Vol. 564: 29–45, 2017
doi: 10.3354/meps11986

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published February 3

Manatee grazing impacts on a mixed species seagrass bed

Lynn W. Lefebvre[1,*], Jane A. Provancha[2], Daniel H. Slone[1], W. Judson Kenworthy[3]

[1]US Geological Survey, Wetland and Aquatic Research Center, Gainesville, Florida, 32653 USA
[2]InoMedic Health Applications, Inc., Kennedy Space Center, Florida 32899, USA
[3]National Oceanic and Atmospheric Administration, National Ocean Service, Beaufort Laboratory, Beaufort, North Carolina 28516, USA

ABSTRACT: The endangered manatee *Trichechus manatus* is one of few large grazers in seagrass systems. To assess the long-term impacts of repeated grazing on seagrasses, we selected a study site within Kennedy Space Center in the northern Banana River, Brevard County, Florida, that was typically grazed by large numbers of manatees in spring. Two 13 × 13 m manatee exclosures and 2 paired open plots of equal size were established at the study site in October 1990. Shoot counts, biomass, and species composition of the co-dominant seagrass species, *Syringodium filiforme* and *Halodule wrightii*, were sampled 3 times per year in all 4 plots between October 1990 and October 1994. We used a Bayesian modelling approach, accounting for the influence of depth, to detect treatment (exclosed vs. open) effects. *S. filiforme* shoot counts, total biomass, and frequency of occurrence significantly increased in the exclosures. By July 1993, mean biomass values in the exclosures (167 g dry wt m^{-2}) greatly exceeded those in the open plots (28 g dry wt m^{-2}). *H. wrightii* decreased in the exclosures by 1994. Initially, both *S. filiforme* and *H. wrightii* responded positively to release from manatee grazing pressure. As *S. filiforme* continued to become denser in the exclosures, it gradually replaced *H. wrightii*. Our findings may be helpful to biologists and managers interested in predicting seagrass recovery and manatee carrying capacity of repeatedly grazed seagrass beds in areas of special significance to manatees and seagrass conservation.

KEY WORDS: Co-dominance · Exclosures · *Halodule wrightii* · Manatee grazing · Seagrass · Species diversity · Species recovery · *Syringodium filiforme*

INTRODUCTION

Sirenians are the largest marine herbivores known to graze on seagrasses (Thayer et al. 1984, Lefebvre et al. 2001, Valentine & Duffy 2006, Marsh et al. 2012). Manatees and dugongs have undoubtedly coevolved with seagrasses over millions of years, and may have been more diverse and abundant than present-day populations (Domning 1981, Domning 2001, Marsh et al. 2012). Today, within their contemporary geographic range, manatees are either absent or in relatively low abundance (Lefebvre et al. 2001) and some marine ecologists have argued they may be functionally extinct with respect to their principal food resources, the seagrasses (Valentine & Duffy 2006).

There are, however, localized aggregations of manatees that exert significant grazing pressure on seagrasses. In Florida, manatees move to natural and artificial warm water refuges (e.g. freshwater springs, power plant effluents) during the winter (Hartman 1979, Packard 1981, Shane 1984, Reynolds & Wilcox 1994, Deutsch et al. 2003). A significant portion of the manatee population on the Altantic coast of Florida migrates seasonally through the Indian River Lagoon (IRL) between Brevard County and south Florida (Deutsch et al. 2003). High densities of grazing manatees in some areas of the IRL have been reported to disturb up to 40 % of the seagrass beds (Packard 1984) and remove 80–96 % of the seagrass leaf biomass (Packard 1984, Lefebvre et al. 1999) and

---

*Corresponding author: llefebvre@usgs.gov

50–67% of the root and rhizome biomass in grazing scars (Lefebvre et al. 1999). In northern Florida, prior to wider summer dispersal, manatee density increases in foraging areas of the northern Banana River (NBR) (Provancha & Provancha 1988, Deutsch et al. 2003). A small-scale experiment (six 2.25 m^2 manatee exclosures) in the NBR showed that manatee feeding significantly reduced the above-ground biomass of *Syringodium filiforme* in as little as 6 wk (Provancha & Hall 1991).

