

Patch dynamics and species shifts in seagrass communities under moderate and high grazing pressure by green sea turtles

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ABSTRACT: We studied 2 seagrass beds in the Mexican Caribbean that were grazed by green turtles. Grazing impact was moderate at Puerto Morelos (<20 % of the area was grazed), whereas at Akumal, 45 to 55 % of the bed was grazed. The turtles practiced rotational (cultivation) grazing and thereby increased the nitrogen leaf content in the dominant seagrass *Thalassia testudinum* by 30 to 33 %. Average seagrass leaf productivity decreased under grazing at Puerto Morelos from 3.09 to 0.93 g dry wt m⁻² d⁻¹, whereas it did not change significantly at Akumal (0.88 to 1.17 g dry wt m⁻² d⁻¹). At Puerto Morelos, the turtles maintained grazing plots for 13 mo to >2 yr, creating a mosaic of patches that were grazed, ungrazed or recovering from grazing. Cover of the faster-growing *Halodule wrightii* and rhizophytic algae increased in the grazing plots, whereas that of the dominant but slow-growing *T. testudinum* decreased. After the turtles stopped grazing the plots, the cover of *T. testudinum* gradually increased again, but recovery to pre-grazing conditions lasted >1 yr and was not observed in this study. Cover of *Syringodium filiforme* decreased when the turtles opened up new grazing areas but remained stable afterwards because the turtles usually avoided consumption of this seagrass. At Akumal, the system approached carrying capacity for grazing, and the turtles returned to grazing plots that had not fully recovered from past grazing. Here, the dominant climax seagrass *T. testudinum* became less abundant from 2008 until 2012, resulting in a less patchy landscape with low seagrass biomass and higher prevalence of the early seral species *H. wrightii*.

KEY WORDS: *Chelonia mydas* · *Halodule wrightii* · Plant–herbivore interactions · *Thalassia testudinum*

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INTRODUCTION

Many centuries ago, green turtles *Chelonia mydas* L. were among the most important consumers of tropical seagrasses, and probably had a great impact on past seagrass communities. But since the 1600s, their populations have decreased >90 % because of human overexploitation (Jackson 1997). For a long time, it was thought that seagrass ecosystems were mainly determined by bottom-up regulation because

the role of (large) herbivores was considered insignificant (Valentine & Heck 1999, Valentine & Duffy 2006). However, large herbivores, such as sea turtles and sirenian mammals, may influence the structure, dynamics and specific composition of tropical seagrass communities (Bjorndal 1980, Thayer et al. 1984, Preen 1995, Aragones & Marsh 2000, Kelkar et al. 2013). Today, the worldwide abundance of green turtles is increasing because of conservation efforts (Seminoff 2004, Broderick et al. 2006). In sev-

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eral areas, the effects of the growing turtle density on seagrass beds have become noticeable (Ballorain et al. 2010, Lal et al. 2010, Christianen et al. 2013, Kaladharan et al. 2013, Kelkar et al. 2013), and in the US Virgin Islands (Williams 1988), Bermuda (Murdoch et al. 2007, Fourqurean et al. 2010) and Terawan, Indonesia (Christianen et al. 2014), the turtles have reached critical densities and have caused local collapse of the seagrass beds.

The green turtle has a pan-tropical distribution and is the only sea turtle species that mainly feeds on seagrasses as adults, but it also eats algae (André et al. 2005) and jellyfish (Lutz et al. 2002). Green turtles in the Caribbean usually return to the same grazing plots, possibly because plant nutritional quality increases when plants are cropped regularly. Older seagrass leaf tissues are richer in fiber and have less nitrogen, and artificial clipping of the seagrass *Thalassia testudinum* results in increasing nitrogen and decreasing lignin contents (Dawes & Lawrence 1979, Bjorndal 1980, Thayer et al. 1984, Zieman et al. 1984). Thus, by maintaining cropped patches (grazing plots), the turtles eliminate refractory tissues and increase the nitrogen content in the leaves (Bjorndal 1980, Zieman et al. 1984). Also, leaf growth may increase through compensatory resource allocation, as has occasionally been reported for terrestrial plants (Briske 1996), but this has not been established for seagrasses. Preen (1995) named this grazing pattern cultivation grazing. In the long term, the carbohydrate reserves in the rhizomes decrease, inhibiting foliar development (Moran & Bjorndal 2005, Fourqurean et al. 2010), and most likely the turtles abandon the cultivated plots at that time (Bjorndal 1980, Zieman et al. 1984). Although the grazing habit of green turtles in the Caribbean is well known, the patch dynamics associated with cultivation grazing have not been well studied until present.

Previous studies on the effects of turtle grazing on seagrasses in the Caribbean only included the large, slow-growing climax grass *T. testudinum* (Bjorndal 1980, Thayer et al. 1984, Zieman et al. 1984, Murdoch et al. 2007, Fourqurean et al. 2010). But Caribbean seagrass communities often consist of 2 or 3 seagrass species, with a diverse community of rooted (rhizophytic) algae (van Tussenbroek et al. 2014), and little is known about the response of the other marine plants to turtle grazing. Plant species may respond to grazing in a different manner, and in terrestrial systems, herbivores often cause shifts in plant community and specific composition (Briske 1996, Augustine & McNaughton 1998). In the tropical Indo-Pacific, faster-growing species such as *Halophila*

ovalis and *Zostera capricornii* are more resilient to clipping (simulating grazing) than the slower-growing *Cymodocea serrulata* (Kuiper-Linley et al. 2007). Indo-Pacific multi-specific tropical seagrass communities undergo shifts in species dominance, with a higher abundance of faster-growing seagrass species under regimes of intensive grazing by dugongs (Preen 1995) or sea turtles (Kelkar et al. 2013). However, such responses at the community level have not yet been established for tropical Caribbean seagrass beds.

This study was conducted at 2 sites in the Mexican Caribbean that are exposed to different grazing regimes; the first site at Puerto Morelos has only been regularly visited by turtles for several years (van Tussenbroek unpubl. data), whereas the second site at Akumal has been visited by turtles for at least 2 decades (Maldonado Cuevas et al. 2006). Preliminary examination of the study sites suggested that grazing intensity is much higher at Akumal than at Puerto Morelos. Through a comparative study of these contrasting sites, we address the following questions: (1) Does rotational grazing increase the growth and nutrient content of seagrasses in the grazing plots? (2) Is the response of the seagrasses to turtle grazing species specific? (3) Do patterns of rotational grazing depend on grazing intensity? (4) What are the effects of (rotational) grazing on seagrass community structure and composition? Considering the recovery of populations of green turtles throughout the tropical seas, it is important to understand the impacts of these turtles on coastal habitats, and through this study, we hope to increase our understanding of how grazing by turtles influences the structure and specific composition of Caribbean seagrass communities.

MATERIALS AND METHODS

Study sites

Both study sites are on the eastern coast of the Mexican Yucatan Peninsula (Fig. 1). The Puerto Morelos reef lagoon is delimited on the seaward side by a fringing reef, running from north to south, at distances of 350 to 1600 m from the coast. The lagoon has a depth of <1 to 6 m (usually 2.5 to 4.0 m), and its calcareous sand bottom is covered with an extensive mixed seagrass community dominated by *Thalassia testudinum*, accompanied by *Syringodium filiforme*, *Halodule wrightii* and rhizophytic algae (Rodríguez-Martínez et al. 2010). This system used to be oligotrophic but has suffered from gradual eutrophication

