

# Patterns of top-down control in a seagrass ecosystem: could a roving apex predator induce a behaviour-mediated trophic cascade?

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## Summary

1. The loss of large-bodied herbivores and/or top predators has been associated with large-scale changes in ecosystems around the world, but there remain important questions regarding the contexts in which such changes are most likely and the mechanisms through which they occur, particularly in marine ecosystems.

2. We used long-term exclusion cages to examine the effects of large grazers (sea cows, *Dugong dugon*; sea turtles *Chelonia mydas*) on seagrass community structure, biomass and nutrient dynamics. Experiments were conducted in habitats with high risk of predation (interior of shallow banks) and lower risk (edges of banks) to elucidate whether nonconsumptive (risk) effects of tiger sharks (*Galeocerdo cuvier*), a roving predator, structure herbivore impacts on seagrasses.

3. In lower-risk habitats, excluding large herbivores resulted in increased leaf length for *Cymodocea angustata* and *Halodule uninervis*. *C. angustata* shoot densities nearly tripled when released from herbivory, while *H. uninervis* nearly disappeared from exclusion cages over the course of the study.

4. We found no support for the hypothesis that grazing increases seagrass nutrient content. Instead, phosphorus content was higher in seagrasses within exclosures. This pattern is consistent with decreased light availability in the denser *C. angustata* canopies that formed in exclosures, and may indicate that competition for light led to the decrease in *H. uninervis*.

5. Impacts of large grazers were consistent with a behaviour-mediated trophic cascade (BMTC) initiated by tiger sharks and mediated by risk-sensitive foraging by large grazers.

6. Our results suggest that large-bodied grazers likely played important roles in seagrass ecosystem dynamics historically and that roving predators are capable of initiating a BMTC. Conservation efforts in coastal ecosystems must account for such interactions or risk unintended consequences.

**Key-words:** *Chelonia mydas*, community dynamics, competition, dugong, exclosure, green turtle, herbivory, nonconsumptive effects, nutrient dynamics, risk effects, seagrass community, trophic cascade

## Introduction

Trophic downgrading of ecosystems – the loss of large-bodied herbivores and/or top predators – has been

associated with large-scale changes in terrestrial, freshwater and marine ecosystems around the world (Estes *et al.* 2011). Predators can modify primary producer community structure, biomass and nutrient composition indirectly, both by removing herbivorous prey individuals (predation or direct killing) and by inducing behavioural changes in herbivores ('risk' or 'nonconsumptive' effects) (e.g. Pace

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*et al.* 1999; Preisser, Bolnick & Benard 2005; Schmitz 2006). There remain, however, important gaps in our understanding of the prevalence and mechanisms of herbivore-mediated indirect impacts of predators on primary producer communities. Indeed, recent studies of these indirect relationships have raised questions about whether small-scale experiments might scale up to diverse ecosystems, vertebrate predators may be less likely to trigger trophic cascades than insect predators, and roving predators are likely to initiate behaviour-mediated trophic cascades (Shurin & Seabloom 2005; Schmitz 2008; Kauffman, Brodie & Jules 2010).

Increasingly, ecologists have recognized the potential importance of nonconsumptive (or risk) effects of predators in structuring herbivore–primary producer interactions. In some situations, risk effects may rival or even exceed the influence of direct predation on prey populations, communities and plant nutrient dynamics (Werner & Peacor 2003; Preisser, Bolnick & Benard 2005; Creel & Christianson 2008; Creel 2011). Despite this, relatively few studies of cascading effects of risk [e.g. behaviourally mediated indirect species interactions (BMII) or behaviour-mediated trophic cascades (BMTC)] have been carried out in large-scale ecosystems with intact populations of predators and herbivores. One notable exception is Yellowstone National Park, where the restoration of wolf (*Canis lupus*) populations apparently triggered behavioural changes in elk (*Cervus elaphus*) that led in turn to increased recruitment of aspen (*Populus tremuloides*) and changes in the wider community (Ripple & Beschta 2004; Creel *et al.* 2005; Fortin *et al.* 2005; Hernández & Laundré 2005). Recent studies, however, have raised questions about the presence of a BMTC in Yellowstone (e.g. Kauffman, Brodie & Jules 2010; Winnie 2012). More broadly, it has been suggested that roving (or actively hunting) predators, like wolves, might not exert strong behaviour-mediated impacts on communities because their prey have limited scope for effective antipredator behaviour (Schmitz & Suttle 2001; Kauffman, Brodie & Jules 2010). Yet, studies from marine systems suggest that roving predators can impact prey behaviour in heterogeneous landscapes where prey can predictably modify their probabilities of encounter with and/or escape from predators (Heithaus *et al.* 2009; Wirsing, Cameron & Heithaus 2010). Whether these prey spatial responses to roving predators might cascade to lower trophic levels remains to be tested.

Despite the economic importance of seagrass as habitat for many species (Heck, Orth & Hays 2003) and as a carbon sink (Duarte *et al.* 2010; Fourqurean *et al.* 2012), many aspects of seagrass ecology, including the role of herbivory, remain poorly understood. Although early studies suggested little seagrass entered food webs through direct grazing (Fry, Macko & Zieman 1987), recent work has demonstrated that megagrazers (e.g. green turtles, *Chelonia mydas*; and dugongs, *Dugong dugon*) can impact seagrass biomass, production, nutrient cycling and community structure (Thayer & Engel 1982;

de Iongh, Wenno & Meelis 1995; Bjorndal 1997; Aragones & Marsh 2000; Masini, Anderson & McComb 2001; Moran & Bjorndal 2005; Fourqurean *et al.* 2010; Lal *et al.* 2010). Yet, due to trophic downgrading, it remains unclear whether these megagrazers impacts are representative of ecosystem and nutrient dynamics under natural conditions (e.g. Heck & Valentine 2006, 2007) since most studies have occurred in disrupted communities (Jackson 1997; Heck & Valentine 2007). Jackson *et al.* (2001) suggested that seagrass communities historically would have had much lower biomass and a vastly different community structure because of unrestricted grazing by herbivores. However, historical seagrass communities also may have been structured by behavioural responses of large herbivores to their predators (see Heithaus *et al.* 2007a, 2008). This possibility has been largely overlooked. Therefore, current conservation targets and our understanding of pristine ecosystem structure could be the result of a ‘shifting baseline’, resulting in an inaccurate estimation of the role these large grazers and top predators once played in structuring seagrass ecosystems. Here, we explore whether tiger sharks (*Galeocerdo cuvier*), as a roving predator, might elicit a BMTC by inducing predation-sensitive habitat shifts in green sea turtles and dugongs in the seagrass ecosystem of Shark Bay, Western Australia.

