming seagrass, reducing the risk of factors such as hypoxia and diseases that cause seagrass die-off (Christianen *et al.*, 2012; Jackson *et al.*, 2001). Megaherbivore grazing also increases microbial nutrient cycling in seagrass sediments (Perry and Dennison, 1999).

Tropical seagrass responses to grazing pressure are dependent upon the size and densities of herbivores present. Some overall patterns can be observed for tropical meadows, and are summarised in Figure 2.1, but variability between meadows still occurs due to meadow characteristics and differences in spatial or temporal scale of studies. There is variability both

between seagrass species and due to differences between study locations. Studies within the same location have also produced differing results (Mutchler and Hoffman, 2017; Myers and Heck, 2013). Seascape configuration and the proximity of other habitats can have an impact on seagrass meadow fauna and meadows in proximity to other habitats can have increased herbivory (Swindells *et al.*, 2017; Valentine *et al.*, 2008).

Interactions among herbivore functional groups

Grazing by one herbivore group can change seagrass meadows as habitats, in ways that affect other herbivores. Heavy grazing by megaherbivores can diminish the available habitat for mesoherbivores, and the suitability of habitat for macroherbivores. The consumption of epiphytes by mesoherbivores may be positive for herbivores that consume seagrass directly, due to increased seagrass growth. The removal of epiphytes, however, might also negatively affect larger herbivores, many of which gain nutrition from the epiphytic algae, either instead of, or in addition to, seagrass itself (Marco-Méndez *et al.*, 2012, 2015). Larger herbivores may inadvertently consume mesoherbivores while feeding on the seagrass they live among (Marsh *et al.*, 2011). Interactions also occur within grazer groups. Herbivory by fish can increase predation risk to sea urchins by reducing habitat complexity and making them more visible (Pagès *et al.*, 2012). Grazing can cause changes to seagrass habitat complexity, which can affect where fish choose to feed, with higher fish herbivory in more complex sites (Unsworth *et al.*, 2007). Chemical changes in seagrass tissue composition caused by herbivory can be beneficial to herbivores. Nitrogen content can increase in response to herbivory, making the seagrass more nutritionally rich (Aragones *et al.*, 2006). However, these changes can be negative, with reductions in starch and increases in fibre (Aragones *et al.*, 2006; Jimenez-Ramos *et al.*, 2017). Phenolic compounds defend seagrasses against herbivores by changing seagrass palatability, and their production shows differing responses to grazing pressure, exhibiting both increases (Martínez-Crego *et al.*, 2015) and decreases (Vergés *et al.*, 2008).
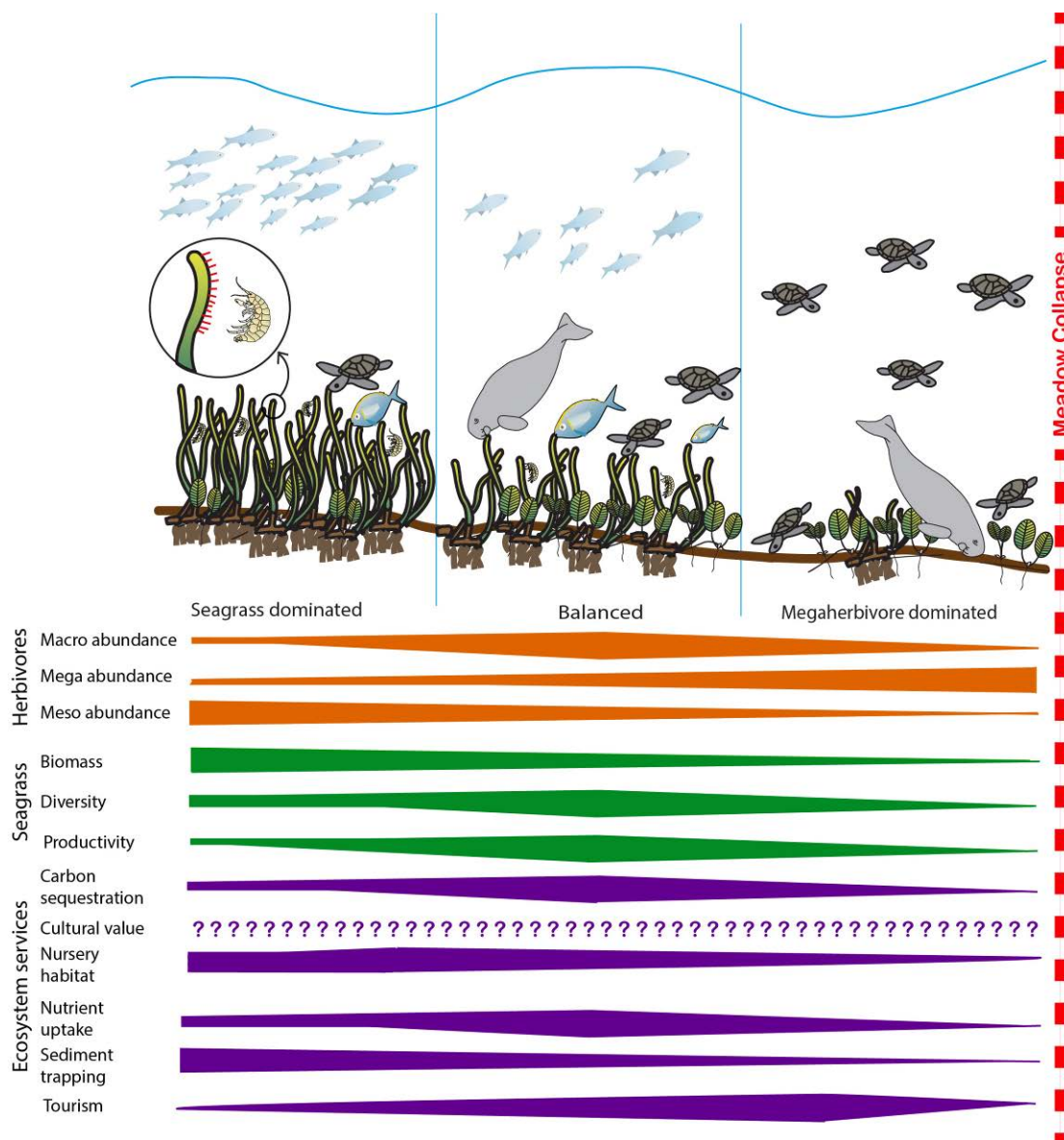
Figure 2.1: Summary of the expected change in herbivore abundance, key seagrass meadow properties and selected ecosystem services as habitats shift from seagrass-dominated to megaherbivore-dominated. At low levels of herbivory, disturbance is minimal and seagrass biomass dominates the system. As herbivory increases, the system moves towards a balanced state where productivity increases in response to herbivory and productivity-associated ecosystem services delivery increases (i.e. carbon sequestration and storage, nutrient uptake leading to improved water quality). In this system, the diversity of both seagrass and herbivore assemblages are generally at their highest. As herbivory increases further, seagrass biomass, diversity and productivity decreases and most ecosystem services delivery reduces before the meadow becomes overgrazed and collapses, at which point ecosystem services delivery ceases. Cultural ecosystem service delivery may be influenced by herbivory, but responses will be highly variable and changes in cultural ecosystem service delivery with increasing herbivory cannot be confidently predicted (Díaz *et al.*, 2006; Garcia Rodrigues *et al.*, 2017). Bars illustrate likely direction of change and do not signify predicted linear relationships. Images: Catherine Collier, Diana Kleine, Tracey Saxby and Dieter Tracey Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/imagelibrary/).

Herbivory as an agent of ecosystem service change

Grazing intensity and type (e.g. shredding, cropping or excavating) structures seagrass meadows and influences the level and type of ecosystem services provided. If the intensity of herbivory is moderate, productivity may increase, resulting in more nutrient uptake by the seagrass (Christianen *et al.*, 2012). Grazing that leads to loss of biomass and reductions in shoot height may alter intermediate services provided by seagrasses. Including potential reductions in a meadow's capacity to: act as a nursery habitat (Heck *et al.*, 2003; Nagelkerken *et al.*, 2002; Sheaves *et al.*, 2014), trap sediment (De Boer, 2007), and sequester carbon (Atwood *et al.*, 2015; Lavery *et al.*, 2013). At very high levels of herbivory, seagrass productivity may be unable to keep pace with removal rates and the meadow could collapse, as shown in Figure 2.1 (Christianen *et al.*, 2014; Fourqurean *et al.*, 2010; Heithaus *et al.*, 2014). In this case, ecosystem services would cease to be delivered, and stored biomass or sediment carbon could be released back into the environment (Fourqurean *et al.*, 2012; Macreadie *et al.*, 2015). Meadow loss on a large scale also results in mortality and changes in fecundity in seagrass-dependent herbivore populations (Fuentes *et al.*, 2016; Meager and Limpus, 2014). How plant-herbivore interactions change ecosystem services depends on location, season, habitat type, seagrass species and the herbivore community composition. Some services are more valuable in certain locations; e.g. the amount of carbon sequestered by seagrasses depends on seagrass species and the environmental context in which the meadow occurs (Lavery *et al.*, 2013; Serrano *et al.*, 2016). Other factors that influence seagrass and herbivores will also change ecosystem service delivery by mediating plant-herbivore interactions as shown in Figure 2.2. Bottom-up anthropogenic stressors and environmental conditions (e.g. light and nutrient levels) can influence seagrass structure, and the top-down influence of predator presence determines where herbivores are more likely to feed (Atwood *et al.*, 2015; Bessey *et al.*, 2016). The response of services to anthropogenic or abiotic disturbance is dependent on the type and intensity of the stressor, and can be context-dependent (Díaz *et al.*, 2007b). Sometimes the impact of herbivores on seagrass ecosystem service delivery is unexpected; for example even when meadows are heavily grazed, the below-ground biomass can still provide an important coastal protection service (Christianen *et al.*, 2013).

By altering the species composition in seagrass meadows and creating disturbance, herbivores can change biodiversity in seagrass communities. Because seagrass is disturbed by grazing activity, both colonising and more persistent species will be present, increasing

seagrass diversity (Figure 2.1) (Kelkar *et al.*, 2013b; Rasheed, 2004). Terrestrial ecosystems with more plant species provide higher levels of ecosystem services (Gamfeldt *et al.*, 2013). Increases in diversity are associated with increased provision of ecosystem services and greater multi-functionality of systems, attributed to greater interspecific niche complementarity (Cardinale *et al.*, 2012; Gamfeldt *et al.*, 2013; Lefcheck *et al.*, 2015); however, the high level of complexity in diverse communities may also lead to a greater number of negative interactions and trade-offs (Duncan *et al.*, 2015). The dominant plant species in ecological communities can be the predominant drivers of ecosystem functioning (mass ratio: c.f. terrestrial grassland examples: Díaz *et al.*, 2007a; Grime, 1998). The identity of dominant seagrass species, and their interactions with herbivore groups, may also play a role alongside, or instead of, high functional diversity to influence seagrass ecosystem service delivery.

There are links between intermediate and final seagrass ecosystem services, some of which are well established, such as changes in seagrass primary production and mesoherbivore removal of epiphytes mitigating nutrient pollution (Christianen *et al.*, 2012). Yet for others, the relationship is unclear. Ecosystem services and human well-being are linked, but the relationship is neither consistent nor linear, so it is difficult to predict how well-being outcomes respond to pressure (Baker *et al.*, 2015).

Herbivores themselves are also important for the ecosystem services delivered by a seagrass meadow. The ecosystem service benefits of tourism, hunting, fishing and cultural values depend explicitly on the presence of herbivores (Butler *et al.*, 2012; Cullen-Unsworth *et al.*, 2014). Cultural ecosystem services provided by seagrass meadows are important, but they are understudied, difficult to quantify and are rarely incorporated into management (Garcia Rodrigues *et al.*, 2017; Ruiz-Frau *et al.*, 2017). Understanding cultural services in the tropics is important, as spiritual and religious values of seagrasses are significant and qualitative information on this is available (Cullen-Unsworth *et al.*, 2014; De La Torre-Castro and Rönnbäck, 2004). Dugongs and green turtles have been referred to as cultural keystone species for communities in the tropics (Butler *et al.*, 2012). Some cultural services such as education, tourism and research require human inputs for benefits to be realised. Others, such as religious, spiritual and bequest value, can be viewed as final services as they rely on a functioning seagrass-herbivore system.

In Figure 2.1, I summarise how seagrass and herbivore interactions manifest to effect the delivery of key ecosystem services. My model suggests that at low levels of herbivory, the

system is seagrass dominated, characterised by high seagrass biomass and moderate levels of productivity and diversity. As herbivory increases, the system moves towards a balanced state where productivity increases in response to herbivory and productivity-associated ecosystem services (i.e. carbon sequestration and storage, nutrient uptake leading to improved water quality) delivery increases. In this system, I hypothesise the diversity of both seagrass and herbivore assemblages are generally at their highest and the biomass of both seagrass and herbivores are maintained at moderate levels. As herbivory increases further, seagrass biomass, diversity and productivity decreases and most ecosystem services delivery reduces before the meadow becomes overgrazed and collapses, at which point ecosystem service delivery ceases. In the model cultural ecosystem service delivery has not been quantified, while it is recognised as being important and may be influenced by herbivory, responses are likely to be highly variable and are not well understood (Díaz *et al.*, 2006; Garcia Rodrigues *et al.*, 2017). Figure 2.1 hypothesises that a balanced system will maximise the broadest range of ecosystem services. While some individual services may peak in either seagrass dominated systems (e.g., nursery habitat and sediment trapping) and others in herbivore dominated systems (e.g. tourism), the presence of intermediate levels of biomass and higher diversity of both seagrasses and herbivores ensures that the greatest number of services will be provided by this balanced state.

Ecosystem service interactions

Ecosystem services can interact with each other as they respond to pressure. Where people and seagrass interact, there are many trade-offs and synergies in service delivery (Arthur *et al.*, 2013; Bas Ventin *et al.*, 2015; Garcia Rodrigues *et al.*, 2017). For example, an increase in both large herbivore numbers and seagrass biomass beyond a threshold value is unlikely, so services associated with herbivores will increase, while those associated with seagrass habitat decrease, resulting in a trade-off. Synergies may also occur but are poorly understood in relation to herbivore pressure.

Understanding interactions and trade-offs in a seagrass meadow and making them explicit is imperative for predicting future changes in delivery, trade-offs and outcomes of management decisions (Mouchet *et al.*, 2014). Even well-intentioned measures can have unintended consequences, or perverse outcomes. Implementing no-take marine protected areas (MPAs) can result in higher local intensities of fish herbivory and consumption of seagrass production (Alcoverro and Mariani, 2004). MPAs designed to protect green turtles, can cause

aggregations that overgraze the seagrass and lead to meadow collapse (Christianen *et al.*, 2014). This effect may be exacerbated if declines in top predators that control green turtles allow green turtle populations to exceed historical numbers (Burkholder *et al.*, 2013; Heithaus *et al.*, 2014). However, green turtles are threatened in tropical seagrass areas and are at high risk of climate change-associated declines (Fuentes *et al.*, 2011), creating a trade-off in potential management priorities.

A pathway for effective management of herbivores, seagrasses and their services

Conservation practitioners and managers can use many legislative instruments to protect seagrasses and their herbivores. These can be global, national or local in scale and with different objectives; i.e. to protect a certain area, a given species or ecosystem type. This range in scale and scope mean that differing pieces of legislation do not always work well together. Management actions can have local consequences, or affect services that have global implications, such as carbon sequestration. To conserve tropical seagrasses and the services they provide, a holistic approach is needed and, to avoid any unconscious bias influencing decisions, weightings should be made explicit. With an awareness of all the interactions at play, we can understand the impact of management decisions and how best to achieve objectives sustainably and across different scales (Arkema *et al.*, 2015).

Management actions will generally prioritise a given set of ecosystem services, which will then require a different seagrass community structure as shown in Figure 2.1, however the variation in seagrass properties and associated services will depend on the types and numbers of herbivores present. Simultaneous multiple benefits could potentially be maximised with minimal impact on the desired set of ecosystem services, by managing for a balanced system (Figure 2.1). Management decisions that shift systems to either seagrass or herbivore dominated are likely to produce trade-offs across a range of services. Where management decisions are skewed away from the maintenance of a balanced system, undesirable outcomes for some ecosystem services are possible and, in the worst-case scenario, complete collapse can occur. For example, if services such as sediment trapping are a priority, managers may wish to aim more towards a seagrass-dominated state, however trade-offs will occur in some other services as a result and should be factored into management decisions. Managing for the balanced system will likely maximise biodiversity benefits, which are a global-scale target. Despite this, a balanced system may not reflect the community desires for seagrass

ecosystem service priorities, a critical component in any management framework (Figure 2.2). While I contend a balanced system is likely to be the most sustainable in the long term, managing for other states is possible and I provide the framework for understanding the consequences of these through the interactions of management decisions with seagrasses, herbivores and their controls in Figure 2.2. The states shown in Figure 2.1 are not separate groups, but are on a continuum such that managers can aim towards a system which is more seagrass or herbivore dominated depending on their ecosystem service priorities and the local community priorities.

Knowledge of the complex interactions between herbivores, seagrasses and delivery of ecosystem services is required to achieve balanced systems or other desired management outcomes and the consequences of these. Figure 2.2 highlights the critical precursors and major pathways and interactions to consider in the tropics for effective management of seagrass-herbivore interactions. This figure illustrates how interactions between herbivores can alter seagrass properties and modify ecosystem service delivery, but also illustrates the top-down and bottom-up factors and management pathways which can influence ecosystem services. Where possible, it is desirable to assess the relative importance of interactions and to incorporate them into management processes. Predicting all interaction outcomes is impossible, but understanding patterns in interaction outcomes can provide guidance to managers (Côté *et al.*, 2016). Conserving seagrass meadow fauna in the tropics requires targeted management, especially given the overexploitation of these animals, and of herbivores in particular, with many populations still vulnerable or endangered (Jackson *et al.*, 2001; Unsworth and Cullen, 2010).
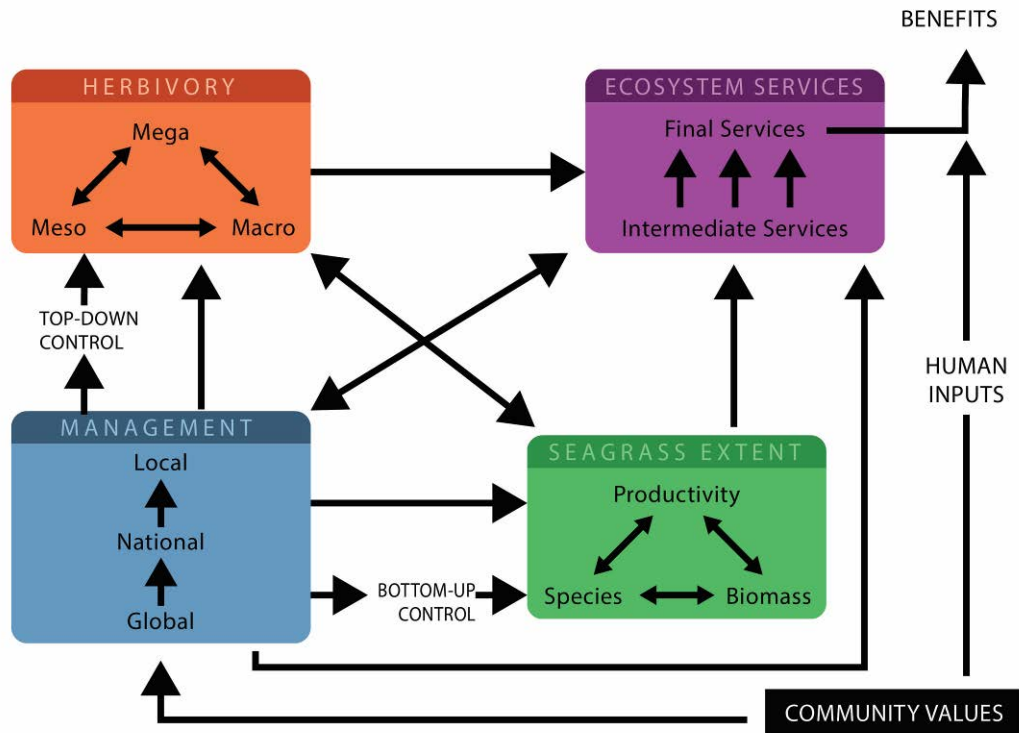
Figure 2.2: The interactions in a seagrass-herbivore system for managers and researchers to consider, to maintain a balanced system. Different herbivores interact with each other to modify seagrass properties and ecosystem services which depend on herbivore numbers, herbivore numbers are determined by top-down controls. Management measures can be dictated by global policy and can be national or local/community based. These measures which control human activities will influence seagrass properties, herbivores and ecosystem services and will in turn be influenced by the relative importance of the various community values and important ecosystem services. Seagrass extent is determined by productivity, species and biomass as well as bottom-up controls, this influences both the ecosystem services provided and the number of herbivores feeding. Ecosystem services are influenced by seagrass extent, herbivores and management measures and require human inputs for benefits to be realised.

To design effective, balanced management, or gain an understanding of the consequences of management decisions directed in favour of a particular service, an awareness of the elements detailed in Figure 2.2 is required. These involve:

1) understanding the desirable management outcome and community values, and making their perceived relative importance explicit;

2) evaluating potential undesirable outcomes for the environment and local community including possible trade-offs;

3) identifying top-down and bottom-up controls in the system that can be manipulated by management actions; and

4) monitoring seagrass ecosystem services and adapting management plans accordingly.

Enabling sustainable management of tropical seagrass ecosystem services requires critical research gaps on how plant-herbivore interactions shape ecosystem service delivery to be addressed. In particular, research is needed to understand how:

1) different herbivore size classes interact to structure seagrass meadows.

2) ecosystem services interact in response to herbivory pressure.

3) the local community values the relative importance of the trade-offs.

4) management actions help to realise benefits of incorporating community values into actions, especially with regard to cultural services.

Conclusions

I contend that a balanced system that promotes diversity of plant and herbivore assemblages is likely to be desirable for sustaining and maintaining delivery of multiple seagrass ecosystem services as shown in Figure 2.1. Seagrass communities are complex systems with potential for poor outcomes if we fail to understand the interactions, trade-offs and unintended consequences that can occur. Figure 2.2 highlights the pathways for managers to be aware of, and to act through, to maximise opportunities to achieve desired outcomes for seagrasses, herbivores and ecosystem services. Seagrass ecosystem services in tropical meadows are poorly understood (Ruiz-Frau *et al.*, 2017), and there are research gaps in relation to herbivore activity that need to be addressed, in addition to the more general seagrass ecosystem services research gaps identified in Nordlund *et al.* (2017). A focus on cultural ecosystem services will allow a more informative valuation of the social, economic and ecological benefits of tropical seagrass systems. It is clear that herbivory is a major structuring influence in tropical seagrass systems and needs to be considered alongside traditional "seagrass only" focused assessments for effective management of these critical habitats and their services. Many of my conclusions are based on hypothetical relationships derived from theory or temperate seagrass systems. Nevertheless, as well as a guide to management decisions based on current knowledge, my framework is useful to show critical areas for future research.

Chapter 3

Chapter 1:
Introduction

Chapter 2:
The role of herbivory in structuring tropical
seagrass ecosystem service delivery

Chapter 3:
Herbivory has a major influence on structure and condition
of a Great Barrier Reef subtropical seagrass meadow

Chapter 4:
Green turtle grazing plot
formation creates structural
changes in a multi-species GBR
seagrass meadow
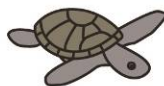
Chapter 5:
Spatial and temporal
patterns in macroherbivore
grazing in a multi-species GBR
seagrass meadow

Chapter 6:
Spatial and temporal variability
of green turtle and dugong
herbivory in seagrass meadows
of the southern GBR

Chapter 7:
General discussion

Chapter 3

Herbivory has a major influence on structure and condition of a Great Barrier Reef subtropical seagrass meadow

Chapter 2 highlights the impacts of herbivory on seagrass meadows and the potential interactions between herbivore groups in structuring seagrass meadows. In this chapter I investigate how the herbivore community as a whole can structure a sub-tropical seagrass meadow in Gladstone, Queensland.

This chapter is published in Estuaries and Coasts in the Special Issue: Seagrasses Tribute to Susan Williams:

All authors helped to conceive the design of this experiment, ALS led all fieldwork activity with assistance from PHY and the Seagrass Ecology Lab team. ALS conducted all lab and data analysis with assistance from Seagrass Ecology Lab staff and volunteers. ALS prepared the manuscript with comments from MAR and PHY.

Abstract

Grazing by all members of a herbivore community can act to structure the ecosystems they feed on. The outcome of this grazing pressure on the plant community also depends on the interaction between the different herbivore groups that are present. I carried out a three-month multi-level field exclusion experiment to understand how different groups of herbivores act both individually and interactively to structure a subtropical seagrass meadow in the Great Barrier Reef. Megaherbivore grazing had the largest impact on this seagrass meadow, significantly reducing aboveground biomass and shoot height, whereas there was no measurable impact of meso- or macroherbivores on seagrass metrics or epiphyte biomass. Megaherbivores here grazed broadly across the meadow instead of targeting grazing in one area. The principal seagrass-herbivore dynamic in this meadow is that megaherbivores are the main group modifying meadow structure, and other grazer groups that are present in lower numbers do not individually or interactively structure the meadow. I demonstrate that herbivory by large grazers can significantly modify seagrass meadow characteristics. This has important implications when designing and interpreting the results of monitoring programs that seek to conserve seagrass meadows, the ecosystem services that they provide, and the herbivores that rely on them. Collectively my results and those of similar previous studies emphasize there is unlikely to be one seagrass and herbivory paradigm. Instead, for individual meadows, their unique species interactions and differences in biotic and abiotic drivers of seagrass change, are likely to have a strong influence on the dominant seagrass-herbivore dynamic.

Introduction

Seagrass meadows are some of the most productive ecosystems in the marine environment, providing a food source for a range of herbivores as well as a suite of other ecosystem functions and services (Heck and Valentine 2006; Nordlund *et al.,* 2016). Grazing by the herbivore community can structure seagrass meadows. The impact of this grazing depends on the numbers and types of herbivore present, and how these different herbivore groups interact (Scott *et al.,* 2018; Chapter 2). The community of herbivores that graze in seagrass meadows is diverse in terms of the species, body sizes and foraging strategies used, that result in a range of alterations to seagrass meadow structure. These herbivores can be classified based on their size; mesoherbivores include the small invertebrates that live and feed in the seagrass meadow, macroherbivores include fish and urchins that forage in the meadow, and

megaherbivores are the largest grazers that consume significant amounts of biomass (Scott *et al.,* 2018; Chapter 2). Grazing by each of these herbivore groups will modify the seagrass meadow in ways that can affect the other grazer groups and will influence the cumulative impact that all grazers have on the meadow (Ebrahim *et al.* 2014; Bessey *et al.* 2016).

Mesoherbivores are the small invertebrates (e.g. amphipods, isopods and gastropods) that generally graze on the epiphytic algae that grow on seagrass leaves (Orth and Van Montfrans 1984), but can also graze on the seagrass leaves themselves (Brearley *et al.,* 2008; Lewis and Anderson 2012; Rossini *et al,.* 2014). Mesoherbivore control of epiphyte loads on seagrass leaves can be important to maintaining meadow health, by mitigating against negative impacts of excess nutrients, that can lead to reductions in seagrass biomass (Hughes *et al.,* 2004; Myers and Heck 2013; Reynolds *et al.,* 2014). Some mesoherbivores feed on the seagrass itself and can cause significant damage to leaves by feeding and burrowing into leaves (Brearley et al. 2008; Lewis and Anderson 2012; Rossini *et al.,* 2014).

Macroherbivores fall into two main groups, fish and sea urchins. Fish graze by taking bites out of seagrass leaves and sea urchins graze by shredding off parts of the leaf (Thayer *et al.,* 1984). Grazing by fish can have dramatic impacts on meadow structure, reducing shoot height and aboveground biomass (Tomas *et al.,* 2005; Pagès *et al.,* 2012), impacting meadow establishment (Bessey *et al.* 2016) and can greatly exceed daily seagrass productivity (Holzer *et al.,* 2013). Sea urchins can dramatically overgraze seagrass meadows in areas where their populations have increased rapidly or individuals aggregate (Eklöf *et al.,* 2008; Langdon *et al.,* 2011).

The largest herbivores that forage in seagrass meadows and consume significant amounts of seagrass biomass are the megaherbivores (e.g. turtles, sirenians and waterfowl). Megaherbivores can reduce structural complexity in seagrass meadows by decreasing; aboveground biomass, shoot density, shoot length and shoot width (Preen 1995; Aragones and Marsh 2000; Fourqurean *et al.,* 2010). Megaherbivory can also modify the species composition of seagrass meadows (Preen 1995; Aragones and Marsh 2000; Hearne *et al.,* 2018). The intensity of herbivory can either stimulate seagrass meadow productivity (Aragones *et al.,* 2006; Christianen *et al.,* 2012), or cause productivity decreases and the production of fewer, shorter new leaves in some meadows (Kuiper-Linley *et al.*, 2007; Kelkar *et al.*, 2013; Johnson *et al.,* 2019). In extreme cases, overgrazing by green turtles can lead to meadow collapse, as shoots become progressively narrower and thinner in response to grazing (Fourqurean *et al.,* 2010; 2019). Green turtles can focus their grazing in a small area

to form 'grazing plots' where they continually graze the nutrient rich regrowth and significantly reduce aboveground biomass in a small part of the meadow (Bjorndal 1980; Williams 1988; Moran and Bjorndal 2005; Molina-Hernández and Van Tussenbroek 2014; Scott *et al.*, 2020; Chapter 4). Dugongs and manatees consume both above and belowground biomass as they form feeding trails through a meadow (Marsh *et al.*, 1982; Preen 1995; Lefebvre *et al.*, 2000), whereas green turtles only crop the aboveground material, except for rare occasions where they have been observed feeding on belowground rhizomes (Christianen *et al.*, 2014; Scott *et al.*, 2020; Chapter 4).

All three of these herbivore groups may be foraging in seagrass meadows concurrently, so their individual impacts will interact to produce overall outcomes on meadow structure. Such changes to the structure of a seagrass meadow can influence the food web it supports. For example, less structurally complex meadows support smaller fish in a lower abundance (Jinks *et al.*, 2019) and provide less settlement substrate for larvae (Thayer *et al.*, 1984). So, as herbivores feed and change meadow structure, they modify the suitability of the seagrass meadow as a habitat and foraging ground for other herbivores, and even for themselves. These interactions can be seen between different herbivore groups, such as megaherbivore feeding on aboveground seagrass biomass reducing infaunal invertebrate community abundance (Skilleter *et al.*, 2007; Johnson *et al.*, 2020). Interactions also occur within a herbivore group, such as grazing by fish increasing predation risk to sea urchins in the same meadow (Pagès *et al.*, 2012). We currently have a limited knowledge of how interactions between herbivore groups may play out to produce meadow scale outcomes in seagrass meadows, particularly in tropical and subtropical areas where large populations of megaherbivores are present.

Seagrass meadows where grazing causes reduced structural complexity can still function as part of a healthy seagrass-herbivore system. Throughout their evolutionary history, seagrasses were grazed by a more abundant and diverse population of megaherbivores, and much of the seagrass productivity would have been consumed by herbivores (Domning 2001). Whereas in many seagrass meadows today, human exploitation has reduced numbers of large grazers, and a large proportion of seagrass productivity enters the detrital food chain (Jackson *et al.*, 2001; Valentine and Duffy, 2006). Megaherbivores rely on seagrass as a food source, but seagrass meadows may also rely on megaherbivory to some extent (e.g. removal of detrital matter and dispersal of seagrass seeds), and seagrass declines in Queensland may have, in part, been caused due to the colonial overexploitation of megaherbivores (Jackson, 2001;

Thayer *et al.,* 1984, Tol *et al.,* 2017). These beneficial impacts of megaherbivory on seagrass meadows will not occur if megaherbivores are able to overgraze seagrass meadows. In the modern ocean, where predator numbers are declining and green turtle conservation measures have been successful, top-down control on megaherbivores is reduced, allowing them to overgraze meadows to the point of collapse in some locations (Arthur *et al.,* 2013; Christianen *et al.,* 2014; Fourqurean *et al.,* 2019). In grazed seagrass meadows with predators present, a low biomass seagrass meadow can indicate a healthy seagrass-herbivore system, however where there are no predators, or other stressors present, a low biomass meadow could indicate an ecosystem heading towards collapse (Heithaus *et al.*, 2014).