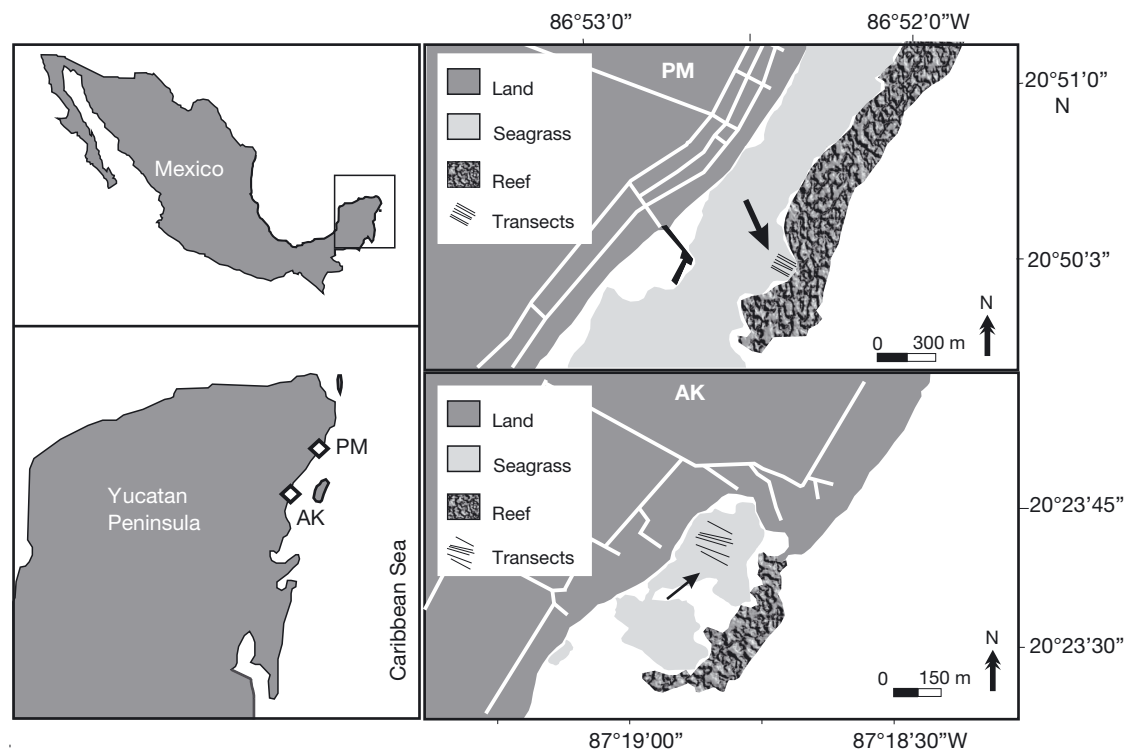


Fig 1. Study sites (indicated by arrows), with approximate outlines of seagrass beds and reefs. PM = Puerto Morelos, AK = Akumal

over recent decades (Carruthers et al. 2005, Rodríguez-Martínez et al. 2010, Sánchez et al. 2013). The grazing pressure by sea turtles in this reef lagoon is low, although there are several preferred sites, 1 to several hectares in size, frequently visited by turtles. Our study site in the southern reef lagoon ($20^{\circ}50'27.2''$ N, $86^{\circ}52'26.1''$ W) has a depth of 1.8 to 3.8 m and has been visited regularly by turtles since 2010 (B. I. van Tussenbroek unpubl. data). Akumal, the second study site, has 3 bays with well-developed beaches that are frequent turtle nesting sites. The study site in the northern bay ($20^{\circ}23'44.9''$ N, $87^{\circ}18'47.9''$ W, Fig. 1) has a limestone bottom covered by a relatively thin sand layer (max. 0.4 m deep) colonized by seagrasses (*T. testudinum*, *S. filiforme* and *H. wrightii*) and sparse rhizophytic algae. The main reef is ~300 m from the coast, but the bay has various small reefs near (~50 m distance) the beach. This bay supports an intensive tourist industry (beach tourism, boating and snorkeling) and is eutrophic (Mutchler et al. 2007, Baker et al. 2010). The seagrass beds, covering 4 to 5 ha in total, occur at 1.5 to 2.5 m depth and have been intensively grazed by resident and visiting turtles for approximately 2 decades (Maldonado Cuevas et al. 2006).

Preliminary analysis of grazing frequency

In June 2011, both study sites were inspected while snorkeling. The inspection started at a haphazardly chosen point in the center of the site, and the next observation points were selected with the aid of 2 random number tables, the first indicating distance in m (1 to 10) and the second indicating cardinal direction (1 to 8, with 1 indicating N and 5 indicating S) to the next point. When a following point was outside the study site, a new random starting point within the site was selected to continue the monitoring. At each point, the nearest *T. testudinum* shoot was located, registering the presence/absence of turtle bites in the leaves. Turtle bites in the broad-leaved *T. testudinum* were identified by a clean-cut horizontal scar (Fig. 2) in all leaves of a shoot and are easily distinguished from bites of large parrotfish (which leave partial circular scars in older leaf sections) or sea urchins (which leave more 'messy' scars because they tend to tear the leaves and usually do not remove all leaves of a shoot at the same level). Also, neither large parrotfish nor sea urchins were very abundant in our study sites. The turtles did not graze dispersed shoots in the seagrass beds, but their graz-

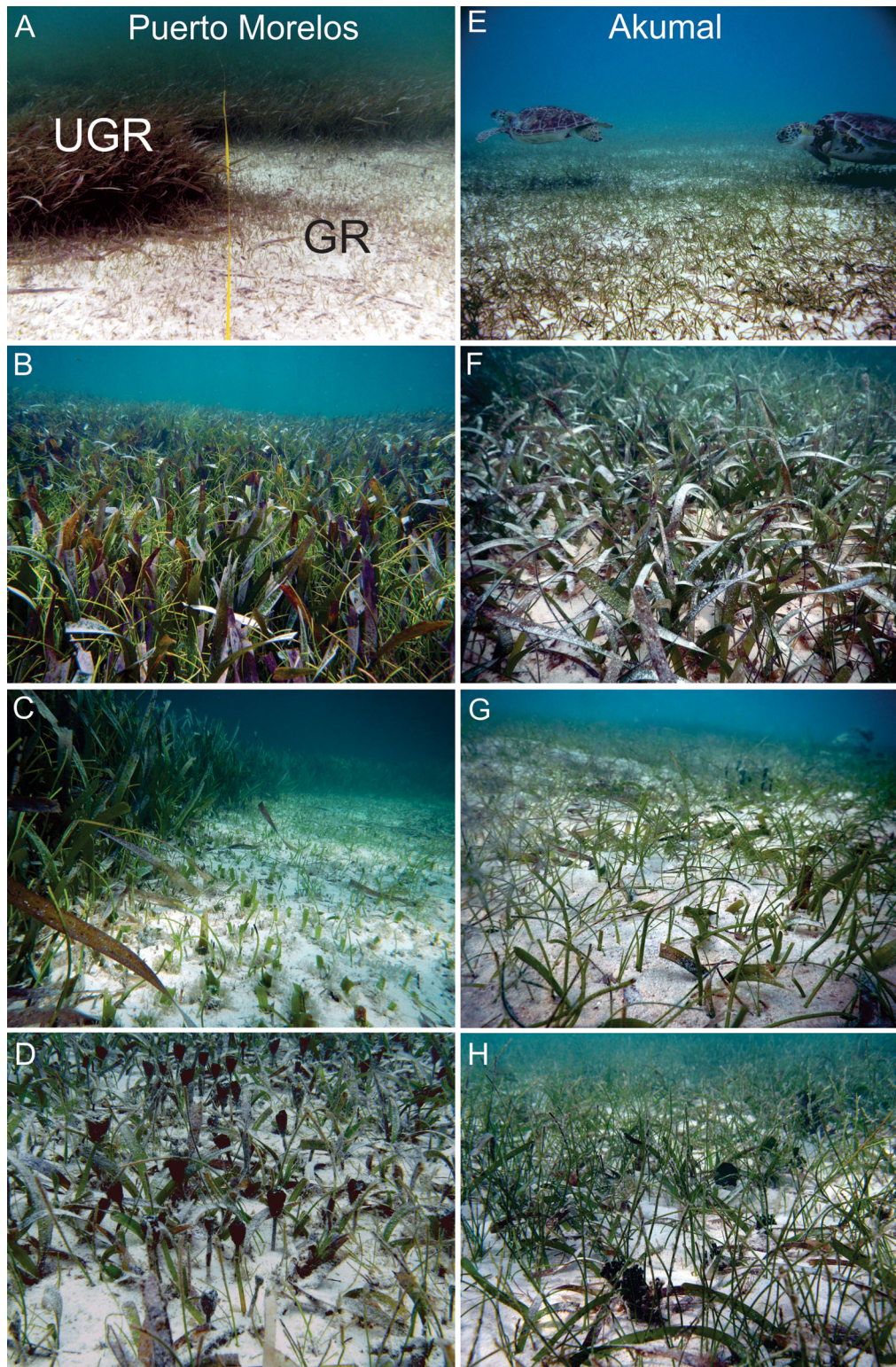


Fig. 2. Photos of seagrass beds at Puerto Morelos (A–D) and Akumal (E–H), showing overviews of the grazed areas (A,E), with details of the condition of the seagrass bed when ungrazed (B,F), recently grazed by turtles (C,G) and recovering from turtle grazing (D,H). At Puerto Morelos, the grazed (GR) and ungrazed (UGR) areas were clearly defined. Differences in vegetation between grazed and ungrazed areas were less obvious at Akumal than at Puerto Morelos

ing efforts were concentrated in grazing plots that had the appearance of a recently 'trimmed' grass bed (Fig. 2). A total of 204 points were examined at Puerto Morelos, and 238 points at Akumal; the frequency of turtle bites in *T. testudinum* shoots was used as a proxy of grazing intensity.