The NBR, Brevard County, Florida, has seasonally high numbers of manatees foraging in extensive mixed-species seagrass beds (Provancha & Provancha 1988, Deutsch et al. 2003). As part of the Kennedy Space Center (KSC), this area has been closed to public boating since 1963, making it one of the largest protected areas of suitable manatee habitat on the Atlantic coast of Florida (Provancha & Provancha 1988). The number of manatees visiting this defacto manatee sanctuary has steadily increased during the past 3 decades; over 1200 manatees were counted in a single survey in the spring of 2014 (Provancha & Provancha 1988, J. A. Provancha unpubl. data).

Two successive harmful phytoplankton blooms in 2011 and 2012 eliminated most of the seagrass coverage in the NBR (St. John's River Water Management District et al. 2012, Phlips et al. 2015). The loss of seagrasses has raised concerns that the localized manatee carrying capacity may be impaired in this and other important feeding areas in the region. As management plans are being developed to mitigate for the large-scale loss of seagrasses, questions also arise as to what effects manatees may have on the distribution, abundance and species composition of naturally recovering and restored populations of seagrasses.

To address some of these questions we analyzed data from a 4 yr exclosure study designed to examine the effects of manatee grazing on species composition, local spatial distribution, shoot density, and above- and belowground biomass of seagrasses in the NBR. Monthly aerial surveys provided information on manatee presence in the NBR during our study, and radio telemetry and observations from a 4 m high tower at the study site provided indirect evidence of potential grazing pressure. The site was a well-documented manatee foraging area consisting of a mixed seagrass community of *Halodule wrightii* and *Syringodium filiforme* (Provancha & Hall 1991), both important species in manatee diets (Packard 1984, Ledder 1986, Lefebvre et al. 1999). Whereas prior manatee grazing studies (Provancha & Hall 1991, Lefebvre et al. 1999) were smaller-scale and shorter-term, the exclosure study we report here was long enough (4 yr) to examine the complex interaction of seasons and interannual variability of seagrasses with the effects of grazing. Additionally, the relatively large size of the exclosures (169 m^2) and large spacing between the treatment plots improved our confidence in interpreting the data by diminishing the potentially confounding effects of clonal integration that smaller plots may experience.

MATERIALS AND METHODS

Study site

The study site was in the NBR (Fig. 1), north of the NASA Causeway (SR 405) in the Merritt Island National Wildlife Refuge and the Kennedy Space Center (KSC). The 0.66 ha site was selected on the basis of manatee distributions observed during aerial

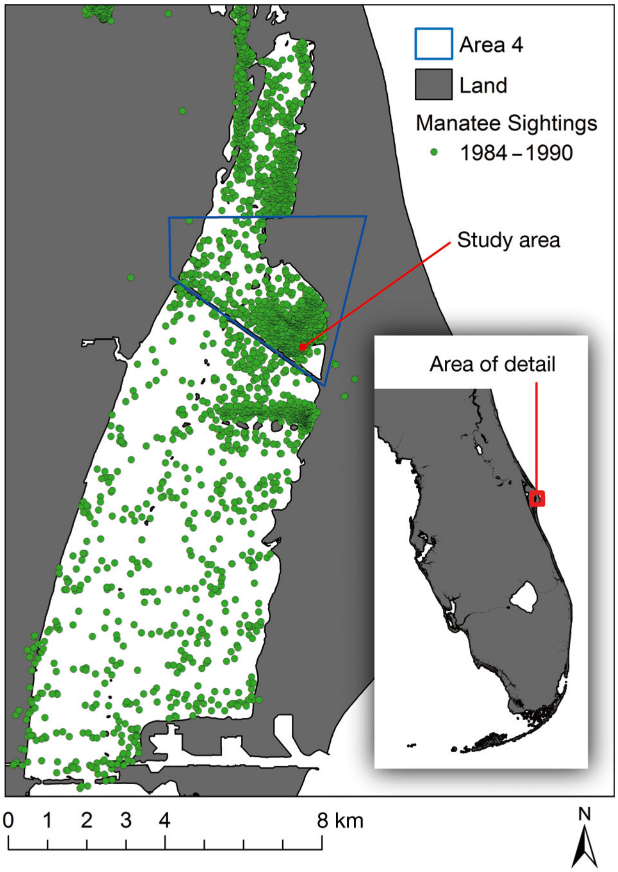

Fig. 1. Location of the study site in the northern Banana River, Brevard County, Florida, USA, showing the locations of manatee sightings from monthly aerial surveys, 1984–1990 and Area 4. Data Source: Kennedy Space Center