The Great Barrier Reef (GBR) contains extensive, diverse seagrass meadows that support a highly diverse community of herbivores with many different foraging strategies (Aragones and Marsh 2000; Coles *et al.,* 2015; Scott *et al.*, 2018; Chapter 2). The epiphytes in GBR seagrass meadows can form an important food source to food webs (Jinks *et al.,* 2019), however we know little about the role of the mesoherbivores that consume these epiphytes in GBR meadows. Mesoherbivory on epiphytes can be significant in some subtropical seagrass meadows and can control epiphytes in the tropical GBR (Myers and Heck 2013; Ebrahim *et al.*, 2014, Hoffmann *et al.,* 2020), although this is not as well understood as in temperate environments (Baden *et al.*, 2010; Reynolds *et al.,* 2014; Duffy *et al.,* 2015). While macroherbivory can be significant in temperate and tropical seagrass meadows (Unsworth *et al.,* 2007; Pagès *et al.,* 2012), this has not been studied in the GBR. The role of mesoherbivory is generally well studied in temperate seagrass meadows but has received little attention in the tropics. Conversely, studies on megaherbivory are more common from the tropics. This difference in attention does not rule out that each of them may be fundamentally important in tropical locations (see reviews by Kollars *et al.,* 2017 and Orth and Van Montfrans 1984). There are large populations of megaherbivores in the GBR, both green turtles (*Chelonia mydas*) and dugongs (*Dugong dugon*) graze on seagrass meadows throughout the GBR (Marsh *et al.,* 1982; Limpus 2008). The diversity of both herbivores and seagrasses in the GBR, and their long evolutionary history together, makes this an ideal environment to investigate plant-herbivore interactions on the community scale.

In this chapter, I examine how different groups of herbivores can structure intertidal seagrass meadows and identify the potential interactions between the exclusion of herbivore groups in structuring meadows. I carried out a multi-level field exclusion study in an intertidal subtropical seagrass meadow in Gladstone Harbour in the southern GBR. This study adds to

our understanding of how herbivore groups interact to structure seagrass meadows in an area where significant megaherbivore feeding is known to occur (Rasheed *et al.,* 2017; Limpus *et al.*, 2018; Chartrand *et al.*, 2019).

Material and methods

Study site

Manipulative field experiments using treatments to exclude herbivores were carried out in an intertidal seagrass meadow at South Trees in Gladstone Harbour, Queensland, Australia (23°51.5'S, 151°19.4'E) (Figure 3.1). The seagrass meadow at South Trees has a continuous cover of ~153ha and is dominated by low biomass *Zostera muelleri* ssp. *capricorni* with some *Halodule uninervis* and *Halophila ovalis* also present in the meadow (Chartrand *et al.* 2019). My study site was dominated by over 95% *Z. muelleri* ssp. *capricorni* with *H. ovalis* making up a small component of the understory in parts of the meadow. The seagrass meadow here has been found to support a unique community of fish and form an important base of the food web in the harbour (Connolly *et al.* 2006). Gladstone Harbour has large populations of green turtles and dugongs as well as other herbivore groups (Connolly *et al.* 2006; Rasheed *et al.* 2017; Limpus *et al.* 2018).
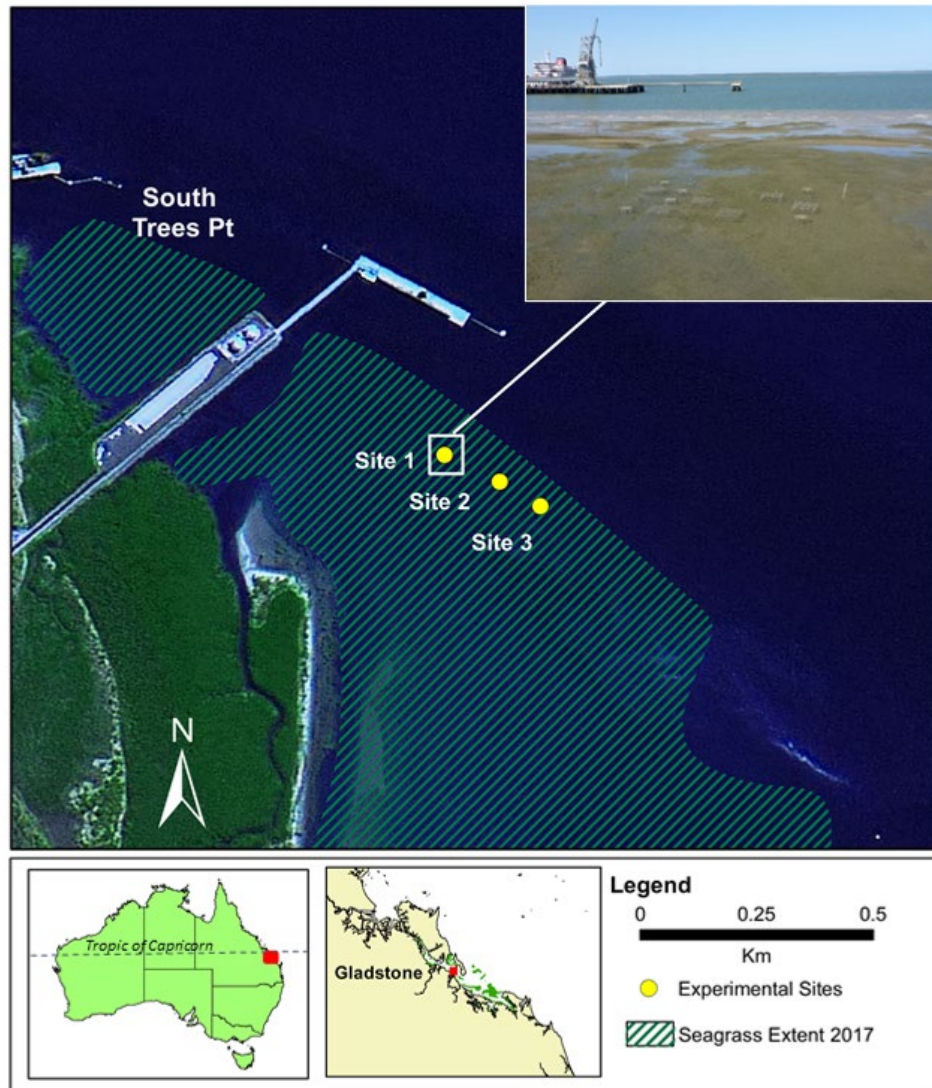
Figure 3.1: Map of study location showing all three sites and an example of the experimental layout at each site.

Experimental design

Herbivore exclusion cages and chemical deterrents were deployed at three sites within the same seagrass meadow at South Trees (Figure 3.1). Sites were 100m apart and all sites were the same tidal height on the mud bank and were exposed for 2-3 hours on low spring tides (<0.9m). Exclusions were set up for three months between 21st August and 17th November in 2017 during the active growing season for seagrasses in the region (Chartrand *et al.* 2016). Each herbivore group was excluded using a different method and these exclusions were combined to understand interactions among groups (summarised in Figure 3.2). A chemical deterrent was used to exclude mesoherbivores, slow release plaster blocks with 7.5% carbaryl were deployed and replaced every two weeks (Poore *et al.* 2009). These were attached to a

peg and covered in chicken wire to prevent them being ingested by other organisms. To exclude macroherbivores, a modified 1m diameter x 0.5m high crab pot was used (macroherbivore cage), this was covered in 10mm monofilament mesh. Steel cages 2m x 2m x 0.5m with a 20 x 20cm mesh were used to exclude megaherbivores. These plots were compared to control plots (0.5m^2) and a procedural control. For the macroherbivore cage this was a frame with no mesh (macroherbivore frame) and for the carbaryl blocks, plaster blocks with no carbaryl added were used. There were eight treatments in total (control, plaster, carbaryl, macro frame, macro cage, macro cage plus carbaryl, mega cage and mega cage plus carbaryl), every site had three replicates of each treatment, giving a total of 9 replicates of every treatment across all three sites.

Plots were arranged in a 6 x 4 grid, with a 2.5m gap between each plot (Figure 3.1), meaning the experimental area of a site was 15.5 x 9.5m. Treatments were divided equally between each site and within a site treatments were allocated randomly to a plot on the grid.

To minimise the impacts of cages on light reaching the seagrass meadow, macroherbivore cages were swapped out and replaced with clean cages every two weeks, and megaherbivore cages were cleaned of any fouling growth at this time. Benthic light measurements reaching the seagrass canopy were taken inside a control plot, a macroherbivore cage and a megaherbivore cage using 2π cosine-corrected irradiance loggers (Submersible Odyssey Photosynthetic Irradiance Recording System, Dataflow Systems Pty. Ltd., New Zealand) calibrated using a cosine corrected Li-Cor underwater quantum sensor (LI-190SA; Li-Cor Inc., Lincoln, Nebraska USA) and corrected for immersion using a factor of 1.33 (Kirk, 1994). Loggers measured photosynthetically active radiation (PAR) and recorded readings every minute for a full two-week tidal cycle, these readings were used to measure total daily light (mol photons m^{-2} day^{-1}) reaching seagrasses in each treatment. Temperature was measured in the same treatments throughout the experiment (Thermodata Pty Ltd, Melbourne, Australia).
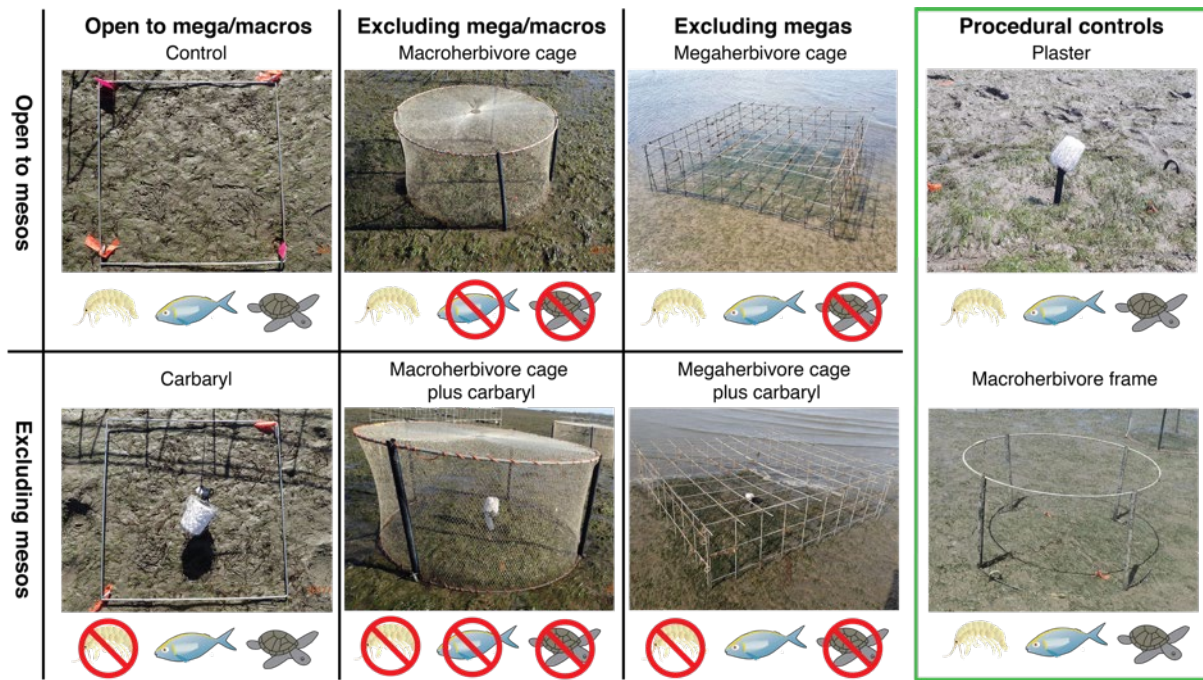
Figure 3.2: Treatments used to exclude each herbivore group individually and interactively with procedural control treatments outlined in green.

Sampling

Measurements were taken from every plot to record shoot height and aboveground biomass at the start and end of the experiment. Three shoot height measurements were made in each plot in the field, by grasping a handful of seagrass leaves and measuring the shoot length, ignoring the longest 20% (Duarte and Kirkman, 2001). Photos were taken from plots to estimate aboveground biomass (Mellors 1991; Rasheed 2004; Rasheed and Unsworth 2011).

At the end of the experiment, a 15cm diameter core was taken from each plot to measure belowground biomass and epiphyte load. Mesoherbivores were sampled from every plot at the end of the experiment by passing a sharpened metal plate underneath a 15cm core at sediment level, this core was enclosed with a 500µm sieve, seagrass material and associated fauna were rinsed and drained in the sieve before being frozen. Seagrass cores were processed in the lab by defrosting samples and separating the above and below ground biomass where the leaf meets the rhizome. Seagrass biomass samples were dried in the oven at 60°C for 10 days and then weighed, two weights were taken to ensure samples had fully dried. Epiphytes were scraped from all wet leaves in a tray using a microscope slide, these were sieved through a 125µm sieve to isolate the epiphytes from the larger tray and dried in the oven at 60°C for three days, epiphyte weight was standardised to the dry weight of seagrass in the core. Mesoherbivore samples from plaster, carbaryl, macroherbivore cage and

macroherbivore cage plus carbaryl treatments were processed by rinsing seagrass through a 1.4mm and 500µm sieve in the lab, all potentially grazing invertebrates were separated and identified to morphologically similar groups within an order or class based on key features that could be observed under the microscope.

To characterise the herbivorous fish present in this meadow, data were obtained from *Jinks et al.* (2019). This study used a beam trawl with a 2mm mesh to sample five trawls at my South Trees meadow in the growing season of 2016. These trawls were undertaken at night while drifting at a speed of 2 knots maximum and all animals were identified, counted and measured (see Jinks *et al,.* 2019).

Statistical analysis

Data were analysed to look at relationships between caging treatments and interactions between herbivore groups using a generalised linear model (GLM) with a Gaussian distribution. The response variables; change in aboveground biomass, change in shoot height, belowground biomass, mesoherbivore abundance and epiphyte load tested individually in the GLM. Change in aboveground biomass was the difference in aboveground biomass based on rank from photos for each plot from the start and end of the experiment. As multiple shoot height measurements were taken from each plot at both sampling intervals, these were averaged for each sampling time to provide a single value for each plot to calculate the difference between the beginning and end. For all GLM analyses, residual and q-q plots of normalised residuals of the model were inspected for heteroscedasticity and non-normality.

To test for interactions between the three key herbivore groups on the response variables, three new factors were added to the data ("Mega", "Macro" and "Meso"), these variables were dummy-coded for each replicate. Where the herbivore group were excluded in a treatment, the variable was assigned a 1, and where the herbivore group could feed a 0 was assigned. These dummy-coded variables were included in a three-way interaction in the GLM to test for their effect on change in biomass, change in shoot height, belowground biomass and epiphyte load. The interactions between Meso:Macro and the three way interaction between all groups could not be evaluated, as it was not possible to design a field treatment which allowed megaherbivores to graze but excluded macroherbivores, therefore this combination could not be analysed.

To look for differences in response variables between factors, a GLM was carried out with both site and caging treatment included as fixed factors. As only three sites could be set up

within the meadow due to logistical and time constraints, this did not provide enough levels to include site as a random factor (Zuur *et al.*, 2013). Therefore site was included as a fixed factor in the GLM to avoid imprecise estimates of a mixed model with limited levels of a random factor. The MuMin package was used to dredge all model options and find the most parsimonious model that was within two points of the lowest AIC value (Bartoń 2019), site did not have a significant effect on any variable so was not included in the final model. An F-test was used to determine the significance of each variable in the best-fit model using the anova() function in R. Post hoc analysis was conducted to compare treatment groups using a Tukey test in the emmeans package (Lenth 2019). Multivariate analysis was used to look for changes in the mesoherbivore community species composition using the vegan package (Oksanen *et al.* 2019).

To test for differences in abundance between mesoherbivore groups, a two way ANOVA including both site and treatment was carried out for each group. Multidimensional scaling was used to create an ordination plot and visualise differences between mesoherbivore communities in different treatments. Two dimensions were used to create the multidimensional scaling plots as this gave a stress value close to 0.2, the stressplot() function was used to check the ordination gives a successful summary of the relationships. Statistical analyses were conducted in R v.3.5.2. (R Core Team 2019) and model outputs were plotted using ggplot2 (Wickham 2016) and the ordiplot function in the vegan package. Differences in mesoherbivore assemblages among exclusion treatments (fixed effect) were analysed based on Bray Curtis distance matrices with 999 permutations using permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2008). PERMANOVA was performed using the PRIMER-v6 statistical software package.

Results

At the end of the three-month experiment, there was a visible change in seagrass inside cages that were protected from grazing, compared to the grazed meadow (Figure 3.3). PAR and temperature data show these were not reduced inside cages (Figure 3.4). Excluding megaherbivores increased aboveground seagrass biomass and shoot heights (Figure 3.5) over the three-month exclusion experiment, however there were no additional detectable impacts of macroherbivore or mesoherbivore grazing, or interactions between these groups, on these seagrass metrics. There was no impact of herbivory on belowground seagrass biomass (Figure 3.5). Both mesoherbivore numbers and epiphyte load were very low at this site and

the addition of carbaryl did not significantly further reduce numbers of mesoherbivores (Figure 3.6). There was no difference in epiphyte load under any of the exclusion treatments (Figure 3.6). For all variables analysed, no effect of site was detected when all model options were dredged, so treatment was the only variable included in the final model.

Beam trawls showed that the key resident herbivorous fish present at this meadow were *Siganus fuscescens*, these made up a major component of the fish community at this site, however only smaller individuals were found between 2-5cm and numbers were low (see Table A.1).
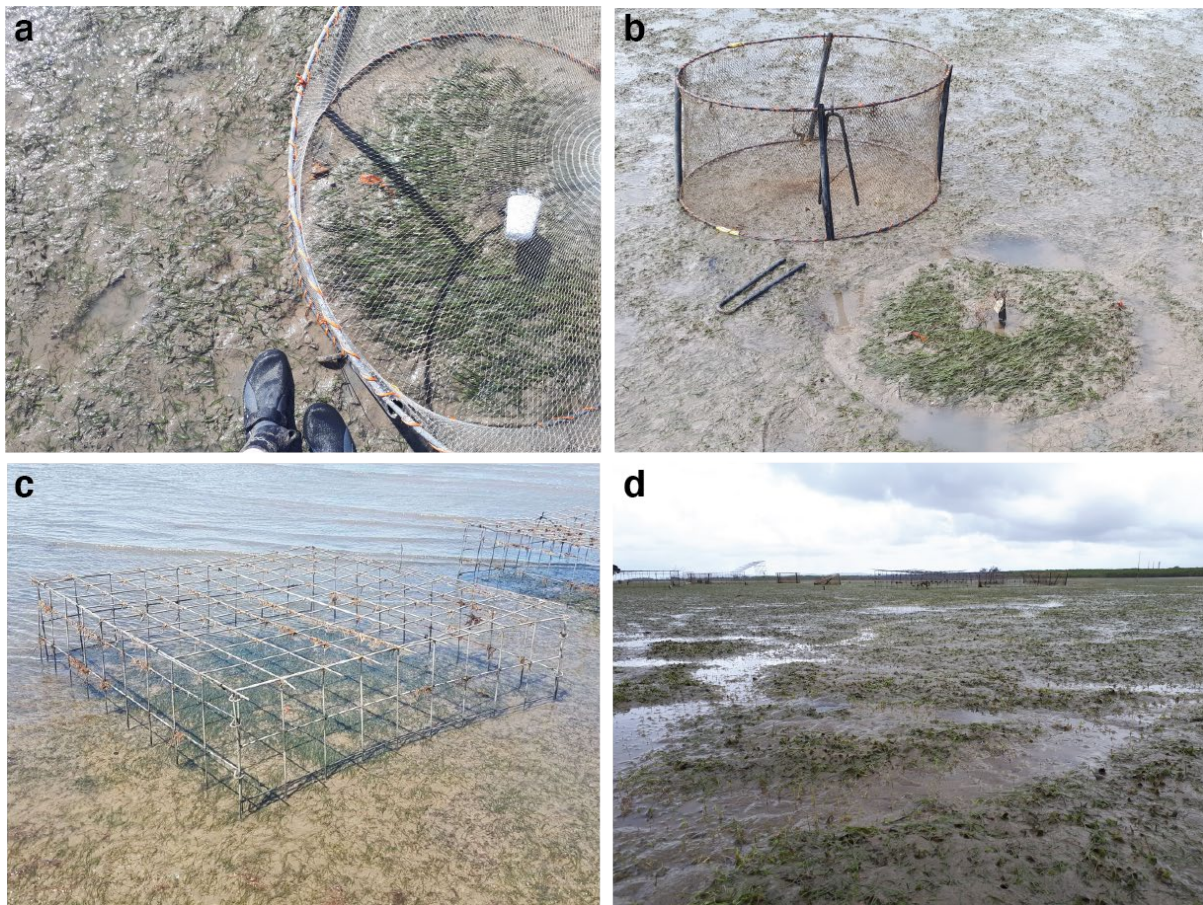
Figure 3.3: Differences between seagrass plots inside and outside of cages at the end of the experiment in macroherbivore exclusion cages (a) and (b) and megaherbivore exclusion cages (c), megaherbivore feeding was observed at the site with recent dugong feeding trails observed (d).

Logger data (Figure 3.4) shows minimal reductions to light in both cage treatments across the full tidal cycle and light remains well above the 6 mol m^{-2} d^{-1} threshold *Z. muelleri* ssp. *capricorni* requires at my study site (Chartrand *et al.,* 2016). The temperature data from the macroherbivore cage and control plot (Figure 3.4) show a minimal difference in temperature between these treatments, where the macroherbivore cage had a slightly higher average

temperature but the difference between treatments did not exceed 0.6°C. Unfortunately, the logger in the megaherbivore cage failed so no data was available for comparison.
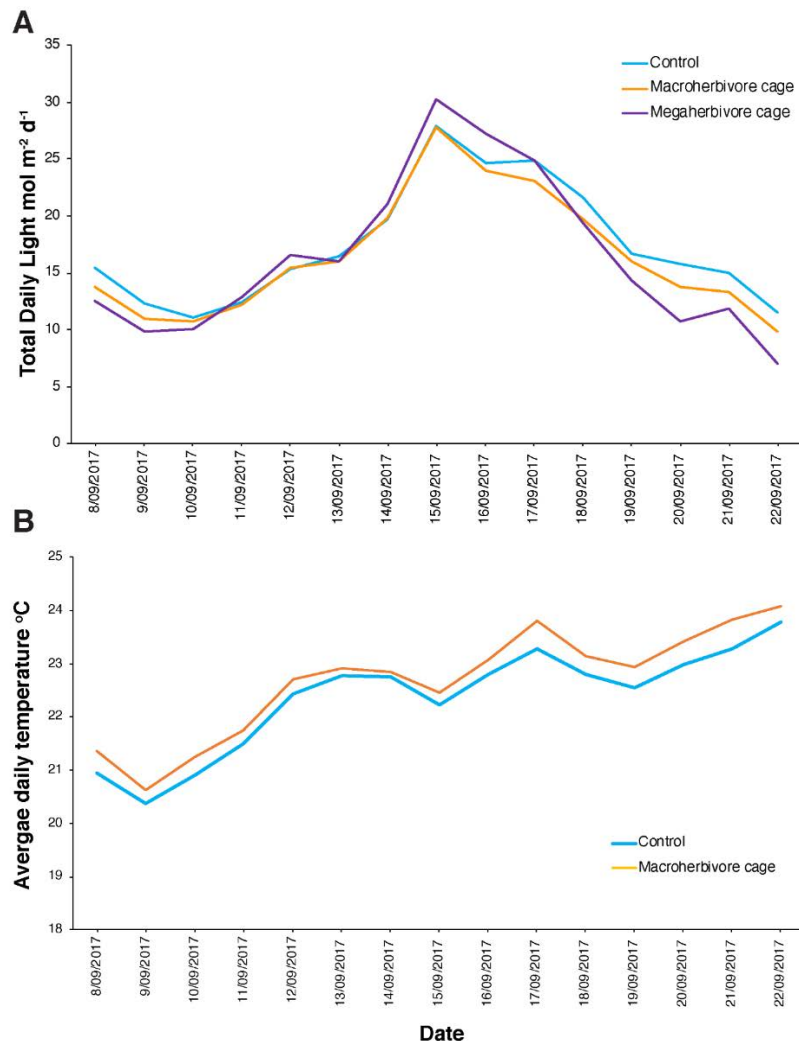
Figure 3.4: Total daily light in control, macroherbivore cage and megaherbivore cage treatments (a), and average daily temperature in control and macroherbivore cages (b).

Aboveground biomass

There was a difference in the change in aboveground biomass between treatments (Figure 3.5) ($F_7 = 7.4264$ P<0.0001). The interaction analysis showed that the only exclusion to impact change in aboveground biomass was megaherbivore exclusion (P<0.0001) and there was no interaction between herbivore groups. Post hoc tests showed that the control treatment had a lower change in aboveground biomass (P<0.05) than all of the caged treatments (macroherbivore cage, macroherbivore cage plus carbaryl, megaherbivore cage and megaherbivore cage plus carbaryl). However, the change in biomass in the control was not different (P>0.05) from the other uncaged treatments (plaster, carbaryl and macroherbivore

frame). Excluding both macro and megaherbivores causes an increase in aboveground seagrass biomass, and the highest biomass values at the end of the experiment (Table A.2), however this increase is driven by the exclusion of megaherbivores, as the other interaction treatments do not change this outcome. This experiment was conducted in the growing season so an overall increase in aboveground biomass would be expected. The only treatments to have a negative change in biomass were uncaged, particularly the control plots which had no barrier at all to grazing, indicating herbivores were consuming seagrass productivity. This is supported by the observation of dugong feeding trails at the site during the experiment (Figure 3.3).

Shoot height

All treatments showed an overall increase in shoot height over the three-month experiment, which was expected during the growing season, however the control treatment had the smallest increase in shoot height during this time (Figure 3.5). There were no interactions between herbivore groups in their impact on shoot height and the interaction analysis showed the only group where exclusion impacted shoot height was the megaherbivore exclusion ($P<0.001$). There was a difference in the change in shoot height between treatments ($F_7 = 9.542$ $P<0.0001$). The post hoc test showed the treatments that excluded megaherbivores had a greater increase in shoot height than the uncaged control and there were no differences between the macroherbivore and megaherbivore cages, indicating that there was no additional impact of macroherbivory to overall seagrass changes, also shown in the interaction analysis. The partially caged procedural control was similar to both the control and macroherbivore/megaherbivore caged treatments, indicating the procedural control had some impact on herbivory, likely due to deterring megaherbivores to some extent.

Belowground biomass

There was no effect of treatment on belowground biomass (Figure 3.5) ($F_7 = 0.6871$ $P = 0.6825$) and there were no interactions between exclusion types detected. Belowground biomass sampling is destructive so was not measured at the start of the experiment, so there may be some spatial differences across the site. However, the lack of pattern between treatments is still very evident with all of the mean values between 100 and 120 gDW/m^2.
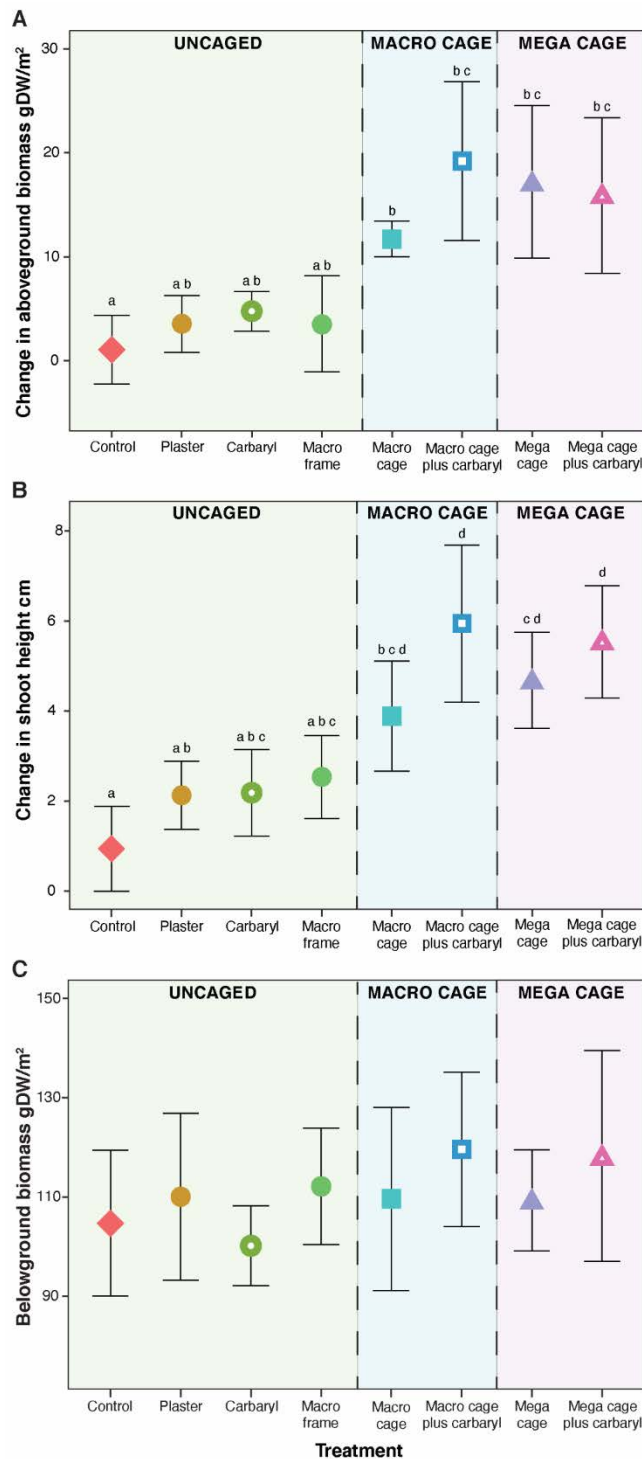
Figure 3.5: Change in aboveground seagrass biomass (a) and shoot height (b) in treatments from the start of the experiment in August to the end in November and belowground biomass at the end of the experiment (c). Letters show treatments that were similar in the Tukey test. Plot shows mean +/- 95% confidence intervals. The diamond indicates the control plot, circles indicate uncaged plots, squares indicate macroherbivore cages and triangles indicate megaherbivore cages, open symbols indicate mesoherbivores were excluded.

Epiphyte load and mesoherbivores

Both the numbers of mesoherbivores and the epiphyte load were uniformly very low across all treatments with no treatment effects on either variable detected in the three months of the study. There was no difference in total mesoherbivores in the treatments sampled (F_3 = 0.6085 P = 0.6144) (Figure 3.6). There was no shift in the mesoherbivore community detected using PERMANOVA (pseudoF_3 = 1.1369, P = 0.298) or observed in the multidimensional scaling ordination plot, where all groups had a high degree of overlap (see supplementary information). The only mesoherbivore group to differ significantly in abundance in treatments was Cumacea (F_3 = 3.233, P<0.05) where abundances in the macroherbivore cage were higher than the plaster block treatment (P<0.05). There was a trend of lower numbers of mesoherbivores in the carbaryl treatments (Figure 3.6), indicating the carbaryl was having some effect of excluding them. There was a consistent trend of lower abundances of isopods in both carbaryl treatments, and the carbaryl treatment had lower numbers of amphipods than other treatments, however the patterns are mixed in the other groups. The protection provided from predation by the macroherbivore cage, which also excluded the fish that prey on mesoherbivores, did not cause an increase in mesoherbivore numbers compared to the uncaged plaster.

