

# Importance of teleost macrograzers to seagrass composition in a subtropical ecosystem with abundant populations of megagrazers and predators

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**ABSTRACT:** Herbivores can play an important role in structuring seagrass communities, yet understanding the relative importance of megagrazers (dugongs and sea turtles) and macrograzers (fishes) has been hampered by a lack of studies in ecosystems with healthy predator populations. This study used a series of nested enclosure–transplant experiments to investigate the impacts of fishes on seagrass species composition in a subtropical ecosystem (Shark Bay, Australia) with abundant populations of megagrazers and predators. Three species of fast-growing seagrasses (*Cymodocea angustata*, *Halodule uninervis*, and *Halophila ovalis*) were transplanted into enclosure cages that were located in shallow seagrass beds and systematically excluded grazers. Experiments were conducted during an entire warm season, and during both a warm and cold period. Fish trapping and belt transects were used to determine the relative abundance of herbivorous fishes, megaherbivores, and air-breathing piscivores. Mainly fishes, rather than megagrazers, affected the establishment and persistence of transplanted seagrasses during the warm season, dominating the top-down effects on both *H. uninervis* and *H. ovalis*. Grazer impacts were minimal during the cold period, except for fish grazing on *H. ovalis*, with dugongs abandoning the study area. Fish grazer density during the cold period trial did not differ from that of the warm period, but predator density (cormorants) was significantly greater. These data suggest that fish can play an important role in structuring subtropical seagrass systems, that herbivore impacts are seagrass-species dependent, and that seagrass beds may be shaped by herbivore responses to their predators.

**KEY WORDS:** Consumptive effects · Dugongs · Fishes · Herbivory · Sea turtles · Top-down control

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## INTRODUCTION

Understanding controls of primary producer community structure and function is a central goal of ecology, and is of increasing importance as humans alter ecosystems (Duffy 2003, Estes et al. 2011). Globally, marine grazers are widely recognized as being able to exert considerable top-down impacts on primary producers, but the relative strength of top-

down control varies markedly among different grazer and primary producer taxa (Poore et al. 2012). Seagrasses were originally thought to be subject to low levels of herbivory due to their poor nutrient value (owing to high C/N ratios; Duarte 1990), low digestibility, and the overharvesting of large marine herbivores (Thayer et al. 1984). However, in places where populations persist, large herbivores ('megagrazer') such as dugongs and green turtles can alter

species composition, structure and biomass of seagrass communities (Preen 1995, Moran & Bjørndal 2005). Furthermore, because fishes can have food-processing mechanisms that optimize energetic supplies from nutrient-poor food sources (Ferreira et al. 1998), they are also capable of altering seagrass ecosystems through direct grazing (Kirsch et al. 2002, Tomas et al. 2005).

Both mega- and macrograzers can play an important role in structuring seagrass communities (Heck & Valentine 2006, 2007). Overgrazing by green turtles in seagrass beds can lead to denudation of vegetation (Fourqurean et al. 2010), yet the importance of seagrass consumption by fishes in shaping species composition is less appreciated. White et al. (2011) found that fish grazing in the southwest of Western Australia did not influence the growth and structure of seagrass, since biomass removal was small. Nevertheless, seagrass can comprise large portions of fish diets (e.g. up to 40% in pinfish off North Carolina: Weinstein et al. 1982; 80% in the Florida Keys: Kirsch et al. 2002; 73% off the northeast coast of Spain: Tomas et al. 2005; and up to 100% in Shark Bay, Western Australia: Bessey & Heithaus 2015), with fishes reportedly removing up to 80% of net above-ground production (Kirsch et al. 2002, Tomas et al. 2005). In areas where herbivorous fishes and mega-grazers coexist, their relative importance in structuring seagrass ecosystems is poorly understood.

Complicating studies of top-down control further, but making them of considerable importance, is the trophic downgrading of ecosystems through the loss of large-bodied grazers and their predators (Post & Pedersen 2008, Estes et al. 2011). Top predator declines and removals are often associated with large-scale changes to communities, triggering trophic cascades following top predator and/or large herbivore removals (Estes et al. 2011). Elucidating the relative impacts of macro- and megagrazers on seagrass composition under abundant predator population densities is important for understanding historical interactions, thereby providing context in which herbivory may play a greater or lesser role in ecosystem structure and function under anthropogenic disruptions. The need for enhanced predictive capacity, especially in systems where management decisions must be made before sufficient system-specific data are available, is particularly important.

The seagrass ecosystem of Shark Bay, Western Australia, has been used as a model system to explore top-down effects for more than a decade, and provides the opportunity to simultaneously investigate both mega- and macrograzer impacts in a seagrass

ecosystem with abundant predator populations (reviewed in Heithaus et al. 2012). Shark Bay features extensive seagrass beds and large populations of tiger sharks *Galeocerdo cuvier*, large piscivores (dolphins *Tursiops cf. aduncus* and cormorants *Phalacrocorax varius*), megagrazers (green turtles *Chelonia mydas* and dugongs *Dugong dugon*), and fish macrograzers (*Pelates octolineatus* and *Monacanthus chinensis*). Previous studies have established that tiger sharks can induce spatial shifts in the foraging habitats and tactics of both megagrazers and piscivores, resulting in considerably lower foraging rates in habitats where the risk of tiger shark predation is increased (i.e. interior areas of shallow seagrass beds), despite high densities within the larger system (Heithaus 2005, Heithaus & Dill 2006, Heithaus et al. 2009, 2012). Long-term enclosure studies in Shark Bay have shown no observable impact of megagrazers on the dominant seagrass species, *Amphibolis antarctica*, in interior habitats, but did show a decline in the fast-growing species, *Halodule uninervis*, even in spite of megagrazers exclusion (Burkholder et al. 2013). Indeed, fast-growing seagrass species are scarce in interior compared to edge habitats (Bessey 2013). In addition, the percent cover of dominant seagrass species (*A. antarctica* and *Posidonia australis*) is greater in interior areas of seagrass beds, providing increased cover for foraging teleost macrograzers. It is therefore hypothesized that teleost herbivory may be playing an important role in reducing the species composition within these interior seagrass habitats.