Leaf growth, tissue nutrient contents and biomass

Seagrass leaf growth and tissue nutrient contents were determined in turtle-grazing and nearby ungrazed (control) areas. The turtle-grazing areas were randomly selected from the observed grazing plots along permanent line transects (see next section), and they had been grazed at least from the beginning of July 2011 (Puerto Morelos) or August 2011 (Akumal); 76 to 100% of all leaves in the selected areas presented turtle bite marks. Leaf growth and productivity of *T. testudinum* were determined using a leaf-marking technique following van Tussenbroek & Brearley (1998), and *S. filiforme* and *H. wrightii* were clipped following Kowalski et al. (2009). Measurements were made in circular areas (20 cm diameter) protected with 35 cm high mesh wire exclosures to avoid disturbance by turtle grazing during the measurements. All leaves of *T. testudinum* within each exclosure were marked 3 cm above substratum level with a syringe needle, and all leaves of *S. filiforme* and *H. wrightii* were clipped at this level. Additionally, all seagrass leaves growing within 30 cm of the perimeter of the control exclosures were clipped with scissors to a height similar to the grazed plots (to ~3 cm) to avoid bias from translocation or shading by (connected) large foliar shoots. After 8 to 9 d, the leaves of *T. testudinum* were marked again at 3 cm height, and the foliar shoots were retrieved by cutting the vertical rhizome below the substratum. The leaves of *S. filiforme* and *H. wrightii* were cut at 3 cm height. At Puerto Morelos, there were 12 sampling stations (6 in grazed and 6 in ungrazed areas), and growth and productivity were measured from 29 November to 7 December 2011. At Akumal, the dominant seagrass *T. testudinum* was less abundant, so we increased the number of replicates to 8 in the grazing plots and the ungrazed (control) areas, and measurements were taken from 18 to 27 January 2012. In the laboratory, the leaves of *T. testudinum* were cut at the level of the basal (recent) and older marks, leaving only the new-growth sections. Epiphytes were removed by scraping with a razor blade, and the lengths of the new-growth sections

were determined with a ruler. The clipped leaves of *S. filiforme* and *H. wrightii* were also cleaned of epiphytes, and their lengths (corresponding to new growth) were determined. Leaf elongation rates were calculated as the lengths of new-growth sections divided by the number of days they were left to grow. The fractions were dried at 65°C and weighed with an analytical balance, and the production rates (as g dry wt m⁻² d⁻¹) were calculated. Per sample, the dried new-growth sections of *T. testudinum* and *S. filiforme* (samples of *H. wrightii* were too small for analysis) were ground to a fine powder; carbon and nitrogen contents were determined in duplicate using a CHN analyzer, and phosphorus content was determined by colorimetric analysis (performed at J. Fourqurean laboratory, Florida International University). Differences in productivity, elongation rates, shoot density and nutrient contents between grazed and ungrazed (control) areas were analyzed with a Student's *t*-test applied to the average values of the samples. Because there were only 5 to 8 replicates per treatment, the significance level (α) was fixed at 0.1 to reduce the probability of a Type II error. A Bonferroni correction was applied to α when testing 2 or more parameters from the same sample.

At the same sampling stations, aboveground and belowground plant parts were sampled with a steel corer (11.2 cm diameter, ~30 cm deep) following van Tussenbroek et al. (2014). The core samples were taken at the beginning of November 2011 at Puerto Morelos and at the beginning of December 2011 at Akumal. Six (Puerto Morelos) or 8 (Akumal) core samples were taken in each type of area (grazed or control). The samples were rinsed with fresh water to remove all sand and refrigerated for a maximum of 14 d until further processing. The tissues of each species were separated into aboveground (green leaf tissue) and live belowground fractions. Lengths of the horizontal rhizome sections (both horizontal and vertical rhizomes for *H. wrightii*) were measured with a ruler. After removal of epiphytes with a razor blade, the length of the longest leaf per shoot was determined with a ruler, and its width (diameter in the case of *S. filiforme*) was measured at the base with dial calipers (0.02 mm precision). Dead (brown) sections of all leaves were discarded. The samples were dried to constant weight in an oven at 65°C for 24 to 48 h, and their weights were determined with an analytical balance. Differences in biomass and morphometric parameters of the 3 seagrass species were analyzed with a Student's *t*-test applied to the average values of the core samples.

Patterns of rotational grazing

The development of grazing plots was followed in permanent transects for 2 yr. Six permanent 100 m long line transects were established in each study site (Fig. 1). At Puerto Morelos, the extremes and middle points (at 50 m) were marked with iron stakes. The distances between subsequent transects were determined with a random number table. At Akumal, iron stakes could not be fixed in a permanent manner because of the shallowness of the sand and because they were continuously removed by visitors. Permanent moorings near the coast were used as starting points, and end points were located with a GPS at the start of each observation.

During each observation, two 50 m long metric tapes were placed between the marked extremes of a transect. Divers observed the vegetation 10 cm on both sides of the 100 m long line transect and identified sections with different visible characteristics, taking into account density, cover, composition of vegetation groups and degree of turtle grazing. The initial and final distance of each segment was noted, together with the relative abundance of seagrasses and rhizophytic algae. Relative abundance was determined with the Braun-Blanquet scale, designed for the study of terrestrial vegetation (Braun-Blanquet 1932, our Table 1). Herbivory pressure, estimated as the prevalence of turtle bites in seagrass leaves, was evaluated using the same scale, but the percentages represent frequency instead of coverage, where 'r' represents rare bites, '+' represents less than 1% of the shoots with bites, '1' represents 1 to 5% of the shoots with bites, etc. In addition, video transects were taken with commercial underwater cameras for future reference. Observations were made during the day (between 11:00 and 16:00 h) every 2 or 3 mo from July 2011

until July 2013 at Puerto Morelos and from August 2011 to September 2012 at Akumal.

Grazing history at Akumal

At Akumal, seagrass vegetation throughout the bay was observed in 2008 (July to August) and 2012 (July) to evaluate possible effects of the increasing turtle population on seagrass abundance. The observations were made at 84 points at 50 m distance from each other, obtained through geo-referencing grid points on a Google Earth™ image of the area. A 1 × 1 m quadrat was dropped at each point, and relative abundance of the seagrass species was determined using the above-mentioned Braun-Blanquet scale. In addition, the presence of turtle bites on the seagrasses was recorded. Relative abundance in 2008 and difference in abundance from 2008 until 2012 were mapped with Surfer (ver. 8, Golden Software) using the triangulation with linear interpolation algorithm.

RESULTS

Grazing intensity

Grazing intensity was lower at Puerto Morelos, where 19.1% of the 204 inspected *Thalassia testudinum* shoots had turtle bites, than at Akumal, where 54.3% of the 238 shoots presented turtle-grazing scars.

Seagrass growth and nutrient content

Rotational grazing did not stimulate leaf growth (elongation rate), productivity or foliar shoot density of any of the seagrass species at both study sites (Table 2). At Puerto Morelos, these parameters were negatively influenced by grazing (except for foliar shoot density of *T. testudinum*), whereas at Akumal, we found no differences in the grazing plots and control areas, but the values were low in general (Table 2). Tissue nitrogen content of *T. testudinum*, however, was higher in the grazing plots at Puerto Morelos and Akumal, and Akumal also had increased phosphorus content (Table 3). However, tissue nutrient contents of the seagrass *Syringodium filiforme* were similar in the grazing plots and the ungrazed areas at both sites (Table 3).