There was no difference in epiphyte load between treatments (Figure 3.6) (F_7 = 0.8784 P = 0.5283) and no interaction between exclusion types affecting epiphyte load. The epiphyte load present at this time of year at this site was overall very low, and as mesoherbivore numbers were also very low, a dramatic change in epiphyte biomass is unlikely.
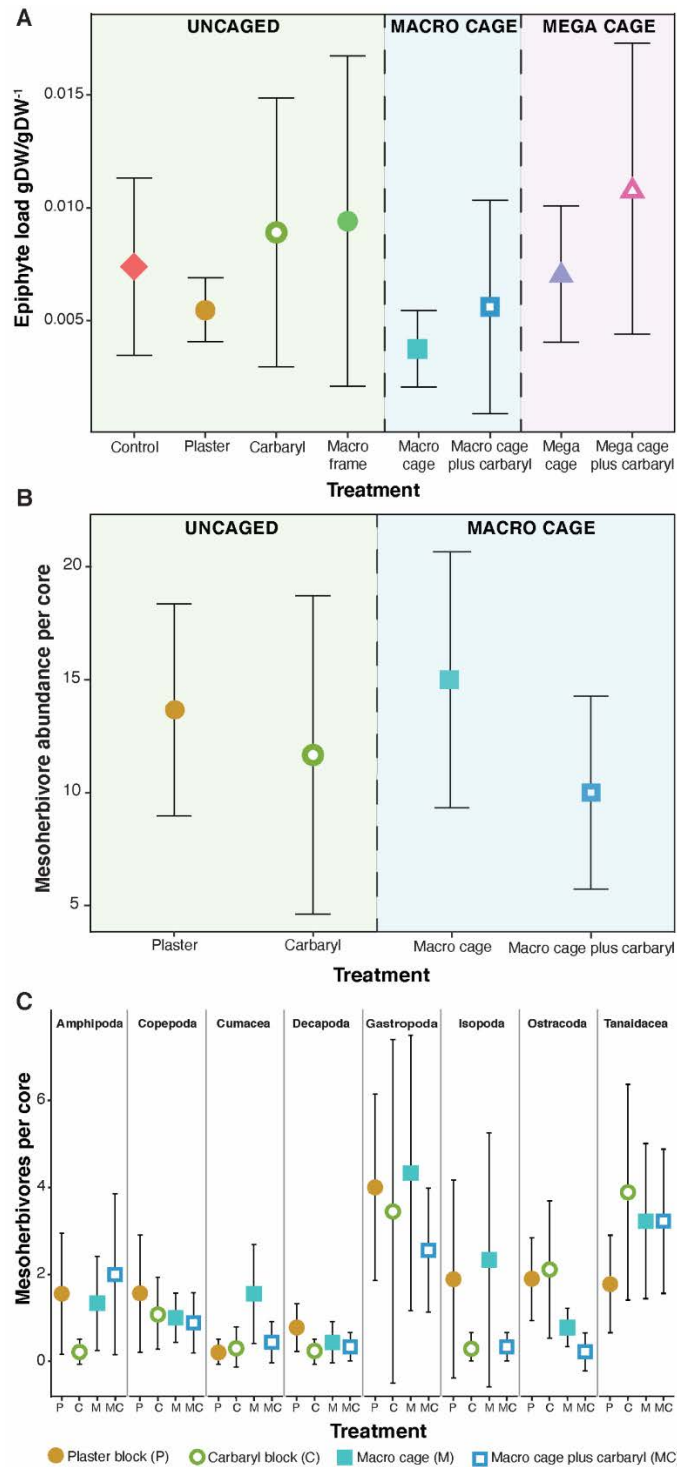
Figure 3.6: Epiphyte load in gDW standardised to gDW of seagrass material in the sample (a), total mesoherbivores core (b) and total mesoherbivores per core split by group (c). Cores represent an area of 176.71 cm^2. Plot shows mean +/- 95% confidence intervals. Circles indicate uncaged plots and squares indicate macroherbivore cages, open symbols indicate mesoherbivores were excluded.

Discussion

Grazing by megaherbivores had a significant impact on overall seagrass meadow structure for this subtropical seagrass meadow. Exclusion of megaherbivores resulted in increases in seagrass biomass and shoot height at all sites over the three-month experiment. The foraging strategy used by megaherbivores in this location did not appear to target small areas by forming grazing plots, instead there was general browsing across the whole meadow with all sites being similarly impacted. No interactions between herbivore groups were detected, possibly because they were insignificant over and above the large megaherbivore impact, due to the low numbers of meso- and macroherbivores present at this site, or because megaherbivore grazing modifies the meadow to an extent where it is less attractive to fish and invertebrates as a habitat and foraging ground (Skilleter *et al.,* 2007; Arthur *et al.,* 2013; Johnson *et al.*, 2020).

Grazing impacts to seagrass caused by megaherbivory were detected across all three sites in this seagrass meadow. My field observations indicated that the grazing impacts to seagrass characteristics I detected were found across the whole meadow including, between and around the sampling locations. Megaherbivore grazing reduced seagrass complexity by decreasing both aboveground seagrass biomass and shoot height, but belowground biomass remained unaffected despite dugong feeding trails that excavate rhizome material observed at the site. Such dramatic losses of aboveground seagrass biomass to megaherbivore grazing have been documented in other locations (Preen 1995; Aragones and Marsh 2000; Fourqurean *et al.*, 2010), in some cases also causing reductions in belowground biomass (Preen 1995). The three-month timeframe of my study may have been too short for the full effects of reduced grazing pressure inside cages to result in an increase of belowground material, with perhaps the initial response of the plant channelled into the rapid expansion of aboveground photosynthetic material (Aragones and Marsh 2000; Christianen *et al.*, 2012). A longer period without grazing pressure may have allowed the accumulation of more belowground material inside exclusion cage plots.

Meadow-scale grazing in Gladstone has been indicated in previous work where dugong feeding trails were observed throughout the year across the entire meadow area at the same South Trees meadow as my study, and green turtles were also observed across the whole meadow (Rasheed *et al.,* 2017; Limpus *et al.,* 2018). My results show that megaherbivores in Gladstone do browse over the entire seagrass meadow without forming grazed plots and

cultivation grazing, as has been observed in other locations (Aragones *et al.,* 2006; Molina-Hernández and Van Tussenbroek 2014) including elsewhere in the GBR (Scott *et al.,* 2020; Chapter 4). This general browsing behaviour that I observed has been documented in other seagrass meadows for both green turtles consuming a preferred species across a meadow (Williams 1988) and dugongs browsing across a meadow (Tol *et al.,* 2016).

Macroherbivores were present in this meadow, as evidenced by small fish bite marks observed on some of the leaves in the meadow and the presence of juvenile *Siganus fuscescens* in beam trawl samples at my study meadow by Jinks *et al.* (2019) (Table A.1). However, there were no differences in seagrass between the macroherbivore excluded treatments and the megaherbivore cages, which allowed fish access and no other interactions between exclusion types. This showed that the increases in seagrass I found in the macroherbivore exclusion treatment were principally due to the coincidental exclusion of the megaherbivores. There could be a range of reasons for the lack of additional effect from exclusion of macroherbivores, but it is possibly a combination of the overwhelming impact of the larger megaherbivores at the site and the relatively low numbers of macroherbivores present.

Gladstone Harbour is important for recreational and commercial fishing (Connolly *et al.*, 2006) which may alter macroherbivory pressure. In other locations, fished areas have more herbivory by urchins than fish, whereas unfished areas had macroherbivory by both fish and urchins (Alcoverro and Mariani 2004). Urchin grazing can have significant negative impacts on seagrass meadows (Eklöf *et al.,* 2008), however at this site there were no urchins observed, nor any distinctive urchin shredding on seagrass leaves. Macroherbivory intensity is dependent on the availability of seagrass (Unsworth *et al.*, 2007), which could explain why in this lower biomass system, macroherbivory levels are lower, compared to other systems where macroherbivory is a significant top down pressure (Tomas *et al.*, 2005; Unsworth *et al.*, 2007; Pagès *et al.*, 2012; Swindells *et al.*, 2017).

In my study site, the seagrass shoots were small with narrow leaves (around 3-5mm wide) and as such mega- and macroherbivory was likely to result in complete shoot removal, rather than smaller damage to leaves, such as bite marks commonly observed in studies of larger growing seagrass. This was realised in the significant change noted in both aboveground biomass and shoot heights and the rarity of bite marks being observed on leaves. Herbivory can of course impact other seagrass metrics, for example by reducing shoot densities, selectively grazing one species, modifying meadow productivity or altering leaf width

(Aragones and Marsh 2000; Lal *et al.,* 2010; Ebrahim *et al.,* 2014). While these were not directly measured as part of my study, it is possible I may have picked up such changes with longer term removal of herbivory pressure.

Both the epiphyte load and mesoherbivore abundances at my site were very low when compared to other studies, across all my treatments, including those where mesoherbivores were not manipulated (Cook *et al.,* 2011; Myers and Heck 2013; Ebrahim *et al.,* 2014). So any changes in epiphyte biomass or mesoherbivore abundances between treatments would be difficult to detect if they occurred. As a result, I did not detect any effect of excluding mesoherbivores on epiphyte biomass, which I believe is overwhelmingly driven by this seagrass meadow not supporting substantial epiphyte growth, and consequently, very low numbers of mesoherbivores.

It is possible my chemical deterrent may have had only limited effectiveness, as the majority of studies which have found strong epiphyte control by mesoherbivores were carried out in temperate meadows (Whalen *et al.*, 2013; Reynolds *et al.*, 2014; McSkimming *et al.,* 2015). However this relationship has also been observed in other subtropical seagrass meadows (Myers and Heck 2013; Ebrahim *et al.*, 2014). Excluding mesoherbivores does not always result in increases in epiphyte load though, in a temperate algal bed, exclusion of amphipod grazers did not increase epiphyte load (Poore *et al.,* 2009) and responses in temperate seagrass meadows can vary depending on seagrass species (Cook *et al.,* 2011). I did not detect a shift in the mesoherbivore community in response to carbaryl treatment, and although I detected a reduction in mesoherbivore numbers, this was not significant so the carbaryl may not have been effective enough in this intertidal environment with strong tidal currents, even though I employed the established method of administering the carbaryl deterrent in other studies (Poore *et al.,* 2009; Cook *et al.,* 2011; Whalen *et al.,* 2013; Ebrahim *et al.,* 2014). This is similar to the findings of Myers and Heck (2013), who found no effect of carbaryl on the mesoherbivore community at a wave exposed site with low numbers of mesoherbivores present, compared to a protected site. Due to the very low numbers of mesoherbivores and low epiphyte cover at my site, my findings indicate that mesoherbivory may be less significant in this and similar subtropical, intertidal, low-epiphyte seagrass meadows, particularly where megaherbivores are present.

There were no interactions between herbivores detected at this meadow in Gladstone. This meadow contains large populations of megaherbivores, but lower numbers of smaller herbivore groups. This contrasts with another subtropical GBR study that found

mesoherbivores were having the largest impact on the meadow by limiting epiphyte growth, whereas macro- and megaherbivores were not structuring the seagrass meadow (Ebrahim *et al.,* 2014). There could be several mechanisms explaining these results. Megaherbivore grazing may modify the seagrass meadow to such an extent that the meadow is a less valuable foraging area for the other herbivore groups. Where megaherbivore grazing creates low biomass seagrass meadows such as in my study, this may reduce the refuges available for smaller herbivores and leave them more open to predation (Pagès *et al.,* 2012). The lack of interactions between groups may also be due to the low biomass of epiphytes on seagrass in Gladstone Harbour, epiphytes have been shown to contribute to the diet of smaller herbivores in this meadow, but there was a switch to a diet of seagrass in larger bodied animals (Jinks *et al.,* 2019). This feeding by smaller herbivores may not be at a high enough intensity to impact the low epiphyte biomass at this site. There could also be an impact of megaherbivores consuming seagrass leaves before epiphytes were able to grow on them, however in my three-month experiment I did not detect any change in epiphytes when seagrasses were released from megaherbivore pressure. Top-down pressure from predation and fishing may also reduce the numbers of macroherbivores within this seagrass meadow, meaning these low populations do not structure the meadows.

The loss of seagrass meadow structure caused by grazing can modify the valuable ecosystem services which the meadow provides. The provision of food for herbivores is an important ecosystem service, however as herbivores graze and change meadow characteristics, they can also modify the other ecosystem services provided by the meadow (Scott *et al.,* 2018; Chapter 2). Ecosystem services that rely on meadow structure such as carbon storage, fish nursery habitat and sediment trapping may be diminished in a grazed meadow (Heck *et al.,* 2003; De Boer 2007; Atwood *et al.,* 2015). In tropical seagrass meadows with no megaherbivores, much of the seagrass productivity enters the detrital chain (Lee *et al.,* 2015). The presence of megaherbivores allows significant amounts of productivity to be exported from the seagrass meadow (Bakker *et al.,* 2016a; Heck *et al.,* 2008).

In Gladstone, the consumption of seagrass material by megaherbivores appears to be an important pathway for the export of seagrass generated primary productivity. Large-scale export of seagrass carbon by megaherbivores may be a possible explanation for the low levels of seagrass-generated blue carbon that have been observed for Gladstone seagrass meadows (Ricart *et al.,* 2020), diminishing their role in climate change mitigation. Changes in structural complexity of a seagrass meadow will alter the structure of the food web that it

supports (Jinks *et al.,* 2019). Such grazer-mediated changes in structure have caused lower fish catches in other locations that have created conflicts between fishers and green turtles (Arthur *et al.,* 2013).

Not all seagrass ecosystem services will be negatively impacted by herbivore pressure, such as those related to the presence of more megaherbivores feeding, including tourism focussed on the presence of charismatic megafauna (Cullen-Unsworth *et al.,* 2014). Megaherbivore excretion can also benefit seagrass meadows by providing a source of nutrients (Bakker *et al.,* 2016a), however this is less likely to be important in areas that are not nutrient limited such as Gladstone Harbour (Gladstone Healthy Harbour Partnership, 2019). A balanced system with a range of herbivores may also lead to maximising the widest range of ecosystem services provided by seagrasses (Scott *et al.,* 2018; Chapter 2).

The relationship between grazers and seagrasses is important for managers to consider as they monitor habitats and implement management measures. Both macroherbivores and megaherbivores can aggregate in Marine Protected Areas, resulting in higher levels of herbivory here (Alcoverro and Mariani 2004; Prado *et al.*, 2008; Christianen *et al.,* 2014). If managers are prioritising the ecosystem services that seagrass meadows provide which rely on meadow structure, it is important to understand how these change with grazer mediated changes in meadow structure. Understanding the plant-herbivore system as a whole is also key for monitoring programs operating in areas with megaherbivore populations, as seagrasses are well adapted to cope with megaherbivory, but may exist in an altered state when grazed (Domning 2001; Jackson 2001; Scott *et al.*, 2018; Chapter 2). Most seagrass monitoring programs that report on or score environmental health are based on metrics of structure such as high biomass or seagrass cover (Duffy *et al.,* 2019). However, because many of these are modified by grazing, a seagrass meadow can appear unhealthy when aboveground structures such as biomass and percent seagrass cover are low, but may actually be part of a healthy seagrass-herbivore system. If grazing exceeds seagrass productivity, overwhelms belowground reserves, or acts in combination with other stressors, it can lead to seagrass declines, or in extreme cases meadow collapse (Arthur *et al.,* 2013; Christianen *et al.*, 2014; Fourqurean *et al.,* 2019). Management measures can modify the plant-herbivore interactions, such as bottom-up controls on seagrasses and top-down controls on herbivores that occur in seagrass meadows. Having more information on these interactions can inform monitoring and management of both seagrasses and herbivores. Understanding whether a

seagrass-herbivore system is in balance, or becoming overgrazed, is essential to prevent meadow decline due to herbivory.

In conclusion, megaherbivore grazing can be a significant top-down structuring influence on subtropical seagrass meadows. By significantly reducing aboveground biomass and shoot height, megaherbivore grazing can impact the range of other ecosystem services provided by the meadow. Due to these significant herbivore mediated changes I suggest that tropical and subtropical systems should ideally be monitored as a coupled seagrass-herbivore assessment.

Chapter 4

Chapter 1:
Introduction

Chapter 2:
The role of herbivory in structuring tropical
seagrass ecosystem service delivery

Chapter 3:
Herbivory has a major influence on structure and condition
of a Great Barrier Reef subtropical seagrass meadow

Chapter 4:
Green turtle grazing plot
formation creates structural
changes in a multi-species GBR
seagrass meadow
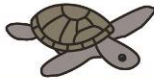
Chapter 5:
Spatial and temporal
patterns in macroherbivore
grazing in a multi-species GBR
seagrass meadow

Chapter 6:
Spatial and temporal variability
of green turtle and dugong
herbivory in seagrass meadows
of the southern GBR

Chapter 7:
General discussion

Chapter 4

Green turtle (*Chelonia mydas*) grazing plot formation creates structural changes in a multi-species Great Barrier Reef seagrass meadow

Chapter 3 showed the overwhelming importance of megaherbivory in structuring an intertidal seagrass meadow in an industrial location. This chapter builds on Chapter 3 by investigating the impact of megaherbivory within a diverse, shallow, subtidal, tropical seagrass meadow located within a Marine Protected Area on the GBR with large populations of green turtles. This chapter adds to our understanding of how different megaherbivore feeding strategies can structure GBR seagrass meadows in different ways depending on the feeding method used, and documents new grazing behaviours not previously seen in GBR seagrass meadows.

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All authors helped to conceive the design of this experiment and assisted with fieldwork, ALS led all fieldwork activity. ALS conducted all lab and data analysis with assistance from Seagrass Ecology Lab staff and volunteers. ALS prepared the manuscript with comments from MAR and PHY.

Abstract

The Great Barrier Reef (GBR) contains extensive seagrass meadows with abundant and diverse herbivore populations. Typically, meadows in the region are multi-species and dominated by fast growing opportunistic seagrass species. However, we know little about how herbivores modify these types of seagrass meadows by grazing. I conducted the first megaherbivore exclusion study in the GBR at Green Island (Queensland) to understand how green turtle grazing structures these multi-species tropical seagrass meadows. After excluding green turtles for three months, we found that grazing only impacted seagrasses at one site, where green turtles created a grazing plot by actively feeding on both above and below ground seagrass structures, a rare observation for the species. Within this grazing plot at the end of the experiment, the un-caged control treatments open to grazing had a 60% reduction in both above and below ground biomass, and shoot height was reduced by 75% but there was no impact of grazing on seagrass species mix. This chapter shows that grazing plot formation by green turtles occurs in GBR fast growing seagrass communities and reduces both above and below ground seagrass biomass, this behaviour may be targeting elevated leaf nutrients, or nutritional content of rhizomes. This study is the first documented case of grazing plot formation by green turtles in the GBR and suggests that grazing pressure has a major influence on seagrass meadow structure.

Introduction

Herbivory is a key structuring force in terrestrial grassland ecosystems (Augustine and McNaughton, 1998; Borer *et al.,* 2014). While grazing dynamics in terrestrial grasslands are well-understood (Augustine and McNaughton, 1998; Díaz *et al.,* 2007b; WallisDeVries *et al.,* 1999), their equivalent in marine environments, grazing on seagrass meadows, has received less attention. Grazers in terrestrial grasslands operate in systems with a majority of low nutritive forage material, so prioritize selection of high quality forage to obtain the nutrients that they are limited by (Owen-Smith and Novellie, 1982; Senft *et al.,* 1987). Large terrestrial herbivores can focus their feeding on small areas to maintain a grazing lawn of low biomass, high quality food (Hempson *et al.,* 2015). These well-established patterns of herbivory that operate in many terrestrial grasslands could potentially occur in a similar manner in marine systems such as seagrass meadows. Herbivory on seagrasses has been identified as an important top-down influence affecting the structure and functioning of a seagrass meadow (Heck and Valentine, 2006; Valentine and Heck, 1999). However, many of the plant-

herbivore interactions taking place in seagrass meadows and the mechanisms behind them have not been quantified (York *et al.,* 2017).

The Great Barrier Reef (GBR) has one of the world's largest areas of seagrass (Coles *et al.,* 2015) that supports a diverse herbivore community, including the largest remaining population of green turtles in the world - located in the northern GBR (Limpus, 2008). The abundance and diversity of seagrasses and large megaherbivore populations in the GBR create conditions similar to those under which seagrasses evolved and adapted to cope with high herbivory pressure (Domning, 2001; Jackson *et al.,* 2001). Seagrasses share a range of adaptations to herbivory with terrestrial grasses, most importantly their relatively inaccessible belowground rhizome biomass and their ability to compensate for biomass lost to grazing (Heck and Valentine, 2006; Valentine and Heck, 1999). In modern times, seagrass-herbivore interactions have been modified by human activity to various effects. Loss of seagrasses from anthropogenic stresses has reduced food for megaherbivores (Waycott *et al.,* 2009). Overfishing, hunting and collection of eggs from nesting sites have in some locations led to declines in megaherbivore populations, freeing seagrass meadows from grazing pressure (Marsh *et al.,* 2005). Overharvesting of top predators in other locations have allowed herbivores to thrive and increased grazing pressure on seagrasses (Burkholder *et al.,* 2013; Estes *et al.,* 2011).

The megaherbivores that graze on GBR seagrass meadows, green turtles (*Chelonia mydas*) and dugongs (*Dugong dugon*), can consume large amounts of seagrass biomass and significantly alter meadow structure (Bakker *et al.,* 2016a). In tropical environments, these herbivores reduce seagrass shoot height, shoot width, shoot density and biomass as well as causing shifts in the species composition of meadows (Aragones *et al.,* 2006; Arthur *et al.,* 2013; Lal *et al.,* 2010). In some cases, turtle overgrazing has resulted in detrimental impacts on seagrass meadows, driving them towards collapse, often gradually via downgrading to a lower successional state (Arthur *et al.,* 2013; Christianen *et al.,* 2014; Fourqurean *et al.,* 2019; Lal *et al.,* 2010; Murdoch *et al.,* 2007). Any changes to seagrass meadow structure caused by grazing will change the ecosystem services provided by the meadow, for example heavily grazed meadows may be a less valuable fishery habitat (Arthur *et al.,* 2013; Heck *et al.,* 2003; Scott *et al.,* 2018; Chapter 2).

Changes in seagrass meadow structure caused by large herbivores depend on the density of herbivores, and how these herbivores feed (Kelkar *et al.,* 2013; Molina-Hernández and van Tussenbroek, 2014). Green turtles have been observed using several foraging strategies,

which cause differing impacts on the seagrass meadow: Green turtles can maintain grazed plots by consistently re-cropping blades in the same area, they may initiate these plots by cropping shoots at the base and allowing old aboveground material to float away (Bjorndal, 1980; Johnson *et al.,* 2019; Molina-Hernández and van Tussenbroek, 2014; Ogden, 1980). They can also be more dynamic in their grazing by maintaining a mosaic of grazed plots and moving among them (Molina-Hernández and van Tussenbroek, 2014). And green turtles can also exhibit a general browsing strategy, cropping all of the seagrass across a meadow without obviously targeting patches (Molina-Hernández and van Tussenbroek, 2014; Nowicki *et al.,* 2018, Scott *et al.,* 2021a; Chapter 3). These feeding behaviours can be modified by top-down factors, for example predator presence can modify green turtle grazing behaviour (Burkholder *et al.,* 2013; Heithaus *et al.,* 2014) and green turtles can aggregate in marine protected areas (Christianen *et al.,* 2014; Scott *et al.,* 2012). The foraging strategies that green turtles use will vary depending on a combination of location specific seagrass attributes and the top-down influences at a given site.

Green Island has a population of resident juvenile green turtles and is one of the oldest no-take marine protected areas in the GBR. Green Island is surrounded by a large intertidal and subtidal seagrass meadow comprised of ten species, that is an important food source for green turtles (Fuentes *et al.,* 2006; Rasheed, 2004). The opportunistic, fast growing seagrass species present at Green Island represent the local climax community for this area, which has likely evolved and expanded under continued grazing pressure (Rasheed, 2004). The Green Island area is however subject to indigenous hunting, with estimates that the nearby community may take as many as 260 green turtles annually from the wider Cairns area (Limpus, 2008), which could influence the numbers of adult green turtles feeding around Green Island (Fuentes *et al.,* 2006). The large area of seagrass dominated by opportunistic fast-growing species and top-down controlled turtle population at Green Island, means that the grazing pressure here is likely to be moderate, meaning there is an abundance of food for herbivores. This seagrass community structure is likely to have been shaped by the plant-herbivore dynamics at this site, with continued grazing pressure from green turtles.

The purpose of this study was to use exclusion cages to examine how grazing by megaherbivores at Green Island modifies seagrass meadow structure and species composition. Exclusion cages have been used extensively in field studies to understand how grazing impacts both terrestrial grasslands and seagrass meadows (Forbes *et al.,* 2019). However, the majority of seagrass exclusion studies have been in sub-tropical locations and

with monospecific seagrass meadows of long-lived species (Armitage and Fourqurean, 2006; Burkholder *et al.,* 2013; D'Souza *et al.,* 2015; Ebrahim *et al.,* 2014; Fourqurean *et al.,* 2010; Williams, 1988). In the GBR, where meadows are often multi-species and dominated by fast growing opportunistic species, there have been no similar studies.

For the first time, this study examines how a green turtle population in the GBR structures the extensive and diverse opportunistic seagrass meadows here and adds to the knowledge of megaherbivore-seagrass interactions in the tropics. Specifically, I tested the effect on seagrass biomass, shoot morphology, tissue nutrients and species composition of green turtle grazing by removing herbivory pressure through exclusion cages.

Material and methods

Study site

Herbivore exclusion experiments were conducted in a subtidal seagrass meadow at Green Island (16°45.5'S, 145°58.3'E) (Figure 4.1), a vegetated sand cay located on the inner edge of the GBR, 27 km northeast of Cairns (Queensland, Australia). The most common megaherbivore present here are green turtles. Dugongs are present in the area but only rarely observed in the Green Island seagrass meadows and not at all during the course of my study. Other herbivores present in the meadow include fish, urchins and mesoherbivores (Pers. Obs.).
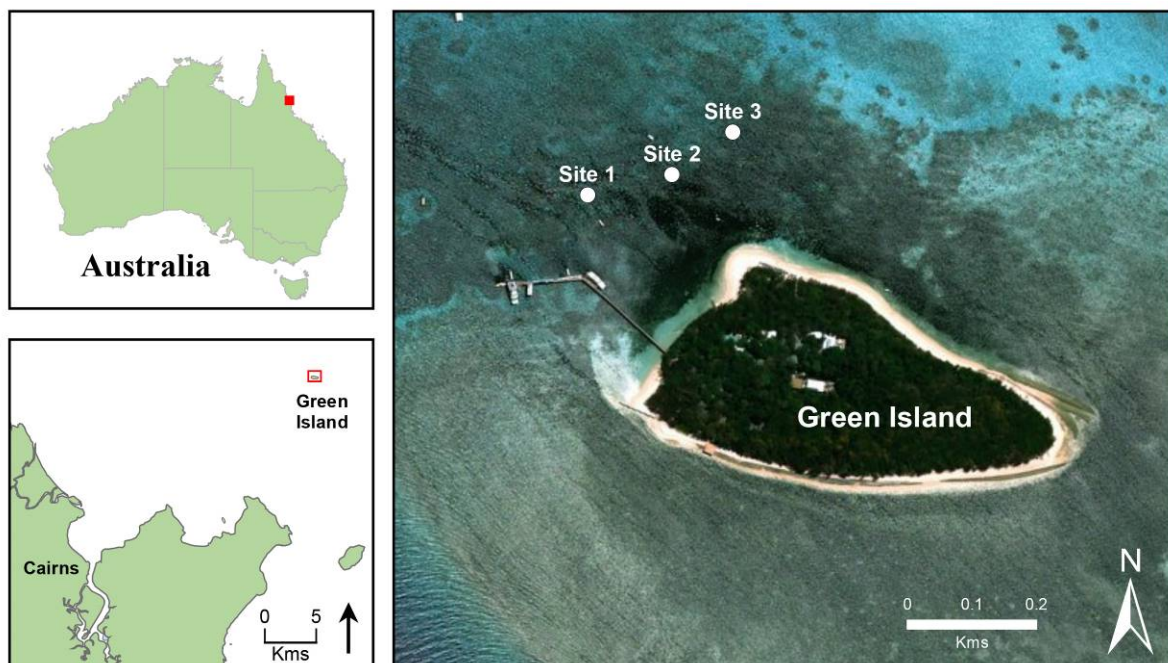
Figure 4.1: Location of study sites at Green Island.

Experimental design

Megaherbivore exclusion cages were deployed at three sites within the same meadow (Figure 4.1). Sites were 200m apart and all sites were at an average depth of 1m below chart datum, and with the same mixed-species seagrass community present at all sites, dominated by *Halodule uninervis*, *Syringodium isoetifolium* and *Cymodocea rotundata*. Exclusions were set up and monitored monthly for a duration of three months. Steel cages 2m x 2m x 0.5m with a 20 x 20cm mesh were used to exclude megaherbivores, these allowed other herbivores (fish, urchins and mesoherbivores) to access the seagrass (Figure 4.2). Three control and three cage treatments were deployed at each site. Each treatment was randomly allocated to a square within a 6 x 4 grid with at least a 2.5m gap between each plot, meaning the experimental area at each site was 15.5 x 9.5m. Treatments were divided equally between each site, giving three replicates of each treatment per site and a total of nine replicates of each treatment across all sites.

To check for possible shading impacts of the cages, benthic light measurements reaching the seagrass canopy were taken inside a megaherbivore cage and a control plot using 2π cosine-corrected irradiance loggers (Submersible Odyssey Photosynthetic Irradiance Recording System, Dataflow Systems Pty. Ltd., New Zealand) calibrated using a cosine corrected Li-Cor underwater quantum sensor (LI-190SA; Li-Cor Inc., Lincoln, Nebraska USA) and corrected for immersion using a factor of 1.33 (Kirk, 1994). Loggers measured photosynthetically active radiation (PAR) and recorded readings every 15 minutes for one month, these readings were used to measure total daily PAR (mol photons m^{-2} day^{-1}) reaching seagrasses. Light data showed that megaherbivore cages did not reduce the total daily PAR reaching the seagrass inside megaherbivore cages (see Figure B.1).

Sampling

Three shoot height measurements were made in each plot in the field every month, by grasping a handful of seagrass and measuring the shoot length of the entire canopy and ignoring the longest 20% (Duarte and Kirkman, 2001).

Shoot density was determined in the field at the beginning (August) and end (November) of the experiment, with four replicate counts of all species in a 10 x 10cm quadrat carried out in each plot.

When turtle feeding was observed at site 3 after two months, GoPro cameras were deployed to confirm that turtle grazing had caused the observed losses in seagrass. A camera was

mounted on a cage at the grazed site and recorded video for 1.5hrs while the site was not being surveyed.

At the end of the experiment, three replicate 15 cm diameter cores were taken from each cage and control plot, these cores were frozen and analysed in the lab for shoot counts, above and below ground biomass weights. Seagrass cores were processed in the lab by defrosting samples, counting the number of shoots for each species and separating the above and below ground biomass where the leaf meets the rhizome. For biomass samples, the seagrass was dried in the oven at 60°C for 10 days and then weighed. In response to the observed grazing plot formation, seagrass tissue nutrient content from inside megaherbivore cages at sites 1 (no grazed plot formed) and 3 (grazed plot formed) was measured from the three most abundant seagrass species (*Cymodocea rotundata*, *Halodule uninervis* and *Syringodium isoetifolium*). Epiphytes were removed in the lab by scraping with a microscope slide and seagrass was dried for 10 days at 60°C. Dried seagrass was finely ground prior to analysis, 0.5g of dried material was analysed for each species and two samples were analysed from all three species in each megaherbivore cage plot. Carbon content was measured by placing a sample into an oxygen-rich atmosphere in a combustion furnace regulated at 1400°C, the carbon is then quantified as the gas flow of the CO_2 content using an infrared measurement cell (Rayment and Lyons, 2011a). Nitrogen and phosphorus were measured by digesting leaf material with a mixture of salicylic and sulfuric acid with hydrogen peroxide, this was diluted and analysed by automated colorimetry in a two-channel analyser instrument (Rayment and Lyons, 2011b).