This study used a series of nested enclosure–transplant experiments to quantify the relative impacts of mega- and macrograzers on fast-growing seagrass species (*Cymodocea angustata*, *H. uninervis*, and *Halophila ovalis*) within shallow seagrass bed areas. Experiments were conducted for an entire warm season, and for a short duration during both a warm and cold period to explore temporal differences in grazer impacts. During the course of the short-term enclosure experiments, the relative abundances of air-breathing piscivores, megagrazers, and teleost grazers were determined using belt transect surveys and fish trapping.

## MATERIALS AND METHODS

### Study system

Shark Bay, Western Australia (25° 45' S, 113° 44' E), is a ca. 13 000 km<sup>2</sup> semi-enclosed subtropical bay featuring ca. 4000 km<sup>2</sup> of seagrass beds. Monospecific

stands of the temperate seagrasses *Amphibolis antarctica* and *Posidonia australis* dominate the community (Walker et al. 1988), with higher seagrass cover in the interior of seagrass beds compared to the edge habitats of the study area (Bessey 2013). Several fast-growing species, especially *Halophila ovalis*, *Halodule uninervis*, and *Cymodocea angustata*, occur patchily throughout the bay (Burkholder et al. 2013). During the current study, the percent cover of all three of these fast growing seagrass species was higher in edge habitats and relatively scarce in interior habitats, despite all species being available for transplant experiments at deeper water donor beds throughout the year (Bessey 2013). Fish communities in the study area were dominated by the herbivorous teleost *Pelates octolineatus*, and seagrass can comprise up to 100% of their stomach contents (Heithaus 2004, Bessey & Heithaus 2015).

Transplant-exclosure experiments were conducted in cleared, sandy patches alongside dominant seagrasses on shallow beds (~2 m depth) in the Eastern Gulf, located 7 km offshore of Monkey Mia. Water temperatures are >20°C during September to May (warm season), and <20°C during June to August (cold season) (Heithaus & Dill 2006).

Megagrazers were classified as all animals excluded by a 20 cm<sup>2</sup> opening mesh (almost exclusively dugongs and green turtles), and macrograzers as animals that could pass through the large mesh but were excluded by 1.2 × 1.3 cm mesh (almost exclusively fishes). This study focussed only on the direct effects of mega- and macrograzer exclusion, but any obvious differences in the abundance of invertebrate grazers or epiphyte loads between treatments were noted.

### Experimental design

Exclosure studies were conducted using a randomized, nested, split plot design (Fig. 1). Megagrazer treatment plots (not excluded or excluded) each contained 3 types of macrograzer treatment subplots (open, cage control, full cage) that were replicated 3 times within megagrazer treatments. Plots were spaced approximately 10 m apart at 3 replicate sites, which were also spaced 10 m apart. Three plant fragments of each seagrass species (*C. angustata*, *H. uninervis*, and *H. ovalis*) were transplanted into the subplots (~30 cm<sup>2</sup>). Each fragment contained at least 3 shoots along a rhizome with an intact rhizome apical

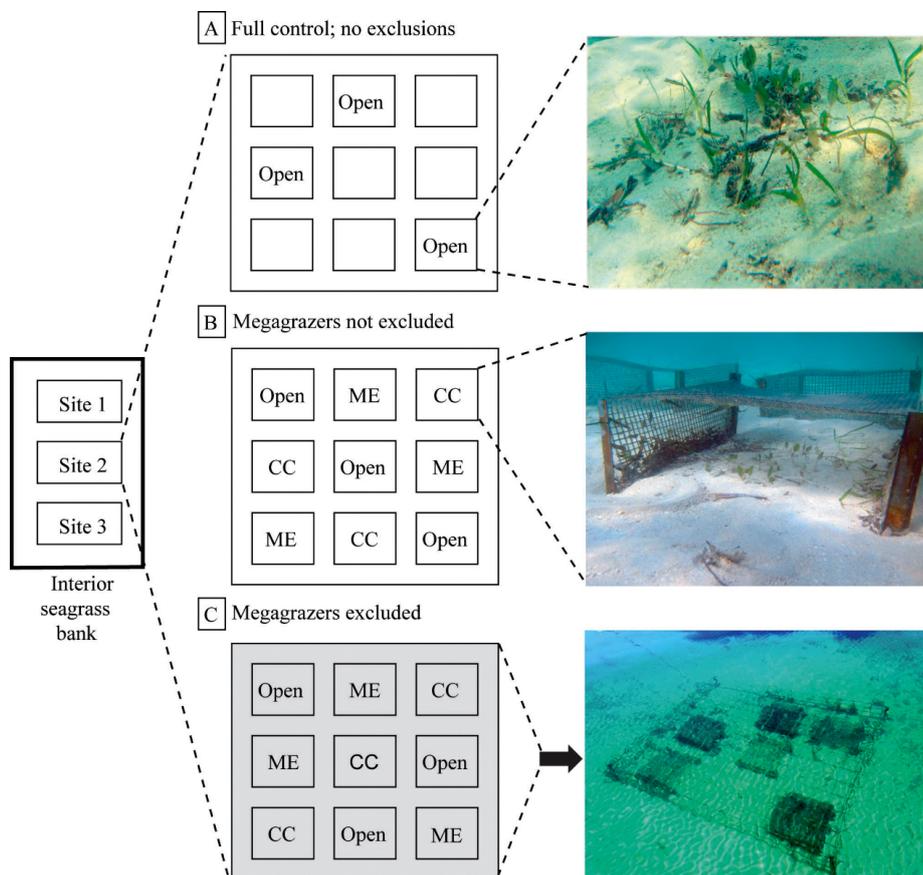


Fig. 1. Experimental design, showing replicate sites (Sites 1–3) within one interior seagrass bed. Each site contained (A) full control plots (no exclusions) and megagrazer treatment plots with (B) megagrazers not excluded and (C) megagrazers excluded. Each plot was 2.6 × 3.0 m, and consisted of nine 30 cm<sup>2</sup> macrograzer treatment subplots, spaced 50 cm apart. Macrograzer exclusion cage (ME) subplots contained 30 × 30 × 20 cm tall cages made of ~1 cm wire mesh; cage controls (CC) were the same as macrograzer cages but had open ends, enabling fishes to access the subplot and still encounter the presence of a cage; open subplots (Open) had no cage

