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

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ABSTRACT: Megaherbivore grazing (e.g. by turtles, and sirenians) 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. We ran an experiment in the Great Barrier Reef to test the question: How does megaherbivory vary on a regional scale? We used megaherbivore exclusion cages in 5 meadows along a 50 km region of coastline around Gladstone in the southern Great Barrier Reef World Heritage Area to understand variability in megaherbivory between meadows. We found differences in the impacts of megaherbivore grazing on seagrass biomass and shoot heights between meadows. 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 seagrass to grazing pressure. Our 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.

KEY WORDS: Megaherbivore · *Chelonia mydas* · *Dugong dugon* · Grazing · Subtropical · Seagrass ecosystems · Plant–herbivore interactions · Food web

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1. INTRODUCTION

Seagrass meadows are highly productive ecosystems and an important food source, particularly for megaherbivores (e.g. green turtles and sirenians) who may rely heavily on seagrass for their diet and can consume significant amounts of seagrass productivity (Scott et al. 2018, Esteban et al. 2020). These large-bodied grazers can act as ecosystem engineers, structuring seagrass meadows by modifying meadow char-

acteristics as they feed, and impacting the ecosystem services a meadow provides (Scott et al. 2018).

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, Scott et al. 2020). Losses in belowground biomass due to grazing can occur where green turtles feed on rhizomes (Christianen et al. 2014, Scott et al. 2020), and when dugongs employ excavation foraging (Shep-

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pard et al. 2010, Rasheed et al. 2017). In extreme cases, overgrazing can result in total loss of seagrass meadows (Kelkar et al. 2013, Christianen et al. 2014, Fourqurean et al. 2019). Seagrass overgrazing is particularly prevalent in areas where green turtle conservation measures have been 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 within 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. 2019) and depend on the number of turtles present (Kelkar et al. 2013).

The responses of seagrasses to pressures such as herbivory can also vary between seagrass species, spatially and temporally, and will depend on top-down and bottom-up controls (Kuiper-Linley et al. 2007, Kilminster et al. 2015). These responses may vary according to meadow habitat, location and associated variability in the stresses and environmental settings (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 spatially, especially as megaherbivores move between meadows (Limpus et al. 2018, Scott et al. 2018).

In the Great Barrier Reef (GBR), 2 megaherbivores that consume large amounts of seagrass are present: green turtles *Chelonia mydas* and dugong *Dugong dugon* (Sheppard et al. 2010, Esteban et al. 2020). These megaherbivores can graze broadly across seagrass meadows as a whole (Scott et al. 2021) or in a more targeted fashion, e.g. green turtles can form grazed plots (Scott et al. 2020). Dugongs may focus their grazing on higher biomass (Tol et al. 2016, Rasheed et al. 2017) or higher-nutrient seagrass (Sheppard et al. 2010). Megaherbivore feeding in the GBR can structure seagrass meadows; the impact of this depends on the megaherbivore population present and their grazing behaviour, along with the compensatory response of the meadow (Kuiper-Linley et al. 2007, Scott et al. 2020).

We used exclusion cages to quantify the impact of megaherbivore grazing at 5 sites in the Gladstone

(Queensland, Australia) region encompassing a 50 km section of coastline. Megaherbivory has been identified as the most important top-down process affecting the seagrass meadows here (Scott et al. 2021), with both green turtles and dugongs feeding at all of the study meadows (Rasheed et al. 2017, Limpus et al. 2018, Scott et al. 2021).

2. MATERIALS AND METHODS

Megaherbivore exclusion cages were deployed at 5 different meadows in a coastal barrier island system of the southern GBR near Gladstone (Fig. 1) for 3 mo between August and November in 2018. The characteristics of these meadows are summarised in Table 1 and shown in Fig. 1. The meadows at these sites contain 3 seagrass species: *Zostera muelleri capricorni*, *Halophila ovalis* and *Halodule uninervis*.

Megaherbivore exclusion cages were 2 × 2 m wide and 0.5 m high and made of galvanised steel with a 20 × 20 cm mesh. These cages excluded megaherbivores but allowed other herbivores access to the plots to graze. Three megaherbivore exclusion cages were deployed at each site with 3 control plots of the same size marked with pegs. Plots were randomly allocated to a square within a 4 × 3 grid with at least a 3 m gap between plots. Previous work in Gladstone has shown these megaherbivore exclusion cages do not impact the light environment (see Scott et al. 2021).