Statistical analysis

Data were analysed using a generalised linear model with a log-link and a gamma distribution. Both site and treatment were included as predictor variables, with the response variables aboveground biomass, belowground biomass and shoot density tested individually for all seagrass species combined. For shoot height data over the duration of the experiment, month was also included as a predictor variable and the plot identity used as a random factor. The MuMin package was used to dredge all model options and find the most parsimonious model that was within two points of the lowest AIC value (Bartoń, 2019). An F-test was used to determine the significance of each variable in the best-fit model using the anova() function in R. Post hoc analysis was conducted to compare treatment groups using a Tukey test in the emmeans package (Lenth, 2019). Residual and q-q plots of normalised residuals of the model were inspected for heteroscedasticity and non-normality. Statistical analyses were conducted

in R v.3.5.2. (R Core Team, 2019) and model outputs were plotted using ggplot2 (Wickham, 2016). Differences in seagrass community among exclusion treatments, site and date (fixed effect) were analysed based on Bray Curtis distance matrices with 9999 permutations using a three way fully orthogonal permutational multivariate analysis of variance (PERMANOVA) with pairwise analysis (Anderson, 2008). PERMANOVA was performed using the PRIMER-v6 statistical software package. A SIMPER analysis was used to determine the species making the largest contribution to differences between sites. The nutrient data were compared using T-Tests to compare each nutrient in each species between sites 1 and 3. A Bartlett-test was used to check for equal variances and adjust the analysis if variances were not equal.

Results

Grazing at sites 1 and 2 did not impact any of the seagrass metrics measured, green turtles created a grazing plot covering approximately 50 x 50m at site 3 (Figure 4.2) leading to reduced aboveground biomass (Figure 4.3), belowground biomass (Figure 4.4) and shorter shoots (Figure 4.5). Shoot density was not impacted by megaherbivore grazing at site 3 (Figure 4.6) and grazing did not cause a shift in species composition (Figure B.2). Monthly shoot height measurements (Figure 4.5) show that the majority of the shoot height reduction at site 3 took place between September and October, after the experiment had been running for two months. At this time, the grazed plot was observed at site 3 (Figure 4.2). At the end of the experiment, seagrass inside megaherbivore cages within the grazed plot area had a higher nutrient content compared to seagrass inside megaherbivore cages at site 1 where no grazed plot was formed.
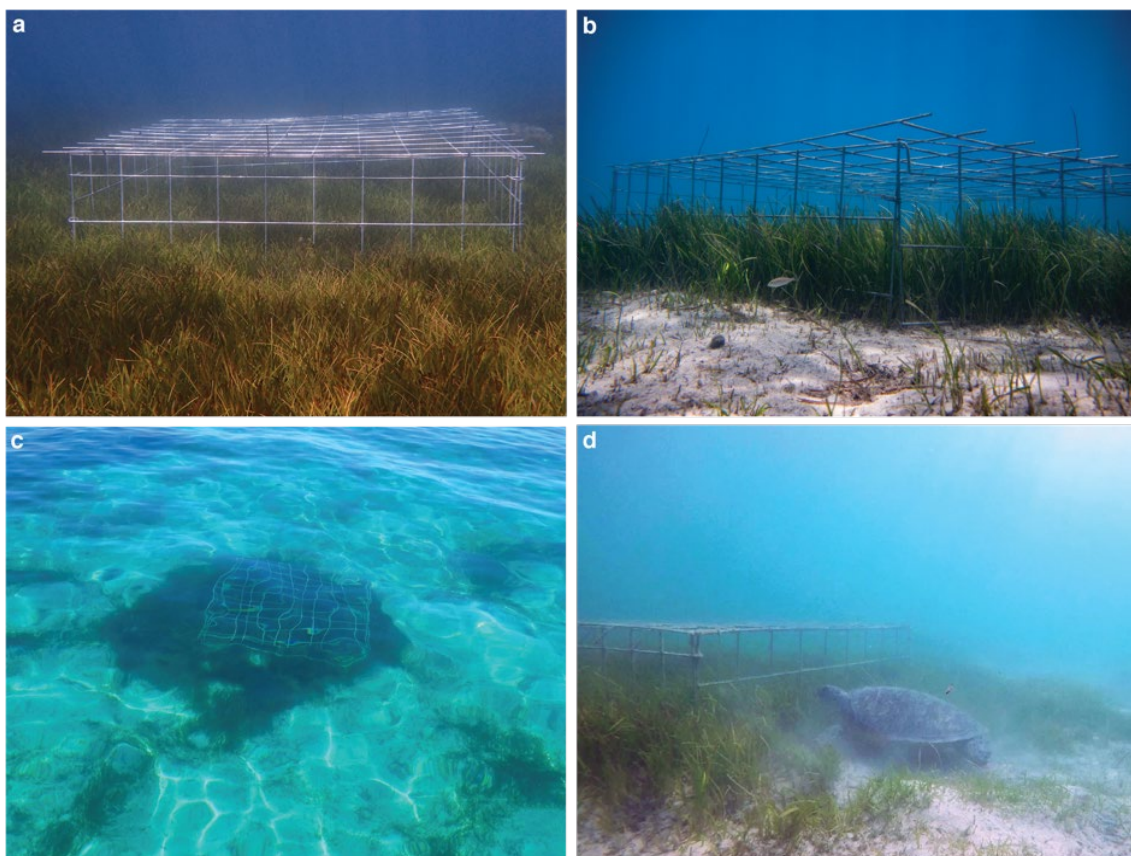
Figure 4.2: Megaherbivore cage at (a) an ungrazed site and (b and c) at site 3 where grazing took place two months into the experiment. Turtles were filmed grazing at site 3 (d).

Effect of grazing on seagrass metrics

There was a significant interaction between site and treatment on aboveground seagrass biomass ($F_2=10.7592$, $p<0.001$). Aboveground biomass at sites 1 and 2 was not impacted by grazing, whereas at site 3 post hoc tests show the open to grazing control plots had less aboveground biomass (67.16 +/- 11.7 SE gDW m^{-2}) than caged plots (167.12 +/- 20.5 SE gDW m^{-2}; Figure 4.3).
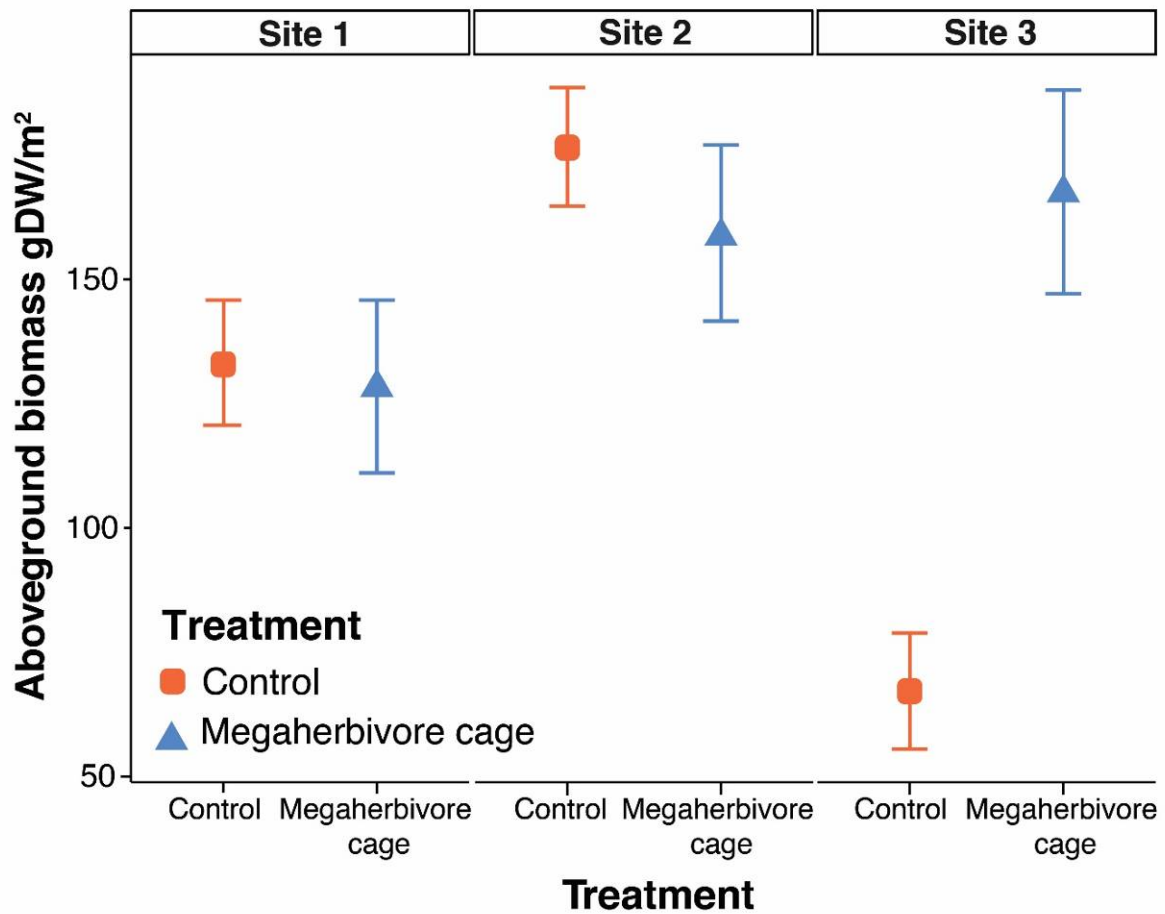
Figure 4.3: Mean aboveground seagrass biomass at all three sites in caged and control treatments with standard error.

Belowground seagrass biomass was also reduced by grazing activity at site 3 (Figure 4.4). There was a significant interaction between site and treatment on belowground seagrass biomass ($F_2=3.6863$, $p<0.05$). Post hoc tests show that at site 3, the open to grazing control plots had less belowground biomass than the megaherbivore cages.
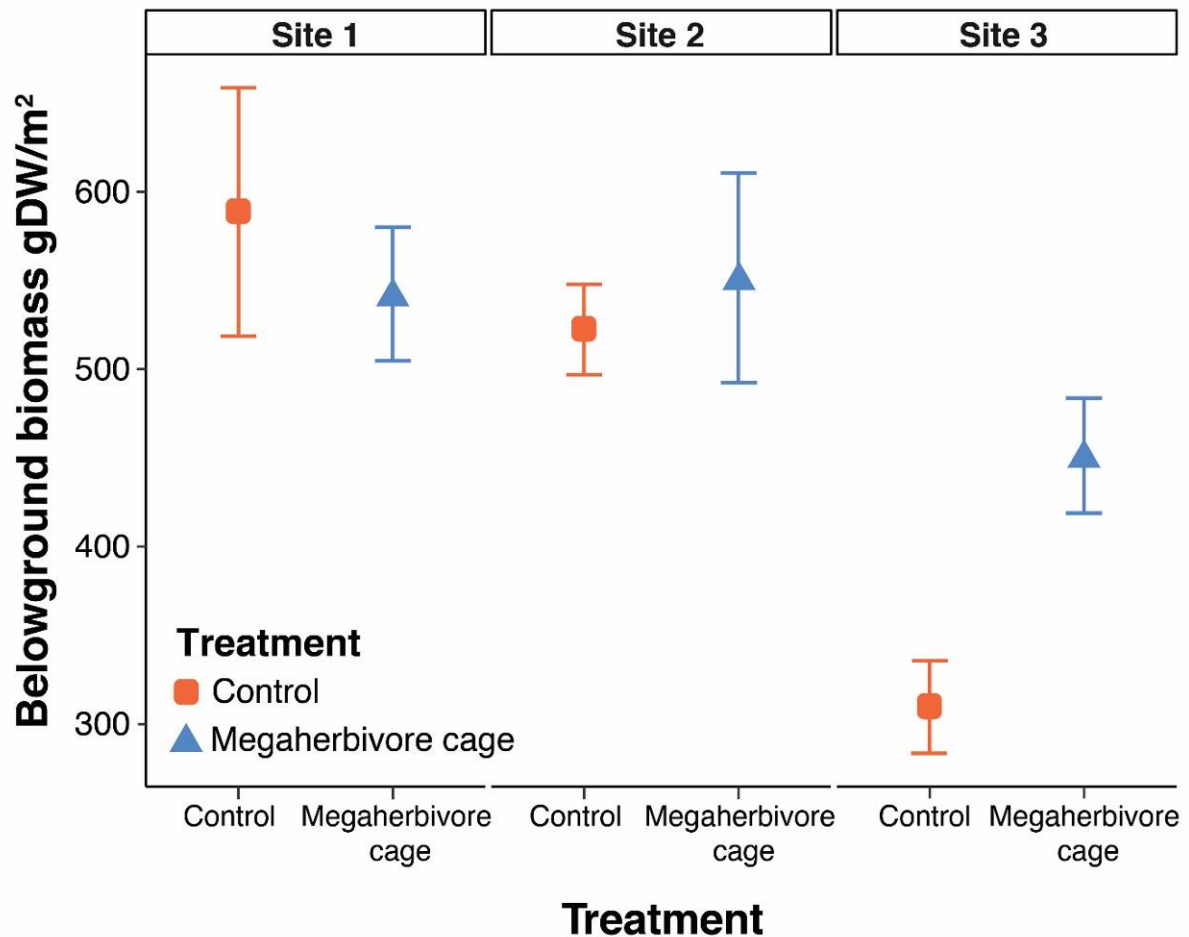
Figure 4.4: Mean belowground seagrass biomass at all three sites in caged and control treatments with standard error.

There was a significant interaction between month, site and treatment for seagrass shoot height ($F_2 = 12.9884$, $p < 0.001$) as shown in Figure 4.5. Post hoc tests showed that there were significant pairwise differences at site 3 in October and November and site 2 when the experiment was set up in August and also in September where the open to grazing control treatments had a shorter shoot height than the megaherbivore exclusion cages. The changes caused by grazing are only seen at site 3 from October onwards when mean shoot height was 9.1 (+/- 1.5 SE) cm in control plots compared to 24.3 (+/- 0.8 SE) cm inside exclusion cages. Grazing further decreased shoot height at site 3 in November when mean shoot height in control plots was 7.2 (+/- 0.8 SE) cm compared to 20.7 (+/- 0.7 SE) cm inside the cages.
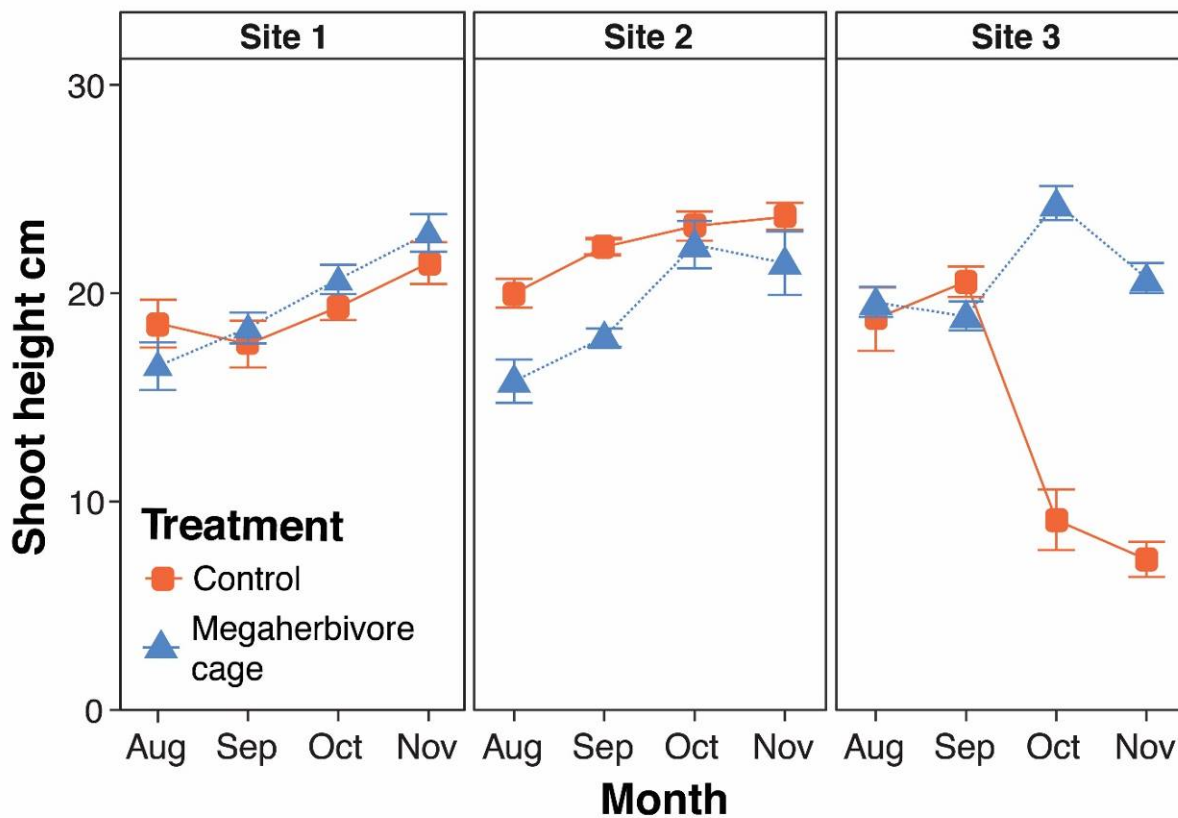
Figure 4.5: Mean shoot height throughout the experiment at all three sites in caged and control treatments with standard error.

The open to grazing control plots at the grazed site 3 had fewer shoots than the ungrazed caged plots at the site and the lowest shoot density of all treatments. However shoot density was not significantly different between treatments or sites after three months ($F_2 = 4.8753$, $p = 0.1324$) (Figure 4.6).
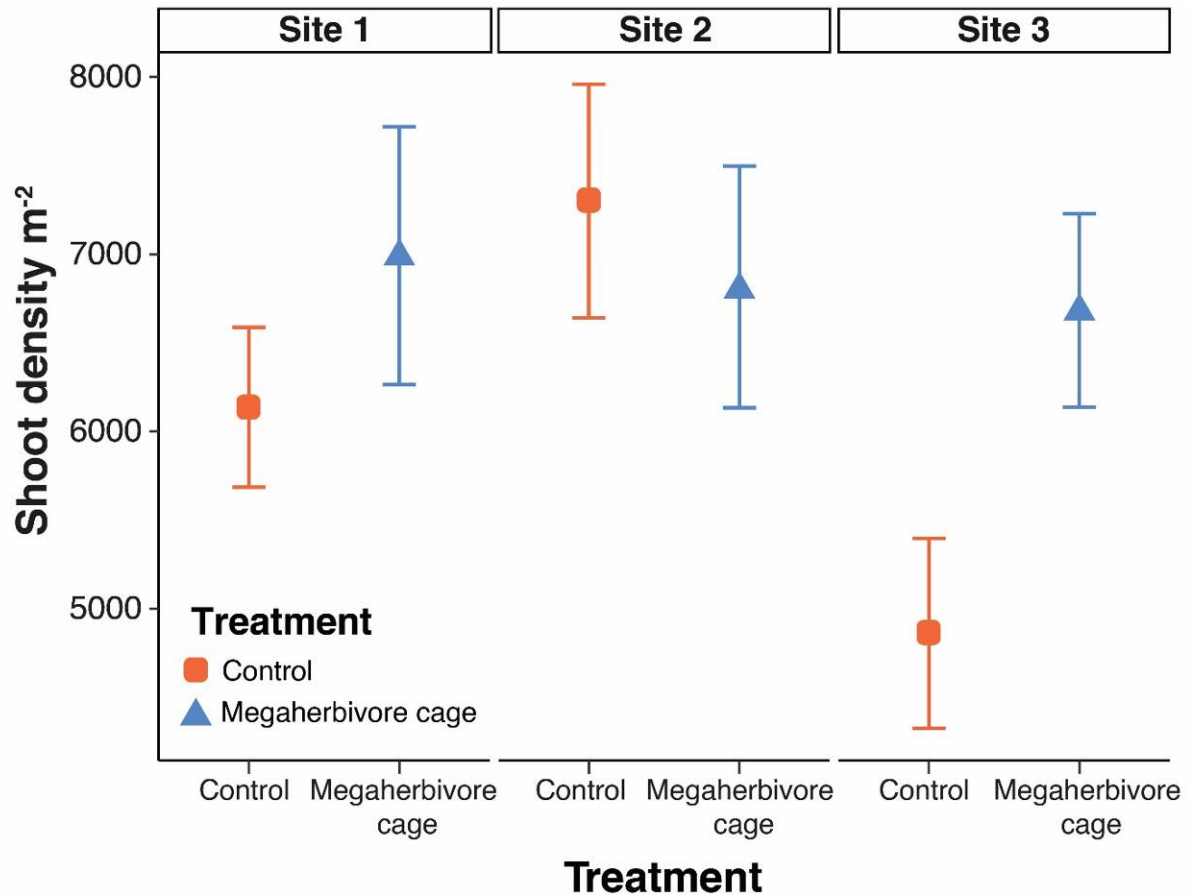
Figure 4.6: Mean shoot density per m^2 with standard error at all three sites in caged and control treatments.

Seagrass species composition was not different between the start and end of the experiment, or between treatments, however there was a difference in seagrass species composition between sites (PseudoF$_{2, 24}$ = 4.1678, p<0.05). Pairwise comparisons show differences were between sites 1 and 3 (t_{16} = 2.56, p<0.001) and sites 2 and 3 (t_{16} = 2.53, p<0.001), however there were no differences between sites 1 and 2 (t_{16} = 0.43, p = 0.88). The SIMPER analysis indicates that differences between site 3 and the other two sites are driven by a lower abundances of *H. uninervis* and *S. isoetifolium* at site 3, however *S. isoetifolium* remains the most abundant species at site 3 (see Figure B.2 and Table B.1).

Nutrient analysis

Nutrients were higher inside the megaherbivore exclusion cages within the grazed plot at site 3 compared with site 1 where no grazing plot was formed (Figure 4.7) at the conclusion of the experiment. Nitrogen was higher at site 3 for *C. rotundata* (T= -2.445, p=0.035), *H. uninervis* (T= -2.309, p= 0.062) and *S. isoetifolium* (T= -3.806, p=0.004). Carbon was higher at site 3 in *H. uninervis* (T = -3.218, p=0.015). Phosphorus was higher at site 3 in *C. rotundata* (T = -2.076, p=0.065) and *S. isoetifolium* (T = -3.2126, p = 0.009).
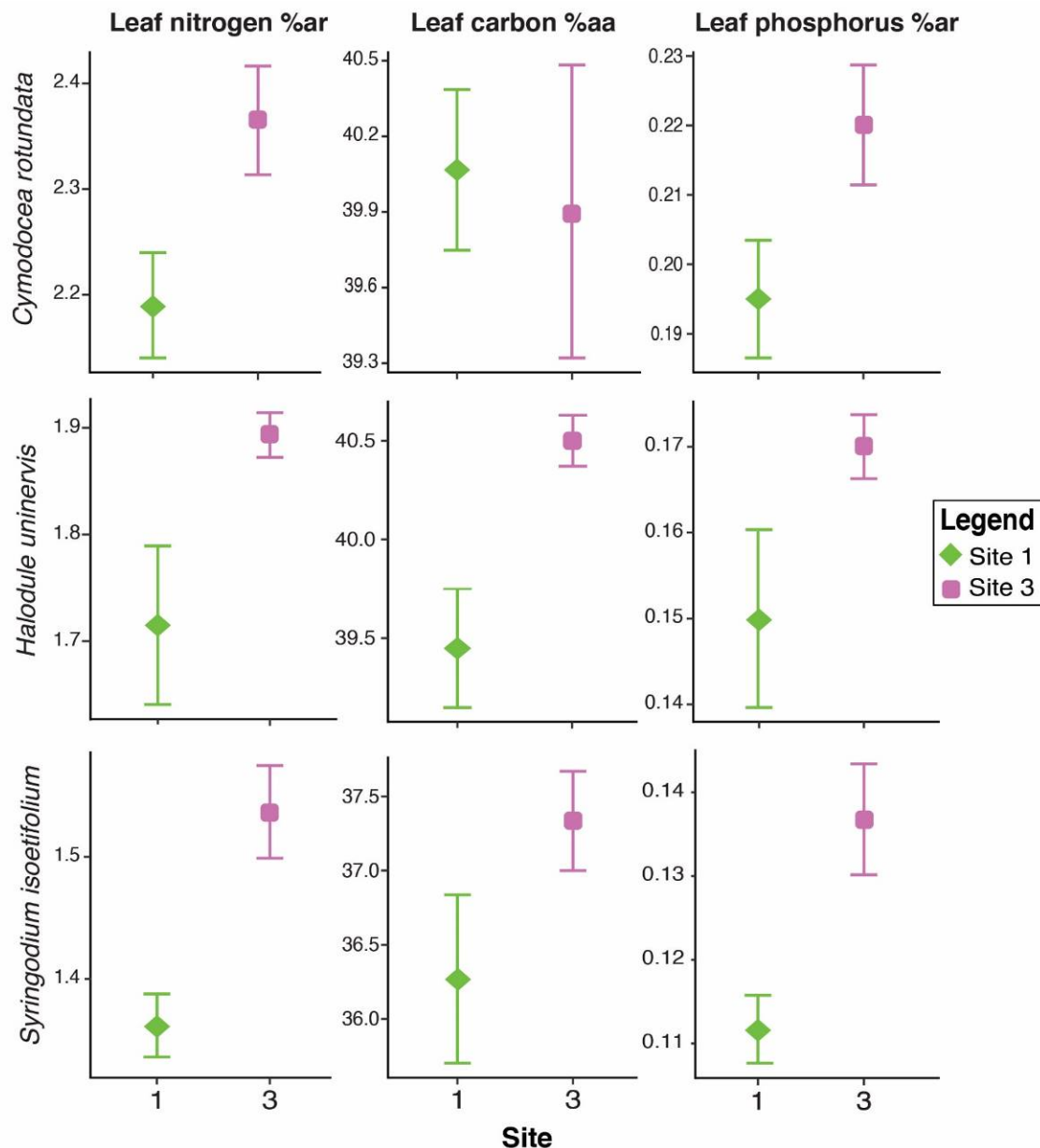
Figure 4.7: Nutrient concentrations at site 1 and 3 for *Cymodocea rotundata*, *Halodule uninervis* and *Syringodium isoetifolium*. Plots show mean and standard error.

Discussion

The Great Barrier Reef has one of the world's largest and most diverse areas of seagrass, which supports one of the world's largest populations of green turtles (Coles *et al.,* 2015; Limpus, 2008). Despite this, we are only just beginning to understand the plant-herbivore interactions that structure GBR seagrass meadows and modify the ecosystem services that they provide. Here, I have documented a concentrated grazing event within one area of a seagrass meadow that impacted meadow structure in several different ways. My study is the first time that this type of grazing has been documented in the GBR, and the first time that turtles feeding on below ground rhizomes have been recorded here. Although this is the first time that we have documented targeted grazing, it is likely to be a repeated behaviour at Green Island. Historical seagrass surveys have noted meadow 'blowouts' at Green Island that appeared to shift over time (Mellors *et al.,* 1993), and a seagrass recovery study in the same meadow as my study noted grazing disturbances that impacted meadow structure at a similar scale (Rasheed, 2004).

The Green Island seagrass meadow appears well-adapted to cope with this level of herbivory. Despite the resident population of large herbivores, this meadow has been able to persist through time (Mellors *et al.,* 1993; Rasheed, 2004). The multi-species seagrass assemblage is able to recover rapidly from small scale impacts as demonstrated by previous experimental work in the meadow (Rasheed, 2004). It is likely that the mix of colonising and opportunistic seagrass species that constitute the meadow has developed in part due to the herbivory pressure that allows for the maintenance of such a diverse suite of competing plant species. Herbivory pressure may have caused this meadow to switch from a *H. uninervis* dominated meadow in 1995 – 1997 (Rasheed, 2004), to a meadow dominated by the colonising *S. isoetifolium* in 2017. *S. isoetifolium* has been shown to be a rapid coloniser of disturbed plots at Green Island that once established is able to persist at the expense of other species (Rasheed 2004). Although formation of the grazing plot did not impact species composition at this site over the duration of my study, the lowest abundances of *H. uninervis* were observed in controls within the grazed plot at site 3, indicating that turtle grazing may cause declines in the later successional species *H. uninervis.* Site 3 also had the lowest abundances of *H. uninervis* at the start of the experiment, possibly due to previous green turtle grazing pressure. It is possible given longer time frames of herbivore exclusion than the 3 months of my study, that the caged plots may have shifted in species composition toward later successional species.

Green turtle feeding established a grazing plot that substantially reduced seagrass aboveground biomass and structure in terms of shoot height in one of the three sites sampled in this meadow. This type of feeding has been seen in other locations, for example Molina-Hernández and van Tussenbroek (2014) recorded a mosaic of maintained grazing plots under a moderate grazing regime in the Mexican Yucatan Peninsula where green turtles would crop blades at the base and then graze the regrowth. These plots were usually continually grazed for a period of 13 months to over 2 years. Similar creation of long term maintained grazed plots has been observed previously in the Bahamas, the Caribbean, the Gulf of Mexico and the Indo-Pacific (Bjorndal, 1980; Christianen *et al.,* 2014; Hearne *et al.,* 2018; Johnson *et al.,* 2019; Ogden, 1980; Williams, 1988). This grazing enables green turtles to cultivate patches of seagrass and graze the nutrient-rich easily-digestible regrowth, which has higher energy and is richer in nitrogen and phosphorus (Bjorndal, 1980; Moran and Bjorndal, 2007). In my study, the maintenance of this grazed plot was not monitored over the longer term. However, the site was visited three months after the experiment ended, and the grazed seagrass had not recovered to the same condition as the surrounding meadow. The concentrated feeding observed at Green Island could be an indication that green turtles here are also maintaining grazing plots for short periods of at least a few months before moving on to another area of the meadow, likely using this foraging strategy alongside a more general browsing strategy.

Green turtle grazing did not reduce shoot density at Green Island. Reductions in shoot density have been observed when large herds of dugongs feed (Preen, 1995), between low and high turtle density areas (Lal *et al.,* 2010) and in long term megaherbivore exclusions (Burkholder *et al.,* 2013). However, in tropical seagrass meadows, simulated grazing does not result in changes in shoot density (Johnson *et al.,* 2020; Moran and Bjorndal, 2005; Mutchler and Hoffman, 2017). Changes in shoot density may only be observed at very high grazing pressure or over long time scales. In my study the mean shoot density of treatments open to grazing within the grazed plot at site 3 was the lowest observed, indicating grazing was causing some declines in shoot density. If the turtles continued to graze in this area then it is possible that shoot density would have continued to decline further.

Belowground seagrass biomass was also lower in the control treatments at site 3 where the grazed plot was formed. Belowground seagrass root and rhizome material is higher in carbohydrates than the aboveground seagrass material (Lanyon, 1991; Sheppard *et al.,* 2007) and is an important food source for dugong, who dig to excavate the rhizomes as they feed (Marsh *et al.,* 1982; Preen, 1995). The green turtles at Green Island may have excavated this

area as a means to easily access the belowground material, to meet a dietary need for starch. Stomach lavage samples from juvenile green turtles around Green Island have found rhizomes consumed incidentally, with only one sample with rhizomes between 5-25% of diet volume (Fuentes *et al.,* 2006). I obtained video footage at the site that further supports this hypothesis, showing turtles pulling out shoots and rhizomes and consuming the whole shoot and associated rhizome material. This type of belowground feeding has only been documented once previously by Christianen *et al.* (2014), however in that case the green turtles had already consumed most of the aboveground biomass across the entire meadow, whereas in my study there was still extensive aboveground biomass available in other areas of the meadow. At Green Island, turtles appeared to be selecting to feed on belowground structures out of choice rather than necessity. This belowground feeding behaviour may only be a viable strategy, in terms of access to rhizomes and nutritional benefit, in fast growing tropical meadows. The meadows at Green Island have less woody rhizomes than most previous studies where turtle grazing has been examined, these previous studies have focused on slower growing seagrass species with woodier less digestible rhizomes.