meristem ( $n = 9$  to 15 total shoots  $\times$  species<sup>-1</sup>  $\times$  subplot<sup>-1</sup>). The rhizomes of the fragments of each species were buried into the sediment with the middle of the segments overlapping, forming an asterisk pattern, and secured with 10 cm wire staples at the middle and ends of segments. Macrograzer full cage subplots (ME) were 30  $\times$  30  $\times$  20 cm tall cages made of 1.2  $\times$  1.3 cm mesh chicken wire. Cage control subplots (CC) were identical to full cages but were missing 2 sides, and open subplots (Open) contained the seagrass transplants without any small cage structure. Subplot positions were randomly assigned within each plot such that each row and column only had 1 of the 3 treatments. Subplots were spaced ~50 cm apart from one another. Megagrazer enclosure plots consisted of a 2.6  $\times$  3.0 m steel rebar top with 20 cm<sup>2</sup> mesh that rested atop 40 cm tall rebar side panels. To explore if megagrazers were repelled by macrograzer cages or if cage structure acted as shelter attractive to fishes, one experiment featured only Open subplots that were placed 10 m away from any other cage structure (full control). Enclosure cages were erected during the end of a cold period during late August 2009, and maintained for the entire warm season.

Cages were cleaned at least every 2 wk and seagrass shoot densities were quantified at the beginning of the experiment, after 24 h, 5 d, 9 d, 21 d, bimonthly for 2 mo, and then once a month through Month 4. The densities of any remaining seagrasses were quantified at the time of cage removal, and at 24, 96, and 210 h after cage removal during May 2010.

To explore temporal variation, separate 3 wk experiments were established, as described above, during a warm (April) and cold (July) period in 2011. Seagrass shoot densities were quantified at the beginning of the experiment, after 24 h, and then at the end of each week for the 3 wk period.

To determine the abundance of air-breathing piscivores and large herbivores, visual surveys were conducted along pre-established belt transects (~3.2 km long) through the interior of seagrass beds for 2 mo surrounding the warm (April/May) and cold (July/August) period enclosure trials. Three separate seagrass beds were surveyed, including the bed where short-term enclosure trials were conducted. During each of the warm and cold period enclosure trials, 22 and 16 passes, respectively, were completed on different days. Belt transects were driven at 6 to 9 km h<sup>-1</sup> in a 5.5 m boat containing at least 3 observers. Observers recorded the number and GPS location of all cormorants, turtles, dugongs, and dolphins sighted within a 60 m (cormorants and turtles), 400 m

(dugongs), and 800 m (dolphins) sighting belt before the boat passed their position. Sighting bias was minimized by conducting surveys in Beaufort wind conditions of 2 or less, and observers noted the location of each individual piscivore to ensure they were counted only once. Piscivore and large herbivore density (e.g. no. dugong km<sup>-2</sup>) was calculated as  $n_t A_t^{-1}$  where  $n_t$  is the number of individuals sighted on transect  $t$ , and  $A_t$  is the area of the transect (km<sup>2</sup>).

Fish trapping was conducted in interior seagrass banks over 2 different days surrounding both the warm (April/May), and cold period (June/July) enclosure trials. Rectangular fish traps (34  $\times$  24  $\times$  21 cm; 1.2  $\times$  1.3 cm mesh; 10 cm conical entrances that tapered from a 6 to a 4 cm diameter opening) baited with 100 g of squid were deployed for between 2 and 4 h. A total of 13 and 9 traps were randomly deployed over seagrass banks during the warm and cold periods, respectively. The purpose of fish trap deployments was to confirm the presence of fish grazers within seagrass banks during both the warm and cold period, and to provide an indication of relative abundance of the 2 most commonly occurring species (*P. octolineatus* and *Monacanthus chinensis*). A previous study within the study site found no significant difference in catch abundances of *P. octolineatus* between the warm and cold season, and found this species to be the most abundant by an order of magnitude (Heithaus 2004).

### Statistical analysis

Generalized linear models with Poisson distribution and a log link function were used to estimate treatment effects on each seagrass species, where the response variable was shoot count. Individual counts over time within treatments were considered repeated measures and an autoregressive correlation structure was specified. The Wald's statistic (which approximates the linear regression test) was used to test for differences among nested model fits. The null hypothesis of the Wald test is that the coefficients for model variables are equal to zero. A test that fails to reject the null hypothesis suggests that removing that variable from the model will not substantially affect the fit. These statistics were achieved by using the 'geepack' package in R (Hojsgaard et al. 2006). Separate analyses were conducted for Open subplots of full controls and megagrazer treatments. Since these analyses required complete datasets with no missing data, one site had to be dropped from the analysis of the short-term, cold period trial because

fish had entered a macrograzer cage in one plot. Ultimately, to estimate the impacts of mega- and macrograzers, the proportional change in shoot densities was calculated over the entire experiment based on the type of grazing they allowed (i.e. no grazing, fishes grazing only, fishes and megagrazing), then a Tukey's multiple comparison test was performed. The contribution of fishes could be estimated by comparing macrograzer cages to subplots allowing only macrograzing, while megagrazers impacts could be derived from the difference between Open subplots in megagrazer treatment plots compared to fish impacts.

Non-parametric statistics (Mann-Whitney *U*-tests) were used to compare belt transect and fish trapping data. All analyses were conducted in R v.2.14.0 (R Development Core Team 2015).