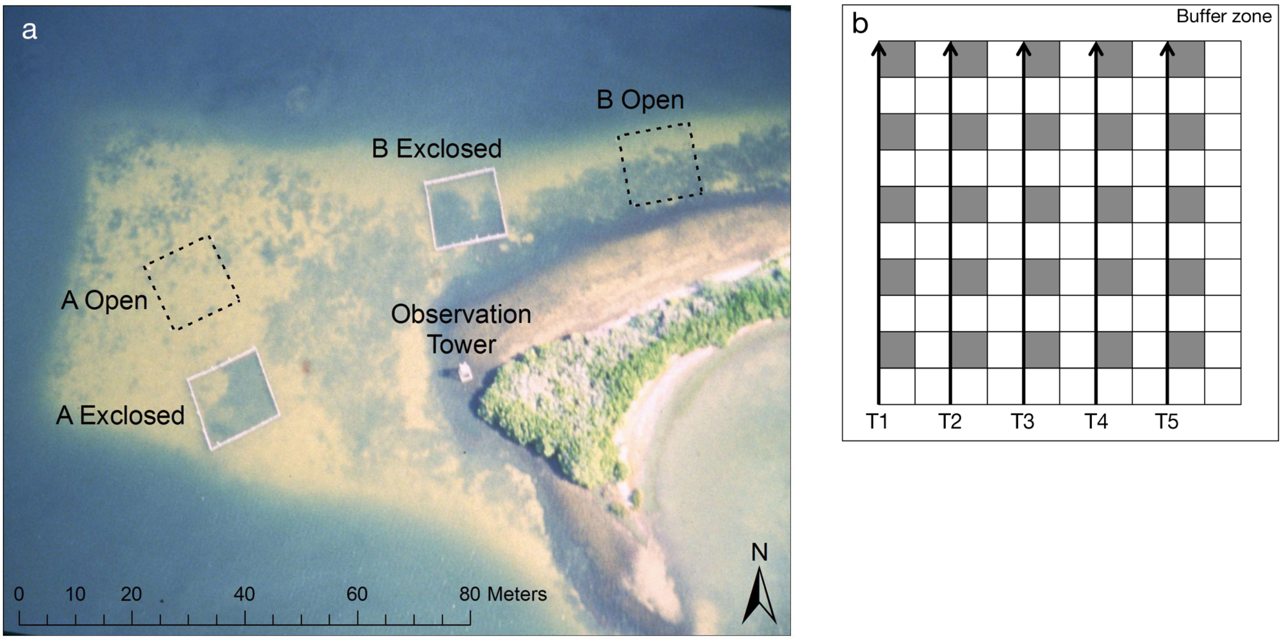

Fig. 2. (a) Locations of exclosures, paired open plots, and observation tower within the study site. Photograph was taken in August 1992, the second year of the study. Area A (including plots A Open and A Exclosed) was the 'shelf' to the west of the observation tower; Area B (including plots B Open and B Exclosed) extended to the north and east of the observation tower (photo credit: authors). (b) Sampling design for determination of species composition in the 4 study plots. The ends of 5 transects were permanently marked (T1–T5). In each of 12 sample periods, the numbers of subquadrats occupied by *Syringodium filiforme* and *Halodule wrightii* were counted in every other 1 m^2 quadrat (shown in gray) on the right of each transect

surveys in spring 1990 (J .A. Provancha unpubl. data) and earlier surveys (1985–1987; Provancha & Provancha 1988). A vegetation survey conducted in March 1990 indicated it was representative of seagrass beds in the NBR; *Syringodium filiforme* and *Halodule wrightii* were abundant (Provancha & Scheidt 2000). An observation tower was installed at 28.5050° N, 80.5905° W in January 1991, approximately mid-way between Areas A and B (Fig. 2a). During our study period, salinity typically ranged from 25–32 ppt and water temperatures ranged from 14°C (winter) to 32°C (summer). Depth ranged from 50–130 cm. See Supplement 1 in the Supplements at www.int-res.com/articles/suppl/m564p029_supp.pdf for further site description.