Table 1. Braun-Blanquet scale used in this study and numerical assignation to the values assigned in this study for graphical purpose. An individual is a foliar shoot for seagrasses and a singly rooted thallus for rhizophytic algae

Value	Abundance	Numerical value
r	Rare: 1 or 2 individuals	0.1
+	Few individuals	0.5
1	Various individuals or cover up to 5%	1
2	Many individuals or cover 6–25%	2
3	Cover 26–50%	3
4	Cover 51–75%	4
5	Cover 76–100%	5

Table 2. Average values (\pm SD) of the total foliar productivity of the community, with foliar productivity, leaf elongation rates and foliar shoot density of each seagrass species in ungrazed (control) and grazing plots at Puerto Morelos and Akumal and the results of *t*-tests. After Bonferroni correction, $\alpha = 0.033$ for the *t*-tests of the 3 parameters of each species (3 dependent variables, $\alpha = 0.1$ because of small sample size). Relative change: difference of the value in grazing plots respective to controls. nd = not determined because of limited sample size, ns = not significant

	n	Control Value	n	Grazed Value	Relative change	<i>t</i> -test <i>t</i>	<i>p</i>
PUERTO MORELOS							
Total foliar productivity ($\text{g m}^{-2} \text{d}^{-1}$)	6	3.09 ± 0.56	6	0.93 ± 0.45	-69.9%	6.594	0.001
<i>Thalassia testudinum</i>							
Foliar productivity ($\text{g m}^{-2} \text{d}^{-1}$)	6	1.97 ± 0.47	6	0.72 ± 0.36	-63.5%	5.193	0.001
Elongation rate ($\text{mm leaf}^{-1} \text{d}^{-1}$)	6	4.48 ± 0.36	6	2.82 ± 0.50	-37.1%	6.626	0.001
Foliar shoot density (no. m^{-2})	6	658 ± 142	6	589 ± 165	ns	0.772	0.458
<i>Syringodium filiforme</i>							
Foliar productivity ($\text{g m}^{-2} \text{d}^{-1}$)	6	1.11 ± 0.19	6	0.19 ± 0.14	-82.8%	9.454	0.001
Elongation rate ($\text{mm leaf}^{-1} \text{d}^{-1}$)	6	5.92 ± 0.56	6	4.15 ± 0.33	-29.9%	6.658	0.001
Foliar shoot density (no. m^{-2})	6	1819 ± 393	6	530 ± 290	-70.1%	6.465	0.001
<i>Halodule wrightii</i>							
Foliar productivity ($\text{g m}^{-2} \text{d}^{-1}$)	6	0.008 ± 0.015	6	0.04 ± 0.04	ns	1.383	0.197
Elongation rate ($\text{mm leaf}^{-1} \text{d}^{-1}$)	2	5.44 ± 0.98	4	2.46 ± 0.25	nd	nd	nd
Foliar shoot density (no. m^{-2})	6	21 ± 38	6	451 ± 474	ns	2.210	0.052
AKUMAL							
Total foliar productivity ($\text{g m}^{-2} \text{d}^{-1}$)	8	1.17 ± 0.63	8	0.88 ± 0.46	ns	1.214	0.245
<i>Thalassia testudinum</i>							
Foliar productivity ($\text{g m}^{-2} \text{d}^{-1}$)	8	0.83 ± 0.85	8	0.62 ± 0.55	ns	0.587	0.568
Elongation rate ($\text{mm leaf}^{-1} \text{d}^{-1}$)	6	4.27 ± 0.39	6	3.73 ± 0.83	ns	1.449	0.190
Foliar shoot density (no. m^{-2})	8	283 ± 297	8	365 ± 463	ns	1.451	0.172
<i>Syringodium filiforme</i>							
Foliar productivity ($\text{g m}^{-2} \text{d}^{-1}$)	8	0.46 ± 0.18	8	0.33 ± 0.36	ns	0.904	0.387
Elongation rate ($\text{mm leaf}^{-1} \text{d}^{-1}$)	8	5.07 ± 1.36	8	4.27 ± 1.24	ns	1.223	0.242
Foliar shoot density (no. m^{-2})	8	1190 ± 632	8	673 ± 308	ns	2.080	0.064
<i>Halodule wrightii</i>							
Foliar productivity ($\text{g m}^{-2} \text{d}^{-1}$)	8	0.09 ± 0.12	8	0.06 ± 0.07	ns	0.686	0.505
Elongation rate ($\text{mm leaf}^{-1} \text{d}^{-1}$)	5	4.30 ± 1.74	5	2.84 ± 0.40	ns	1.826	0.135
Foliar shoot density (no. m^{-2})	8	1186 ± 1408	8	1185 ± 1663	ns	0.000	1.000

Species-specific response to grazing pressure

The seagrasses lost aboveground leaf biomass because of grazing, reducing their photosynthetic capacity, which in due course decreased their belowground tissues, but the latter response was species specific (Table 4, Fig. 3). Although the leaf biomass of *T. testudinum* in the grazing plots was reduced considerably compared with that in the control areas, rhizome biomass (or length) was not significantly different in the grazed and ungrazed (control) areas at Puerto Morelos, and it was only slightly (but not significantly) reduced in the grazing plots at Akumal (Table 4, Fig. 3). Also, at Akumal, where the seagrasses have been grazed for more than 2 decades and where grazing pressure was higher, biomass of this species was much lower. The rhizome biomass (and length) of *S. filiforme*, in contrast, was considerably reduced in the grazing plots (Table 4, Fig. 3).

Halodule wrightii was virtually absent at Puerto Morelos, and differences between grazing plots and ungrazed areas were insignificant, but at Akumal this species was more abundant, and its belowground rhizome biomass and length even increased a little (although not significantly) in the grazing plots, despite a considerable decrease in leaf biomass (Table 4, Fig. 3). Leaf widths (or diameters) were lower in the grazing plots than in the control areas (except for *H. wrightii* at Puerto Morelos).

Patterns of rotational grazing

At Puerto Morelos, the turtle-grazing plots had clearly defined borders (Fig. 2). The turtles initiated the opening up of small areas (1 to 3 m in transect length), and we observed that the turtles, when preparing a new grazing area, cropped all plants

Table 3. Average values (\pm SD) of nutrient contents in the new-growth sections of *Thalassia testudinum* and *Syringodium filiforme* leaves in grazed and ungrazed (control) areas at Puerto Morelos (December 2011) and Akumal (January 2012) and the results of *t*-tests. n does not always correspond with that from Table 2 because sample size was insufficient for analysis. After Bonferroni correction, $\alpha = 0.033$ for the *t*-tests of the 3 parameters of each species. Relative change: difference of the value in grazing plots respective to controls. nd = not determined, ns = not significant

	n	Control Value	n	Grazed Value	Relative change	<i>t</i>	<i>p</i>
PUERTO MORELOS							
<i>Thalassia testudinum</i>							
Carbon content (% dry wt)	6	37.36 \pm 0.93	5	37.77 \pm 0.76	ns	−0.789	0.451
Nitrogen content (% dry wt)	6	1.83 \pm 0.18	5	2.43 \pm 0.30	32.8 %	−3.941	0.007
Phosphorus content (% dry wt)	6	0.14 \pm 0.01	5	0.16 \pm 0.03	ns	−1.832	0.128
C:N ratio	6	24.0 \pm 2.1	5	18.4 \pm 2.3	nd	nd	nd
C:P ratio	6	712.5 \pm 50.6	5	626.4 \pm 104.3	nd	nd	nd
N:P ratio	6	29.9 \pm 3.3	5	34.3 \pm 5.5	nd	nd	nd
<i>Syringodium filiforme</i>							
Carbon content (% dry wt)	5	37.40 \pm 0.54	4	38.07 \pm 2.19	ns	−0.596	0.590
Nitrogen content (% dry wt)	5	1.76 \pm 0.09	4	2.04 \pm 0.311	ns	−1.893	0.176
Phosphorus content (% dry wt)	5	0.11 \pm 0.01	4	0.12 \pm 0.02	ns	−0.811	0.495
C:N ratio	5	24.8 \pm 1.2	4	22.0 \pm 2.1	nd	nd	nd
C:P ratio	5	882.9 \pm 101.6	4	837.3 \pm 138.3	nd	nd	nd
N:P ratio	5	35.6 \pm 3.0	4	38.5 \pm 9.1	nd	nd	nd
AKUMAL							
<i>Thalassia testudinum</i>							
Carbon content (% dry wt)	5	39.26 \pm 1.6	6	40.21 \pm 0.85	ns	−1.213	0.272
Nitrogen content (% dry wt)	5	2.34 \pm 0.17	6	3.05 \pm 0.25	30.3 %	−5.588	0.001
Phosphorus content (% dry wt)	5	0.12 \pm 0.02	6	0.16 \pm 0.02	33.3 %	−3.222	0.010
C:N ratio	5	19.9 \pm 0.9	6	15.5 \pm 1.1	nd	nd	nd
C:P ratio	5	918.1 \pm 225.8	6	653.8 \pm 113.9	nd	nd	nd
N:P ratio	5	46.7 \pm 13.6	6	42.3 \pm 7.3	nd	nd	nd
<i>Syringodium filiforme</i>							
Carbon content (% dry wt)	6	39.83 \pm 2.73	3	40.82 \pm 1.64	ns	−0.568	0.521
Nitrogen content (% dry wt)	6	2.35 \pm 0.37	3	2.86 \pm 0.50	ns	−1.557	0.214
Phosphorus content (% dry wt)	6	0.11 \pm 0.04	2	0.13 \pm 0.02	ns	−1.031	0.359
C:N ratio	6	20.1 \pm 2.4	3	16.9 \pm 2.1	nd	nd	nd
C:P ratio	6	1013.5 \pm 365.8	2	783.3 \pm 107.3	nd	nd	nd
N:P ratio	6	51.7 \pm 22.3	2	43.1 \pm 4.2	nd	nd	nd