Grazing location may also have been influenced by seeking higher nutritional content of seagrass leaves, reflecting common grazing strategies of terrestrial grassland herbivores (Hempson *et al.,* 2015). After the grazing plot was established at site 3, I examined the leaf tissue nutrients in the caged plots at site 3 where seagrass remained unaffected by turtle grazing and compared them with the caged plots at site one where no grazing plot was formed. Leaf tissue nitrogen and phosphorus concentrations within site 3 were higher than those at site one outside of the grazing plot. These samples were taken at the end of the experiment after the grazing plot was established, so should be interpreted with caution, however the elevated nutrient concentrations at site 3 may offer a possible explanation, leading green turtles to target this area to initiate a grazing plot. This type of grazing optimisation has been observed for dugongs in the GBR (Aragones and Marsh, 2000; Aragones *et al.,* 2006; Preen, 1995) and for green turtles in other tropical locations (Bjorndal, 1980; Hearne *et al.,* 2018; Williams, 1988).

Seagrass meadow characteristics and the scale, intensity and frequency of disturbance are important when considering the impacts of grazing on ecosystem services (Eklöf *et al.,* 2008; Scott *et al.,* 2018; Chapter 2). Tropical seagrasses are able to recover from grazing disturbances quickly (Aragones and Marsh, 2000; Rasheed, 2004, 1999), so the delivery of some ecosystem services such as fish habitat and sediment trapping (De Boer, 2007; Heck *et*

al., 2003) would likely be restored within a matter of months after grazers have moved on. However, some changes may take longer to reverse, such as nutrient cycling and carbon storage and sequestration (Aoki *et al.,* 2019; Johnson *et al.,* 2019; Macreadie *et al.,* 2015). The grazing plot formation I observed at Green Island appeared to occur in only a relatively small area of the overall meadow (approx. 50 x 50m area), with the majority of the seagrass meadow relatively unaffected by green turtle grazing. This could be because the fast growing, opportunistic species in this meadow are adapted to cope with low levels of grazing pressure. Under these circumstances, the overall meadow structure would be relatively unaffected and ecosystem services likely preserved, even if this is part of a mosaic such as observed in other locations (Molina-Hernández and van Tussenbroek, 2014).

Top-down control from higher predators in a seagrass meadow also influences how grazing can modify seagrass meadows and their ecosystem services. A balance in ecosystem services may be difficult to maintain in seagrass meadows where there is a reduction in top-down control on herbivores. Where shark populations are reduced resulting in weaker top-down control on green turtle populations, meadows can become overgrazed as has been documented in other locations (Christianen *et al.,* 2014; Fourqurean *et al.,* 2019; Lal *et al.,* 2010; Murdoch *et al.,* 2007). Humans can also exert top-down control on herbivores and green turtle populations worldwide have been recovering after hunting ceased and effective conservation measures were implemented in many locations (Balazs and Chaloupka, 2004; Broderick *et al.,* 2006; Chaloupka *et al.,* 2008). On the GBR, apex predators like tiger sharks have been considerably reduced over the last half century (Roff *et al.,* 2018), however, the Green Island green turtle population is still under some pressure from indigenous hunting, exercising a top down control on herbivory (Limpus, 2008).

This study shows that green turtles in at least one location in the GBR use a concentrated feeding strategy with possible establishment and maintenance of grazing plots. Such concentrated grazing may be beneficial for herbivores as it could potentially cultivate nutrient-rich areas of the meadow to allow green turtles to access carbohydrate rich belowground seagrass material. The seagrass meadow at Green Island appears to be well adapted to cope with this herbivory pressure, being maintained with a diverse mix of colonising and opportunistic species capable of rapid growth and recovery. Indeed, this species mix may be a result of long-term and persistent herbivory pressure. Seagrasses have been subject to megaherbivore grazing for over 50 million years, and often at a high intensity and frequency (Domning, 2001). Historically, associations between large megaherbivore

populations and seagrass meadows have resulted in closely cropped seagrass meadows where grazing plots merged to cover the entire meadow (Jackson, 2001; Williams, 1988). In the extensive, high biomass meadow at Green Island dominated by opportunistic species, it appears likely that green turtles use the formation of grazing plots and consumption of below-ground material to efficiently meet their nutritional needs in a similar manner to terrestrial herbivores. Establishment of a grazing plot at Green Island significantly impacted both above and belowground seagrass structure in some areas within meadows, which could alter ecosystem service delivery. These grazing plots at Green Island are likely to be formed in a mosaic within the larger meadow. This study is the first time that such concentrated impacts of green turtle grazing have been documented in the GBR and further study would reveal more about how turtles might initiate, maintain, and move between grazed plots. The establishment of grazing plots may also be present at other similar seagrass communities within the GBR and Indo-Pacific. As green turtle populations worldwide continue to recover, it is important to understand and monitor the plant-herbivore interactions operating in seagrass meadows, to inform both conservation and management measures for both the animals and their food source.

Chapter 5

Chapter 1:
Introduction

Chapter 2:
The role of herbivory in structuring tropical
seagrass ecosystem service delivery

Chapter 3:
Herbivory has a major influence on structure and condition
of a Great Barrier Reef subtropical seagrass meadow

Chapter 4:
Green turtle grazing plot
formation creates structural
changes in a multi-species GBR
seagrass meadow

Chapter 5:
Spatial and temporal
patterns in macroherbivore
grazing in a multi-species GBR
seagrass meadow

Chapter 6:
Spatial and temporal variability
of green turtle and dugong
herbivory in seagrass meadows
of the southern GBR

Chapter 7:
General discussion

Chapter 5

Spatial and temporal patterns in macroherbivore grazing in a multi-species tropical seagrass meadow of the Great Barrier Reef

Chapters 3 and 4 show the large structuring impact that megaherbivory can have on a seagrass meadow. However, macroherbivores such as fish and urchins are present on the GBR and could be influencing meadow structure in some locations. Although Chapter 3 showed this was not the case in Gladstone, in this chapter I investigate the impact of macroherbivory in the meadows around Green Island. I chose this site because the seagrass here is structurally complex so a favourable habitat for macroherbivores, and close to coral reef habitat. I also observed both bite marks from herbivores, and the herbivores themselves, while conducting fieldwork for Chapter 3. Green Island is a particularly interesting place to study this dynamic as it is one of the oldest no take Marine Protected Areas on the GBR.

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All authors helped to conceive the design of this experiment, ALS led all fieldwork activity with assistance from PHY and the Seagrass Ecology Lab team. ALS conducted all lab and data analysis. ALS prepared the manuscript with comments from MAR and PHY.

Abstract

Macroherbivory is an important process in seagrass meadows worldwide, however the impact of macroherbivores on seagrasses in the Great Barrier Reef (GBR) has received little attention. I used exclusion cages and seagrass tethering assays with cameras to understand how the intensity of macroherbivory varies over space and time in the seagrass meadows around Green Island, and what impact this has on overall meadow structure. Rates of macroherbivory were comparatively low, between 0.25 – 44% of daily seagrass productivity, however rates were highly variable over a one-year period, and among sites. Loss of seagrass material to macroherbivory was predominantly due to fish, however urchin herbivory was also taking place. Macroherbivory rates were of insufficient intensity to impact overall meadow structure. No macroherbivory events were identified on cameras that filmed in the day, indicating that feeding may be occurring in large infrequently present shoals, or at night. While relatively low compared to some meadows, seagrass macroherbivory was still an important process at this site. I suggest that in this highly protected area of the GBR, where the ecosystem and food webs remain largely intact, macroherbivory was maintained at a low level and was unlikely to cause the large-scale meadow structuring influence that can be seen in more modified seagrass systems.

Introduction

Seagrasses are some of the most productive ecosystems on the planet, capable of turning over their entire standing crop in as little as three to four days for some tropical meadows (Rasheed *et al.*, 2008). This productivity supports diverse food webs through detrital pathways and direct consumption by herbivores, as well as accumulation of detritus in sediments which acts as a carbon sink or is exported to adjacent ecosystems (Duarte and Cebrián, 1996; Hyndes *et al.*, 2014). On a global scale, consumption of seagrass material is relatively low, however in the tropics grazing rates can be much higher (Heck *et al.*, 2020). Grazing of seagrasses by megaherbivores (e.g. green turtles and dugongs) is an important process in tropical regions such as the Great Barrier Reef (GBR) and can have large-scale impacts on seagrass meadows (Aragones and Marsh, 2000; Scott *et al.*, 2020, 2021a; Chapters 3 and 4). However, we know less about the impacts of macroherbivores (e.g. fish and urchins), in GBR seagrass habitats.

Rates of macroherbivory in seagrass meadows can be very high, in some locations exceeding the daily productivity of the meadow. In temperate and subtropical meadows, herbivorous fish can consume all of the daily seagrass productivity and in peak grazing events, can consume over ten times the daily productivity (Holzer *et al.*, 2013; Kirsch *et al.*, 2002; Tomas *et al.*, 2005). In tropical seagrass meadows, estimates of macroherbivore seagrass consumption range from 3 - 26% of daily seagrass productivity (Lee *et al.*, 2015, 2016; Tertschnig, 1989; Vonk *et al.*, 2008), to ten times daily productivity at times (Unsworth *et al.*, 2007), with grazing dominated by herbivorous fish (Lee *et al.*, 2015, 2016). Urchin herbivory can be high in temperate environments, where urchins can consume over 80% of aboveground seagrass biomass (Burnell *et al.*, 2013; Carnell *et al.*, 2020). Less is known about the role of urchin grazing in tropical meadows, but aggregations of urchins can cause large declines in slow growing tropical seagrasses, and urchin herbivory can exceed fish herbivory in some tropical meadows (Alcoverro and Mariani, 2002; Hay, 1984).

The intensity of seagrass grazing by macroherbivores also varies over space and time. Temporal changes in both seagrass productivity and macroherbivore grazing mean that proportional losses of seagrass to macroherbivory can vary seasonally, and losses to macroherbivory are greatest when seagrass productivity is at its lowest, (Kirsch *et al.*, 2002; Tomas *et al.*, 2005; Wressnig and Booth, 2008). Seasonal changes mean macroherbivores can impact meadow establishment and recovery to different degrees at certain times of year (Bessey *et al.*, 2016; Valentine *et al.*, 2000). Macroherbivory also changes on local and landscape spatial scales. This variability can be due to location-specific factors; e.g. sheltered sites can have five times the losses from macroherbivory than exposed meadows (Cebrián *et al.*, 1996). More complex seascapes can also have higher populations of macroherbivores with increased rates of macroherbivory (Unsworth *et al.*, 2007), e.g. scarid fish grazing can double in seagrass meadows that are in proximity to mangroves (Swindells *et al.*, 2017) and reef associated fish can feed in halos around reefs (Chiquillo *et al.*, 2020; Valentine *et al.*, 2008).

In some locations, the results of macroherbivore grazing can lead to substantial changes in seagrass meadow structure, particularly when grazers are present in large numbers, aggregate in groups or where top-down controls are removed. High macroherbivore grazing rates can result in seagrass meadows with higher shoot densities (Planes *et al.*, 2011), less aboveground seagrass material (Carnell *et al.*, 2020; Planes *et al.*, 2011), lower rhizome sugar content (Planes *et al.*, 2011), losses of belowground material (Carnell *et al.*, 2020; Peterson *et al.*,

2002) and lower flowering intensity (Planes *et al.*, 2011). When grazing reduces primary production and canopy height, macroherbivores can reduce meadow function, particularly when grazing on already fragmented seagrass meadows or when large aggregations of macroherbivores overgraze meadows (Eklöf *et al.*, 2008; Gera *et al.*, 2013). These losses in meadow function due to herbivory can have implications for the ecosystem services delivered by a seagrass meadow (Carnell *et al.*, 2020; Eklöf *et al.*, 2008; Peterson *et al.*, 2002; Rose *et al.*, 1999; Scott *et al.*, 2018; Chapter 2). Seagrass grazing by fish can modify the meadow to such an extent that it is a less valuable habitat and foraging ground for other macroherbivores. For example, fish herbivory can reduce meadow structure and increase predation risk for urchins (Heck and Valentine, 1995; Pagès *et al.*, 2012).

In multi-species seagrass meadows, macroherbivores may show a preference for a given species of seagrass and can impact establishment of fast growing species (Bell *et al.*, 2019; Bessey *et al.*, 2016; Mariani and Alcoverro, 1999; Vonk *et al.*, 2008). In some cases, macroherbivores can show a grazing preference based on nutritional characteristics of the plant (Bell *et al.*, 2019; Goecker *et al.*, 2005; Holzer *et al.*, 2013; McGlathery, 1995; Prado and Heck, 2011), but this is not always the case (Kirsch *et al.*, 2002), and the availability of seagrass can be the most important factor influencing grazing (Unsworth *et al.*, 2007).

The GBR consists of a network of Marine Protected Areas (MPAs) that offer varying levels of protection including no take zones that offer the highest levels of protection through to areas where most forms of fishing are allowed (Ogilvie, 2016). We know that MPAs can have a strong influence on macroherbivores through modification of top-down controls that can result in both positive and negative outcomes for seagrass meadows that may differ for fish and urchins (Alcoverro and Mariani, 2004; Bessey *et al.*, 2016; Finke and Denno, 2005; Hay, 1984; Planes *et al.*, 2011; Prado *et al.*, 2008). Therefore, the potential outcomes from the pressures of macroherbivory for seagrass meadows in the GBR are likely to be variable. For example, where coastal seagrass meadows in the GBR have been heavily impacted by turtle and dugong grazing, macroherbivory was found to have an insignificant role in further influencing meadow characteristics (Scott *et al.,* 2020; Chapter 3). However, our understanding of other meadow types and locations in the GBR is limited, especially for areas that have the highest level of protection. This is surprising given the focus on macroherbivores in reef systems, where they play a key role in maintaining GBR reef resilience and promoting coral recovery (Bellwood *et al.,* 2003, 2004; Ceccarelli *et al.,* 2011; Cheal *et al.,* 2016).

In this study I examine patterns of macroherbivory over a year in a multi-species tropical seagrass meadow in Green Island (Queensland, Australia) one of the oldest no-take MPAs on the GBR (Baxter, 1990; Ogilvie, 2016). Green Island is home to a diverse fish and invertebrate community, many of these are herbivorous or omnivorous, with a diverse piscivorous fish population also present (AIMS, 2017). I established macroherbivore exclusion experiments to test whether macroherbivory at this site was having an influence on seagrass meadow structure. I also used seagrass tethering assays to test how macroherbivory varies over space and time around Green Island and used tethers and meadow cores to test whether macroherbivores showed a preference for a given species of seagrass in this multi-species meadow.

Material and methods

Study site

Experiments were conducted at three sites within intertidal and shallow subtidal seagrass meadows around Green Island, a vegetated coral cay 27km off the coast of Cairns, Queensland, Australia (Figure 5.1). Green Island is one of the oldest MPAs on the GBR and was first protected in 1937 then declared a Marine National Park in 1974, and since then no fishing has been permitted around the island (Baxter, 1990; Ogilvie, 2016). The seagrass here is diverse with ten species found around the Island (Fuentes *et al.*, 2006; Rasheed, 2004), and a range of macroherbivores. There are four species of siganid found around Green Island and adults of both shoaling species present, *Siganus fuscescens* and *Siganus lineatus* have been shown to feed on seagrass as an important part of their diet (Pitt, 1997). Visual census surveys around Green Island have found 14 species of parrotfish and herbivorous surgeonfish (AIMS, 2017). Sea urchins are also present in the meadows at Green Island, *Diadema* spp. have been recorded around the coral reef (Baxter, 1990), and I have observed *Tripneustes gratilla* in the seagrass meadow. Differences in the characteristics between the sites examined in this study at Green Island are outlined in Table 5.1. The sites were comprised of six species; *Cymodocea rotundata*, *Cymodocea serrulata*, *Halodule uninervis*, *Halophila ovalis*, *Syringodium isoetifolium* and *Thalassia hemprichii*. For sites 1 and 3, the exclusion cages and tethers were placed in the same location, at site 2 exclusion cages were placed within an area of lower density seagrass to investigate if this was caused by herbivory, but the tethers were placed closer inshore within an area of higher canopy height and shoot density.

Exclusion cage experiments

Manipulative field experiments to exclude macroherbivores were carried out at sites 1, 2 and 3 shown in Figure 5.1 and described in Table 5.1. Macroherbivore exclusion cages were made from a modified 1m diameter x 0.5m high crab pot that was covered in 10mm monofilament mesh (Figure 5.2). Exclusion cages were deployed in the seagrass meadow for a total of seven weeks from April to June 2018. Exclusion cages were deployed at each site in a grid layout with six cages, six control plots and six procedural controls - macroherbivore exclusion cages with holes cut in the sides to allow macroherbivores to access the seagrass (Figure 5.2). Treatments were arranged haphazardly in the grid and plots were 2m apart.

Figure 5.1: Map of study sites.

To monitor and minimise the impact of shading caused by the cages, they were regularly cleaned and light measurements were taken. Macroherbivore cages at all three sites were manually cleaned twice a week for the duration of the experiment and were periodically swapped out for clean cages. Benthic light measurements reaching the seagrass canopy were taken inside a control plot and a macroherbivore cage for the first month of the experiment using 2π cosine-corrected irradiance loggers (Submersible Odyssey Photosynthetic Irradiance Recording System, Dataflow Systems Pty. Ltd., New Zealand) calibrated using a cosine corrected Li-Cor underwater quantum sensor (LI-190SA; Li-Cor Inc., Lincoln, Nebraska USA) and corrected for immersion using a factor of 1.33 (Kirk, 1994). Loggers measured

photosynthetically active radiation (PAR) and recorded readings every 15 minutes, these readings were used to measure total daily light (mol photons m^{-2} day^{-1}) reaching the seagrass in both cage and control plots.

At the end of the seven-week exclusion experiment, an 11cm diameter (10.6cm internal diameter) core sample was taken from every cage, control and procedural control plot. These cores were stored in the freezer and processed in the lab for aboveground biomass, shoot counts and counts of fish bite marks and urchin shreds. Samples were gently defrosted in the lab and above and below ground material separated where the shoot meets the rhizome. Shoots were counted for each species and the number of bite marks due to herbivory was also recorded. Aboveground biomass material for each species was then dried in the oven at 60°C and weighed after one week of drying.

Table 5.1: Characteristics of the different sites used in this study

Site	Species composition	Depth	Mean aboveground biomass gDW m^{-2}	Mean shoot density m^{-2}	Habitat	Experiment
1	*C. rotundata* *T. hemprichii*	0 – 2 m	213.8	1605	In meadow	Cages and tethering
2	*H. ovalis* *T. hemprichii*	0 - 2.5 m	13.1	1208	In reef patch	Cages
2a	*C. rotundata* *T. hemprichii*	0 - 2.5 m	-	-	In meadow	Tethering
3	*C. rotundata* *C. serrulata* *H. uninervis* *S. isoetifolium* *T. hemprichii*	1 – 3 m	181.3	8649	In meadow	Cages and tethering

Tethering experiments

Seagrass tethering experiments were used to quantify macroherbivory over time using an established technique (Kirsch *et al.*, 2002), modified by changing the length and type of rope, number of seagrass shoots and duration of time in the meadow. Tethering experiments were carried out at sites 1, 2a (from August onwards) and 3 shown in Figure 5.1 and Table 5.1 every 2 months from June 2019 to April 2020. These experiments used the two most common species across all three sites; *C. rotundata* and *T. hemprichii.* Both species were collected from the meadow at each site by selecting blades that were not heavily covered in epiphytes

and showed no signs of grazing and arranged in tethers. Each tethered shoot was made up of two outside blades and one middle blade of the seagrass taken from the same meadow and from the same shoot where possible (Unsworth *et al.*, 2007), all blades were photographed before being spliced into a 30cm rope (the tether). Each tether had two shoots of *C. rotundata* and two shoots of *T. hemprichii* spliced into it, these tethers were pegged into the seagrass meadow with the same orientation and shoot height as the surrounding meadow (see Figure 5.2). Ten tethers were placed in the seagrass meadow at each site in two rows of five, tethers were separated by 0.5m and the two rows of tethers were 0.5m apart. Tethers remained in situ for a total of three days, and after collection each blade was photographed again. Photos were used to calculate the surface area of blades at the start and end of the experiment, and the surface area lost to herbivory using ImageJ (Rasband, 1997). Photos were also used to count bite marks and categorise these as: urchin shreds, large fish bites (>5mm), small fish bites (< 5mm) or megaherbivory by green turtles (see Figure 5.2). Shoots were frozen and subsequently weighed in the lab following defrosting and drying in an oven at 60°C for four days.
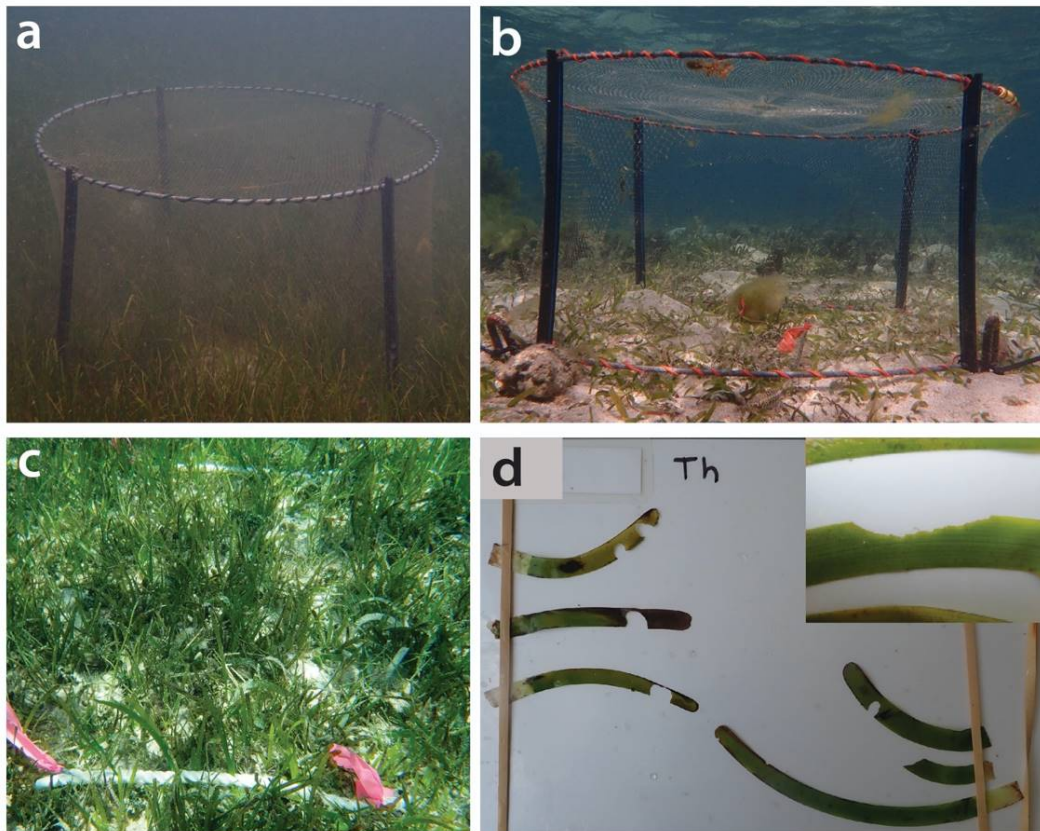
Figure 5.2: (a) Macroherbivore exclusion cages; (b) procedural control cages that allowed macroherbivores to access seagrass; (c) tethers deployed in the meadow; (d) and fish bite marks seen on tethered seagrass with urchin shred mark (d – inset).

Remote underwater cameras (GoPro model) were used to film tethered seagrass at each site to record herbivore grazing behaviour. Cameras were placed around the tethers and left recording for 60 – 90 minutes at each site, two recordings were carried out at all sites on days one and two of tether deployment, where tidal conditions allowed. All footage was viewed to look for the presence of herbivores. For three camera deployments per site per sampling event, a random 15 minute section of video was watched in detail and all fish were identified and the number in that section of video was recorded along with the MaxN (maximum number of individuals in a frame) (Harvey *et al.,* 2007).

Seagrass meadow productivity measurements were carried out at all sites in June 2018 and at site 1 in February 2020. Shoots of all species were pierced with a syringe half way up the leaf sheath and then harvested after 1 – 3 weeks, new growth was weighed in the lab and calculated as mg Dry Weight (DW) d^{-1} per shoot to enable comparisons with losses from tethered shoots (Zieman, 1974). To compare productivity measurements to losses due to macroherbivory, average productivity from all measurements of each species was used, with June measurements used for the dry season months and February measurements used for wet season months.

Statistical analysis

All data were analysed using a generalised linear model (GLM) using R v.3.5.2. (R Core Team, 2019) and model outputs were plotted using ggplot2 (Wickham, 2016). Exclusion cage data were analysed using a GLM with a gamma distribution and log-link, site and treatment were included as fixed factors with the response variables aboveground biomass, belowground biomass and shoot density tested individually. Tether data were analysed using the MASS package (Venables and Ripley, 2002) and a GLM with a negative binomial distribution and log-link with site, seagrass species and month included as fixed factors with the response variables total bite marks and surface area lost to macroherbivory. An F-test was used to determine the significance of each variable in the best-fit model using the anova() function in R. Post hoc analysis was conducted to compare treatment groups using a Tukey test in the emmeans package (Lenth, 2019). If a variable was not significant in the ANOVA, this was excluded from the model in the post hoc analysis.

To analyse the number of bite marks per blade from cores taken at the end of the experiment, an ANOVA was used to test for differences in bite marks per blade of each species. Each site was analysed separately due to the different species compositions at each.

Results

Macroherbivore grazing at Green Island varied throughout the year and between sites, in terms of the amount of seagrass consumed (Figure 5.3a). Numbers of bite marks on tethers also varied over space and time, but not between seagrass species. Peaks in herbivory were being driven by numbers of fish bite marks rather than urchins (Figure 5.3b). Macroherbivores consumed between 0.25 – 44% of aboveground daily seagrass productivity (Table 5.2). There was a difference in the weight of seagrass lost to herbivory between the two species used on the tethers, but there was no clear preference for either of the seagrass species in terms of the number of bite marks on each (Figure 5.3a). However, results from the analysis of cores across the meadow as a whole, show that less common seagrass species such as *H. ovalis* and *C. serrulata* may be targeted by fish grazers at Green Island (Figure 5.4). Despite being present, macroherbivores did not measurably impact seagrass meadow properties such as shoot density, aboveground biomass and species composition within the meadow (Figure 5.5).

Rates of herbivory

Loss of seagrass material on tethered seagrass throughout the year differed between sites, months and species with interactions between site:month and month:species ($p<0.05$). Losses to macroherbivory were lowest at site 2 throughout the year, and highest at site 3 in the August/October peak (Figure 5.3a). Post hoc analysis showed differences between the two seagrass species on the tethers at site 3 in August, and site 2 in October ($p<0.05$), where losses of *T. hemprichii* were higher than *C. rotundata*. There was no difference between months at sites 1 or 2, but site 3 had higher losses to herbivory in October than June.

Spatial and temporal variability in herbivory

The total number of fish, urchin and turtle bite marks per tether differed between sites and months ($p<0.05$), but not between seagrass species (Figure 5.3b). There was an interaction between site and month regarding the total number of bite marks on tethers ($p<0.05$). Herbivory peaked at all sites in October, with a second peak occurring at site 1 in June (Figure 5.3b).

Post hoc tests showed that within site 1, bite marks were fewer in April than the June and October peaks. Within site 2 there were no differences between months, and within site 3 there were fewer bite marks in June than the peak months of August and October.

Throughout most of the year, bite marks were highest at site 3 and lowest at site 2. The only months with no differences in bite marks between sites were April and December. The peaks in herbivory at all sites were driven by higher numbers of fish bites rather than urchin feeding (Figure 5.3b). All types of bite marks were contributing to herbivory pressure at all three sites during the experiment, small fish bite marks were highest at site 3 throughout much of the year, whereas turtle and urchin bites were higher at site 1.
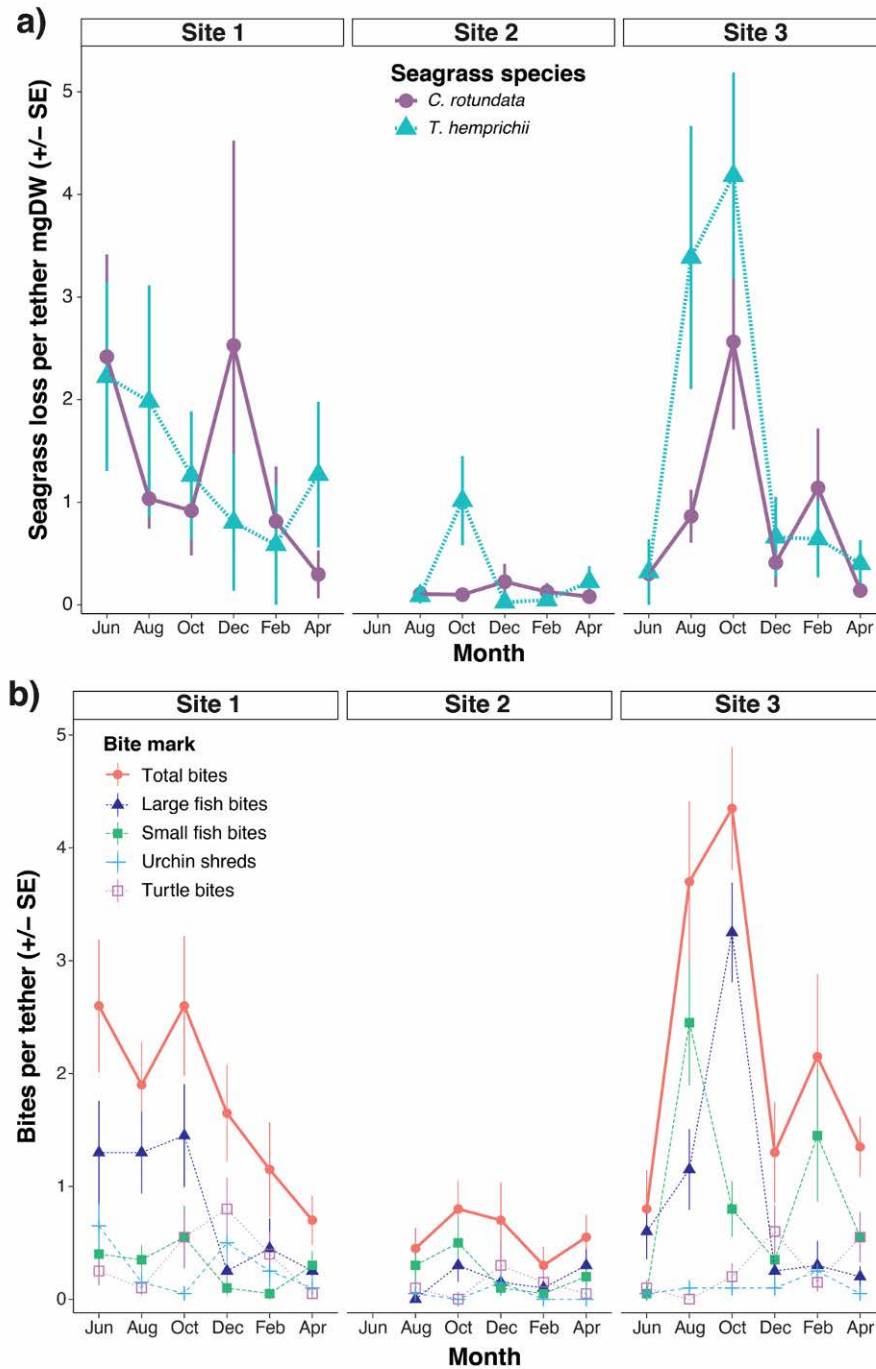
Figure 5.3: Seagrass loss (mgDW) per tether due to macroherbivory (turtle bites excluded) during the experiment (a) and bites per tether showing the overall total and types of bite marks present (b).