**RESULTS**

The full experimental control used seagrasses that were transplanted into Open subplots 10 m away from any other cage structure. Open subplots, which could be grazed by both megagrazers and fishes, declined regardless of whether they were near macrograzer cages or away from any structures (Fig. 2). Neither site nor megagrazer treatment were significant variables for *Cymodocea angustata* nor *Halophila ovalis* shoot counts (Table 1; relevant statistics highlighted). However, site and megagrazer treatment were significant predictors for *Halodule uninervis*. Starting shoot counts of *H. uninervis* were greater within one site compared to that of the other two, and in plots located away from any other cages, shoot counts reached zero by Day 90, unlike those in

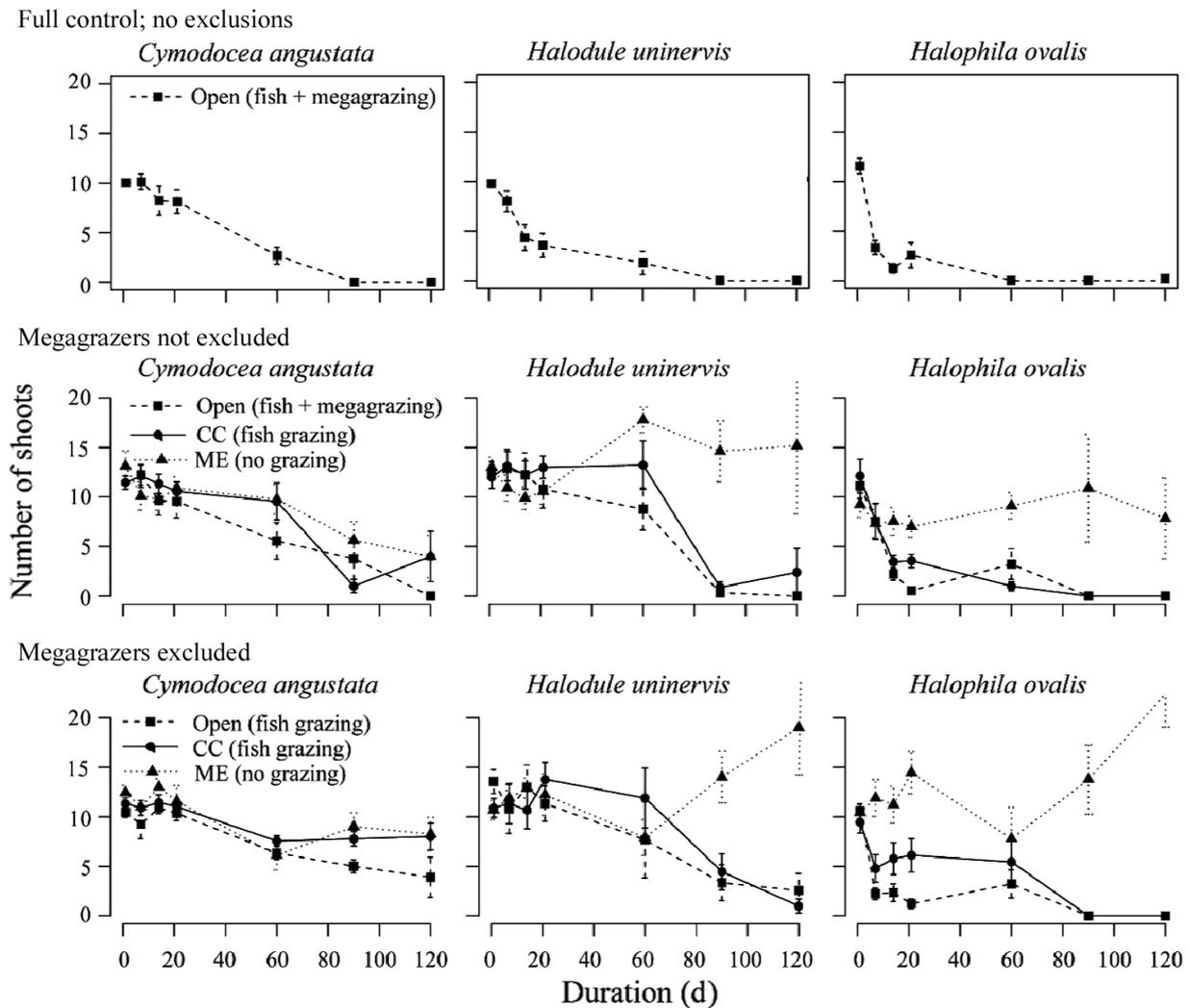


Fig. 2. Mean ( $\pm$ SE) seagrass shoot counts for full control plots, and for both megagrazer and macrograzer treatments during the 4 mo enclosure study (September 2009 to January 2010)

Table 1. Analysis of deviance results from generalized model fits for the 4 mo (September 2009 to January 2010) enclosure study of Open subplots, and the remaining subplots, by seagrass species. Significant variables discussed in the text are highlighted

	<i>Cymodocea angustata</i>			<i>Halodule uninervis</i>			<i>Halophila ovalis</i>		
	df	$\chi^2$	p	df	$\chi^2$	p	df	$\chi^2$	p
<b>Longer term: Open subplots only</b>									
Site	2	1.40	0.49	2	8.60	0.01	2	0.00	0.90
Megagrazer	2	3.70	0.16	2	12.30	<0.01	2	0.00	0.83
Site × megagrazer	4	9.20	0.06	4	10.40	0.03	4	8.00	0.08
Duration	6	68.40	<0.001	6	43.90	<0.001	6	1683.00	<0.001
Duration × megagrazer	12	204.90	<0.001	12	103.40	<0.001	12	65.00	<0.001
<b>Longer term: full control excluded</b>									
Site	2	4.20	0.12	2	7.70	0.02	2	3.00	0.27
Megagrazer	1	1.90	0.17	1	0.00	0.85	1	2.00	0.17
Site × megagrazer	2	0.90	0.63	2	4.40	0.11	2	4.00	0.16
Macrograzer	2	11.80	<0.01	2	13.20	<0.01	2	64.00	<0.001
Megagrazer × macrograzer	2	0.20	0.89	2	0.50	0.79	2	4.00	0.17
Macrograzer (site × megagrazer)	8	34.10	<0.001	8	52.90	<0.001	8	18.00	0.02
Duration	6	63.20	<0.001	6	6.00	0.42	6	35.00	<0.001
Duration × megagrazer	6	19.10	<0.01	6	3.60	0.74	6	10.00	0.11
Duration × macrograzer	12	16.10	0.19	12	61.80	<0.001	12	398.00	<0.001
Duration × megagrazer × macrograzer	12	28.50	<0.01	12	16.70	0.16	12	26.00	0.01

megagrazer exclusion plots which never reached zero. Although all species of seagrasses declined in open subplots over time, there were indeed differences in the rate of decline between megagrazer treatment plots (Table 1; significant interaction of duration × megagrazer).