With its large shark and large herbivore populations, Shark Bay offers a unique opportunity to investigate the role of top predators and large herbivores in structuring seagrass ecosystems. We used exclusion cages to test *a priori* predictions of spatial variation in top-down impacts of large herbivores based on known predation-sensitive foraging behaviour of dugongs (Wirsing, Heithaus & Dill 2007a,b,c) and green turtles (Heithaus *et al.* 2007a). Briefly, predation risk from tiger sharks results in both grazer species concentrating their foraging effort in safer areas along the edges of shallow banks while avoiding the more dangerous interior portions of the banks (see Heithaus, Wirsing & Dill 2012). Therefore, we predicted that (i) megagrazers impacts on seagrasses would be stronger in edge microhabitats than in interior portions of banks and (ii) the release from grazing pressure would result in increased seagrass biomass, reduced nutrient content of seagrasses and possible shifts in community structure in edge, but not interior, microhabitats.

## Materials and methods

### STUDY SITE

The study was conducted in the Eastern Gulf of Shark Bay, Western Australia (~ 25°45' S, 113°44' E). Shark Bay is a shallow (<15 m) subtropical bay that is dominated by seagrass beds covering approximately 4000 km<sup>2</sup> (Walker 2003). Shark Bay is one of the few remaining seagrass ecosystems in the world with near pristine populations of both large-bodied herbivores (green turtles and dugongs; Preen *et al.* 1997; Heithaus *et al.* 2005) and

the roving predators (tiger sharks) that feed on them (Heithaus, Wirsing & Dill 2012) thereby affording a unique opportunity to examine the effects of large herbivores and their predators on seagrass community dynamics. The seagrass community, which experiences minimal anthropogenic impacts, is a diverse assemblage of temperate and tropical seagrass species. The dominant species in the bay are slower-growing temperate species, including *Amphibolis antarctica*, *Posidonia australis* and *Posidonia coriacea*. Smaller, faster-growing species, primarily of tropical origin, including *Halophila ovalis*, *Halophila spinulosa*, *Halophila decipiens*, *Halophila minor*, *Halodule uninervis*, *Cymodocea angustata* and *Syringodium isoetifolium* (Walker, Kendrick & McComb 1988; Burkholder, Fourqurean & Heithaus 2013), are less abundant. Biomass turnover rates of *Amphibolis antarctica* and *Posidonia* sp. (3.8–3.9 year<sup>-1</sup>) are much slower than those of smaller taxa like *Cymodocea* spp. (11.7–12.0 year<sup>-1</sup>), *Halodule* spp. (13.9 year<sup>-1</sup>) and *Halophila* spp. (17.2–32.4 year<sup>-1</sup>) (Duarte 1991).

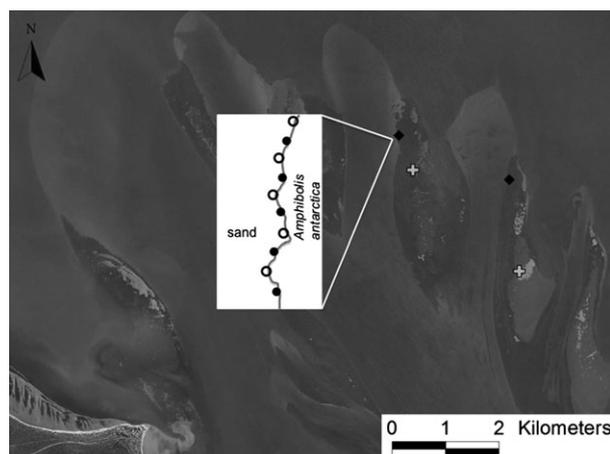
Our approximately 160 km<sup>2</sup> study site in the Eastern Gulf of Shark Bay is characterized by a series of shallow (<4.5 m) banks, mostly covered by seagrass, separated by deeper channels (6–11 m) that are approximately 0.6–2.1 km wide and mostly unvegetated. Shallow habitats can be further subdivided into two microhabitats – interior portions of banks and bank edges – that vary in the risk tiger sharks pose to large-bodied herbivores, the abundance of these large herbivores and seagrass community structure and biomass (see Heithaus *et al.* 2007a; Wirsing, Heithaus & Dill 2007b; Burkholder, Fourqurean & Heithaus 2013). For large herbivores, edge microhabitats are higher risk than interior microhabitats, and both dugongs and green turtles preferentially forage in these edge microhabitats during periods of high shark abundance, which last 9–12 months of the year (Heithaus *et al.* 2007a; Wirsing *et al.* 2006, Wirsing, Heithaus & Dill 2007b; Heithaus, Wirsing & Dill 2012). Green turtles are present year-round in the study area, but during low-risk periods in winter, turtles reduce their foraging rates considerably (Broderick *et al.* 2007; J. Thomson, unpublished data), making it unlikely that turtles would exert considerable top-down control during low-risk periods. Dugongs forage in both interior and edge microhabitats during brief periods when tiger shark abundances are lower and dugongs are present in the study area (Wirsing, Heithaus & Dill 2007a,b,c; b). During the majority of the year, however, dugongs have either moved to thermally favourable habitats outside the study area (when shark abundances are lowest; Wirsing, Heithaus & Dill 2007a) or are present in the study area when tiger shark abundance is high, and therefore forage in edge microhabitats. Additionally, dugongs reduce ‘dangerous’ excavation foraging and increase their use of a ‘safe’ cropping foraging tactic, which allows for increased vigilance, when sharks are present (Wirsing, Heithaus & Dill 2007c). Thus, like green turtles, dugong foraging impacts are expected to be concentrated in edge microhabitats. Based on these predation-sensitive behaviours, we predicted that excluding herbivores from foraging would have large consequences for seagrasses in edge microhabitats and minimal impacts on seagrasses within interior microhabitats.