Proportion of productivity consumed

The amount of seagrass productivity consumed by macroherbivores varied depending on the time of year, species of seagrass and ranged between 0.25 and 44% of seagrass productivity (Table 5.2). This variation depended on the time of year, species of seagrass and the site, with the highest outright and proportional losses of productivity to macroherbivores at sites 1 and 3 (Table 5.2).

Table 5.2: Percentage of daily seagrass productivity consumed as a percentage of daily productivity per shoot in the wet season (February, October, December) and dry season (April, June August). Productivity and seagrass consumption shown as mean ± 1SE

Site	Season	Species	Productivity (mg day^{-1} shoot^{-1})	Seagrass consumption (mg day^{-1} shoot^{-1})	Productivity consumed by macroherbivores
1	Wet	Cr	1.68 ± 0.56	0.21 ± 0.41	8-25%
		Th	1.57 ± 0.56	0.15 ± 0.29	6-13%
	Dry	Cr	1.32 ± 0.48	0.19 ± 0.28	4-30%
		Th	1.63 ± 0.93	0.30 ± 0.45	13-23%
2	Wet	Cr	1.68 ± 0.56	0.02 ± 0.06	1-2%
		Th	1.57 ± 0.56	0.06 ± 0.15	0.25-11%
	Dry	Cr	1.32 ± 0.48	0.13 ± 0.44	1-30%
		Th	1.63 ± 0.93	0.09 ± 0.26	1-13%
3	Wet	Cr	1.68 ± 0.56	0.27 ± 0.36	4-25%
		Th	1.57 ± 0.56	0.30 ± 0.39	7-44%
	Dry	Cr	1.32 ± 0.48	0.07 ± 0.12	2-11%
		Th	1.63 ± 0.93	0.26 ± 0.46	3-33%

Identity of macroherbivores

The herbivores responsible for bite marks on the tethers were not observed on the over 70 hours of remote video footage in any month. The only herbivorous fish seen were small siganids (Table B.1), no urchins were seen on the cameras, but these were occasionally observed in the meadow during this study. Siganids were observed on the video footage in very large numbers at site 3 in February, however the majority of these were juveniles.

Species preference

Bite mark data from all seagrass species in the control plots at the end of the exclusion experiment was analysed to look for overall patterns in seagrass species preference in this diverse meadow (Figure 5.4). There was no difference in the number of bite marks between *C. rotundata* and *T. hemprichii* at site 1 F_1=1.72 (p = 0.231), which was also supported by comparing these two species in the tethering experiment. At site 2 *H. ovalis* had more bites

per blade than *T. hemprichii* $F_1=3.63$ (p=0.09) and at site 3 *C. serrulata* had more bites per blade than *C. rotundata* and *H. uninervis* $F_1=4.83$ (p=0.03).
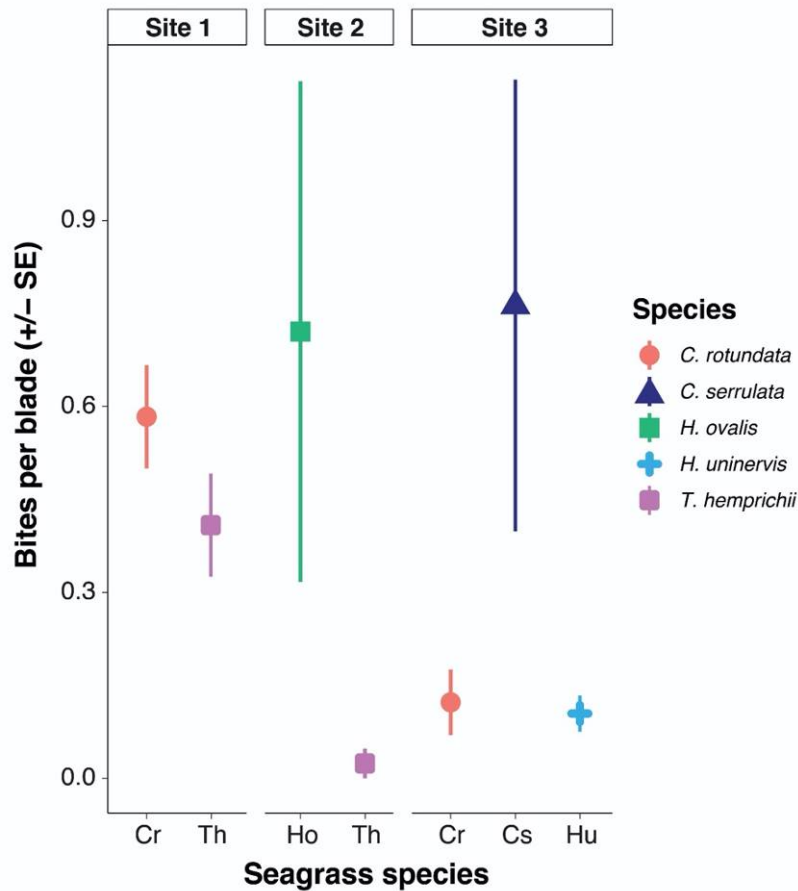
Figure 5.4: Bites per seagrass blade in control plots of all species found at all sites.

Impact of macroherbivory on the seagrass meadow

At the end of the exclusion caging experiment, there was no effect of excluding macroherbivores on seagrass metrics, with no treatment differences in aboveground biomass ($F_2 = 0.5$ p = 0.6), belowground biomass ($F_2 = 0.6$ p = 0.5), or shoot density ($F_2 = 0.04$ p = 0.9). There was no effect of excluding macroherbivores in the bare area within the meadow at site 2 and the exclusion cages did not have an impact on the seagrass meadow. While there were no differences caused by macroherbivory, there were differences between sites in aboveground biomass ($F_2 = 76.9$ p<0.001), belowground biomass ($F_2 = 83.2$ p<0.001), and shoot density ($F_2 = 56.13$ p<0.001). Aboveground biomass was lowest at site 2 (Figure 5.5a), shoot densities were lowest at sites 1 and 2 (Figure 5.5b) and belowground biomass was lowest at site 2 (Figure 5.5c).

While insufficient to cause a change in overall seagrass biomass in treatments, analysis of bite mark numbers in seagrass blades revealed a difference in the number of bite marks

between treatments ($F_2 = 9.1$ p<0.001), between sites ($F_2 = 35.5$ p<0.001) and there was a site by treatment interaction ($F_4 = 3.7$ p<0.05). Post hoc analysis shows that bite marks were less frequent in cages that excluded macroherbivores than control plots (p<0.05) at sites 1 and 3, but there was no difference at site 2 and very low levels of bite marks overall (Figure 5.5d). Light logger data shows that cages did not reduce the total daily PAR reaching plots (Figure C.1).
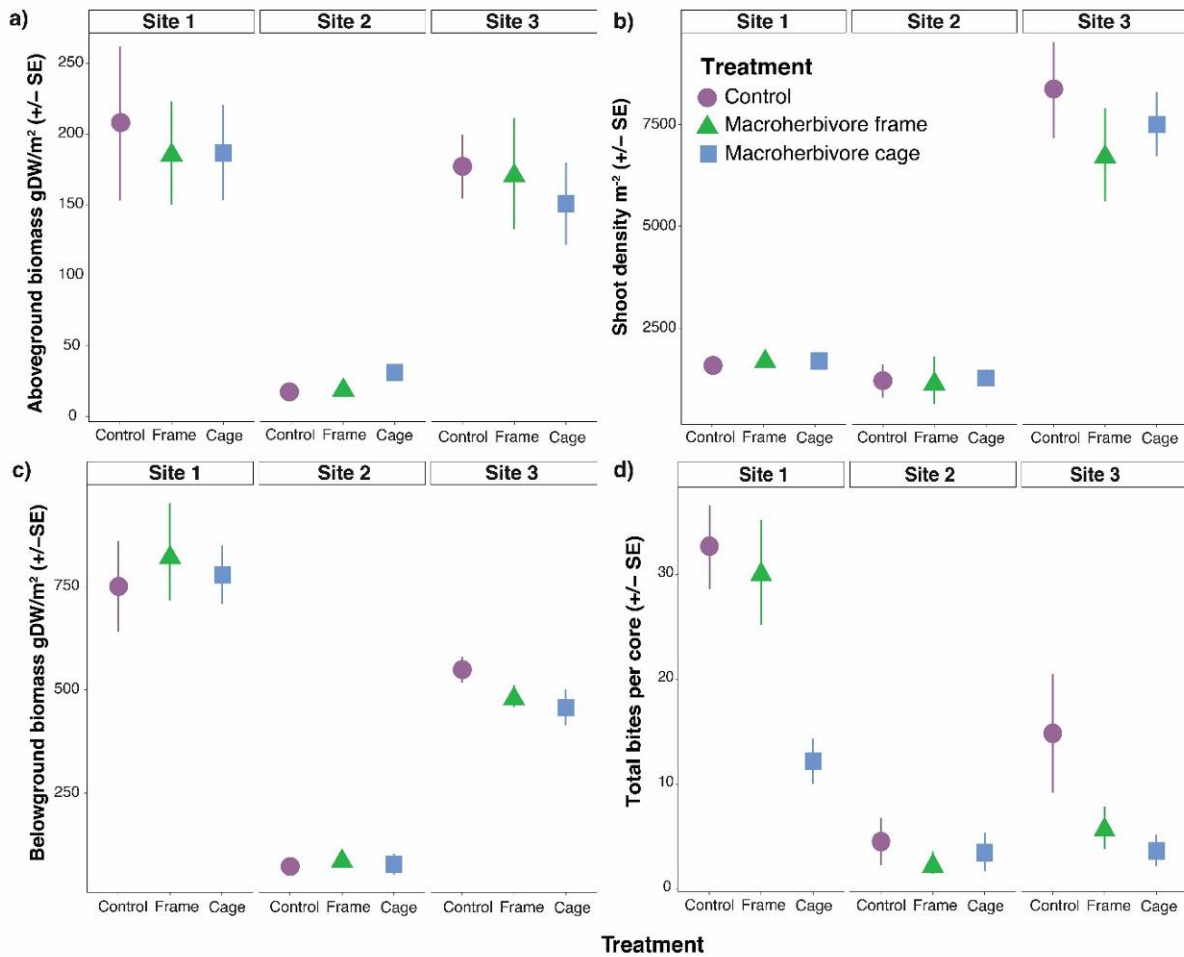
Figure 5.5: Aboveground biomass (a), shoot density (b) belowground biomass (c) and bite marks per core (d) in all treatments at all sites at the end of the exclusion cage experiment.

Discussion

This study examined macroherbivory in a tropical multi-species seagrass meadow in the Great Barrier Reef. Macroherbivory varied greatly both spatially and temporally, ranging from 0.25% to as much as 44% of the daily seagrass productivity. While evidence of grazing was present in the meadow, macroherbivory did not result in large-scale detectable impacts to seagrass meadow structure and biomass. Macroherbivores did not show a clear preference for either of the two most common species in the meadow, but may prefer the rarer species.

Rates of macroherbivory at Green Island were consistently low compared with temperate and subtropical meadows (Holzer *et al.*, 2013; Kirsch *et al.*, 2002; Tomas *et al.*, 2005) and compared with studies from some other tropical locations (Gullström *et al.*, 2011; Unsworth *et al.*, 2007). The levels of macroherbivory at Green Island were more similar to rates documented in tropical seagrasses in the South China Sea, where herbivores removed up to 16% of seagrass productivity (Lee *et al.*, 2015, 2016) and to herbivory rates found worldwide (Cebrián and Duarte, 1998). As macroherbivory at Green Island appeared to be highly variable, there may be peak grazing events that I did not observe during the timeframe of my study, where a larger amount of seagrass productivity is removed. Targeted grazing by siganids has previously been observed at Green Island, with large shoals of up to 100 individuals moving from the reef dominated areas where they rest, to the southwest seagrass flats (close to site 1 in this study) to feed (Pitt, 1997).

These rates of seagrass herbivory are also low compared to macroherbivory on algae within coral reefs in the GBR, where algal biomass removal rates in a 4 hour period can be between 6 – 36% (Loffler *et al.*, 2015), but these rates can vary depending on the type of macroherbivore present (Ceccarelli *et al.*, 2011). Siganids are important herbivores on GBR reefs, however they have very low rates of herbivory on seagrasses (Fox and Bellwood, 2008).

Green Island is one of the oldest Marine Protected Areas in the GBR (Baxter, 1990; Ogilvie, 2016). In other parts of the world, protected areas have been shown to modify macroherbivory and result in increased herbivory inside Marine Protected Areas (Ferrari *et al.*, 2008; Hay, 1984; Prado *et al.*, 2008). This may occur because of the number of trophic levels in the food web being protected. For example, where apex predators are functionally extinct and only three trophic levels are present, MPAs release fishing pressure on piscivores and result in reduced macroherbivore populations or changes in foraging behaviour (Carroll

et al., 2019). When apex predators are present and protected (four trophic levels) they reduce piscivore numbers and increase the populations of macroherbivores. However, when long-term protection and conservation measures are applied to a system, interactions generally become more diverse and complex and this can dampen these trophic cascades leading to more stable systems (Duffy *et al.*, 2007; Finke and Denno, 2005). In the case of Green Island, it is possible that because top-predators are also protected, larger fish and sharks are able to exert top-down control on the herbivore populations here and modify their feeding behaviour (Burkholder *et al.*, 2013). Large predatory fish and blacktip sharks were frequently observed in the seagrass meadows at all sites and all times of year throughout the duration of the experiment and on the video footage collected during the study (Figure C.2). A lack of top-down control due to overfishing of herbivore predators has been shown to contribute to overgrazing by macroherbivores in other locations (Wallner-Hahn *et al.*, 2015) and the presence of predators can control macroherbivore populations (Carroll *et al.*, 2019; Gullström *et al.*, 2011). The presence of predators can also modify the feeding behaviours of megaherbivores over space and time, based on their perceived risk of predation (Burkholder *et al.*, 2013; Heithaus *et al.*, 2007; Wirsing *et al.*, 2007) and it is possible the macroherbivores at Green Island are also attempting to avoid predators while foraging.

The levels of macroherbivory at Green Island were insufficient to cause a measurable impact on overall seagrass meadow structure. This contrasts with other locations where high grazing rates by macroherbivores have caused dramatic losses in above and below ground biomass (Carnell *et al.*, 2020; Peterson *et al.*, 2002; Planes *et al.*, 2011; Ruíz *et al.*, 2009), but is a similar pattern to other work from the GBR which found no impact of macroherbivores on seagrass meadow structure (Scott *et al.,* 2021a; Chapter 3). In a previous study at Green Island, I identified the most important herbivore modifying seagrass meadow structure is the green turtle, *Chelonia mydas* (Scott *et al.,* 2020; Chapter 4). These megaherbivores can graze intensively on small patches of seagrass within the Green Island meadow and impact both above and belowground seagrass structure (Scott *et al.*, 2020; Chapter 4) and mesoherbivores can impact epiphyte cover (Hoffmann *et al.*, 2020). However, even these large herbivores did not act across the entire meadow with impacts measured in smaller grazing plots within the meadow leaving the majority unaffected.

Bite marks on tethered seagrass show that macroherbivory at Green Island was dominated by fish, and peaks in macroherbivory were driven by fish bite marks. However, urchin herbivory was also taking place throughout the year at a lower frequency. Urchins have also been found

to be a lower contributor to macroherbivory in other locations (Lee *et al.*, 2015), particularly in areas where fishing is prohibited (Alcoverro and Mariani, 2004; Hay, 1984).

No macroherbivores were observed directly feeding on tethers in over 70 hours of video collected in this experiment, and no large herbivores were seen in any of the footage, however large numbers of schooling juvenile siganids were recorded at site 3 in February. As no macroherbivory events were captured on camera and only rarely observed in the meadow throughout this experiment, macroherbivory may be taking place at night or could be due to large shoals of fish moving through the meadow sporadically. Previous work at Green Island has shown that *Siganus fuscescens* and *Siganus lineatus* feed on seagrass as an important part of their diet, and they can move through the meadows here in large foraging shoals (Pitt, 1997). Both urchins and siganids in tropical seagrasses and GBR reefs can graze at night (Fox and Bellwood, 2011; Tertschnig, 1989; Young and Bellwood, 2011). Although juvenile siganids are associated with the Green Island seagrass meadows, they predominantly feed on turfing algae and animal material within the meadow (Pitt, 1997). Fixed site surveys indicate a diverse suite of herbivorous fish are present at Green Island, including scarids, siganids and acanthurids (AIMS, 2017). The parrotfish genus *Sparisoma*, that cause high rates of seagrass loss in the Caribbean and other areas, are not present in the Indo-Pacific (Hoey and Bellwood, 2008), and although their functional equivalents *Calotomus* spp. and *Leptoscarus vaigiensis* are rare in the GBR (Hoey and Bellwood, 2008), they have been shown to consume large amounts of seagrass in other areas in the Indo-Pacific (Gullström *et al.*, 2011; Unsworth *et al.*, 2007).

Although rates of macroherbivory were low overall, there was small-scale spatial variability between sites around Green Island, and macroherbivory rates changed over time at each site. Such spatial and temporal variability in macroherbivory has been previously documented and depends on factors that cause patchiness in abundances of herbivores (Lee *et al.*, 2015; Tomas *et al.*, 2005; Wressnig and Booth, 2008). At Green Island, the neighbouring coral reef habitat may play a key role, as reef-associated fish can feed on seagrass, and in some locations cause bare halos in seagrass around reefs by grazing and preventing the establishment of some seagrass species (Chiquillo *et al.*, 2020; Randall, 1965; Valentine *et al.*, 2007). Similar halos were observed around some reefs at Green Island but were not investigated as part of this study. The depth of meadows may also have been important, herbivory was highest at site 3 for much of the year, the deepest site in the study (other sites were intertidal). Other studies have also found mid-depth subtidal sites have higher

macroherbivory (Lee *et al.*, 2015; Sluka and Miller, 2001) and larger herbivorous fish can occur deeper than juveniles (Gullström *et al.*, 2011). Seasonal and temporal variability in macroherbivory is also very common in other locations, and targeted herbivory by shoals of fish, is what allows these meadows to persist even when herbivore consumption exceeds daily primary productivity for short periods of time (Kirsch *et al.*, 2002; Unsworth *et al.*, 2007).

Macroherbivores at Green Island did not show a preference for either *C. rotundata* or *T. hemprichii* in the tethers, however data from cores at the exclusion study sites showed they consumed rarer species *H. ovalis* and *C. serrulata*, at relatively greater rates when they were present. Macroherbivores in tropical seagrass meadows have been shown to prefer opportunistic species such as *C. rotundata* over climax species such as *T. hemprichii* (Lee *et al.*, 2015; Mariani and Alcoverro, 1999; Vonk *et al.*, 2008). In other tropical locations, fish have also shown a preference for the faster growing *Syringodium filiforme* or *Halodule uninervis* over *Thalassia* species (Lee *et al.*, 2016; Tribble, 1981). These preferences may also be size dependent, as larger parrotfish are able to feed on seagrass blades with a higher fibre content, meaning they can graze on the high nutrient, high fibre *T. hemprichii* (Lee *et al.*, 2016).

Conclusion

This study found that macroherbivory was generally low in the multi-species seagrass meadow at Green Island. Large fish, small fish and urchins all fed on seagrass here, but this varied over space and time. Despite persistent feeding by macroherbivores throughout the study, it was of insufficient intensity to cause large-scale structural impacts to seagrass biomass, species composition or shoot density in the meadow. This pattern may be characteristic of other GBR seagrass meadows where macroherbivores are present, however, further studies at other locations are needed. Green Island is one of the oldest MPAs on the GBR, where both macroherbivores and their predators are protected, this top-down influence may be controlling rates of macroherbivory in this meadow, an area worthy of further study. Although the level of macroherbivory was comparatively low at Green Island, this is still likely to represent an important pathway for seagrass productivity to enter the food web. This study supports other recent work highlighting that tropical seagrass productivity provides an important component to food webs in the GBR, but shows that this is variable over space and time (Jinks *et al.*, 2019; Scott *et al.*, 2020, 2021a).

Chapter 6

Chapter 1:
Introduction

Chapter 2:
The role of herbivory in structuring tropical
seagrass ecosystem service delivery

Chapter 3:
Herbivory has a major influence on structure and condition
of a Great Barrier Reef subtropical seagrass meadow

Chapter 4:
Green turtle grazing plot
formation creates structural
changes in a multi-species GBR
seagrass meadow

Chapter 5:
Spatial and temporal
patterns in macroherbivore
grazing in a multi-species GBR
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Chapter 6:
Spatial and temporal variability
of green turtle and dugong
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Chapter 7:
General discussion

Chapter 6

Spatial and temporal variability of green turtle and dugong herbivory in seagrass meadows of the southern Great Barrier Reef

Chapter 3 showed that megaherbivores had the dominant influence on the seagrass meadow at South Trees in Gladstone, but there are multiple seagrass meadows within the Gladstone region which megaherbivores are also likely to be influencing. In many locations there are multiple meadows where megaherbivores feed, but our understanding of the spatial and temporal variability in megaherbivory between different closely connected meadows, and over time, is limited. This chapter investigates the variability in the structuring impacts of megaherbivory on a regional scale and over time in the Gladstone region.

This chapter is currently under review in Marine Ecology Progress Series:

All authors helped to conceive the design of this experiment, ALS led all fieldwork activity with assistance from PHY and the Seagrass Ecology Lab team. ALS conducted all lab and data analysis. ALS prepared the manuscript with comments from MAR, PHY and PIM.

Abstract

Megaherbivore grazing (e.g. by turtles, dugongs and manatees) plays a major and well-documented role in structuring seagrass meadows around the world; however, we know little about local-scale (intra- and inter-meadow) variability in megaherbivore grazing. This is surprising given that megaherbivores are highly-selective eaters who may feed by targeting certain meadows, or areas within a meadow. Here, I ran an experiment in the Great Barrier Reef (GBR) to test the question: How does megaherbivory vary on a regional scale? I used megaherbivore exclusion cages at five meadows along a 50km region of coastline around Gladstone (Queensland) in the southern GBR World Heritage Area to understand variability in megaherbivory between meadows. I found differences in the impacts of megaherbivore grazing on seagrass biomass and shoot heights between different meadows in the region. There were also interannual differences in grazing impacts at one meadow that had been studied previously. These differences may be due to megaherbivore population and grazing dynamics, as well as the response of the seagrass to grazing pressure. My results show that seagrass meadows grazed by megaherbivores are dynamic systems that vary on regional spatial scales as well as over time. This is important for management measures that seek to consider the seagrass herbivore system as a whole and understand the implications of monitoring efforts based on seagrass aboveground condition.

Introduction

Seagrass meadows are highly productive ecosystems and an important food source, particularly for megaherbivores who may rely predominantly or completely on seagrass for their diet and can consume significant amounts of seagrass productivity (Bakker *et al.*, 2016a; Esteban *et al.*, 2020). Megaherbivores are large grazers over 10kg in body weight and in seagrass systems include green turtles, manatees, dugongs, and swans (Bakker *et al.*, 2016a). These large bodied grazers can act as ecosystem engineers, structuring seagrass meadows as they feed, and impacting the ecosystem services provided by a meadow (Bakker *et al.*, 2016a; Scott *et al.*, 2018; Chapter 2).

Megaherbivore grazing can have significant impacts on seagrass meadow characteristics. Grazing can reduce aboveground biomass, shoot densities and shoot height in meadows (D'Souza *et al.*, 2015; Lal *et al.*, 2010; Scott *et al.*, 2020; Chapter 4). Losses in belowground biomass due to grazing can also occur where green turtles dig to feed on rhizomes

(Christianen *et al.*, 2014; Scott *et al.*, 2020; Chapter 4), and when dugongs employ excavation foraging to feed on above and belowground material (Rasheed *et al.*, 2017; Sheppard *et al.*, 2010). In extreme cases overgrazing of meadows can occur, resulting in losses of seagrass meadows in some locations (Christianen *et al.*, 2014; Fourqurean *et al.*, 2019; Kelkar *et al.*, 2013a). Overgrazing of meadows is particularly prevalent in areas where green turtle conservation measures have been very effective and their numbers increase rapidly, but predator numbers remain low (Heithaus *et al.*, 2014).

Structuring of seagrass meadows by megaherbivores has been documented in various tropical and subtropical locations (Heithaus *et al.*, 2014), however less is known about how megaherbivory varies between meadows in a region. Dugongs can show high site fidelity to meadows within a location (D'Souza *et al.*, 2015) and can feed in herds (Sheppard *et al.*, 2010). The effects of green turtle grazing can be spatially variable within a bay (Hearne *et al.*, 2018) and depend on the number of turtles present in a meadow (Kelkar *et al.*, 2013a; Lal *et al.*, 2010), which can determine whether a meadow in one location declines or disappears due to overgrazing (Fourqurean *et al.*, 2019).

The responses of seagrasses to pressures such as herbivory can also vary between species, over space and over time and will depend on the top-down and bottom-up controls that operate in a meadow (Kilminster *et al.*, 2015; Kuiper-Linley *et al.*, 2007). Some seagrass species may be more tolerant to grazing. In subtropical Queensland seagrass meadows, *Halophila ovalis* was found to be the most tolerant species, followed by *Zostera muelleri* ssp *capricorni,* with *Cymodocea serrulata* the least tolerant (Kuiper-Linley *et al.*, 2007). These responses may vary according to the habitat and region where the meadow is located and the associated variability in the stresses and environmental settings within an area (Kilminster *et al.*, 2015).

Understanding the plant-herbivore system as a whole, particularly in seagrass meadows with megaherbivores present, is important to manage these ecosystems effectively. Effective management of multiple meadows in a region requires an understanding of how the impacts of herbivory vary in space and time between these closely connected meadows (Scott *et al.*, 2018; Chapter 2).

In the Great Barrier Reef (GBR), two seagrass megaherbivores are present – green turtles (*Chelonia mydas*) and dugongs (*Dugong dugon*). Green turtles will preferentially consume seagrass where it is available and dugongs predominantly graze on seagrasses, both of these

can consume large amounts of seagrass (Esteban *et al.*, 2020; Sheppard *et al.*, 2010). These megaherbivores can graze broadly across seagrass meadows as a whole (Scott *et al.*, 2021a; Chapter 3) or in a more targeted fashion where green turtles can focus their foraging on smaller areas of the meadow to form grazed plots (Scott *et al.*, 2020; Chapter 4). While dugongs in the GBR may focus their grazing on higher biomass (Rasheed *et al.*, 2017; Tol *et al.*, 2016) or high nutrient content (Sheppard *et al.*, 2010) areas of a meadow. Megaherbivore feeding in the GBR can act to structure the seagrass meadows here and the impact of this depends on the megaherbivore population present and their grazing behaviour (Scott *et al.*, 2020; Chapter 4).

I used exclusion cages to quantify the impact of megaherbivore grazing at five sites in the Gladstone region encompassing a 50km section of coastline. Megaherbivory has been identified as the most important top-down process affecting these seagrass meadows (Scott *et al.*, 2021a; Chapter 3), with green turtles grazing at the meadow-scale throughout the meadow and dugongs also feeding at all of the study meadows in the region (Limpus *et al.*, 2018; Rasheed *et al.*, 2017; Scott *et al.*, 2021a; Chapter 3).

Methods

Megaherbivore exclusion cages were deployed at five different meadows in a coastal barrier island system of the southern GBR near Gladstone (shown in Figure 6.1) for three months between August and November in 2018. The characteristics of these meadows are summarised in Table 6.1 and shown in Figure 6.1, the meadows at these sites contain three seagrass species; *Zostera muelleri* ssp *capricorni*, *Halophila ovalis* and *Halodule uninervis*.

Table 6.1: Site characteristics at the start of the experiment (beginning of the growing season)

Site	Dominant species	Habitat	Mean aboveground biomass gDW m^{-2} ± SE	Mean shoot height mm ± SE
Pelican Banks	*Z. capricorni*	Intertidal sand/mud	11.13 ± 0.7	46 ± 2.0
Wiggins Island	*H. ovalis*	Intertidal mud	1.61 ± 0.3	2.7 ± 0.1
South Trees	*Z. capricorni*	Intertidal sand/mud	8.90 ± 0.5	83 ± 3.9
Wild Cattle Island	*H. uninervis*	Subtidal sand	6.58 ± 0.6	95 ± 5.0
Rodds Bay	*Z. capricorni*	Intertidal sand/mud	21.99 ± 1.7	148 ± 6.4

Megaherbivore exclusion cages were 2m x 2m wide and 0.5m high and made of galvanised steel with a 20 x 20cm mesh. These cages excluded green turtles and dugongs but allowed other herbivores access to the plots to graze. Three megaherbivore exclusion cages were deployed at each site with three control plots of the same size marked with pegs, these were randomly allocated to a square within a 4 x 3 grid with at least a 3m gap between plots.

Five shoot height measurements were taken from every plot at the start and end of the experiment, by measuring the shoot length of the entire canopy and ignoring the longest 20% (Duarte and Kirkman, 2001). Photos were taken from every plot at the start and end of the experiment to estimate aboveground biomass (Rasheed, 1999).

The South Trees meadow location repeated sampling that had occurred the previous year, which enabled a temporal comparison of herbivory at that site (Scott *et al.*, 2021a; Chapter 3). Shoot height and change in aboveground biomass data from South Trees over a 3 month period from August to November 2017 (Scott *et al.*, 2021a; Chapter 3), collected using the same methods was compared to data collected in 2018.
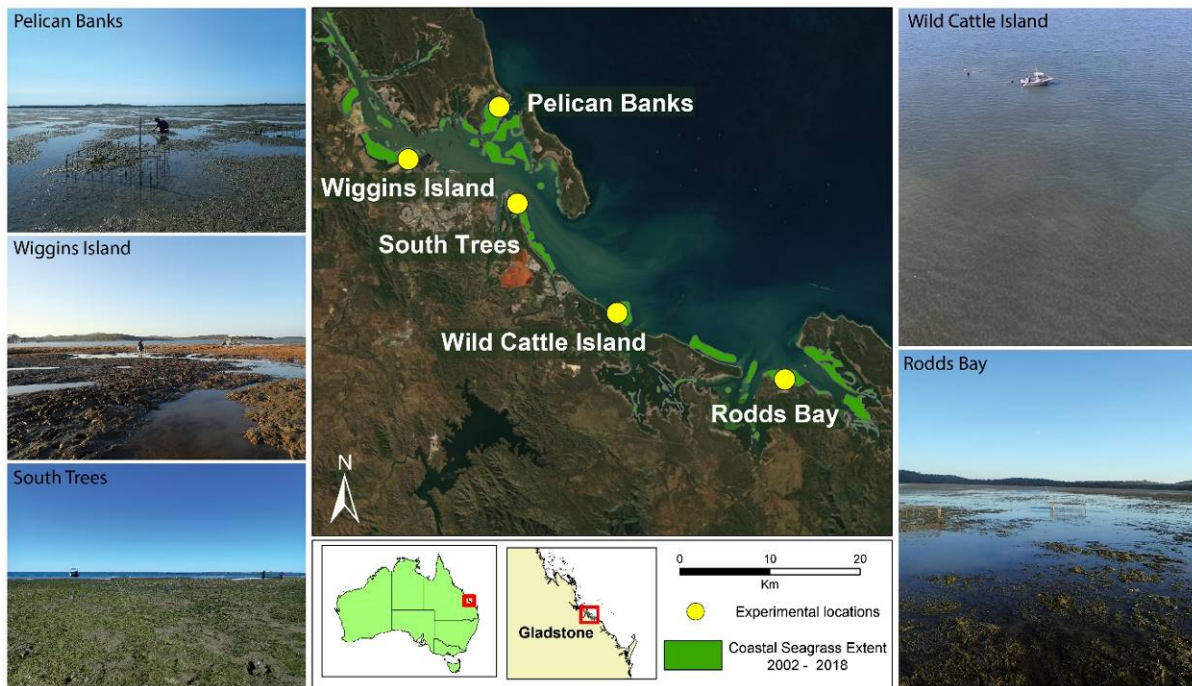
Figure 6.1: Location of experimental sites in Gladstone Harbour with coastal seagrass distribution from Chartrand *et al.* (2019) and photos of all sites.