Over the course of the full 4 mo experiment, macrograzer treatment was a significant variable for all transplanted seagrass species, *C. angustata*, *H. uninervis*, and *H. ovalis* (Table 1, Fig. 2; relevant statistics highlighted). *C. angustata* counts declined slightly when macrograzers were excluded, whereas *H. uninervis* and *H. ovalis* counts remained the same or increased. Inside cage control and open subplots, counts of *H. uninervis* and *H. ovalis* showed large and similar levels of decline regardless of megagrazer treatment, suggesting macrograzers eliminated these preferred seagrasses. Interestingly, both cage control subplots and open subplots in both megagrazer plot types showed little impact of grazing over the first 20 to 60 d of the experiment (which corresponded with cooler water temperatures) for *C. angustata* and *H. uninervis*. After Day 60, *H. uninervis* began to decline quickly, while *H. ovalis* had declined rapidly over the first 1 to 10 d in all subplots subject to macrograzers. These findings, combined with the increase of seagrasses within macrograzer cages, supports the observations that seagrass transplants were successful. All seagrass species declined when macrograzer cages were removed at the end of the experiment (Fig. 3), but more *C. angustata* shoots remained

(mean proportion ± SE:  $0.53 \pm 0.11$ ) than *H. uninervis* ( $0.13 \pm 0.05$ ) and *H. ovalis* ( $0.27 \pm 0.10$ ) ( $F_{2,130} = 13.557$ ,  $p < 0.001$ ; Fig. 4).

Short-term experiments revealed that grazer impacts varied considerably between the warm and cold period trials (Figs. 4 & 5, Table 2). During the warm period, macrograzers virtually eliminated all transplanted *H. uninervis* and *H. ovalis*, while all seagrass species persisted in macrograzer enclosure subplots (Fig. 4), supporting the success of transplants. Macrograzer impacts were minimal during the cold season (Fig. 5), except for *H. ovalis*.

The proportional change in shoot densities over the entire experiment, based on the type of grazing allowed, demonstrated that fishes (macrograzing) dominated top-down impacts on transplanted seagrasses in interior seagrass habitats, but these impacts were concentrated during the warm season (Fig. 6). The exclusion of both megagrazers and fishes resulted in increases (during the 4 mo experiment) or maintenance (during 3 wk experiments), of transplanted seagrass abundances, confirming transplants had been successful. In contrast, seagrass in plots that allowed fish grazing were virtually eliminated, but only during the warm season. During all seagrass counts, no noticeable differences in the abundances of invertebrate grazers or epiphyte loads were observed among treatments.

Belt transects revealed that cormorant density (a highly abundant predator of *Pelates octolineatus*; Bessey & Heithaus 2013) was higher during the cold

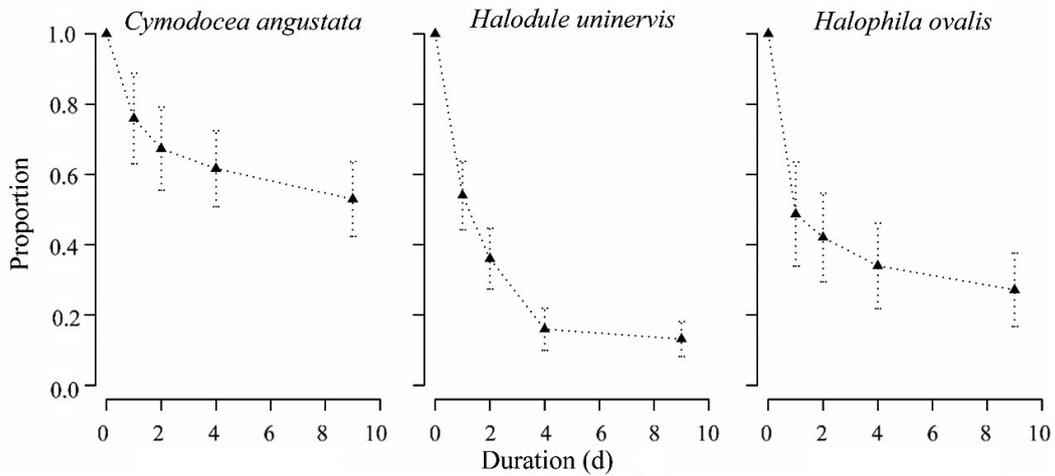


Fig. 3. Mean ( $\pm$ SE) declines in seagrasses exposed to grazing after 4 mo of macrograzer exclusion (cage removal experiment)