#### FIELD METHODS

From September 2007–May 2010, we used exclusion cages to determine the impacts of megaherbivore grazing on seagrass community structure, shoot density, blade length and nutrient content within both high- and low-shark risk areas (interior and

edge microhabitats, respectively). The cages consisted of a 2.5 × 3 m top of galvanized rebar with 20 × 20 cm mesh suspended approximately 20 cm above the substrate with aluminium fence droppers secured with wire and zip ties. Rebar sides of the same material as the tops were attached to the top and extended into the substrate. Shoot densities and blade length were assessed in four fixed quadrats (60 cm × 60 cm each) within each cage approximately bimonthly over the course of the study. Cages were cleaned of drifting debris and fouling as needed. Control plots were designated by a single fence dropper that facilitated serial measurements at four fixed quadrats (60 cm × 60 cm each). Cages were constructed on the margin of *A. antarctica* beds, extending into sand substrate where tropical seagrass species are most prevalent (Burkholder, Fourqurean & Heithaus 2013). Because of herbivore preferences for fast-growing species in this system (Burkholder, Heithaus & Fourqurean 2012) and apparent resilience of *A. antarctica* to grazing (Burkholder, Heithaus & Fourqurean 2012; Burkholder, Fourqurean & Heithaus 2013), we focused our analyses on the three fast-growing taxa in our study area (*C. angustata*, *H. uninervis* and *H. ovalis*).

We constructed cages and controls in interior and edge microhabitats. Interior cages/controls were constructed in waters 1.5–3 m deep, and edge cages/controls were constructed in waters 3–5 m deep. We established 20 control and 20 experimental plots (five cages and five controls at edge and interior microhabitats across two separate banks) in September 2007 (Fig. 1). Plots within habitats and banks were spaced at least 30 m apart. In January 2008, one set of five edge microhabitat cages and controls were compromised due to strong currents associated with extreme weather (no such problems occurred at other sites). In November 2008, we re-established these plots in a new location where they were maintained for the duration of the experiment concluding in May 2010. The re-established set of edge experiments ran for nearly 600 days, while the initial set of edge cages that were not compromised and both sets of interior cages ran for nearly 1000 days. There was no significant change in seagrass communities or densities between day 600 and day 1000 for the three sets of experiments that were maintained. Therefore, we truncated our data sets to 600 days in order to include all plots



**Fig. 1.** The study was conducted in the Eastern Gulf of Shark Bay, Western Australia (a). ‘Edge’ sites are indicated with a black diamond and ‘interior’ sites with grey ‘+’. Cage sites are closed circles, and control sites are open circles.

in analyses. We do not include plots that were only present for approximately 90 days.

At the end of the experiment, we collected seagrass from one quadrat of each plot using a 15-cm-diameter PVC core tube. The core was pushed into the sediment 20 cm and then removed, collecting the seagrass both above-ground (leaves and stems) and below-ground (roots and rhizomes). Seagrass samples were stored on ice in the field and immediately frozen to  $-20^{\circ}\text{C}$  upon return to shore until they could be processed for elemental analysis.

At the conclusion of the experiment, the enclosure cages were removed and the sites were revisited at 24 and 72 h after deconstruction to examine above-ground seagrass tissue removal. The timing of sampling was constrained by logistical considerations and not based on any *a priori* reasoning other than we expected grazing pressure to cause a rapid decrease in seagrass biomass. The same four fixed quadrats (60 cm  $\times$  60 cm) were sampled for shoot densities. To compare removal rates among species and plots with differing starting shoot densities, we converted remaining densities at each time step to the proportion of seagrass remaining. Only plots with more than 10 total blades at the removal of the exclusion cage were included in analyses.

#### LABORATORY METHODS

Upon return to the laboratory, all seagrass tissue was rinsed in deionized water. Leaf tissue was separated from stems and gently scraped with a razor blade to remove epibiota. Leaves were dried for at least 24 h in a food dehydrator (Ezidri Ultra FD1000) and then crushed to a powder with mortar and pestle for elemental content analysis. Carbon (C) and nitrogen (N) contents of samples were measured using an elemental analyzer (Fisons NA1500), and phosphorus (P) content was measured using a dry-oxidation/acid hydrolysis method (Fourqurean, Zieman & Powell 1992).

#### Results

Combined shoot counts of fast-growing seagrasses, derived from initial counts in both caged ( $n = 20$ ) and control plots ( $n = 20$ ), varied between edge and interior areas at the beginning of trials ( $t = 4.44$ ,  $P < 0.001$ ). Fast-growing seagrasses were abundant in edges (mean =  $278.6$  shoots/m $^2 \pm 60.9$  SE) and scarce in interior plots (mean =  $3.7$  shoots/m $^2 \pm 1.9$  SE). Species composition of fast-growing species also varied between edges and interiors. Only *Halodule uninervis* was found in interior plots (mean =  $3.7$  shoots/m $^2 \pm 1.9$  SE), but at lower densities than in edge plots (mean =  $104.8$  shoots/m $^2 \pm 33.2$  SE;  $t = 3.04$ ,  $P < 0.001$ ). At the initiation of experiments, plots in the edge microhabitat also contained the fast-growing species *Cymodocea angustata* (mean =  $162.5$  shoots/m $^2 \pm 30.1$  SE), *Halophila ovalis* (mean =  $3.8$  shoots/m $^2 \pm 1.9$  SE) and occasionally *Halophila spinulosa* (mean =  $0.03$  shoots/m $^2 \pm 0.03$  SE).