Five canopy height measurements were taken from every plot at the start and end of the experiment, by grasping a handful of seagrass and measuring the length of the overall canopy, ignoring the longest 20% (Duarte & Kirkman 2001). Photos were taken of every plot at the start and end of the experiment to estimate aboveground biomass; ranks from these photos were calibrated with photos of a known biomass (Rasheed 1999). Temperature was measured with loggers every 30 min for a 3 wk period during the experiment (Thermodata).

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. 2021). Canopy height and change in aboveground biomass data from South Trees over a 3 mo period from August to November 2017 (Scott et al. 2021) were compared to data collected in 2018; these data were from independent plots in the same area as those established in 2018 and collected using the same methods.

ANOVA with Tukey post hoc analysis was used to examine differences in the change in aboveground

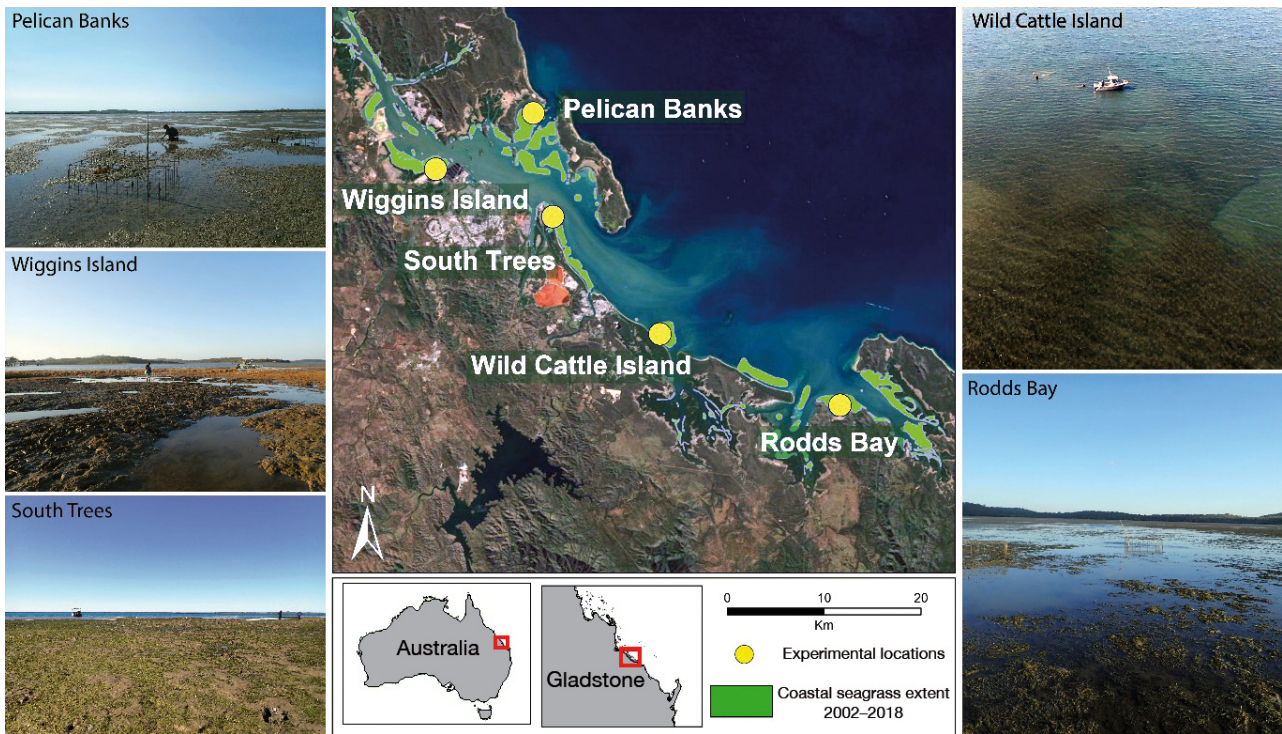


Fig. 1. Location (and photos) of the 5 experimental sites in Gladstone Harbour (Queensland, Australia), with coastal seagrass distribution from Chartrand et al. (2019). Photos: Abigail L. Scott

Table 1. Characteristics of study sites in Gladstone Harbour (Queensland, Australia) at the start of the experiment (beginning of the growing season). Error terms are SE. DW: dry weight; LAT: lowest astronomical tide; na: not assessed