Change in aboveground biomass over the three-month exclusion study, and shoot height measurements at the end of the three-month exclusion from all three cages and control plots at all sites, were compared using an ANOVA and a Tukey post hoc analysis. Residual and q-q plots of normalised residuals of each ANOVA were inspected for heteroscedasticity and non-normality. Statistical analyses were conducted in R v.3.5.2. (R Core Team, 2019) and model outputs were plotted using ggplot2 (Wickham, 2016). Change in aboveground biomass was analysed for four of the five sites in this experiment, the fifth, Wild Cattle Island, was excluded from this analysis because visibility was too poor to take photos of plots at this subtidal site in November. Shoot height measurements at the end of the exclusion study were analysed for four of the five sites in this experiment, Wiggins Island was excluded because muddy sediments and standing water over short *H. ovalis* shoots prevented accurate shoot height measurements in November.

Results

Spatial differences in the impact of megaherbivory

Megaherbivore grazing caused declines in aboveground biomass at some sites within the Gladstone region but not others (Figure 6.3a). There was a location by treatment interaction that determined the change in aboveground biomass over the duration of the exclusion experiment ($F_3 = 10.36$, p<0.001). Post hoc analysis showed that within sites there was a higher change in biomass during the experiment in megaherbivore cages than open to grazing control plots at Pelican Banks and Rodds Bay, but no differences between treatments at South Trees and Wiggins Island. Pelican Banks had a higher change in biomass than all other sites and was the only site to increase in biomass overall during the experiment, Rodds Bay had a lower change in biomass than all other sites and all plots decreased in biomass throughout the experiment (Figure 6.3a). There was no difference between South Trees and Wiggins Island, with no change in biomass at either site throughout the experiment.

There was a difference in shoot height between location ($F_3=32.324$, p<0.001) and treatment ($F_1=14.464$, p<0.001), but no interaction between these two (Figure 6.3b). Shoot heights were shorter in control plots that were open to grazing compared to megaherbivore exclusion cages at all locations, the largest differences in shoot height between treatments were at Pelican Banks. Post hoc analysis showed overall differences between all locations, with shortest shoot heights at South Trees and longest shoot heights at Rodds Bay.
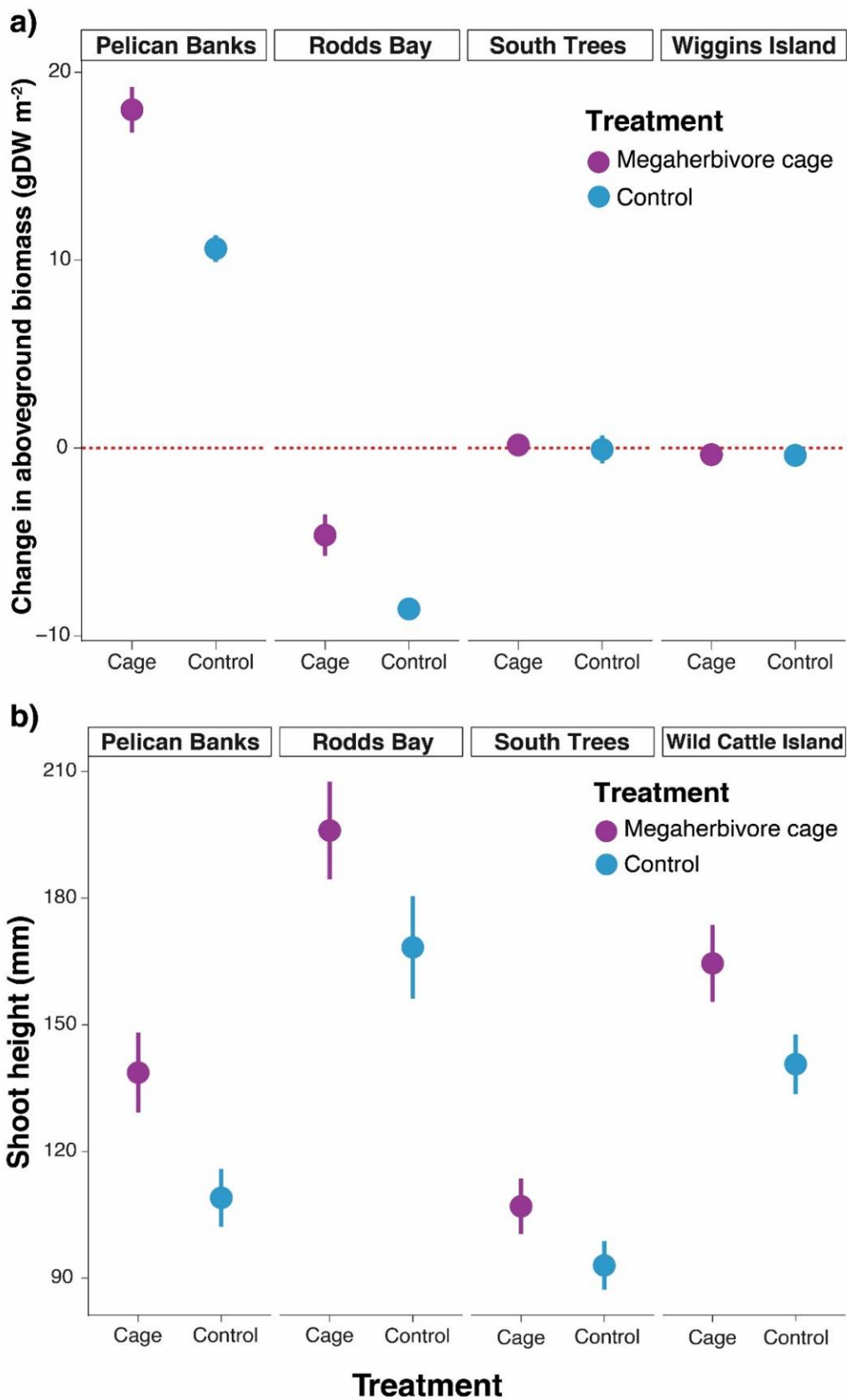
Figure 6.2: Change in aboveground biomass throughout the exclusion experiment (a), shoot height at the end of the experiment (b). Error bars show ± SE.

Temporal differences in herbivory at South Trees

For the South Trees site, where I had previously conducted herbivore exclusions in 2017 (Scott *et al.,* 2021a; Chapter 3), impacts of herbivory differed between 2017 and 2018 (Figure 6.3). There was an effect of treatment (F_1 = 13.91, $p<0.05$) and year (F_1 = 5.88, $p<0.05$) and an interaction between these (F_1 = 5.00, $p<0.05$) on the change in aboveground biomass (Figure 6.3a). There was a significant effect of year (F_1 = 7.86, $p<0.05$) and treatment (F_1 = 12.01, $p<0.05$) on shoot height, but no interaction between these ($F1$ = 2.030 p = 0.16) (Figure 6.3b). Shoot heights inside the open to grazing control plots were shorter than inside the exclusion cages in both years. Post hoc analyses show there was a strong treatment effect in 2017 with both aboveground biomass and shoot height significantly lower in open to grazing control plots compared to within the caged megaherbivore exclusion treatment. In 2018 there was no treatment effect for change in aboveground biomass and a much smaller effect on shoot heights.
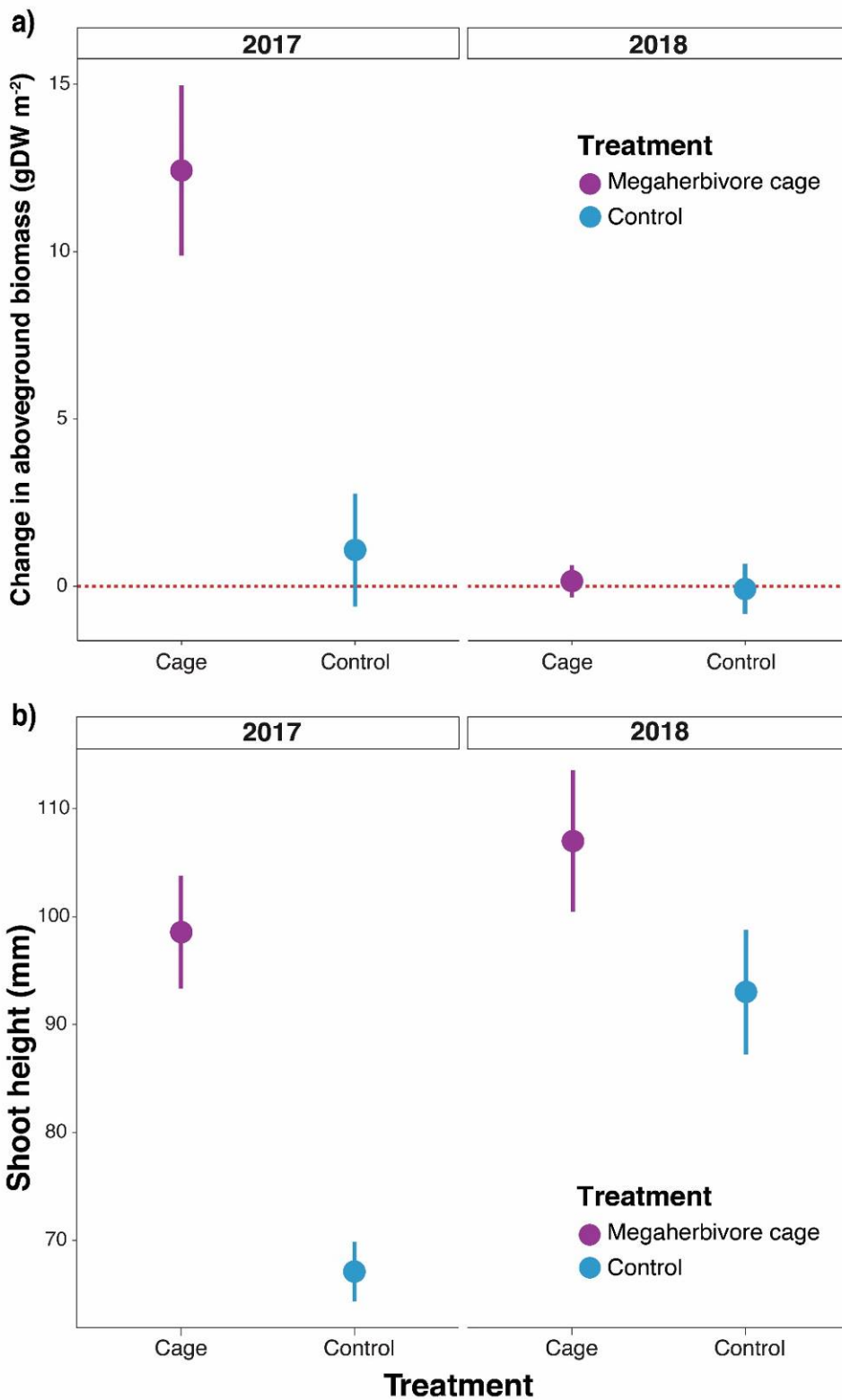
Figure 6.3: Change in aboveground biomass in megaherbivore cage and control plots (a) and final shoot height measurements (b) after three months of megaherbivore exclusion from August to November at South Trees in 2017 and in 2018. Data from 2018 taken from Scott *et al.* (2021a).

Discussion

Grazing by megaherbivores on the southern Great Barrier Reef produced variable impacts on coastal seagrass meadow structure within the region and over time at the same meadow. Megaherbivores were grazing at all four meadows where shoot height was measured, which resulted in shorter shoots in control plots open to grazing compared to exclusion cages. However, reductions in aboveground biomass due to megaherbivore grazing were only seen at Pelican Banks and Rodds Bay. There was a similar pattern at South Trees meadow over time, where shoot heights were reduced by grazing in both years, but aboveground biomass was only impacted by grazing in 2018.

A range of studies from around the world have demonstrated that megaherbivore grazing is an important structuring force in seagrass meadows and can cause reductions in aboveground characteristics of tropical seagrasses (Christianen *et al.*, 2014; D'Souza *et al.*, 2015; Lal *et al.*, 2010) as well as in tropical GBR seagrass meadows (Scott *et al.*, 2020; Chapter 4). Grazing by megaherbivores has previously been identified as the most important top-down structuring force in the subtropical seagrass meadow at South Trees in Gladstone (Scott *et al.*, 2021a; Chapter 3). However, megaherbivores are not always the most important grazer group in subtropical seagrass meadows. For example, in one Queensland seagrass meadow where megaherbivores are present, they do not influence aboveground seagrass characteristics and mesoherbivores (e.g. amphipods, juvenile prawns and juvenile fish) are the most important grazer group impacting meadow properties (Ebrahim *et al.*, 2014). My study supports previous research from Gladstone that shows the megaherbivore populations are acting to structure the meadows here (Scott *et al.*, 2021a), but shows that this pressure is not constant.

The variability in the impact of megaherbivore grazing on seagrass meadows in Gladstone is likely to be driven in part by megaherbivore grazing behaviour, movements and population dynamics. In the GBR, megaherbivores can target higher biomass areas of seagrass meadows (Rasheed *et al.*, 2017; Tol *et al.*, 2016), which may be the case here as Pelican Banks and Rodds Bay had the highest biomass of the seagrass meadows studied, and were both impacted by megaherbivory. South Trees also had a higher biomass in 2017 than 2018 and reductions in aboveground biomass due to grazing were greater at this time. Megaherbivores can also target certain seagrass species when they graze (Kuiper-Linley *et al.*, 2007); however, this did not appear to be the case in Gladstone as although both of the most highly targeted meadows in Gladstone were dominated by *Z. capricorni*, *Z. capricorni* also

dominated one of the meadows least impacted by herbivory. Green turtles were found throughout the Gladstone region when surveyed in 2013 and from 2016 - 2018 (Babcock *et al.*, 2015; Limpus *et al.*, 2018; Prior *et al.*, 2015). Tagged green turtles often showed high fidelity to their foraging sites within Gladstone Harbour (Babcock *et al.*, 2015; Limpus *et al.*, 2018), however some individuals do move between meadows to feed (Babcock *et al.*, 2015; Limpus *et al.*, 2018). Dietary analysis shows green turtles in Gladstone can move in and out of the seagrass meadows in the Harbour and switch their diet to feed on algae (Prior *et al.*, 2015). Monitoring of dugong feeding trails shows that dugong grazing at the same sites as this study varies over time, within areas of a single meadow and also between meadows, indicating dugongs are moving between sites and potentially focussing grazing on higher biomass seagrass meadows in the region (Rasheed *et al.*, 2017). South Trees has only been sampled for green turtles in 2018 and although numbers of turtles were high, the population here was dominated by small immature turtles (Limpus *et al.*, 2018). It is possible that grazing by this juvenile dominated population at South Trees may have had less of an impact on the meadow than the population with more adults at Pelican Banks. A combination of megaherbivore feeding preferences, movements between meadows and population structure could cause the variable impacts seen in the Gladstone region, but was not explicitly measured as part of my study.

The other potential driver of the variability in the impacts of grazing on seagrass is the response of the seagrass meadow to the top-down pressure of megaherbivory. Seagrasses can respond to herbivory by altering their productivity, modifying rhizome or leaf water soluble carbohydrate concentrations and changing leaf properties, however these responses depend on the species of seagrass (Kuiper-Linley *et al.*, 2007). Seagrass responses will differ between regions and depend on the other stressors present at a given time (Kilminster *et al.*, 2015). These responses will determine the overall impact of herbivory on the meadow.

Although I only had the ability to assess temporal variability in grazing impacts on one meadow, I would expect the same variability in megaherbivore grazing on seagrass meadows over time to be seen in other locations in the region. In Gladstone, long-term seagrass monitoring over the past 18 years shows meadow changes that could be driven in part by megaherbivory (Chartrand *et al.*, 2019) with evidence of dugong feeding hotspots within Gladstone shift between and within meadows over time (Rasheed *et al.*, 2017).

Studies from around the world and the GBR have highlighted the importance of considering megaherbivore impacts when evaluating seagrass condition and resilience and the coupling of

both megaherbivore and seagrass monitoring is truly warranted for better system understanding (Christianen *et al.*, 2014; Heithaus *et al.*, 2014; Lal *et al.*, 2010; Scott *et al.*, 2018). However, this study demonstrates that the seagrass-megaherbivore relationship is spatially and temporally dynamic on a regional scale and monitoring programs that seek to assess seagrass and megaherbivores as an integrated system need to consider the drivers and variability of this relationship for effective management outcomes and monitoring. Understanding the regional scale megaherbivore-seagrass dynamics of closely connected meadows could inform management measures that are based on aboveground seagrass metrics to understand seagrass health and may assist in detecting seagrass meadows that are becoming overgrazed.

Chapter 7

Chapter 1:
Introduction

Chapter 2:
The role of herbivory in structuring tropical
seagrass ecosystem service delivery

Chapter 3:
Herbivory has a major influence on structure and condition
of a Great Barrier Reef subtropical seagrass meadow

Chapter 4:
Green turtle grazing plot
formation creates structural
changes in a multi-species GBR
seagrass meadow
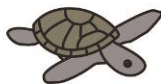
Chapter 5:
Spatial and temporal
patterns in macroherbivore
grazing in a multi-species GBR
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Chapter 6:
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Chapter 7:
General discussion

Chapter 7

General discussion

This chapter summarises the outcomes of my thesis, what these new findings mean for our understanding of seagrass herbivory in the GBR, and the management implications of my research. I also outline future research to build on my work and place my results within the conceptual model of Chapter 2. I conclude that herbivory is an important top-down structuring influence on GBR seagrass meadows, and that plant-herbivore interactions have shaped GBR seagrass communities and continue to influence their characteristics. These plant-herbivore interactions are variable over space and time and depend on the types of herbivore present and their grazing behaviour as well as the response of the seagrass meadow to herbivory. To appropriately monitor and manage seagrass meadows on the GBR and maintain the delivery of ecosystem services, these meadows should be managed as a coupled seagrass-herbivore system where practical.

How do herbivores structure seagrass meadows and their ecosystem services in the Great Barrier Reef?

Key findings

My research shows that, like terrestrial grasslands and seagrass meadows in some other parts of the world, seagrasses in the GBR are structured by the herbivores that graze on them. The impact of the top-down structuring influence of herbivory on seagrass depends on the herbivore community present at a given meadow and is variable over space and time. Megaherbivory has the most significant grazing impact on seagrass meadow structure in both the Green Island and Gladstone meadows that I studied, however the differing megaherbivore foraging behaviours at these two locations changed the scale of the structuring impacts observed. Macroherbivory is taking place in some GBR seagrass meadows, however feeding rates in the locations I studied were lower than those observed elsewhere - perhaps due to a more stable system where multiple trophic levels are protected in the case of Green Island, or seagrass meadows maintained in a lower biomass state that are a less favourable habitat for macroherbivores in the case of Gladstone. Mesoherbivory on epiphytes was also found to be low in Gladstone.

Plant-herbivore interactions in GBR seagrass meadows

Herbivory is an important pathway for the export of plant material in terrestrial ecosystems and in the highly productive seagrass meadows that are found worldwide (Bakker *et al.*, 2006; Burkepile, 2013; Frank *et al.*, 1998; Valentine and Heck, 2020). By consuming seagrass material, herbivores can facilitate the export of this productivity to other ecosystems within the coastal seascape (Heck *et al.*, 2008; Hyndes *et al.*, 2014). My research has shown that herbivores consume significant amounts of seagrass productivity on the GBR, potentially exporting this productivity by transferring it to higher trophic levels or moving it out of the meadow. As megaherbivores can consume large amounts of seagrass biomass, and it is likely this export pathway dominates over detrital export in many GBR meadows (Chapters 3 and 4 - Scott *et al.,* 2020, 2021a).

The grazing behaviour of herbivores on land may select for higher quality forage material to maximise the energy or nutrient intake from the plant material consumed (McNaughton, 1984). Similar grazing optimisation is thought to be occurring in seagrass meadows

(Aragones *et al.*, 2006). My research has shown that green turtles form grazing plots in some locations in the GBR which may allow them to meet dietary requirements for nutrients or carbohydrates (Chapter 4 - Scott *et al.* (2020)). My study documented one grazing plot at Green Island, and a subsequent megaherbivore exclusion experiment observed another grazing plot formed within the same meadow after one year (York, *pers. ob.*). This shows the formation of grazing plots by green turtles at Green Island is a repeated behaviour and may have acted to structure seagrass species composition and nutritional content in this meadow over longer timescales.

Like terrestrial plants, seagrasses have evolved under intense grazing and have adapted to persist even when subjected to very high herbivory pressure (Domning, 2001; Jackson, 2001). Seagrass meadows on the GBR are able to recover from disturbances that cause losses of above and belowground material (Rasheed, 1999, 2004; Rasheed *et al.*, 2014). The fast growth rates of GBR seagrasses allow them to asexually compensate for losses within a meadow through rhizome growth (Rasheed, 1999, 2004). Another essential mechanism for recovery from meadow-scale disturbance are the seed banks produced by meadows, these seeds allow meadows to recover when adult plants are lost (Rasheed *et al.*, 2014). My research indicates that the GBR seagrass meadows I studied are well adapted to persist under current levels of herbivory pressure and even the dramatic grazing impacts I observed in Chapter 4 (Scott *et al.*, 2020) would have only resulted in short term meadow structuring impacts.

Although the meadows I studied consist of opportunistic seagrass species, over their long evolutionary history, grazing is likely to have shaped the seagrass communities present today. Whether this is due to changes in meadow structural properties, productivity or species composition, a GBR seagrass community without herbivores would look very different to the seagrass meadows we see today. For example, small scale disturbances at Green Island can favour the faster opportunistic seagrass species *Syringodium isoetifolium* and cause overall community shifts in the meadow (Rasheed, 2004). There is also anecdotal evidence and observations of shifts to opportunistic species in meadows once dominated by larger persistent seagrass species with the return of intense dugong feeding in other areas of Queensland (e.g. Mornington Island; R. Coles *pers. com.*; Wellesley Islands - Taylor *et al.*, 2007). Although I did not document species shifts in the grazing plots that I observed in Chapter 4 (Scott *et al.*, 2020), changes in community composition are likely to have occurred as the meadow recovered from this grazing event and conditions favoured fast colonising

species. These changes would be observed over much longer time scales than what I studied. The most pervasive impact of megaherbivore grazing, seen at both locations I studied in Chapters 3, 4 and 6 (Scott *et al.*, 2020, 2021a) was the reduction of seagrass shoot heights, showing megaherbivore grazing maintains meadows with shorter shoots and less structural complexity.

Herbivores on land and in the marine environment can act as ecosystem engineers and their grazing behaviour may alter the characteristics of the food source that they rely on (Forbes *et al.*, 2019; Poore *et al.*, 2012). By modifying the functional properties of a seagrass ecosystem, herbivores can also alter the suite of ecosystem services provided by a meadow, including the provision of food for the herbivores themselves (Chapter 2 - Scott *et al.,* 2018). For example, one herbivore group can modify a seagrass meadow to such an extent that it is a less valuable habitat and foraging ground for other herbivores (Pagès *et al.*, 2012). A similar pattern was observed in the Gladstone region where megaherbivory reduced seagrass meadow structural complexity (Chapter 6), and these lower biomass meadows were less valuable for both macroherbivores and mesoherbivores (Chapter 3 - Scott *et al.*, 2021a). Such losses in seagrass complexity due to megaherbivory also impact other ecosystem services provided by a seagrass meadow outlined in Chapter 2 (Scott *et al.*, 2018). The grazed seagrass meadow at South Trees in Gladstone has been shown to be moderately complex compared to other meadows in the GBR, which means it supports fewer larger fish, thereby diminishing the fisheries value of this meadow (Jinks *et al.*, 2019).

The role of different herbivore groups in structuring GBR seagrass meadows

The herbivore community in GBR seagrass meadows is made up of a diverse range of mesoherbivores such as amphipods and isopods, macroherbivores such as fish and urchins, and megaherbivores such as turtles and dugong. Each group of herbivore has a different feeding strategy and all herbivore groups can act individually and interactively to structure seagrass meadows.

At both of the seagrass locations I studied, megaherbivory had the largest top-down structuring impact on the meadow. However, the way megaherbivores structured the meadow was quite different between sites. My exclusion experiment that looked at all groups of herbivores in Gladstone, showed megaherbivores structured the meadow here with no measurable impacts of, or interactions with, any other herbivore groups, and that this impact

was relatively uniform across the entire meadow (Chapter 3 - Scott *et al.* 2021a). At Green Island, the dramatic, localised impacts of green turtle grazing plot formation were evident (Chapter 4 - Scott *et al.* 2020) and although macroherbivory was taking place, the impacts on overall meadow structure were minimal (Chapter 5 - Scott *et al.*, 2021b). Although I did not detect an impact of megaherbivory on the seagrass community structure at Green Island, it is likely that the formation of grazing plots, and movement between these, has shaped the seagrass community over a longer timescale.

In my interactive study, mesoherbivores did not have a large impact on seagrass meadow properties or epiphyte load in Gladstone (Chapter 3 - Scott *et al.,* 2021a). This is a somewhat surprising result given the importance of mesoherbivores in maintaining healthy seagrass meadows in other parts of the world (Hughes *et al.*, 2004). While I did not measure the mesoherbivore epiphyte interaction at Green Island, Hoffmann *et al.* (2020) found that excluding mesoherbivores resulted in an 89% increase in epiphyte load on the seagrass meadow, so it may well be an important factor in maintaining seagrass meadows here and elsewhere on the GBR. The importance of the mesoherbivore epiphyte consumption pathway may depend on the population dynamics of both consumers and resources in the meadow in question (Myers and Heck, 2013). In Gladstone, the abundance of both mesoherbivores and epiphytes was very low and there was no interaction between these, whereas at Green Island the abundance of both were higher and the interaction between the two was important. In my study locations and in much of the coastal GBR, high nutrient levels are generally not a major issue and hence epiphyte overgrowth is not a problem for seagrass survival (Carruthers *et al.*, 2002). Thus, the importance of mesograzing on epiphytes and hence seagrass meadow health may be reduced here compared with higher nutrient locations.

The overwhelming impact of megaherbivory that I observed at both of my study sites fits with other studies carried out on seagrass-megaherbivore dynamics (Christianen *et al.*, 2014; Fourqurean *et al.*, 2019; Heithaus *et al.*, 2014; Lal *et al.*, 2010; Thayer *et al.*, 1984). But this is not always the prevailing dynamic, other studies which excluded multiple herbivore groups in areas with megaherbivores present, found a larger impact of mesoherbivores and macroherbivores than megaherbivores on the meadow (Bessey *et al.*, 2016; Ebrahim *et al.*, 2014). My results show that paradigms adopted for seagrass-herbivore dynamics are not universally applicable, as the range of seagrass meadow settings and systems is diverse and complex, and universal paradigms rarely capture this diversity.

Spatial and temporal variability

The impacts of herbivory are not constant and will vary over space and time, due to both herbivore foraging behaviour and seagrass responses to herbivory pressure, along with other drivers of seagrass change. In Chapters 3 and 4 - Scott *et al.*, (2020, 2021a), I observed contrasting megaherbivore feeding strategies between Green Island and Gladstone. At Green Island, green turtle grazing was targeted in small patches of the meadow and caused dramatic losses of both above and below ground biomass within these patches (Chapter 4 - Scott *et al.*, 2020). Whereas in Gladstone, megaherbivores grazed broadly across the meadow as a whole, causing the meadow to exist in a lower biomass state (Chapter 3 - Scott *et al.*, 2021a). However, this pattern of megaherbivory in Gladstone was found to differ among the meadows in the region, and also between years at South Trees (Chapter 6). Macroherbivory (by fish and urchins) was also variable over time and between the seagrass meadows at Green Island (Chapter 5 - Scott *et al.*, 2021b), throughout much of the year rates of macroherbivory were very low, but in peak months almost half of seagrass productivity was removed by macroherbivores.

My findings emphasise the need to acknowledge variability in seagrass-herbivore interactions in studies that are carried out on smaller temporal or spatial scales. To fully understand the plant-herbivore dynamics in operation in one location, an understanding of the broader spatial and temporal dynamics in herbivory would be required.

The role of a balanced seagrass-herbivore system

In Chapter 2 (Scott *et al.*, 2018) I hypothesise that a balanced seagrass-herbivore system, where moderate levels of grazing take place but seagrass meadow structure is still maintained, could maximise the delivery of a broad range of seagrass ecosystem services. Understanding more about the plant-herbivore interactions in GBR seagrass meadows allows us to test the conceptual model that I presented in Chapter 2 and how herbivory potentially modifies the delivery of ecosystem services. The data I present in Chapters 3-6 show how herbivores can modify seagrass meadow structure and alter the provision of food for other herbivores in two locations. Based on my findings from Chapters 3-6 these two locations could be seen to occupy different positions on the seagrass-herbivore scale, shown in Figure 7.1. Green Island represents a balanced system, whereas the lower biomass grazed meadows in Gladstone are more megaherbivore dominated. In the balanced system at Green Island, we have seen higher levels of macroherbivory (Chapter 5 - Scott *et al.*, 2021b) and

mesoherbivory (Hoffmann *et al.*, 2020), than in the megaherbivore dominated system in Gladstone (Chapter 3 -Scott *et al.*, 2021a). We also see the patterns in seagrass characteristics at Green Island have a higher biomass and more diverse meadow predicted for a balanced system in the conceptual model, and Gladstone has a lower-biomass, lower-diversity meadow characteristic of a megaherbivore dominated system.
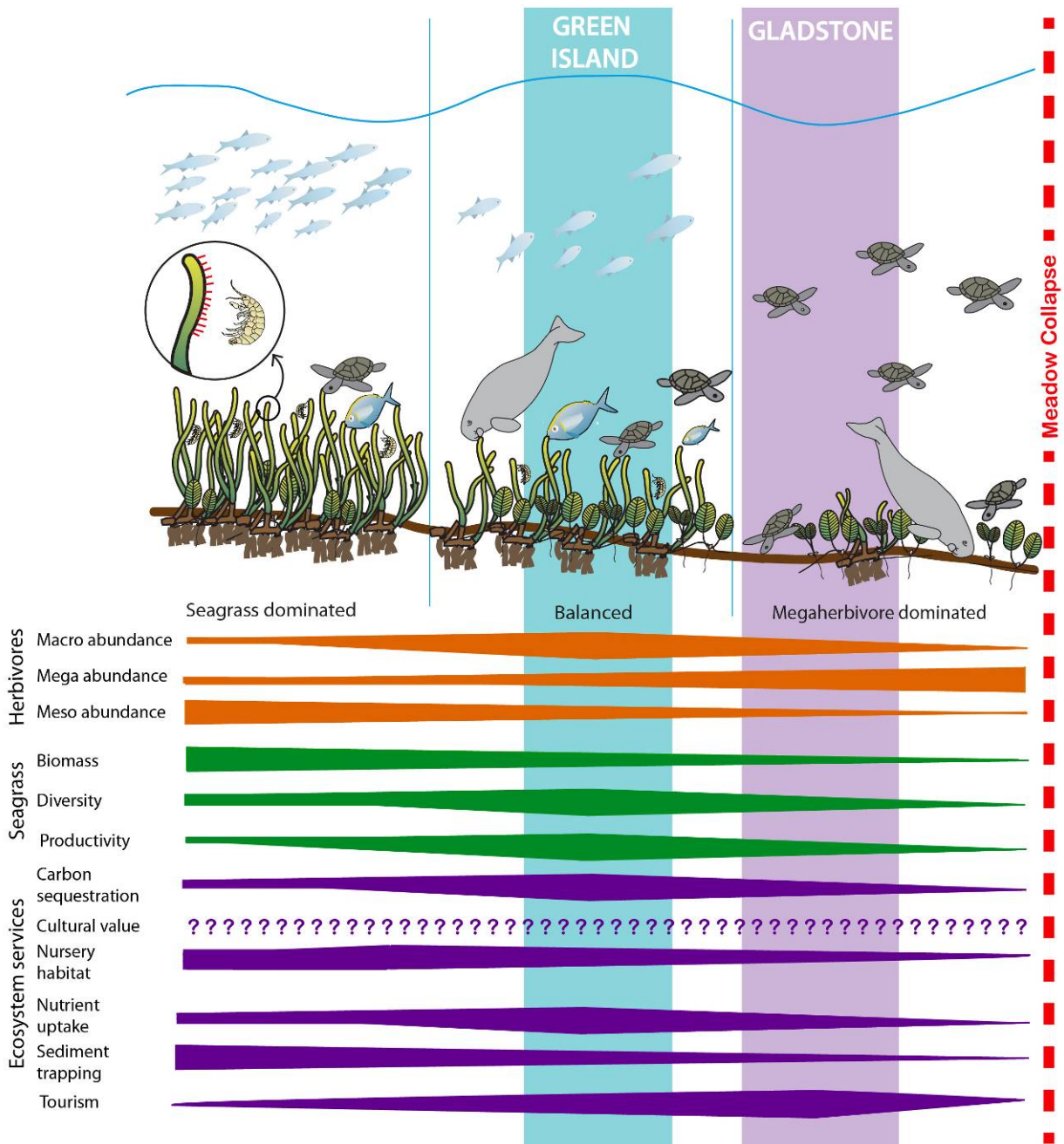
Figure 7.1: Conceptual diagram from Chapter 2 (Scott *et al.*, 2018), modified to show where my two study sites fit within this conceptual framework.