without ingesting the (old) plant tissue, which drifted away. Some of these newly opened areas were abandoned shortly afterwards and were only obvious for 1 to 4 mo (ephemeral or short-term grazing). Most of these initiated plots became larger in the following months until attaining a more or less fixed size after several months, and they were browsed by the turtles for at least 12 mo to over 2 yr (long-term plots; Table 5, Fig. 4). Several long-term grazing plots were abandoned by the turtles during the study, which was obvious because of the absence of shoots with bite scars. These areas recovering from grazing showed sparser seagrasses than the ungrazed sites (Fig. 2). At Akumal, the grazed and ungrazed areas alternated within one to several months, and their boundaries were not as clearly delimited as at Puerto Morelos (Fig. 2). The sizes of the plots also varied between observation times; single plots split up into 2 to 4 sep-

arate plots separated by ungrazed areas the following time, or several small grazing plots fused to become a single plot. The grazing plots attained a larger size at Akumal than at Puerto Morelos (Table 5), and in addition, the total areal cover of grazing plots was much larger at Akumal than at Puerto Morelos (Fig. 4).

Effects of grazing on the seagrass communities

The study area at Puerto Morelos had visible grazing plots with clearly defined limits. The abundance of the seagrass *T. testudinum* decreased after the turtles initiated grazing the plots and continued to decrease for several months, after which it remained stable (Fig. 5). *S. filiforme* also decreased in abundance when the turtles started grazing a plot, but it

Table 4. Average values (\pm SD) of biomass of all seagrasses together (total biomass) and of individual seagrass species, with selected morphometric parameters, in ungrazed areas (control) and grazing plots at Puerto Morelos and Akumal and the results of *t*-tests. After Bonferroni correction, $\alpha = 0.025$ for the *t*-tests of the 4 parameters of each species (4 dependent variables, $\alpha = 0.1$ because of small sample size). Relative change: difference of the value in grazing plots respective to controls. nd = not determined, ns = not significant

	n	Control Value	n	Grazed Value	Relative change	<i>t</i> -test <i>t</i>	<i>p</i>
PUERTO MORELOS							
Total green foliar biomass (g m ⁻²)	6	134.4 \pm 50.4	6	13.4 \pm 8.1	-90.0%	5.806	0.001
Total belowground biomass (g m ⁻²)	6	972.2 \pm 264.3	6	653.2 \pm 241.1	ns	2.167	0.056
<i>Thalassia testudinum</i>							
Green foliar biomass (g m ⁻²)	6	93.3 \pm 46.5	6	9.2 \pm 7.8	-90.1%	4.372	0.006
% Aboveground/total biomass	6	12.5 \pm 3.9	6	1.6 \pm 0.8	-87.2%	8.36	0.001
Leaf width (mm)	6	10.0 \pm 1.2	6	7.3 \pm 1.9	-27.0%	3.004	0.016
Leaf length (cm)	6	18.1 \pm 3.9	6	3.4 \pm 1.1	-81.2%	nd	nd
Length rhizome (m m ⁻²)	6	96.5 \pm 30.2	6	119.0 \pm 57.5	ns	-0.848	0.422
<i>Syringodium filiforme</i>							
Green foliar biomass (g m ⁻²)	6	40.7 \pm 25.0	6	3.2 \pm 1.4	-92.1%	3.667	0.014
% Aboveground/total biomass	6	9.9 \pm 3.4	6	5.2 \pm 3.0	ns	2.571	0.028
Leaf diameter (mm)	6	1.41 \pm 0.22	6	1.13 \pm 0.17	ns	2.508	0.032
Leaf length (cm)	6	13.8 \pm 5.9	6	5.7 \pm 1.3	-58.7%	nd	nd
Length rhizome (m m ⁻²)	6	146.3 \pm 48.3	6	50.3 \pm 37.6	-65.6%	3.84	0.004
<i>Halodule wrightii</i>							
Green foliar biomass (g m ⁻²)	6	0.4 \pm 0.6	6	1.0 \pm 1.0	ns	nd	nd
% Aboveground/total biomass	2	11.6 \pm 1.7	4	6.0 \pm 2.9	-48.3%	nd	nd
Leaf width (mm)	2	0.99 \pm 0.42	4	1.02 \pm 0.51	4.3%	nd	nd
Leaf length (cm)	2	9.0 \pm 1.2	4	3.6 \pm 0.9	-60.0%	nd	nd
Length rhizome (m m ⁻²)	6	6.2 \pm 12.0	6	44.7 \pm 52.7	ns	nd	nd
AKUMAL							
Total green foliar biomass (g m ⁻²)	8	47.1 \pm 25.01	8	6.6 \pm 1.9	-86.0%	4.567	0.001
Total belowground biomass (g m ⁻²)	8	295.3 \pm 104.8	8	221.0 \pm 87.7	-25.2%	1.548	0.145
<i>Thalassia testudinum</i>							
Green foliar biomass (g m ⁻²)	8	33.8 \pm 25.2	8	2.7 \pm 2.5	-92.0%	3.472	0.004
% Aboveground/total biomass	8	15.1 \pm 3.8	6	1.9 \pm 0.5	-87.4%	8.397	0.001
Leaf width (mm)	8	8.1 \pm 1.1	6	5.7 \pm 1.5	-29.6%	3.448	0.005
Leaf length (cm)	8	12.6 \pm 2.7	6	3.0 \pm 0.9	-76.2%	nd	nd
Length rhizome (m m ⁻²)	8	42.3 \pm 24.3	8	38.3 \pm 25.8	ns	0.300	0.769
<i>Syringodium filiforme</i>							
Green foliar biomass (g m ⁻²)	8	5.9 \pm 3.7	8	1.8 \pm 2.8	-69.5%	2.537	0.024
% Aboveground/total biomass	8	10.8 \pm 4.9	5	6.2 \pm 2.5	ns	1.957	0.076
Leaf diameter (mm)	8	1.20 \pm 0.26	5	0.88 \pm 0.05	-26.7%	2.723	0.020
Leaf length (cm)	8	7.7 \pm 2.6	5	3.3 \pm 1.1	-57.1%	nd	nd
Length rhizome (m m ⁻²)	8	25.5 \pm 15.9	8	14.9 \pm 19.7	-41.6%	2.556	0.025
<i>Halodule wrightii</i>							
Green foliar biomass (g m ⁻²)	8	7.4 \pm 6.3	8	2.1 \pm 2.3	-71.6%	2.530	0.004
% Aboveground/total biomass	8	11.3 \pm 3.2	8	4.0 \pm 0.9	-64.6%	6.007	0.001
Leaf width (mm)	8	1.07 \pm 0.09	8	0.67 \pm 0.13	-37.4%	7.277	0.001
Leaf length (cm)	8	8.5 \pm 1.6	8	2.9 \pm 0.5	-65.9%	nd	nd
Length rhizome (m m ⁻²)	8	129.0 \pm 114.4	8	161.3 \pm 189.0	ns	1.720	0.142

remained stable after this initial decrease (Fig. 5). Meanwhile, the relative abundances of *H. wrightii* and rhizophytic algae increased after 2 and 6 mo, respectively, of grazing (Fig. 5). After the turtles abandoned the plots, during the process of vegetation recovery, the abundance of *T. testudinum* and rhizophytic algae increased after 2 to 4 mo, whereas that of *H. wrightii* decreased after 6 mo (Fig. 5). How-

ever, 8 to 12 mo after the turtles had abandoned the grazing plots, the dominant seagrass *T. testudinum* had not reached abundance levels previous to grazing (Fig. 5).