Site	Seagrass species	Habitat	Mean aboveground biomass (gDW m ⁻²)	Mean canopy height (mm)	Mean shoot density (m ²)	Mean temp (°C)	Tide height (m above LAT)
Pelican Banks	<i>Zostera muelleri capricorni</i> with <i>Halophila ovalis</i>	Intertidal sand/mud	11.13 ± 0.7	46 ± 2.0	3154 ± 565	26.7	0.7
Wiggins Island	<i>H. ovalis</i>	Intertidal mud	1.61 ± 0.3	2.7 ± 0.1	na	na	1.0
South Trees	<i>Z. m. capricorni</i> with <i>H. ovalis</i>	Intertidal sand/mud	8.90 ± 0.5	83 ± 3.9	3932 ± 155	26.8	1.0
Wild Cattle Island	<i>Halodule uninervis</i> with <i>H. ovalis</i>	Subtidal sand	6.58 ± 0.6	95 ± 5.0	na	27.4	-1.0
Rodds Bay	<i>Z. m. capricorni</i>	Intertidal sand/mud	21.99 ± 1.7	148 ± 6.4	3093 ± 317	27.1	0.6

biomass and canopy height among sites and between caged and control plots. Residual and q-q plots of normalised residuals of each ANOVA were inspected to ensure the assumptions of homoscedasticity and normality were met. Statistical analyses were conducted in R v.3.5.2. (R Core Team 2019), and data were plotted using 'ggplot2' (Wickham 2016). Change

in aboveground biomass was analysed for 4 of the 5 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. Canopy height measurements at the end of the exclusion study were analysed for 4 of the 5 sites in this experiment as there

were no significant differences at the start of the experiment. Wiggins Island was excluded from canopy height analysis because muddy sediments and water over short *H. ovalis* shoots prevented accurate canopy height measurements in November.

3. RESULTS

Megaherbivores were observed at all of the sites in Gladstone throughout both experiments, and dung feeding trails were also seen in the meadows.

3.1. Spatial differences in the impact of herbivory

Megaherbivore grazing caused declines in aboveground biomass at some sites within the Gladstone region (Fig. 2a). A location:treatment interaction determined the change in aboveground biomass over the duration of the exclusion experiment ($F_{3,22} = 10.36$, $p < 0.001$). Post hoc analysis among sites

showed a greater change in biomass within megaherbivore cages than open-to-grazing control plots at Pelican Banks and Rodds Bay ($p < 0.001$), but no differences between treatments at South Trees and Wiggins Island ($p > 0.05$). Pelican Banks had the highest change in biomass among sites and increased in biomass during the experiment, whereas Rodds Bay decreased in biomass, and South Trees and Wiggins Island had no change in biomass throughout the experiment (Fig. 2a).

There was a difference in canopy height between location ($F_{3,119} = 32.324$, $p < 0.001$) and treatment ($F_{1,119} = 14.464$, $p < 0.001$), but no interaction between them (Fig. 2b). Canopy heights were shorter in control plots compared to megaherbivore exclusion cages at all locations; the largest differences in canopy height between treatments were observed at Pelican Banks. Post hoc analysis showed overall differences between all locations ($p < 0.001$), with shortest canopy heights at South Trees and tallest at Rodds Bay.

3.2. Temporal differences in herbivory at South Trees

For the South Trees site, where we had previously conducted herbivore exclusions in 2017, impacts of herbivory differed between 2017 and 2018 (Fig. 3). There was an effect of treatment ($F_{1,18} = 13.91$, $p < 0.05$) and year ($F_{1,18} = 5.88$, $p < 0.05$), and an interaction between them ($F_{1,18} = 5.00$, $p < 0.05$), on the change in aboveground biomass (Fig. 3a). There was also a significant effect of year ($F_{1,44} = 7.86$, $p < 0.05$) and treatment ($F_{1,44} = 12.01$, $p < 0.05$) on canopy height, but no interaction ($F_{1,44} = 2.030$, $p = 0.16$) (Fig. 3b). Canopy heights inside the control plots were shorter than inside the exclusion cages in both years. Post hoc analyses showed a strong treatment effect in 2017, with both aboveground biomass and canopy height significantly lower in control plots compared to within the caged megaherbivore exclusion treatments ($p < 0.05$). In 2018, there was no treatment effect for change in aboveground biomass and a much smaller effect on canopy heights ($p > 0.05$).