Management implications

One of the older prevailing paradigms in seagrass ecology suggested that seagrass populations are predominantly controlled by bottom-up abiotic factors such as light levels, nutrient availability and water temperatures (Valentine and Heck, 2020). While these are undoubtedly important structuring influences, my studies and other emerging research from around the world (e.g. Christianen *et al.*, 2014; Fourqurean *et al.*, 2019; Heithaus *et al.*, 2014; Hoffmann *et al.* 2020, Lal *et al.*, 2010 Pagès *et al.*, 2018) are highlighting the importance of various herbivore groups in controlling seagrass meadow distribution and function. This bottom-up paradigm is now shifting to also recognise and incorporate the significant top-down influence of herbivory in controlling many seagrass populations (Heck and Valentine, 2007; Valentine and Heck, 2020). In the GBR setting, there are a range of management and monitoring measures in place that focus on these bottom-up abiotic factors for seagrass, including efforts to reduce nutrient and sediment inputs (Australian Government and Queensland Government, 2017) and management of acute anthropogenic impacts that can reduce light such as dredging (Chartrand *et al.*, 2016; York *et al.*, 2015). However, these programs do not generally include the top-down influence of herbivory on seagrass meadows (Coles *et al.*, 2015), my results show this is a critical component shaping at least some of the GBR seagrass meadows and should be considered.

Management actions that modify the seagrass-herbivore system

This understanding of seagrasses and their herbivores is particularly relevant in modern seagrass meadows where humans modify many of the aspects of the plant-herbivore system. Green turtle conservation measures have been very successful in many locations around the world leading to increases in population sizes, however, the predators that have historically controlled green turtle numbers remain in decline (Chaloupka *et al.*, 2008; Heithaus *et al.*, 2014). This has allowed green turtle numbers to increase over and above historical levels in many seagrass meadows, in some cases these populations exceed the carrying capacity of the meadow, and in extreme cases overgrazing of seagrasses results in losses of meadows (Christianen *et al.*, 2014; Fourqurean *et al.*, 2019; Heithaus *et al.*, 2014; Lal *et al.*, 2010). Such declines due to green turtle herbivory create conflicts with people who rely on the ecosystem services that seagrass meadows provide and are detrimental to the herbivores themselves (Arthur *et al.*, 2013). Although there are large populations of green turtles in the GBR, their numbers are not increasing rapidly, and the presence of top-down controls due to

predation and indigenous hunting are likely maintaining turtle populations well below the carrying capacity of the seagrass meadows (Limpus, 2008). However, my research has shown that megaherbivores in the GBR can have significant impacts on seagrass meadow structure and while these currently appear to be part of a balanced system, management measures should seek to maintain this and ensure it does not shift towards an overgrazed system.

Management actions to establish Marine Protected Areas also have implications for plant-herbivore dynamics in seagrass meadows. These impacts depend on the number of trophic levels targeted by the protected area, for example where herbivores are protected and their predators are not, higher abundances of herbivores increase grazing pressure and can cause overgrazing (Ferrari *et al.*, 2008; Fourqurean *et al.*, 2019; Heithaus *et al.*, 2014; Prado *et al.*, 2008). Herbivores can aggregate in Marine Protected Areas, which also causes enhanced seagrass grazing rates (Prado *et al.*, 2008) and overgrazing of some meadows (Christianen *et al.*, 2014). The GBR contains a network of Marine Protected Areas established in 1981, with some areas such as Green Island protected for even longer timeframes (Baxter, 1990), however these protect both herbivores and some of their predators. Therefore predators can control herbivore populations in the GBR and prevent overgrazing.

Implications for assessing seagrass meadow condition

In the GBR and beyond there are a variety of monitoring projects that assess seagrass condition based on aboveground seagrass metrics such as biomass, percent cover, or species present (Coles *et al.*, 2015; Duffy *et al.*, 2019). These metrics are used on a GBR wide scale to understand the health of seagrass meadows and to track how the meadow status changes from year to year. However, my research has shown that aboveground seagrass characteristics in seagrass meadows can be heavily influenced by the top-down control of herbivory (Chapters 3, 4 and 6 - Scott *et al.*, 2020, 2021a). A healthy, highly productive seagrass meadow may have a low biomass if this productivity is being consumed by herbivores. However, a similarly low biomass meadow that is not being grazed may indicate decline and be in need of management intervention due to other impacts such as declining water quality. Understanding this dynamic is further complicated by the spatial and temporal variability in both seagrass productivity and the pressure of herbivory (Chapters 5 and 6).

My research shows that seagrass meadows in the GBR should ideally be managed as a coupled seagrass-herbivore system and monitoring of these meadows should incorporate the top-down structuring influence of herbivory alongside the bottom-up factors already

considered. This is particularly important in areas with high megaherbivore populations. The challenge for scientists and managers is to take this knowledge and incorporate it into management tools that consider seagrass meadows, bottom-up abiotic drivers and the top-down pressure of herbivory populations. Quantifying and identifying the drivers of seagrass change is a key challenge to overcome, and for the GBR is incomplete without including an assessment of herbivory.

Interactions with other threats

Seagrass meadows are threatened by multiple stressors worldwide (Orth *et al.*, 2006; Waycott *et al.*, 2009), many of these stressors are present in GBR seagrass meadows (Coles *et al.*, 2015) and these can be particularly problematic when they interact with a meadow already under grazing pressure. Where other stressors interact with grazing pressure to cause declines in a meadow, this threatens the seagrass itself, the herbivore populations that graze on the meadow, and both the people and adjacent ecosystems that rely on the ecosystem services that the meadow provides.

In northern Australia, large-scale losses of seagrass can be caused by cyclones and associated flooding (McKenna *et al.*, 2015; Rasheed *et al.*, 2014; Rasheed and Unsworth, 2011). Previous seagrass losses caused by cyclone activity have been followed by megaherbivore starvation events (Marsh and Kwan, 2008; Preen and Marsh, 1995). Grazing can change the resilience of a seagrass meadow and alter the ability of a meadow to recover from these types of disturbances (Unsworth *et al.*, 2015). By understanding whether a seagrass-herbivore system is in balance and the levels of grazing pressure present, outcomes of the interactions with other stressors such as low light levels and habitat fragmentation can be better predicted and managed (Chartrand *et al.*, 2016; Gera *et al.*, 2013). This is particularly important in seagrass meadows in the southern GBR such as Gladstone which have been identified as hotspots where multiple anthropogenic stressors could interact to threaten seagrass meadows (Grech *et al.*, 2011).

Future research

Given the large, diverse seagrass meadows and the diverse populations of herbivores in the GBR, it is surprising that we are only just beginning to unravel the complex plant-herbivore interactions that have shaped these meadows throughout their evolutionary past and into the present. My study was the first to quantify the impacts of herbivory in structuring GBR seagrass meadows and has provided new insights into the impact of herbivores on seagrass meadows as well as how this varies spatially and temporally. However, plant-herbivore interactions are complex, and the GBR is a large and diverse system with multiple seagrass communities - so there is still much to understand in terms of the impact of herbivores on seagrass meadows and their ecosystem services within the GBR.

Understanding seagrass herbivory on a GBR wide scale

The GBR contains a diverse range of seagrass species and communities that are likely to be grazed by herbivores. My research focussed on two locations in the GBR with different seagrass communities present, however as I have established there is substantial variability in seagrass-herbivore interactions in different meadow types and locations. York (pers, comm.) have identified large-scale variability in megaherbivore grazing in 11 locations that span the full 2500km length of the GBR, however there are still many meadows where interactions are not understood. A useful avenue of future research would be examining meadows with high populations of megaherbivores, particularly those meadows where declines have been observed. More research on herbivory in other meadow types such as deep water seagrasses would help to understand the value of and ecosystem services provided by these poorly understood ecosystems.

Grazed plot dynamics

The formation of grazed plots has been documented around the world and in Chapter 4, I documented the formation of grazing plots by green turtles for the first time on the GBR. Subsequent work by York (*pers. comm*) has shown that grazing plot formation is a repeated behaviour at Green Island, but we know little about the dynamics of these grazing plots. In other locations green turtles maintain grazing plots for longer periods of time and can move between a mosaic of grazing plots (Johnson *et al.*, 2019; Molina-Hernández and van Tussenbroek, 2014; Williams, 1988). Understanding these grazing plot dynamics in the GBR would show the long-term impacts of this grazing behaviour on seagrass meadows. Other studies have shown that grazing plot formation allows green turtles to feed on nutrient rich

regrowth (Bjorndal, 1980; Moran and Bjorndal, 2007), future work should investigate whether the same pattern is observed in the GBR and whether my observations relating to green turtle dietary requirements are broadly applicable. Tracking of megaherbivores can be a useful tool to understand more about seagrass meadows (Hays *et al.,* 2018), and this would also show more about interactions between megaherbivores and seagrasses, including the formation of, and movement between, grazing plots.

Links to seagrass productivity responses

Studies worldwide have shown a variable response of seagrass productivity to grazing (Aragones *et al.*, 2006; Christianen *et al.*, 2012; Fourqurean *et al.*, 2010; Kelkar *et al.*, 2013a). Due to the narrow leaves of the seagrass blades in Gladstone and the almost complete loss of grazed seagrass at Green Island, I was not able to compare seagrass productivity in grazed and ungrazed treatments. However, the response of seagrass productivity to herbivory remains a key question worthy of further study in the GBR to establish the relationship between herbivore pressure and seagrass productivity. Changes in productivity will also have implications for the ecosystem services delivered by the meadow. More field studies, or simulated grazing studies, would help to understand the response of GBR seagrass productivity to herbivory.

Quantifying the carrying capacity of GBR seagrass meadows for megaherbivores

Many meadows in the GBR are under high megaherbivore grazing pressure and may exist in a megaherbivore dominated state, so understanding the numbers of megaherbivores these meadows currently support, and have the capacity to support, would aid in management. By assessing the seagrass productivity in an area and how much of this is consumed by megaherbivores, assessments of carrying capacity can help to predict and prevent overgrazing of meadows, particularly by green turtles. Intensive seagrass and megaherbivore surveys in meadows that have been identified as megaherbivore dominated systems would help to establish if these grazing levels are sustainable.

Understanding seascape benefits of seagrass productivity export by herbivores

The GBR is made up of connected coastal ecosystems with mangroves, seagrass meadows and coral reefs existing in close proximity to one another. Understanding how herbivores move seagrass productivity between these habitats would give a seascape understanding of the role of herbivory in the GBR. In many locations these habitats are adjacent to one another, so many species are likely to rely on multiple habitats, including seagrass herbivores.

A more general seascape level study of the links between the usage of these habitats is warranted, and the role of herbivores would be a particularly interesting element of such a study.

Links and trade-offs with ecosystem service delivery

In Chapter 2 I identified the role that herbivory plays in ecosystem service delivery in seagrass meadows, and while I had hoped to directly test these trade-offs in ecosystem service delivery for carbon storage in Chapter 6, my long-term field study was not successful in achieving this due to field equipment difficulties. However, the question of the trade-offs in ecosystem service delivery caused by herbivory remains important for management. Future research could identify and quantify the trade-offs in ecosystem service delivery caused by a herbivore dominated system to test the conceptual model set out in Chapter 2.

Developing management tools to incorporate the top-down influence of herbivory

Research into plant-herbivore dynamics in seagrass meadows is highly relevant from a management perspective, however we currently lack the information to easily incorporate this research into management and monitoring in the GBR. Future work should identify how managers and traditional owners can undertake integrated seagrass-herbivore monitoring and develop tools that help to easily and accurately classify meadows according to Figure 7.1.

Concluding remarks

The role of herbivores as ecosystem engineers in seagrass meadows worldwide is well established, however no studies had tested the impact of herbivory on the diverse and extensive seagrass meadows found in the GBR. My research has quantified for the first time the role of herbivores in structuring GBR seagrass meadows with the following key roles of the herbivore community:

- The herbivore community in the GBR structures tropical and subtropical seagrass meadows.

- Megaherbivores have the largest impact on seagrass meadow structure, but the scale and type of the impact depends on how megaherbivores graze.

- In the GBR meadow I studied, the mesoherbivore-epiphyte dynamic seems to be less important in structuring and maintaining the meadow than in other locations.

- Macroherbivores are present but are not consuming large amounts of seagrass productivity, or impacting seagrass structure in a highly protected meadow.

- Macroherbivory and megaherbivory are variable over space and time so the impacts on the seagrass meadow are not easy to predict.

- Herbivory that structures seagrass meadows is also likely to modify ecosystem service provision by a meadow.

- The reductions in seagrass above and belowground biomass caused by megaherbivore grazing could change the quality of the seagrass meadow as a foraging ground for other herbivores as well as altering the delivery of other ecosystem services in these meadows.

My research has presented novel findings that add to the global literature on plant-herbivore dynamics in seagrass meadows. The role of megaherbivores as ecosystem engineers in these meadows has long been suspected, but has been quantified for the GBR for the first time in my study.

These findings have applications for informing management and monitoring of seagrasses and their herbivores and suggest that these should be considered as a coupled seagrass-herbivore system. A greater understanding of the plant-herbivore interactions in GBR seagrass meadows is essential in the face of multiple stressors and worldwide seagrass declines, to conserve GBR seagrass meadows, and the herbivores who rely on them.

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Appendix A

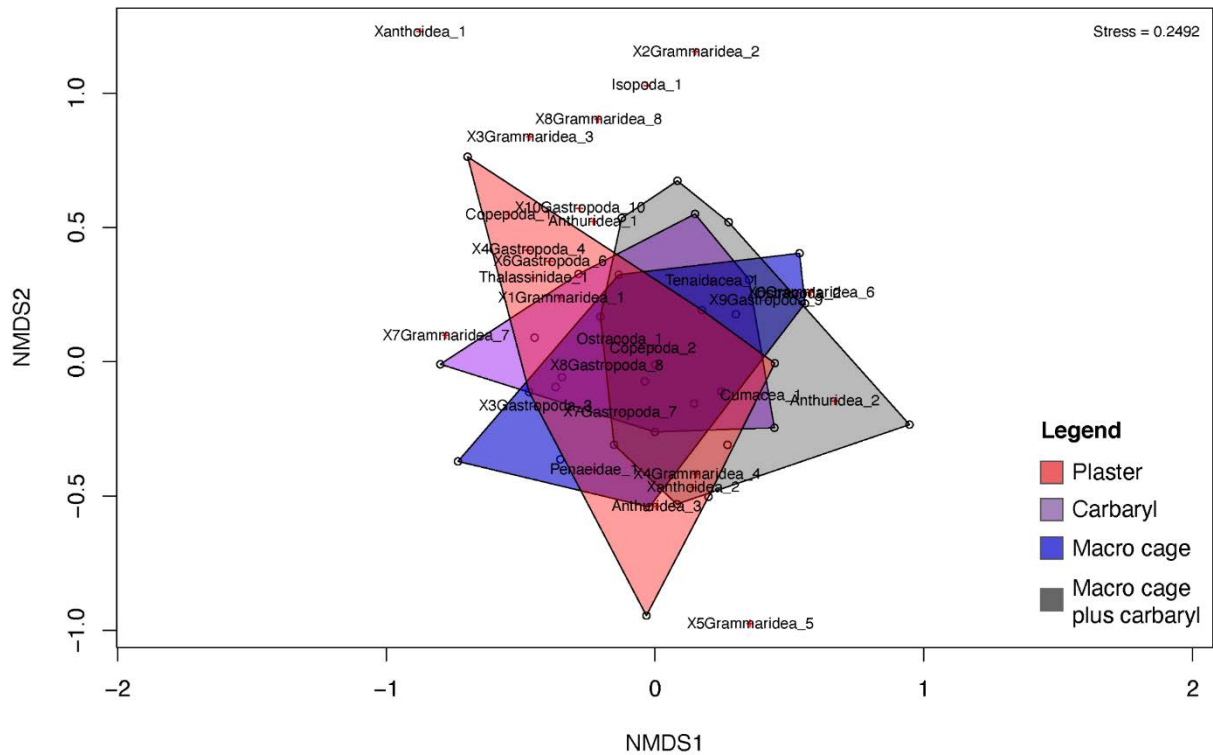# Chapter 3 supporting figures and tables

Table A.1: Mean numbers and size ranges of fish and decapods caught at the site using a small beam trawl (2 mm mesh) in the seagrass meadow (See Jinks *et al*. 2019). Fish species have been divided into trophic groups based on feeding preferences. This trawl targeted fish in the 1 – 5 cm range.

Species and classification	Mean number per 100 m²	Standard error	Size range
Carnivore			
Ancistrogobius yoshigoui	6.50	2.79	1 - 4 cm
Atherinomorus endrachtensis	0.09	0.09	5 cm
Eleutheronema tetradactylum	0.09	0.09	1 - 5 cm
Gerreidae sp. 1	1.86	1.86	2.5 cm
Gerres subfasciatus	0.06	0.06	5 cm
Lethrinus spp.	38.25	8.76	2 - 3 cm
Photopectoralis aureus	0.06	0.06	1 - 4 cm
Platycephalus endrachtensis	0.06	0.06	15 cm
Pomadasys maculatus	0.26	0.26	3.5 cm
Sillago maculata	0.19	0.19	2 cm
Tetraroge barbata	0.26	0.17	2 - 3 cm
Herbivore			
Siganus fuscescens	7.85	1.37	2 - 5 cm
Omnivore			
Crab sp.	0.06	0.06	1 cm
Fangblenny sp.	0.09	0.09	1.5 - 4 cm
Fish sp. 11	0.09	0.09	1 cm
Fish sp. 12	0.09	0.09	1 cm
Fish sp. 16	0.06	0.06	3 cm
Fish sp. 4	0.17	0.17	1.5 cm
Helotes sexlineatus	0.29	0.18	3.5 - 6 cm
Metapenaeus sp.	4.68	2.96	2 - 3 cm
Pelates quadrilineatus	1.88	1.05	1 - 3 cm
Penaeus sp.	3.30	3.20	3 - 6 cm
Prawn spp.	17.79	3.40	1 - 3.5 cm
Swimmer crab sp.	0.33	0.26	2 cm

Table A.2: Mean aboveground biomass (gDW/m^2) and standard error for all treatments at the start of the experiment in August and end in November.

Treatment	Start		End	
	Average biomass gDW/m^2	Standard error	Average biomass gDW/m^2	Standard error
Control	15.8	0.4	16.9	0.2
Plaster	14.1	0.3	17.7	0.2
Carbaryl	14.0	0.2	18.7	0.1
Macro frame	15.2	0.6	18.7	0.4
Macro cage	16.8	0.7	28.5	0.8
Macro cage plus carbaryl	18.8	0.9	37.5	0.9
Mega cage	13.2	0.3	30.4	0.9
Mega cage plus carbaryl	16.2	0.7	32.1	1.1

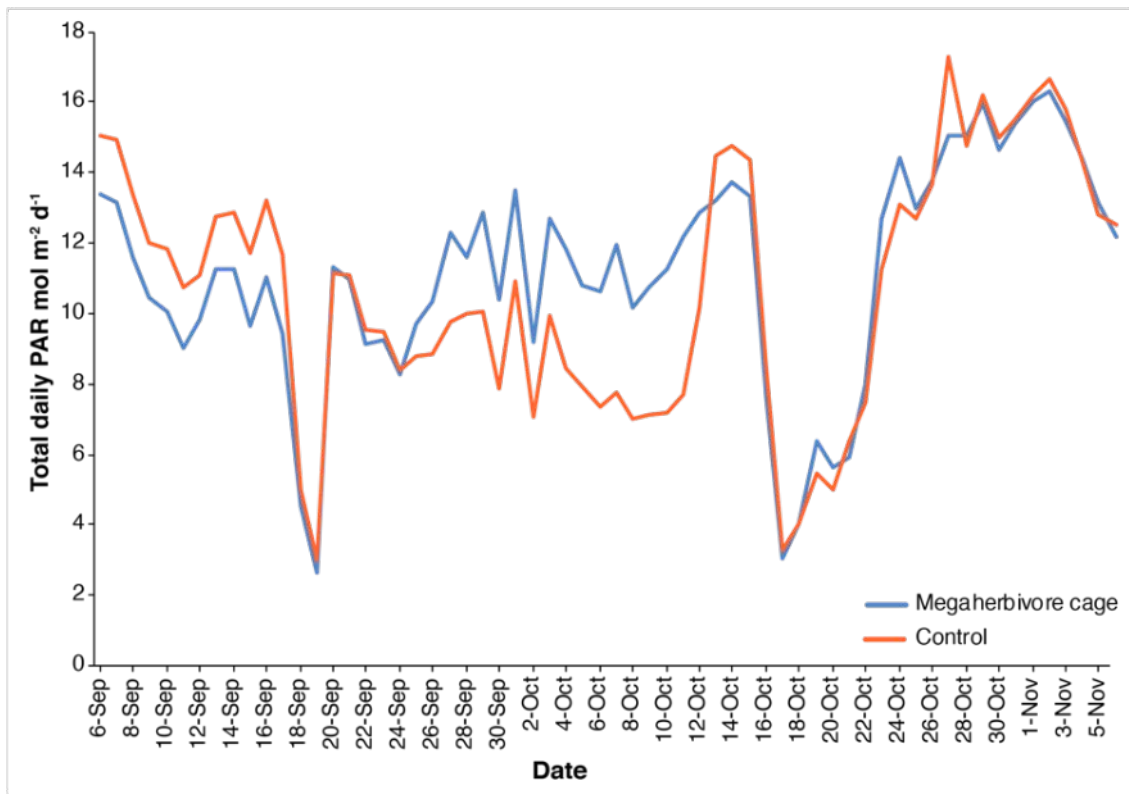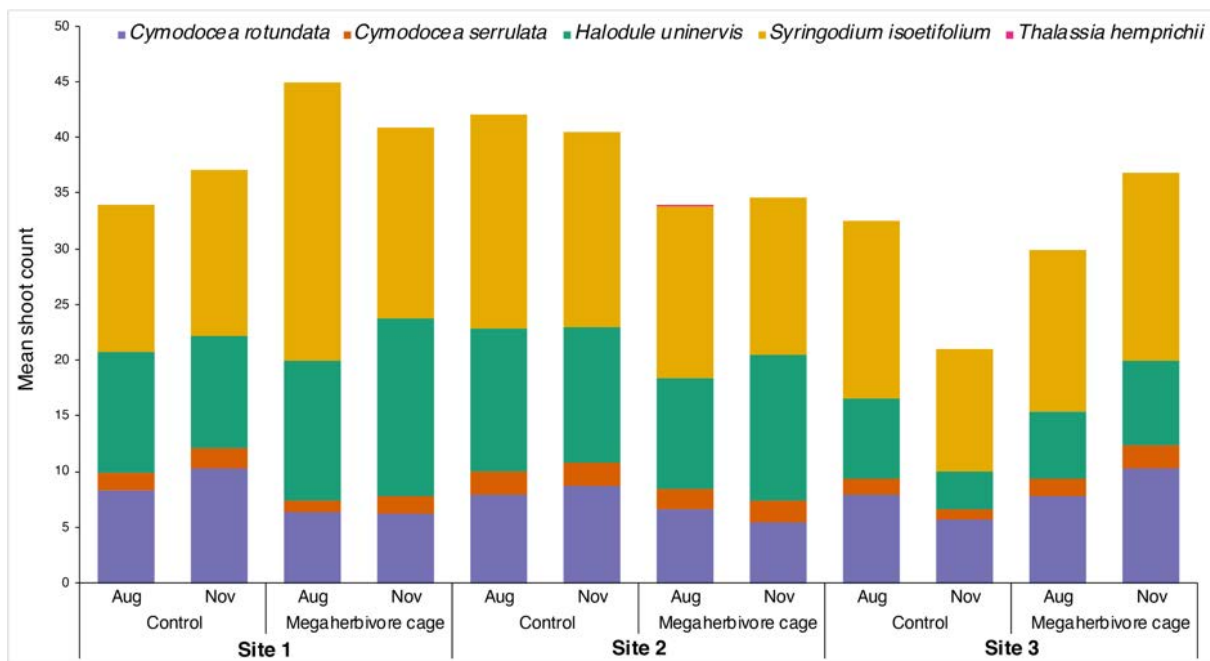**Figure A.1:** Multidimensional scaling output of mesoherbivore species recorded in each treatment.

Appendix B

Chapter 4 supporting figures and tables

Figure B.1: Total daily photosynthetically active radiation in control and megaherbivore cages.

Figure B.2: Mean shoot counts of all species in megaherbivore cage and control plots at all sites at the start (Aug) and end (Nov) of the experiment.

Table B.1: Details of percentage similarity (SIMPER) analyses for seagrass species between sites. Av Contrib. % is the percent contribution of a species to the Groups average similarity (Group Av. Sim.)/dissimilarity (Group Av. Diss.); Av. Abund is the average abundance of each species in a group; Cum.% is the cumulative percent contribution of multiple species to Group Av. Sim. The pairwise comparison with the asterisk indicates the groups that were not significantly different in the PERMANOVA analysis.

Site	Group Av. Sim.	Species	Av. Abund	Av. Sim	Sim/SD	Contrib.%	Cum.%
1	78.69	*S. isoetifolium*	17.52	33.55	4.67	42.63	42.63
		H. uninervis	12.38	26.82	4.79	34.08	76.72
		C. rotundata	7.77	16.21	2.86	20.6	97.31
2	76.86	*S. isoetifolium*	16.58	30.86	1.93	40.16	40.16
		H. uninervis	12.04	28.27	4.76	36.78	76.94
		C. rotundata	7.17	15.05	2.15	19.58	96.51
3	78.83	*S. isoetifolium*	14.56	40.89	8.41	51.88	51.88
		C. rotundata	7.96	20.53	3.31	26.04	77.92
		H. uninervis	6.04	13.99	2.42	17.74	95.66

Sites	Group Av. Diss.	Species	Av. Abund Group 1	Av. Abund Group 2	Av. Diss	Diss/SD	Contrib.%	Cum.%
1, 2*	21.57*	*S. isoetifolium*	17.52	16.58	11.13	1.47	51.6	51.6
		H. uninervis	12.38	12.04	4.29	1.37	19.87	71.47
		C. rotundata	7.77	7.17	3.92	1.28	18.16	89.63
1, 3	25.23	*H. uninervis*	12.38	6.04	9.95	1.57	39.42	39.42
		S. isoetifolium	17.52	14.56	9.1	1.19	36.05	75.46
		C. rotundata	7.77	7.96	4.55	1.25	18.05	93.51
2, 3	27.87	*S. isoetifolium*	16.58	14.56	11.09	1.59	39.78	39.78
		H. uninervis	12.04	6.04	9.68	1.64	34.72	74.5
		C. rotundata	7.17	7.96	4.78	1.37	17.16	91.66

Appendix C

Chapter 5 supporting figures
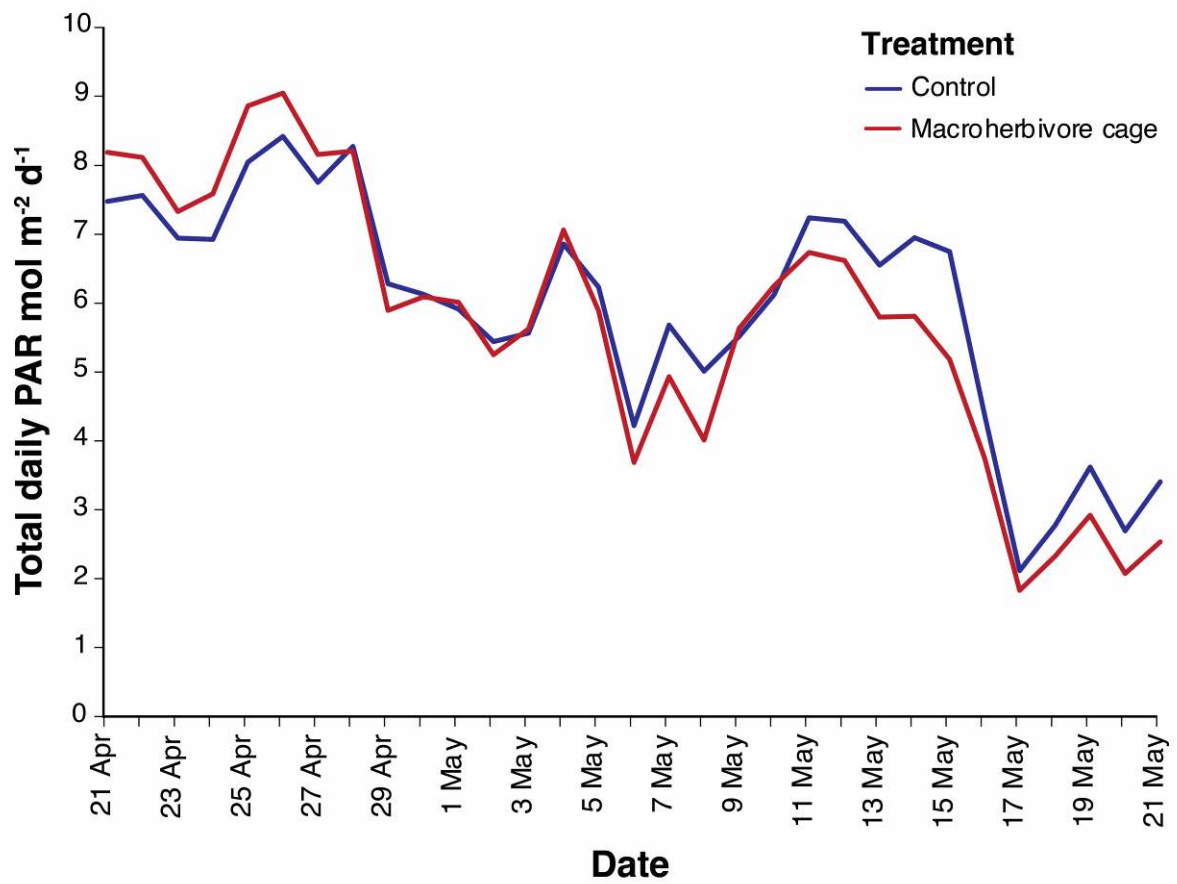
Figure C.1. Total daily light in control and caged plot.

Figure C.2. Blacktip reef shark captured on video.