Total (aboveground and belowground) biomass was considerably lower at Akumal than at Puerto Morelos (Table 4). Also, differences between grazing plots and ungrazed areas were much less marked at

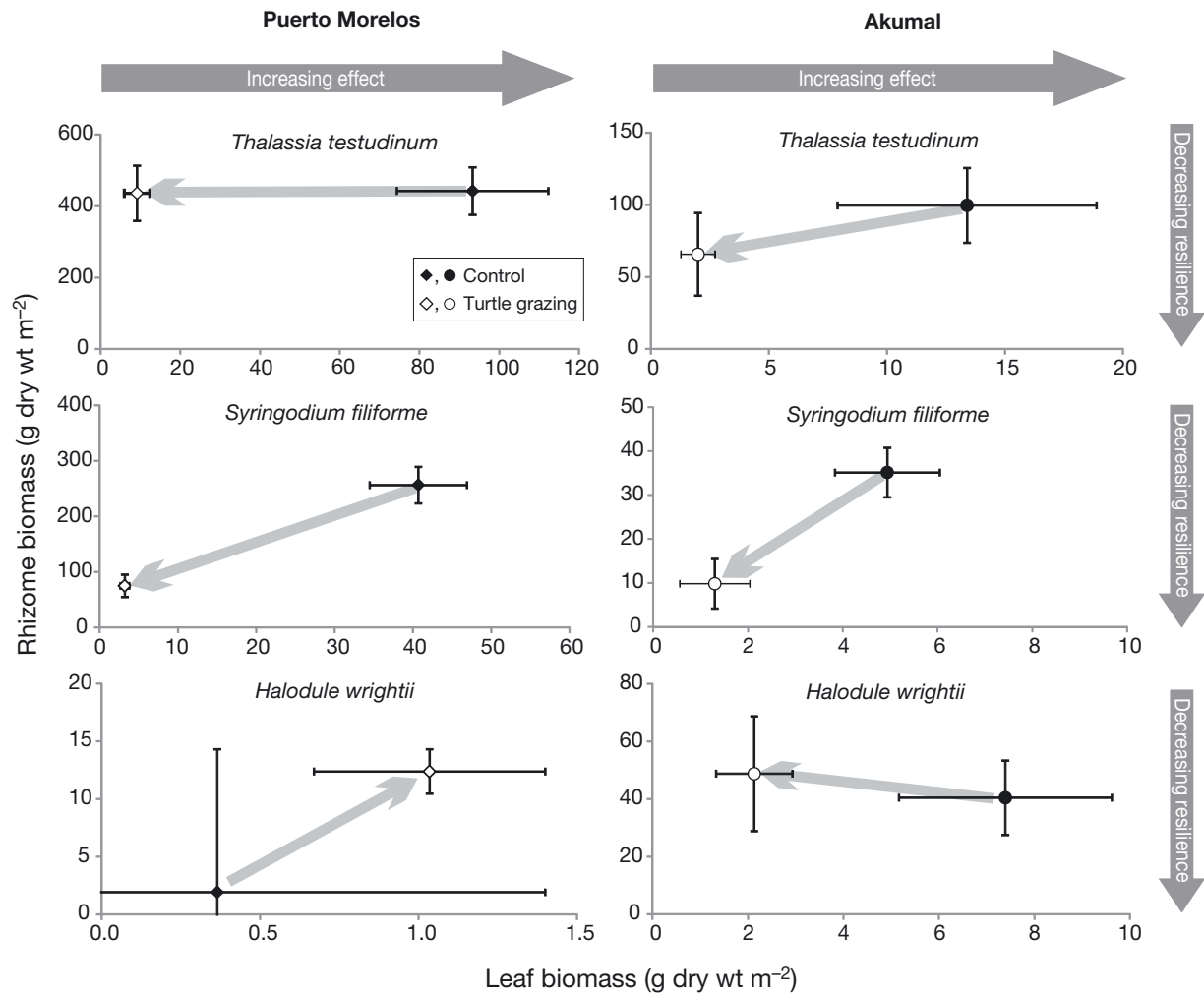


Fig. 3. Leaf biomass of the 3 seagrass species in grazing plots and ungrazed (control) areas vs. biomass of their rhizomes. Loss of photosynthetic leaf tissue from grazing results in loss of belowground tissue, and rhizome biomass can be considered as a parameter of resilience to grazing pressure of the seagrass. The bars represent standard error. The light grey arrows indicate the change in the parameters between control (ungrazed) areas and grazing plots. $n = 6$ at Puerto Morelos, $n = 8$ at Akumal. Note differences in scales of the x and y axes

Table 5. Types of grazing plots registered along permanent transects observed at intervals of 2 to 3 mo from July 2011 until July 2013 at Puerto Morelos (PM) and from August 2011 until September 2012 at Akumal (AK). Grazing plots have short-leaved seagrasses with >40% of the shoots having recent turtle bite-marks. Size is expressed as length along the line transect. Number of grazing plots (n) is not given for Akumal because the grazing plots varied in size (fusing and splitting up) at each observation time, but there were between 2 and 6 grazing plots (avg. 2.8) per 100 m line transect

Plot type	Site	n	Size (m)	Description
Ephemeral	PM	15	1–3	Grazing marks registered only once; may be abandoned attempts to open up new grazing areas
Short-term grazing	PM	4	2–5	Grazing marks observed for 3 to 4 mo
Long-term grazing	PM	17	5–11	Grazing marks observed for at least 13 mo until abandoned or until the end of this study
Intermittent grazing	AK	–	1–75	Grazing marks observed for 1 to 6 mo, but the limits of the grazing plots changed at each observation

Fig. 4. Cover of grazing plots at Puerto Morelos (PM) and Akumal expressed as % grazed sections along 6 permanent 100 m long line transects. For Puerto Morelos, the cover of the types of plots is also given (see Table 5). nd = not determined because not all plot types could be identified; at the beginning of the study, the history of grazing plots was unknown, and at the end of the study, we did not follow up further plot development. Grazing plots at Akumal could not be placed in clear categories because they changed in size and place after 2 to several months