4. DISCUSSION

Grazing by megaherbivores on the southern GBR produced variable impacts on coastal seagrass meadow structure within the region and over time at the same meadow. Megaherbivores grazed at all

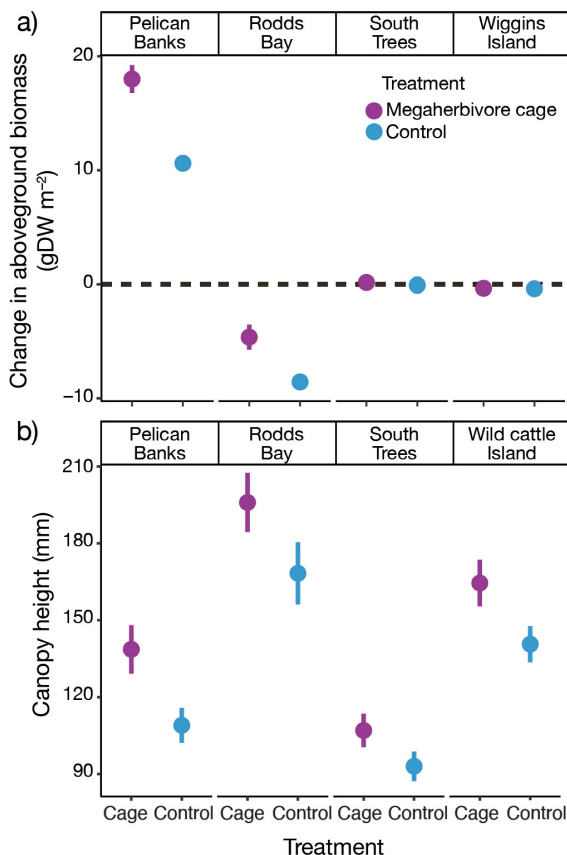


Fig. 2. (a) Change in aboveground biomass throughout the exclusion experiment and (b) canopy height at the end of the experiment. DW: dry weight. Error bars show \pm SE. See Section 2 for information on sites sampled

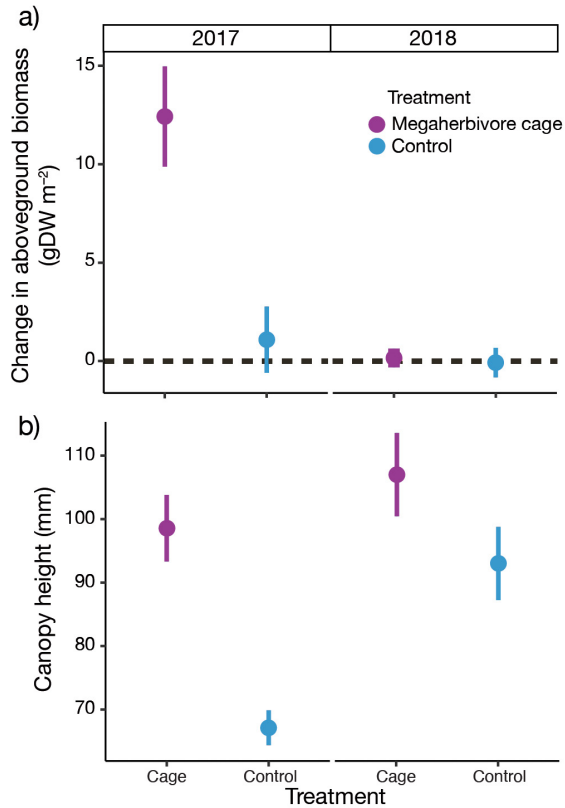


Fig. 3. (a) Change in aboveground biomass in megaherbivore cage and control plots and (b) final canopy height measurements after 3 mo of megaherbivore exclusion from August to November at South Trees in 2017 and in 2018. Data from 2018 taken from Scott et al. (2021). DW: dry weight. Error bars show \pm SE

4 meadows where canopy height was measured, which resulted in a shorter canopy in open-to-grazing control plots compared to exclusion cages. However, reductions in aboveground biomass due to grazing were only seen at Pelican Banks and Rodds Bay. A similar pattern was evident at South Trees meadow over time, where canopy heights were reduced by grazing in both years, but aboveground biomass was only impacted in 2017.