Within interior microhabitats, there was no effect of caging on the cover of the dominant species, *Amphibolis antarctica*. Portions of cages with 100% cover at the beginning of the experiment had identical cover at the end. There was a significant effect of treatment on the change in *H. uninervis*

densities within interior microhabitats ( $t = 2.04$ ,  $P < 0.05$ ), but this difference was driven primarily by variation in starting densities within enclosure and control plots. Indeed, all plots with *H. uninervis* present at the start of the experiment experienced shoot density declines, and by the end of the study, shoots of *H. uninervis* were only present in one plot. There were, however, sporadic temporary increases in shoot densities of *H. uninervis* within both enclosures and control plots, including plots that began with no above-ground shoots (Fig. 2). Despite these sporadic outbreaks, shoot densities quickly declined from densities at the start of the experiment.

Shoot densities of fast-growing seagrass species varied considerably between enclosures and control sites at the conclusion of the experiment in edge trials (Fig. 3). Densities of *C. angustata* were influenced by an interaction of treatment and time (Table 1). Densities increased substantially in enclosures, but did not change in control plots (Fig. 4). The heights of *C. angustata* almost tripled within enclosures, but did not change within control plots ( $t = 20.48$ , d.f. = 341,  $P < 0.001$ ; Fig. 5). Densities of

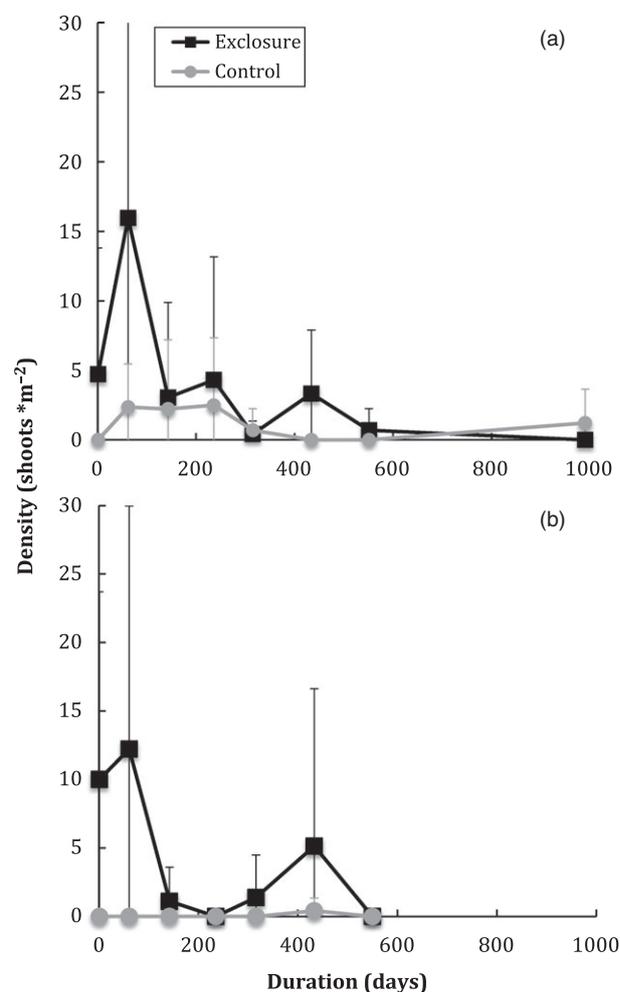


Fig. 2. Temporal variation in the densities of *Halodule uninervis* in enclosure (black squares) and control (grey circles) plots in interior microhabitats of two banks. Error bars represent  $\pm$  SD.



**Fig. 3.** At the initiation of experiments in edge microhabitats, seagrasses were relatively sparse and closely cropped (top). After 600 days (bottom), seagrass heights and densities had increased inside exclosures but remained closely cropped and at lower densities in control plots.

**Table 1.** Factors influencing the density of seagrasses in edge microhabitats. Significant values are in bold

	d.f.	<i>F</i>	<i>P</i>
<i>Cymodocea angustata</i>			
Time	1, 39	2.75	<b>0.009</b>
Treatment	1, 39	3.26	<b>0.002</b>
Time–treatment	1, 39	2.05	<b>0.047</b>
<i>Halodule uninervis</i>			
Time	1, 39	0.61	0.55
Treatment	1, 39	3.15	<b>0.004</b>
Time–treatment	1, 39	3.07	<b>0.005</b>
<i>Halophila ovalis</i>			
Time	1, 39	1.11	0.27
Treatment	1, 39	1.79	0.08
Time–treatment	1, 39	0.59	0.56