Experimental design

Treatment and control plots. Our specific objectives were to evaluate the possible effects of manatee grazing on seagrass shoot density, biomass, and species composition, in an area of confirmed and repeated manatee grazing activity. Economic and logistical constraints limited the study to only 2 replicates of the treatment and control plots: 2 exclosed and 2 open. One pair of treatment and control plots was located in Area A and the other in Area B to account for site effects (Fig. 2a). We used a repeated-measures design, sampling shoot density, biomass, and species composition in all 4 plots multiple times over 4 yr.

Exclosures. Each exclosure (13 × 13 m) accommodated a 10 × 10 m interior sampling plot surrounded by a 1.5 m buffer (plots A Exclosed and B Exclosed) (Fig. 2a,b). An open plot of equal size was delineated with PVC poles adjacent to each exclosure (A Open and B Open). The exclosures were constructed on the study site and the corners of the open plots marked in October 1990.

While excluding manatees, the exclosures allowed fish and most other estuarine species to pass freely through them. They were constructed of galvanized steel water pipe (2.5 cm outer diameter), welded to form 3.2 m long panels (4 per side) with horizontal bars approximately 17.8 cm apart. This inter-bar spacing was the maximum possible that would prevent a manatee calf from being entrapped between the bars. Panels were secured to galvanized or stainless steel posts with cable straps and extended approximately 25–50 cm above the water surface. Large alligators *Alligator mississippiensis*, bull sharks

Carcharhinus leucas, and bottle-nose dolphins *Tursiops truncatus* would also likely have been excluded from the ungrazed study plots. Each exclosure had a gate to permit access by investigators.

Aerial surveys and photographs. Systematic aerial surveys were employed to monitor distribution and abundance of manatees at KSC since 1977 following methods described by Provancha & Provancha (1988) and continued monthly during our study. The segment of the aerial survey route that contained our study site was referred to as Area 4 (Fig. 1).

Between October 1990 and August 1993, oblique photographs of our study site were taken by the manatee aerial survey team with a hand-held camera at a height of approximately 150 m to illustrate visual differences in coverage and density among the exclosed and open seagrass plots.

Ground observations. In the spring of 1991 and 1992 (mid-February to mid-May) observers looked for manatees in the study area from the observation tower located between Areas A and B. They recorded all manatees sighted, particularly noting and plotting the movements of those seen in plots A Open and B Open (Fig. 2).

Radio-telemetry. See Supplement 2.

Sampling strategy. Each plot had a sampling area of 100 m^2 (Fig. 2b). All 4 plots were sampled approximately every 4 mo from October 1990, immediately after exclosure construction, through October 1994. Seasons were defined as spring (Feb/Mar), summer (June/July), and fall (Oct/Nov). Samples were either repeated in the same 1 m^2 quadrats (shoot counts and species composition) or were collected randomly (biomass cores). Data on shoot density and species composition were collected in each sampling period except summer 1994 (total = 12), and biomass data were collected in each sampling period through July 1992 and in July 1993 (total = 7).

Shoot counts. Shoots were counted in 5 randomly selected, permanently established 1 m^2 quadrats per 100 m^2 plot. Three corners of each selected quadrat were marked with 2.5 cm diameter PVC stakes and the quadrat frame, divided into 16 subquadrats, was laid down at the same position in every sampling period. When shoot density was relatively high (>50 shoots per 25 cm^2 subquadrat), shoots were counted in 5 randomly selected subquadrats and averaged to determine the shoot count per 1 m^2 quadrat. In these cases, the same 5 subquadrats were counted in every sampling period.

Biomass. Biomass cores (Kenworthy & Schwarzschild 1998) were taken each season through July 1992 at randomly selected locations within each plot (excluding the permanent shoot-count quadrats). Sample sizes were 10 cores per plot in October 1990, Feb 1991, and Oct 1991; 20 per plot in July 1991, February 1992, and July 1992. One year after the last of the 6 seasonal samples (July 1993), we collected a final biomass sample (20 per plot) to examine long-term changes in biomass. Cores were 15 cm in diameter and inserted as deep as necessary to assure recovery of all root and rhizome material (≈20 cm). Core samples were sorted by species, separated into shoot and root + rhizome components, and dried for 48 h or to a constant weight (nearest mg) at 60°C.