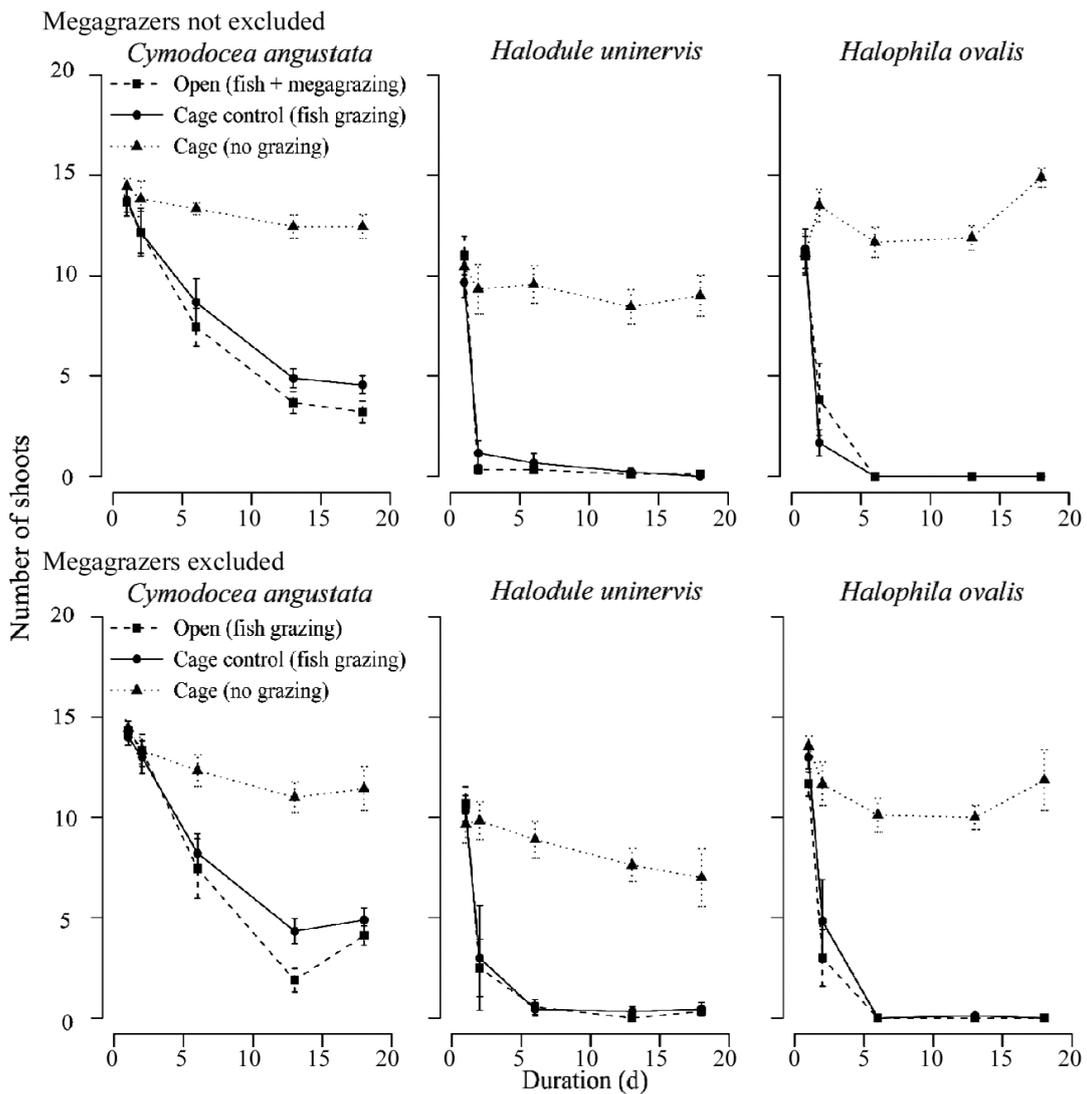


Fig. 4. Mean ( $\pm$ SE) seagrass shoot counts for both megagrazer and macrograzer treatments during the short-term exclusion study in the warm period (April 2011)

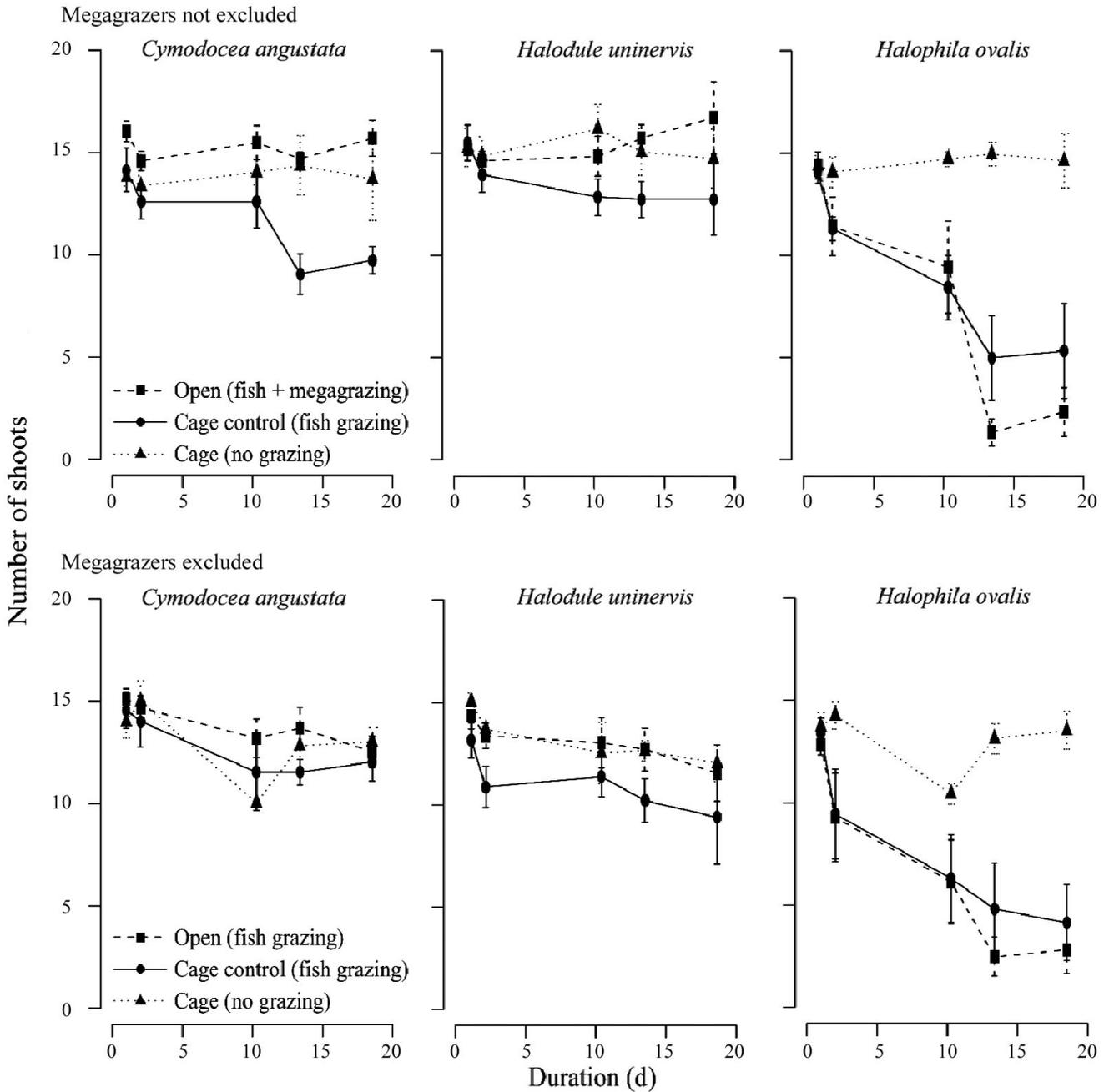


Fig. 5. Mean ( $\pm$ SE) seagrass shoot counts for both megagrazers and macrograzer treatments during the short-term enclosure study in the cold period (July 2011)