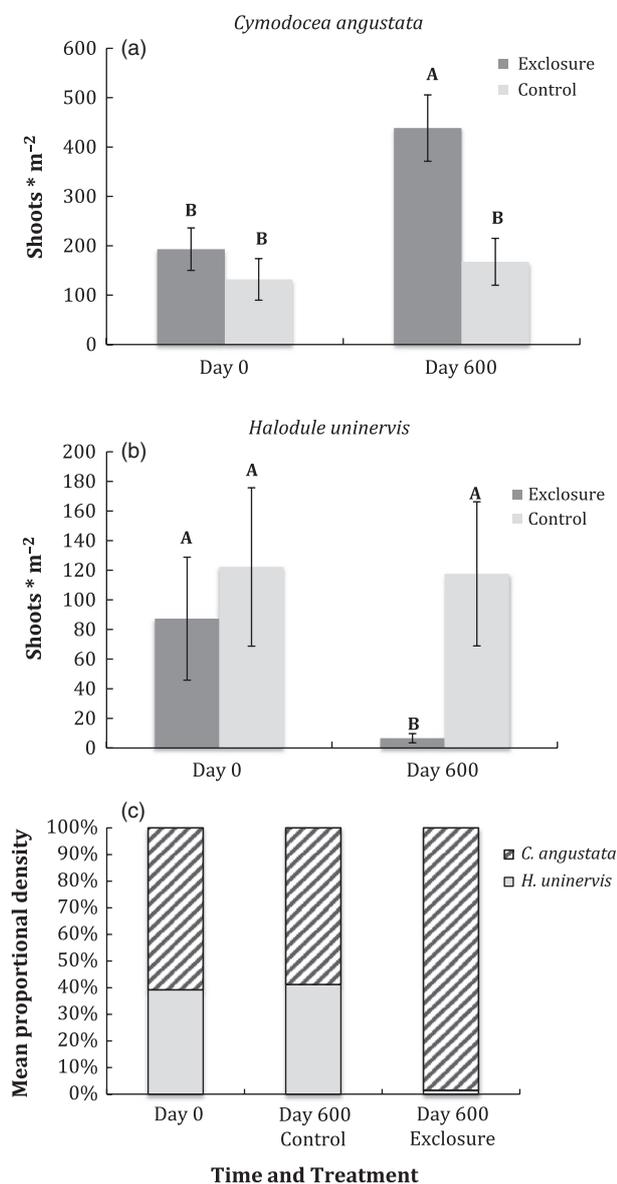
*H. uninervis* varied with the interaction of time step and treatment (Table 1), but not in the same way as for *C. angustata*. *Halodule uninervis* densities declined within exclosures but remained consistent in control plots (Fig. 4). The heights of *H. uninervis*, however, were approximately 1.5 times greater inside exclosures than in control sites at the end of the experiment ( $t = 5.23$ , d.f. = 133,  $P < 0.001$ ; Fig. 5). The density of *H. ovalis* did not vary with any factor (Table 1). There was no difference in blade lengths between treatments ( $t = 1.48$ , d.f. = 31,  $P = 0.07$ ; Fig. 5).

In edge microhabitats, there was no effect of long-term exclusion of megaherbivores on C : N and N : P ratios, for any species (Table 2, Fig. 6). Phosphorus content was higher (i.e. lower C : P), however, in *Cymodocea angustata* and *Halodule uninervis* inside exclusion cages than in control plots. There was no effect for *Halophila ovalis* (Fig. 6).

The proportion of seagrass shoots remaining within plots after removal of cages was influenced by an interaction between species and time ( $F_{2,41} = 4.69$ ,  $P < 0.05$ ). *Cymodocea angustata* densities were reduced by 30% in the first 24 h, but densities were not reduced significantly over the following 48 h (Fig. 7). *Halodule uninervis* densities were reduced by approximately 40% in the first 24 h and continued to decline to an average of 25% of shoots remaining after 72 h. Unfortunately, blade lengths were not measured during the removal experiment. However, 24 h after cage removal, the height of *C. angustata* had been cropped to lengths similar to those of blades found outside the exclosure plots.

## Discussion

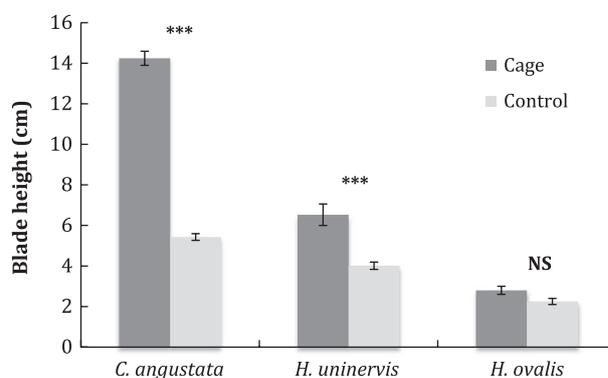
Understanding the importance of top-down control in natural ecosystems is critical for establishing conservation and management baselines and predicting ecosystem responses to natural and anthropogenic change. Yet, there is continued debate about the strength of top-down control and the conditions in, and mechanisms through, which it is more or less likely to occur. Using a combination of previously published studies of the behavioural responses of large herbivores (green turtles, dugongs) to the presence of top predators (tiger sharks) and our exclosure experiments, we provide evidence that (i) top-down control by large herbivores is important in determining plant biomass and species relative abundance in a relatively pristine seagrass ecosystem, and (ii) the spatial pattern of these impacts likely is mediated by risk effects of a roving top predator. Further, our nutrient content data suggest that grazing mediates competition between seagrass species, so that in grazed seagrass meadows, light competition is reduced, leading to higher light availability



**Fig. 4.** Initial and ending shoot densities of (a) *Cymodocea angustata* and (b) *Halodule uninervis* in enclosures and control plots in edge microhabitats. Bars with different letters are significantly different based on *post hoc* Tukey's *post hoc* tests. Error bars represent  $\pm$  SE. (c) The relative densities of *C. angustata* increased considerably in enclosures, while *H. uninervis* became rare.

and lower nutrient content of grazed plants and the continued coexistence of competitors. Our results provide important insights into the dynamics of seagrass ecosystems and, more generally, the potential for roving predators to trigger BMTCs in intact ecosystems.

Marine megaherbivores impact seagrass ecosystems in other locations. For example, Nakaoka, Mukai & Chunhabundit (2002) found that only about 3% of the dry weight of *H. ovalis* remained in foraging trails left by dugongs that excavated seagrass rhizomes. Grazing does not merely reduce biomass of plants within feeding trails. It can also mediate the outcomes of competition



**Fig. 5.** Heights of seagrasses at the conclusion of experiments in the edge microhabitat. Error bars represent  $\pm$  SE. *t*-test \*\*\**P* < 0.0001; NS = not significant.