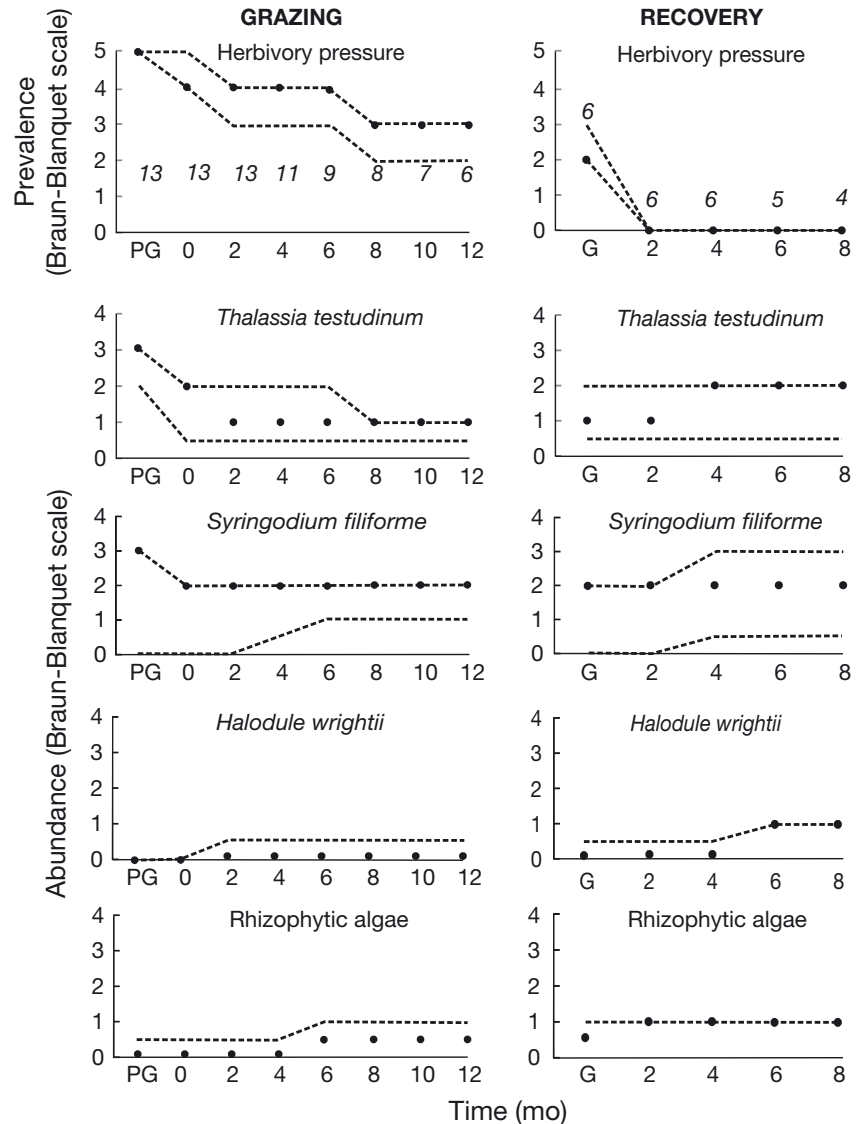
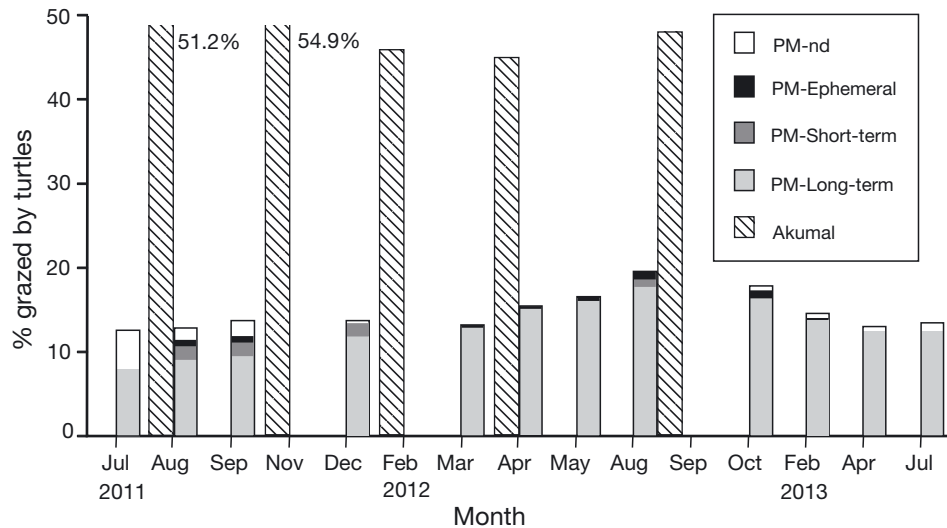


Fig. 5. Changes in grazing prevalence and abundances of the seagrasses and rhizophytic algae (mainly *Rhypocephalus oblongus*, but also *Penicillus* spp., *Udotea* spp. and *Halimeda* spp.) in representative grazing plots (GRAZING: only 12 mo are pictured, but some plots continued to be grazed longer) and plots abandoned by turtles (RECOVERY), obtained from observations of the permanent line transects. The dotted lines indicate minimum or maximum abundance, and the points indicate median values. G = grazed, PG = pregrazing. The point legends in the graphs of herbivory pressure indicate the number of observed patches. See Table 1 for Braun-Blanquet scale

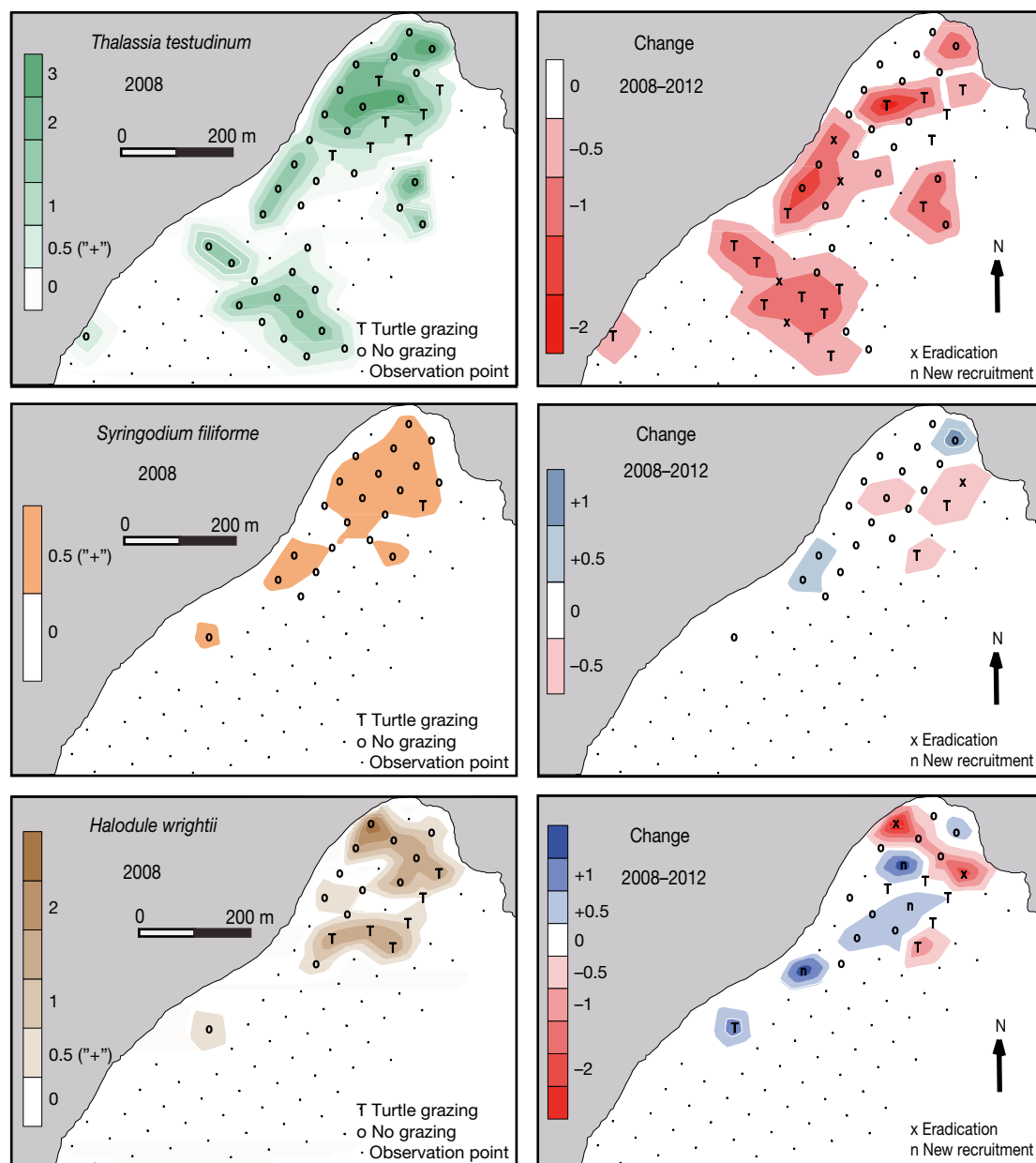


Fig. 6. Abundance (Braun-Blanquet scale; see Table 1) of the seagrasses in Akumal Bay, Mexico, in 2008 and changes in their abundance from 2008 until 2012

Akumal than at Puerto Morelos. In 2008, the seagrass bed at Akumal was dominated by *T. testudinum*, with *S. filiforme* and *H. wrightii* being less abundant (Fig. 6). In 2012, the abundance of *T. testudinum* was reduced, and grazing areas (marked by 'T' in Fig. 6) were more frequent. The seagrass species *H. wrightii*, in contrast, increased in abundance and also colonized new areas (Fig. 2). The population of *S. filiforme* apparently is in equilibrium, as the areas of reduction and increase were approximately equal (Fig. 6)

DISCUSSION

The principal benefit for turtles of cultivation grazing is an increased nitrogen content in the leaves of *Thalassia testudinum*. In the plots exposed to grazing ≥ 4 mo, the leaves of *T. testudinum* were enriched in nitrogen compared to adjacent ungrazed areas. Fourqurean et al. (2010) suggested that the difference in the amount of nitrogen in leaves from grazed vs. ungrazed areas could be a consequence of the accumulation of old leaves with low nutrient content

in plots without browsing. But in this study, we only analyzed the nitrogen content in the new-growth sections of both grazed and ungrazed areas, and nitrogen was higher in the leaves from the first area, suggesting that persistent cropping indeed increases the nutritional quality of the leaves. Primary productivity of the seagrasses in the grazing plots decreased at Puerto Morelos. At Akumal, where grazing intensity was high, primary productivity was equally low in both ungrazed (control) and grazed areas (Table 4).