period ( $147 \pm 43$  ind.  $\text{km}^{-2}$ ) relative to the warm period ( $28 \pm 3$ ) trials ( $W = 333.5$ ,  $p < 0.001$ ), but no significant difference in catch rates of the herbivorous fishes *P. octolineatus* (warm:  $2 \pm 1$  fish trap $^{-1}$ , cold:  $3 \pm 2$ ;  $W = 60.5$ ,  $p = 0.92$ ) or *Monacanthus chinensis* (warm:  $2 \pm 1$ , cold:  $4 \pm 1$ ;  $W = 37.5$ ,  $p = 0.16$ ) were observed. Likewise, no significant differences in dolphin density was detected between warm and cold

period trials ( $W = 199.5$ ,  $p = 0.39$ ). Dugongs (mean  $\pm$  SE:  $0.92 \pm 0.76$  ind.  $\text{km}^{-2}$ ) and turtles ( $1.12 \pm 0.46$  ind.  $\text{km}^{-2}$ ) were sighted along belt transects in the study area during the warm period, but not during the cold period trials. Dugongs are known to abandon the study area during the cold season (Wirsing et al. 2007), while turtles reduce their foraging behaviour (Thomson & Heithaus 2014).

Table 2. Analysis of deviance results from generalized model fits for the short-term enclosure study in the warm (April 2011) and cold (July 2011) periods for each transplanted seagrass species. Significant variables discussed in the text are highlighted

	<i>Cymodocea angustata</i>			<i>Halodule uninervis</i>			<i>Halophila ovalis</i>		
	df	$\chi^2$	p	df	$\chi^2$	p	df	$\chi^2$	p
Short-term: warm season									
Site	2	1.00	0.67	2	3.00	0.26	2	1.00	0.54
Megagrazer	1	0.00	0.81	1	0.00	0.96	1	0.00	0.94
Site × megagrazer	2	1.00	0.48	2	1.00	0.49	2	0.00	0.97
Macrograzer	2	58.00	<0.001	2	64.00	<0.001	2	75.00	<0.001
Megagrazer × macrograzer	2	0.00	0.82	2	1.00	0.70	2	1.00	0.70
Macrograzer (site × megagrazer)	8	35.00	<0.001	8	19.00	0.02	8	63.00	<0.001
Duration	4	87.00	<0.001	4	70.00	<0.001	4	47.00	<0.001
Duration × megagrazer	4	1.00	0.87	4	1.00	0.85	4	1.00	0.91
Duration × macrograzer	8	321.00	<0.001	8	1235.00	<0.001	8	2035.00	<0.001
Duration × megagrazer × macrograzer	8	5.00	0.80	8	20.00	0.01	8	14.00	0.10
Short-term: cold season									
Site	1	0.20	0.66	1	3.00	0.08	1	0.20	0.65
Megagrazer	1	0.40	0.54	1	17.90	<0.001	1	2.50	0.11
Site × megagrazer	1	15.30	<0.001	1	0.20	0.65	1	3.90	0.05
Macrograzer	2	23.40	<0.001	2	16.20	<0.001	2	33.90	<0.001
Megagrazer × macrograzer	2	7.30	0.03	2	0.40	0.80	2	1.10	0.58
Macrograzer (site × megagrazer)	4	59.30	<0.001	4	53.00	<0.001	4	22.70	<0.001
Duration	4	10.00	0.04	4	15.50	<0.01	4	31.20	<0.001
Duration × megagrazer	4	18.80	<0.001	4	28.70	<0.001	4	2.80	0.60
Duration × macrograzer	8	13.70	0.09	8	30.20	<0.001	8	244.40	<0.001
Duration × megagrazer × macrograzer	8	186.40	<0.001	8	11.40	0.18	8	53.00	<0.001

## DISCUSSION

The current study found that fish affected the establishment and persistence of seagrasses transplanted into interior habitats during the warm season, and dominated the top-down impacts on both *Halodule uninervis* and *Halophila ovalis*. During the 4 mo study and the short-term experiment in the warm season, both *H. uninervis* and *H. ovalis* were virtually eliminated from all plots that were exposed to fish grazers. In contrast, both species became established and increased in abundance when protected from fish grazing during the 4 mo study. Visual observations of Open subplots confirmed the presence of bite marks on seagrass shoots and rhizomes in the sediment, suggesting that herbivory, rather than tidal movement or current, had displaced the transplanted seagrasses. The removal experiments indicated that *H. uninervis* and *H. ovalis* were grazed faster than *Cymodocea angustata*. Burkholder et al. (2012) also found these 2 particular seagrass species to be the most highly grazed. For these preferred seagrass forage species, the current study indicates that even if they were to become established, fish grazing has the capacity to eliminate them from shallow seagrass banks. This is consistent with observations that these fast-growing seagrass species are rare on shallow seagrass banks

in the study area. Interestingly, during the cold season, the impacts of grazing were greatly reduced, yet fish grazers maintained a preference for *H. ovalis*.