It is possible that other factors contributed to differences between treatments and sites, but megaherbivory is the most likely cause. Water quality conditions during the study were similar at Wiggins Island, South Trees and Rodds Bay, with higher turbidity and nutrient concentrations, whereas Wild Cattle and Pelican Banks had lower turbidity and nutrient concentrations (Hansler et al. 2020). No birds were observed on or around the cages at any of the sites, so bird fertilization is unlikely to have been an issue around the cages.

A range of studies have demonstrated that megaherbivore grazing is an important structuring force

in seagrass meadows, and can cause reductions in aboveground characteristics of tropical seagrasses globally (Christianen et al. 2014, D'Souza et al. 2015) including the GBR (Scott et al. 2020). Grazing by megaherbivores has previously been identified as the most important top-down structuring force at South Trees (Scott et al. 2021). However, megaherbivores are not always the most important grazer group in subtropical seagrass meadows. In one Queensland meadow, megaherbivores did not significantly influence aboveground seagrass characteristics, and mesoherbivores (e.g. amphipods, juvenile prawns and juvenile fish) were the most important grazer group impacting meadows (Ebrahim et al. 2014). Our study supports previous research from Gladstone showing that megaherbivore populations act to structure the meadows (Scott et al. 2021), but indicates that this pressure is not constant.

The variable impact of megaherbivore grazing on seagrass meadows in Gladstone over space and time is likely to be partially driven by megaherbivore grazing behaviour, movements and population dynamics. In the GBR, megaherbivores can target higher biomass areas of meadows (Tol et al. 2016, Rasheed et al. 2017), which may be the case here, as Pelican Banks and Rodds Bay had the highest seagrass biomass in the study 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. Green turtles were found throughout the Gladstone region when surveyed in 2013 and from 2016 to 2018 (Babcock et al. 2015, Prior et al. 2015, Limpus et al. 2018). Tagged green turtles often showed high fidelity to their foraging sites within Gladstone; however, some individuals move between meadows to feed (Babcock et al. 2015, Limpus et al. 2018). Dietary analysis has shown that Gladstone's green turtles can switch their diet to feed on algae (Prior et al. 2015). Monitoring of dugong feeding trails shows that dugong grazing in the Gladstone region varies over time, within and between meadows, indicating that dugongs move between sites (Rasheed et al. 2017). Grazing behaviour could also be influenced by the variable presence of predators exerting a top-down control on megaherbivores (Heithaus et al. 2014). 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. Without more information about megaherbivores at South Trees, it is difficult to explain differences between years, although they could be due to a combination of megaherbivore behaviour and climatic conditions affecting the light environment and hence seagrass growth (Chartrand et al. 2019). 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 in our study.

Another potential driver of variability in the impacts of grazing on seagrass is the response of the 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 vary among species (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). Differing seagrass responses to herbivory may explain the variability in seagrass change during the growing season, and may be related to previous history of herbivory events in the meadow.

Although we only assessed temporal variability in grazing impacts on 1 meadow, we expect the same variability in megaherbivore grazing on seagrass meadows over time to occur in other locations in the region. In Gladstone, long-term seagrass monitoring over the past 18 yr shows meadow changes that could be driven in part by megaherbivory (Chartrand et al. 2019), with evidence of dugong feeding hotspots shifting between and within meadows over time (Rasheed et al. 2017). This pattern is seen in the temporal variability we found at South Trees.

Studies from around the world and the GBR have highlighted the importance of considering megaherbivore impacts when evaluating seagrass condition, and the coupling of both megaherbivore and seagrass monitoring, and the drivers of these dynamics, is desirable for better understanding of such systems (Christianen et al. 2014, Heithaus et al. 2014, Scott et al. 2018). However, our study demonstrates that the seagrass–megaherbivore relationship is spatially and temporally dynamic on a regional scale, and monitoring programmes 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 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.

Acknowledgements. This research was supported through an Australian Research Council grant LP160100492 and funding from Gladstone Ports Corporation. A.L.S. was supported by the Holsworth Wildlife Research Endowment (Ecological Society of Australia), the National Environment Science Programme Tropical Water Quality Hub and an Australian Government Research Training Program Scholarship. Thanks to the TropWATER seagrass ecology field team for their assistance, and to Y. M. Tan and volunteers M. Ellis and F. Pastorelli for field assistance.

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*Editorial responsibility: Adriana Vergés,
Sydney, New South Wales, Australia
Reviewed by: 3 anonymous referees*

Submitted: December 8, 2020

Accepted: March 19, 2021

Proofs received from author(s): June 3, 2021