The seagrass species were not affected to the same degree by turtle grazing (Fig. 3). *T. testudinum* maintained its belowground biomass after at least 4 mo of continuous grazing, whereas *Syringodium filiforme* lost a substantial portion of belowground tissue, suggesting that *T. testudinum* resisted short-term grazing better than *S. filiforme*. *S. filiforme* most likely lost belowground biomass because it has thinner rhizomes and therefore less carbohydrate reserves to compensate for reduced photosynthesis when its leaves are removed. However, *T. testudinum* most likely will also eventually lose belowground tissues at increasing or long-term grazing pressure, which is indicated by the lower (aboveground and belowground) biomass of this species at Akumal than at Puerto Morelos (Fig. 3). *Halodule wrightii*, in contrast, had a slightly increased belowground biomass in grazing plots and most likely maintained its biomass through colonization. This is supported by the increasing abundance of this species at Puerto Morelos (Table 4, Fig. 3). *H. wrightii* is an early seral species and can attain high rhizome elongation rates ($80.9 \text{ cm yr}^{-1} \text{ apex}^{-1}$, Gallegos et al. 1994) and rapidly colonize newly opened gaps (Bell et al. 1999). Simulated grazing experiments in other areas also revealed species-specific resilience to clipping. In Moreton Bay, Australia, *Halophila ovalis* resisted clipping better than *Zostera capricorni*, and the seagrass *Cymodocea serrulata* was least resilient (Kuiper-Linley et al. 2007). Similar studies in the Lakshadweep Archipelago, India, showed that *Cymodocea rotundata* resisted clipping better than the more long-lived and robust *Thalassia hemprichii* (Kelkar et al. 2013).

Under a moderate grazing regime, as registered at Puerto Morelos (<20% of the area was grazed), the turtles grazed persistently in specific areas (grazing plots) for a considerable period. Such persistent grazing in plots is considered typical for the Caribbean and has been described by Bjorndal (1980) in the Bahamas and Zieman et al. (1984) at St. Croix, US Virgin Islands. But at Puerto Morelos, the turtles grazed in the plots for much longer (13 mo to >2 yr)

than expected, as Bjorndal (1980) found that turtles kept grazing plots up to 12 mo. However, the findings of this study are more consistent with a more recent study by (Moran & Bjorndal 2005) in which *T. testudinum* maintained growth after 16 mo of simulated grazing (clipping). After the turtles had abandoned a grazing plot, we never observed their return to these plots again. Plots recovering from grazing did not have the well-developed seagrass community of ungrazed areas, and the leaves of *T. testudinum* tended to be thinner and shorter. Recovery of the seagrass vegetation in these patches to pre-grazing community structure and composition lasted >12 mo and exceeded the observation time of this work. The turtles at Akumal maintained clearly defined grazing plots until ~2005 (B. I. van Tussenbroek pers. obs.; see also photos taken in 2002 at <http://tortugawatch.com/notations2002.htm>). But at the time of the present study, between 47 and 55% of the seagrass was grazed; the borders of the grazing plots were not clearly defined, and they were only maintained for 2 to several months. In 2005, >90 turtles of different sizes were counted (Maldonado Cuevas et al. 2006), and the turtle population has increased since (M. A. Maldonado Cuevas pers. comm.). Assuming a population of 100 grazing turtles in 2012 at an average weight of $50 \text{ kg turtle}^{-1}$ and an intake of 0.74 to $1.77 \text{ kg dry wt } T. testudinum \text{ kg}^{-1} \text{ turtle yr}^{-1}$ (from Bjorndal et al. 2000), the turtles require 3700 to 5850 kg dry wt foliar tissue of *T. testudinum* annually. The total seagrass area at Akumal is ~5 ha, but considering a seagrass recovery period of $\geq 1 \text{ yr}$, only ~2.5 ha (or less) can be grazed at the same time, allowing for rotation. In 2012, an area of 2.5 ha produced ~4198 kg dry wt, assuming an average foliar productivity for *T. testudinum* and *H. wrightii* of $0.8 \text{ g dry wt m}^{-2} \text{ d}^{-1}$ (we observed that the turtles avoided consumption of *S. filiforme* in this bay). According to these estimates, the productivity of the seagrasses has reached the carrying capacity to feed 100 turtles. This is the plausible reason why the turtles graze plots which are still recovering from past grazing, thereby not allowing for full recovery of the seagrasses and resulting in a low primary productivity of the community. In seagrass meadows in the US Virgin Islands that were reduced in size by boat traffic, Williams (1988) observed that large number of turtles ate all of the *T. testudinum* without creating distinct grazing plots.

Turtle grazing may cause shifts in specific community composition because of the differential resilience to grazing of the seagrass species. For example, the shorter-lived, early successional species *C. rotun-*

data replaced the more long-lived, robust *T. hemprichii* when grazed by turtles in India (Kelkar et al. 2013), and *Halophila ovalis* replaced *Z. capricorni*, *C. rotundata* and *C. serrulata* after experimental cropping in Queensland, Australia (Aragones & Marsh 2000). However, changes in species composition depend on local settings, and Aragones & Marsh (2000) did not find changes in species composition in *Halodule uninervis* beds, despite the nearby presence of the faster-growing *H. ovalis*. At Puerto Morelos, continuous grazing resulted in a seagrass community shift towards a higher relative dominance of the colonizing seagrass species *H. wrightii* and also rhizophytic algae in plots that were grazed continuously over longer periods (Fig. 5). These plants probably benefitted from reduced abundance of the dominant *T. testudinum* from grazing, because its full-grown leaves cause substantial shading (Enríquez & Pantoja-Reyes 2005) and *T. testudinum* is a superior competitor for scarce nutrients (Williams 1990, Rose & Dawes 1999, Davis & Fourqurean 2001). Such herbivore-induced species replacement caused by interference in competitive interactions has also been reported in terrestrial grasslands (Anderson & Briske 1999). Although *S. filiforme* was very susceptible to grazing (see above), and its abundance reduced immediately after opening up of the plots at Puerto Morelos, it remained constant afterwards, even though the turtles returned to the plots (Fig. 5). *S. filiforme* possibly persisted in the grazing plots despite being intolerant to grazing pressure, because we observed that the turtles usually avoided eating this seagrass species. However, the turtles grazed this seagrass occasionally, possibly by accident. This might explain why *S. filiforme* leaves were shorter in the grazed areas than in the ungrazed areas (Table 4), but yet another reason could be that the higher *T. testudinum* canopies in the ungrazed areas protected the *S. filiforme* leaves from breaking (Williams 1987). At Akumal, selective grazing of the dominant *T. testudinum*, and its unlikely recovery because of the increasing density of grazing turtles, has driven a gradual species replacement of the whole seagrass bed towards a higher dominance of the faster-growing, early seral seagrass *H. wrightii* (Fig. 5).

Although the rotational or cultivation grazing observed at Puerto Morelos had a negative effect on the aboveground community biomass in the grazing plots, increased diversity was observed at the community or landscape levels. Grazed and ungrazed areas have different structures (short and long leaves, respectively), and the grazing plots created gaps for the colonization of the faster-growing seagrass species *H.*

wrightii and rhizophytic algae (Fig. 5). Thus, the overall seascape was more diverse when frequented by grazing turtles. But at Akumal, where the turtles had reached a critical density, a more homogeneous community emerged, with an overall lower seagrass biomass (Table 4) and a higher prevalence of faster-growing species (Figs. 2 & 6).

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