Fish grazing impacts appeared to vary temporally, which raises the possibility that grazer impacts may be structured by impacts of predators, or by seasonal changes in metabolic demand. Predation-sensitive foraging of herbivores within the Shark Bay study site would predict fish grazers to have greater impacts on forage species during the warm season. Like megagrazers, dolphins reduce their use of interior portions of banks during the warm months to minimize the risk of predation from tiger sharks (Heithaus & Dill 2006), thus allowing herbivorous fishes to forage more freely. As a result, fishes should have larger impacts on transplanted seagrass species during warm months. In contrast, during the cold months, piscivores can forage in interior seagrass banks with reduced risk from tiger shark predators, as tiger shark abundances are greatly reduced. Herbivorous fishes are still present over dense seagrass beds within interior habitats during the cold season (Heithaus 2004, Bessey & Heithaus 2015), but should be less willing to move out of the protective cover of *Amphibolis antarctica* to forage in open habitats. In addition, cormorant densities were comparatively higher in the cold period. Cormorants are a major predator of

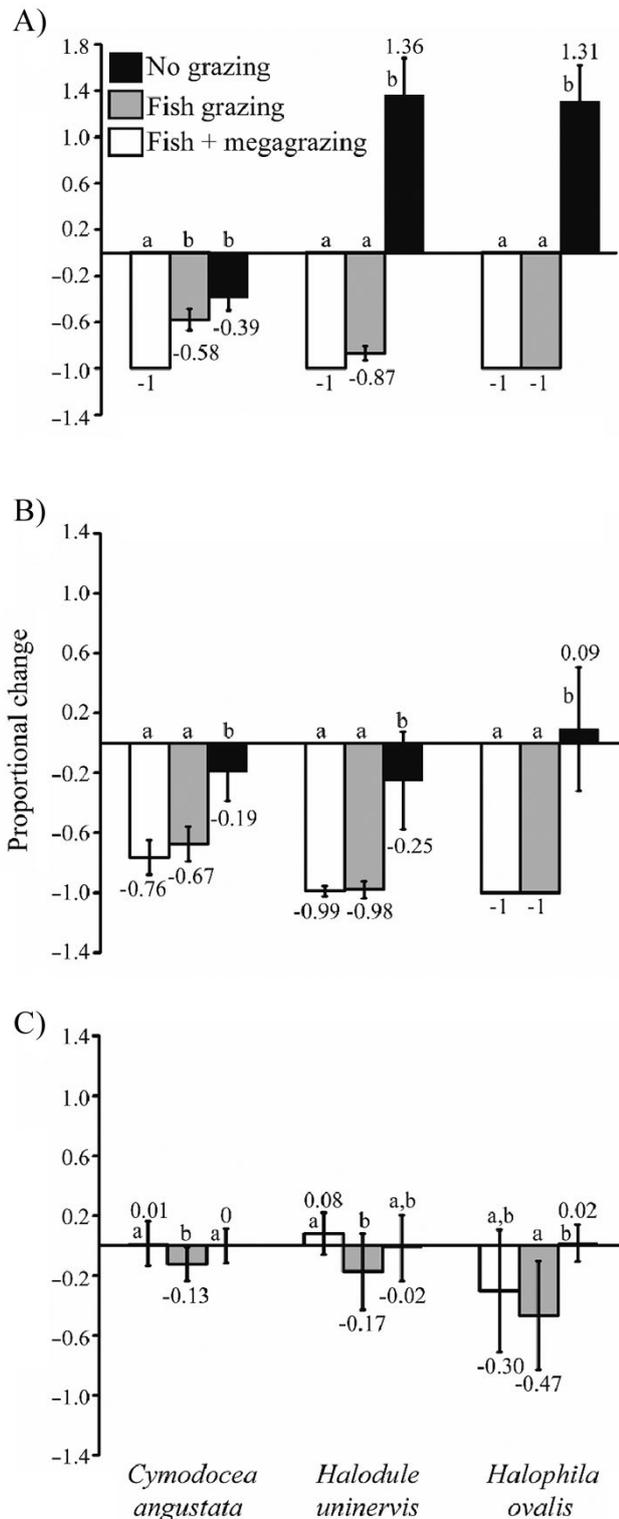


Fig. 6. Proportional change (mean  $\pm$  SE) in seagrasses comparing start and end shoot counts by type of grazing during (A) the 4 mo enclosure study ending in the warm season, (B) the short-term enclosure study in a warm period, and (C) the short-term enclosure study in a cold period. Mean values are presented over bars; letters represent significant differences between groups based on Tukey's multiple comparison tests

*Pelates octolineatus*, and temporal variation in predation risk may be an important factor in structuring the behaviour and foraging impacts of this abundant fish grazer (Bessey & Heithaus 2013). Alternatively, seasonal changes in the metabolic demand of fishes could also account for the reduced impact of fish grazers during the cold period. The metabolic demands of fish are influenced by body mass, temperature, and activity levels, which may influence grazing impacts (Killen et al. 2010). Indeed, feeding rates of fish decline at low temperatures (Jobling 1994), although herbivorous fish require continual food intake for survival (Arrington et al. 2002). This, too, could explain the reduced grazer impacts on *C. angustata* and *H. uninervis* during the cold period trials, with fish still maintaining a preferences for *H. ovalis*. *P. octolineatus*, the most abundant species of fish in the study area, do indeed contain a large portion of seagrass in their stomach content during the cold season (Bessey & Heithaus 2015).

Although previous studies have demonstrated the potential impacts of particular marine herbivore groups on seagrass (Preen 1995, Kirsch et al. 2002, Tomas et al. 2005, Heck & Valentine 2006), an understanding of the relative importance of different grazers has been hampered by a lack of studies in ecosystems with healthy predator populations, where both megagrazers and macrograzers act simultaneously. The importance of herbivory could be attenuated or amplified if grazers are overexploited or are rebounding or released from risk. Indeed, the increase of herbivorous green turtle populations in recent decades, a response to conservation efforts, has led to population densities capable of altering the structure of seagrass meadows (Fourqurean et al. 2010, Lal et al. 2010, Kelkar et al. 2013). Previous marine studies have considered the differential effects of various grazer groups, but their primary focus has been invertebrate mesograzers and fishes in algal systems, or in one instance a simulated eelgrass environment (Duffy et al. 2003, Fox 2004, Matthiessen et al. 2007, Bruno et al. 2008, Vanderklift et al. 2009, Ceccarelli et al. 2011). The current experiment provides *in situ* experimental data in a seagrass system with both healthy grazer (from both mega- and macrograzers) and predator populations. Indeed, we found that fish dominated the top-down impacts on 2 species of seagrass in interior habitats: *H. uninervis* and *H. ovalis*. For these preferred species, fish grazing can eliminate the seagrasses from shallow seagrass banks during times of reduced predation risk, indicating that fish can play an important role in structuring a subtropical seagrass system, that herbi-

vore impacts are seagrass-species dependent, and that seagrass beds may be shaped by herbivore response to their predators.

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