**Table 2.** Results of statistical tests for variation in nutrient content of seagrasses in enclosures and controls within edge microhabitats. Significant values are in bold

Species	d.f.	C : N		C : P		N : P	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
<i>C. angustata</i>	1, 23	2.20	0.15	<b>5.52</b>	<b>0.03</b>	2.78	0.11
<i>H. uninervis</i>	1, 9	1.28	0.29	<b>16.97</b>	<b>0.003</b>	4.68	0.06
<i>H. ovalis</i>	1, 8	2.76	0.14	0.00	0.98	0.57	0.48

among plants in the community and nutrient dynamics. For example, dugong grazing in Queensland, Australia, resulted in a 12-fold increase in shoot densities of *Halophila ovalis*, a fast-growing, pioneer seagrass species, and a 6-fold decrease in shoot densities of the competitively dominant *Zostera capricorni* (Preen 1995). Green turtle grazing can considerably increase the decomposition rate of seagrass species such as *Thalassia testudinum* (Thayer & Engel 1982). Furthermore, repeated grazing of seagrass patches by green turtles in the Caribbean increased seagrass forage quality by causing the production of new leaves that are higher in nutrient content and therefore more easily digested (Bjorndal 1980). Intense overgrazing by green turtles, however, may result in shifts in seagrass community structure (Kuiper-Linley, Johnson & Lanyon 2007; Wabnitz *et al.* 2010) and eventually cause significant declines in seagrass biomass and productivity (Williams 1988; Murdoch *et al.* 2007; Fourqurean *et al.* 2010). The above studies have, in general, been conducted in ecosystems with either greatly reduced or rebounding populations of dugongs and green turtles and reduced populations of predatory sharks (Baum & Myers 2004; Marsh *et al.* 2005; Chaloupka *et al.* 2008; Blaber *et al.* 2009; Ferretti *et al.* 2010). Thus, how megaherbivores might impact seagrass ecosystems where populations of both these grazers and their predators are intact has remained unclear (e.g. Heck & Valentine 2006).

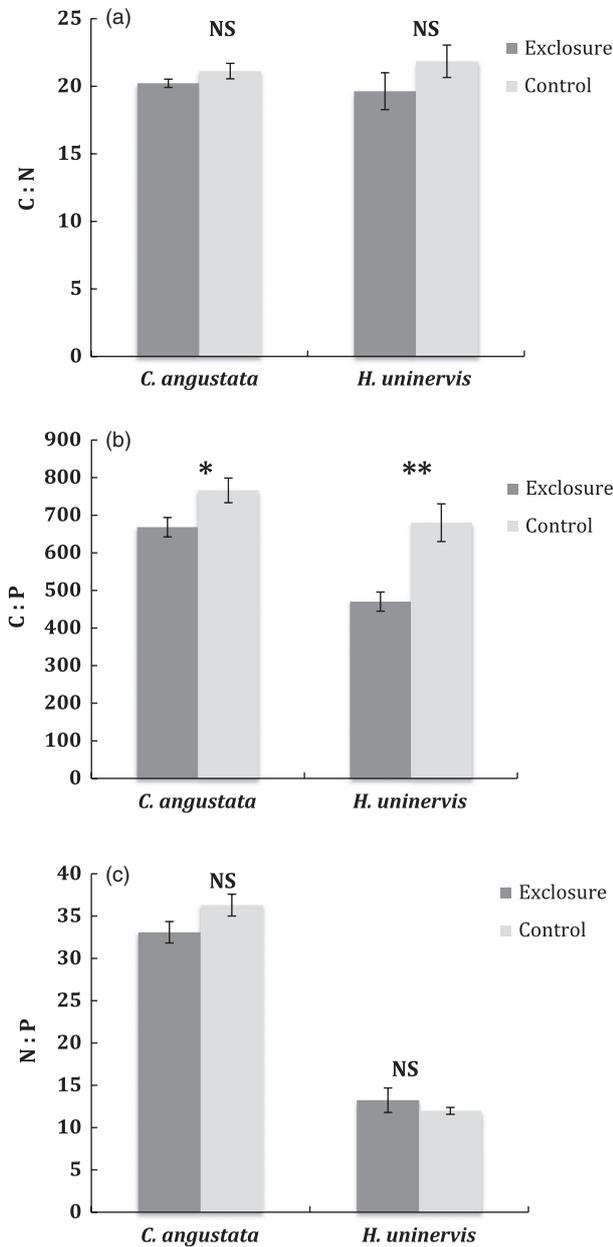


Fig. 6. Nutrient content – (a) C : N, (b) C : P, (c) N : P – of seagrass blades in exclusions and controls at the conclusion of experiments in the edge microhabitat. Error bars represent  $\pm$  SE. *t*-test \*\*\* $P < 0.001$ , \*\* $P < 0.01$ , \* $P < 0.05$ , NS = not significant.

In Shark Bay, populations of both large grazers and top predators are intact (Preen *et al.* 1997; Heithaus *et al.* 2005; Heithaus, Wirsing & Dill 2012), and seagrasses are free from anthropogenic water quality degradation and physical disturbance, which have heavily impacted coastal ecosystems around the world (Orth *et al.* 2006; Waycott *et al.* 2009). Tiger sharks elicit strong antipredator behaviours in marine megaherbivores (Heithaus *et al.* 2007a,b; Wirsing, Heithaus & Dill 2007a,b,c; Wirsing, Heithaus & Dill 2011) that concentrate grazing pressure on seagrasses along the edges of banks, where predation risk is lower, while relaxing grazing pressure within interior microhabi-

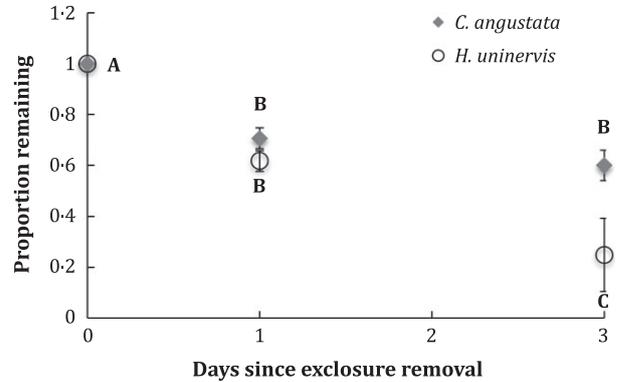


Fig. 7. Proportion of *C. angustata* ( $n = 10$  plots) and *H. uninervis* ( $n = 4$  plots) blades remaining after removal of exclusions in edge microhabitats. Error bars represent  $\pm$  SE. Symbols with different letters are significantly different based on Tukey's *post hoc* tests. Letters above symbols are for *C. angustata* and those below symbols for *H. uninervis*.

tats where risk to large grazers is higher. The reduced densities of megagrazers in the latter areas are accompanied by a substantial reduction in excavation foraging (Wirsing, Heithaus & Dill 2007d), which facilitates fast-growing species (Preen 1995), by those dugongs that do forage under increased risk. In these interior habitats, exclusion cages had little impact on either the dominant seagrass species, *Amphibolis antarctica*, or fast-growing species. Conversely, in edge habitats where megaherbivore grazing is concentrated by shark presence, the exclusion of the megaherbivores greatly influenced the abundance, species composition and nutrient content of seagrasses. These results are consistent with predictions of risk-sensitive foraging by large herbivores and suggest that green turtles and dugongs affect the structure and function of seagrasses in the edge microhabitats where they are concentrated while apparently having little role in structuring the seagrass community within more dangerous interior microhabitats. Thus, spatial variation in megagrazers impacts on seagrasses likely is driven by risk effects of tiger sharks (i.e. a BMTC).

Within edge microhabitats, seagrass communities changed when protected (with exclusion cages) from megagrazers herbivory. *Cymodocea angustata* densities increased substantially, and shoots grew basically as tall as the exclusion cage. *Cymodocea angustata* remained smaller in stature and in lower densities outside the exclusions. In contrast, although *Halodule uninervis* inside exclusions grew taller than it did at control sites, its densities declined in exclusion plots over the course of 600 days. Whether this decline was the result of competitive exclusion by *C. angustata* or its removal by smaller herbivores that could enter the exclusions is unclear, because teleost herbivores show a strong preference for *H. uninervis* over *C. angustata* (Burkholder, Heithaus & Fourqurean 2012). The former explanation may be somewhat more likely because remaining *H. uninervis* shoots might have been expected to be of similar, or shorter, heights to control plots if fish grazing had been

responsible for the declines. Since shading increases the concentrations of limiting nutrients in seagrass tissues (Abal *et al.* 1994) and P is generally limiting in Shark Bay (Smith & Atkinson 1984; Burkholder, Fourqurean & Heithaus 2013), we interpret the increase in P content of seagrass inside exclosures as an indicator of decreased light availability in the longer and denser plant canopies. The increase in length of leaves and decrease in density of *H. uninervis* could be due to the shading caused by the more robust shoots of *C. angustata*. The importance of herbivory by large-bodied grazers in driving observed patterns of seagrass community structure and above-ground biomass in edge microhabitats is further supported by the rapid reduction in densities of *C. angustata* and *H. uninervis* at the conclusion of the experiment, when removal of the exclosures exposed previously protected seagrasses to grazing by turtles and dugongs while not changing access by teleost grazers.

Our results from interior microhabitats are somewhat harder to interpret. Above-ground biomass of fast-growing species was initially lower in interior microhabitats than in edge microhabitats despite similar depths of plots and the presence of fast-growing species in shallow areas in other portions of the bay with different spatial configurations (i.e. much larger continuous shallow banks; Burkholder, Fourqurean & Heithaus 2013). There did appear, however, to be viable below-ground biomass of *H. uninervis* in all plots, because shoots appeared periodically during our sampling. These shoots quickly disappeared in all treatments. These data suggest that large-bodied grazers do not drive the relative lack of fast-growing species in interior microhabitats of our study area, which was expected because of their avoidance of these areas in response to risk from tiger sharks (see Heithaus, Wirsing & Dill 2012). Physical factors or herbivory from smaller-bodied species (i.e. fish) not excluded by our experiments could limit fast-growing seagrasses in interior areas. The latter explanation seems more likely since the fast-growing species often are found in shallow waters in other locations (suggesting that *H. uninervis* can survive in these depths and light intensities) and herbivorous teleosts that could enter our exclosure cages prefer fast-growing species like *H. uninervis* (Burkholder, Heithaus & Fourqurean 2012) and are common in interior microhabitats (Heithaus 2004). Herbivory by other smaller-bodied invertebrate grazers (e.g. isopods, sea urchins) is unlikely important due to their low abundance in the study area (unpublished data). Recent experimental studies in interior microhabitats confirmed that fish grazing is important in these habitats (Burkholder, Heithaus & Fourqurean 2012; C. Bessey, M. Heithaus, J. Fourqurean, D. Burkholder & K. Gastrich, unpublished, but that minimal megagrazers impacts are not simply due to the strength of top-down impacts by fishes (C. Bessey, M. Heithaus, J. Fourqurean, D. Burkholder & K. Gastrich, unpublished).

The nutrient content of the two most common seagrass species varied between control plots and exclosures. In general, grazing by turtles and dugongs is observed to

result in increased nutrient content in seagrass blades, thereby increasing the nutritional value of seagrasses in heavily cropped areas (Bjorndal 1980, 1997; Zieman, Iverson & Ogden 1984; Aragones *et al.* 2006). However, Thayer *et al.* (1984) suggested that heavy grazing by marine megagrazers would eventually result in decreased nutrient content as removal of biomass by grazers depleted the stores of available nutrients in the sediments available to the plants. Here, we found that although there were no changes in C : N ratios of seagrasses released from herbivory, the C : P ratio decreased (i.e. P content increased) when *C. angustata* and *H. uninervis* were released from herbivory. As described above, this pattern could reflect decreased light availability in the denser ungrazed canopies. Alternatively, intense grazing by megaherbivores could decrease sediment nutrient availability in heavily grazed areas, and reduced grazing losses in exclosures resulted in an increase in P available for plant growth.

We were not able to separate the relative importance of green turtle and dugong grazing in driving seagrass responses in edge microhabitats. At the population level, stable isotope analyses suggest that green turtles in the study area do not appear to rely heavily on seagrasses as a food source, although some individuals may have high proportions of seagrass in their diets (Burkholder *et al.* 2011). Therefore, we might expect turtles to have minimal impacts on seagrass communities, even in edge microhabitats where they are concentrated by tiger shark predation risk (Heithaus *et al.* 2007a). Our exclosure experiments, however, suggest that turtles are at least partially responsible for seagrass removal. A halo of grazed seagrass extended into exclosure cages that is consistent with turtles reaching their heads through the mesh to graze grasses they could access (Fig. 8). Dugong heads could not fit through the mesh of our cages to cause a similar pattern. Because population densities of green turtles are high in Shark Bay (Heithaus *et al.* 2005), even a relatively small proportion of individuals primarily consuming seagrasses could impact seagrass communities.

Our results suggest that tiger sharks induce a BMTC in an intact seagrass ecosystem. This BMTC, whereby the presence of sharks concentrates herbivory by large grazers in edge microhabitats and limits their impacts in interior areas, likely promotes spatial heterogeneity in seagrass community structure and biomass. While the potential importance of trophic cascades has been well-established in small-scale experiments and time-series correlations in marine, freshwater and terrestrial settings (e.g. Carpenter & Kitchell 1993; Pace *et al.* 1999; Schmitz, Hamback & Beckerman 2000; Halaj & Wise 2001; Estes *et al.* 2004), this study is the first to experimentally investigate the potential for BMTC to structure marine ecosystems at large spatial and temporal scales and in ecosystems featuring intact populations of large-bodied predators and herbivores. Thus, the potential importance of risk effects in large-scale marine ecosystems must be included in



**Fig 8.** Halos of grazing (white arrows) inside exclosures suggest that green turtles are at least partially responsible for reduced seagrass biomass in edge microhabitats.

conservation and management planning and in setting restoration targets. Indeed, if megagrazers were released from predation risk entirely, there could be considerable shifts in seagrass community structure, biomass and ecosystem services in Shark Bay facilitated by potentially lower grazing pressure on communities found along the edges of banks and increased herbivory in interior habitats. Results from more heavily impacted ecosystems support this hypothesis. In Bermuda, recent management strategies have resulted in increasing green turtle populations (Chaloupka *et al.* 2008) in the presence of reduced tiger shark populations in the region (Baum *et al.* 2003). The increase in turtle populations appears to have triggered increased herbivory and collapses in seagrass biomass (Fourqurean *et al.* 2010). Similar results have been documented in the Lakshadweep Islands, Indian Ocean, with a gradient of turtle density and grazing pressure across a lagoon resulting in decreased shoot density, leaf width, leaf area and above-ground biomass at heavily grazed sites. The grazing pressure gradient also leads to an apparent shift in the seagrass community from a co-dominant bed of *Cymodocea rotundata* and *Thalassia hemprichii* before turtle populations increased to an almost monospecific bed of *C. rotundata* currently found in areas of high grazing pressure (Lal *et al.* 2010).

Our results have important implications for our understanding of community dynamics in general. Indeed, the responses of megagrazers to predators in Shark Bay are akin to those of herbivores in numerous terrestrial and aquatic ecosystems (Heithaus *et al.* 2008, 2009). The

BMTC in Shark Bay similarly mirrors those induced by wolves in Yellowstone (Ripple & Beschta 2004, 2007) and spiders in old-field communities (Schmitz 2006). Recently, however, it has been suggested that roving predators may induce relatively weak risk effects and be less likely to trigger BMTCs than sit-in-wait predators (Schmitz 2005, 2008) because roving predators have a risk signature that is more spatially diffuse (i.e. less predictable by potential prey). The influence of predator hunting mode on whether BMTCs are triggered is supported by data from mesocosm experiments with spiders as top predators and grasshoppers as mesoconsumers (Schmitz 2008, 2009). Kauffman, Brodie & Jules (2010) extended this argument, suggesting that even large-bodied roving predators would be unlikely to initiate BMTC and that, in fact, wolves (a roving predator) in the northern range of Yellowstone did not initiate a BMTC (but see response by Beschta & Ripple 2012).

Because many top vertebrate predators, especially in coastal ecosystems, are roving predators with diffuse risk signatures, it is important to determine whether they are less likely than sit-and-wait predators to initiate BMTCs. Heithaus *et al.* (2009) suggested that roving predators should, theoretically, be capable of inducing strong risk effects and BMTC if prey operate at spatial scales across heterogeneous landscapes that allow them to minimize encounter rates or conditional probabilities of capture through behavioural adjustments (e.g. spatial shifts). Importantly, many mesocosm experiments have been conducted in relatively homogeneous landscapes. For example, Schmitz (2008) examined the effect of hunting mode on predation risk to grasshoppers targeted by roving spiders that occupy the mid-canopy and sit-and-wait spiders that use the upper canopy. Prey moving across larger, heterogeneous landscapes – like sea turtles and dugongs in Shark Bay – have more options to shift into habitats that predictably reduce encounter rates or the probability of capture in encounter situations (Heithaus *et al.* 2009). In Shark Bay, direct risk effects of roving tiger sharks on large-bodied grazers and other taxa and the present experimental study offer evidence for cascading impacts of a roving predator on seagrass community structure and nutrient dynamics. Future studies are needed to understand the contexts and pathways in which roving predators are more or less likely to induce BMTC and to further investigate the pathways through which tiger sharks, and other top marine predators, might indirectly structure coastal marine communities.

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