Species composition. Species composition (expressed as frequency of occurrence) was sampled on 5 permanently established transects in each plot (Fig. 2b). A 1 m^2 quadrat frame, subdivided into 16 subquadrats, was laid down at every other quadrat position (5 per transect) on each of the 5 transects (25 quadrats per plot). The number of subquadrats per quadrat containing seagrass was recorded, by species, at each location and the number of bare subquadrats was also recorded. Species frequency = number of quadrats (out of 25 per plot) with 0, 1, ..., 16 vegetated subquadrats.

Data analysis

Our primary objective was to detect treatment (exclosed vs. open) effects, while controlling for repeated subsampling effort and environmental and temporal effects on response variables among sampling locations and times. A database was created with all possible temporal and spatial sampling locations represented (i.e. each year, season, quadrat, and core sample location). Field data were filled into this database, and all unsampled locations were left as ‘missing’. Given the low replication, unbalanced data structure and complexity of our analyses, we relied on Bayesian hierarchical linear models to estimate variable responses. Because the sampling locations were selected spatially at random (or systematically for composition) from the possible quadrat locations, we were able to assume a pattern of missingness at random and allow the model to estimate the missing response values (Rubin 1976, Lunn et al. 2012).

Fixed effects (model parameters) were Treatment, Area (A or B), Year (1991–1994), Season (spring, summer, fall) and Depth. Each 1 m^2 quadrat was individually identified and grouped within the repeated-measures framework to appropriately aggregate error and avoid pseudoreplication. Species were modeled separately, as we hypothesized that they would respond differently to grazing, resulting in a shift in species composition. First-order interactions were Treatment × Area and Treatment × Year. A second-order interaction, Treatment × Area × Year, was also included after preliminary modeling indicated that Year had a more significant effect than Season. All other potential interactions were left out to simplify the model. Two response variables (Var) were modeled separately for each seagrass species: shoot counts from the permanent 1 m^2 quadrats (=shoot counts) and total biomass from the randomly selected cores (=biomass). Thus, for each species:

$$\begin{aligned}\text{Var} = \text{Treat} + \text{Area} + \text{Depth} + \text{Year} + \text{Season} \\ + \text{Treat}\times\text{Area} + \text{Treat}\times\text{Year} + \text{Treat}\times\text{Area}\times\text{Year} \\ + \text{Error (Quadrat)}\end{aligned} \qquad (1)$$

Shoot counts and biomass were square-root transformed. Because of the large number of samples with 0 shoots, and since our species composition data truncated at 16 subquadrats, untransformed frequency data were modeled assuming a zero-inflated, right-censored Poisson distribution (Slone et al. 2013). Linear models were implemented in R (Version 3.2.1, R Core Team 2015) using the package BRugs (Version 0.8-3; Thomas et al. 2006), which links R to the software package OpenBugs (Version 3.2.3 rev 1012, Lunn et al. 2009). Means of the response variables, based on the same data as the model, were also calculated.

Water depth was measured to the nearest 5 cm at each of the 25 species-composition sample points in the 4 study plots during the spring 1994 sample period. The Arc-GIS tool Topo to Raster was used to interpolate bathymetry for other sample points in the plots (permanent quadrats and biomass cores). Depths were calibrated to a vertical datum (NAVD-88) at mid-tide stage, using the mangrove edge as 'shoreline,' depth = 0. Because we accounted for water depth in our models, we can assume that any differences in seagrass species response to grazing pressure were caused by factor(s) other than depth.

RESULTS

Differences between exclosed and open plots

Manatee occurrence

Monthly aerial surveys (Fig. 3) and radio telemetry (see Supplement 3) between 1991 and 1994 showed a pattern of greatest relative manatee presence near the study site in spring. A notable exception occurred in 1991 when the highest count was in winter: on 15 January 1991, the monthly survey revealed large numbers of manatees in Area 4 of the NBR (Fig. 3). Manatees also appeared to be in or near the open study plots. On 16 January 1991, an underwater examination of the seagrass beds in both open plots revealed evidence of recent grazing activity (cropped blades and exposed, broken rhizomes) on both *Syringodium filiforme* and *Halodule wrightii*.

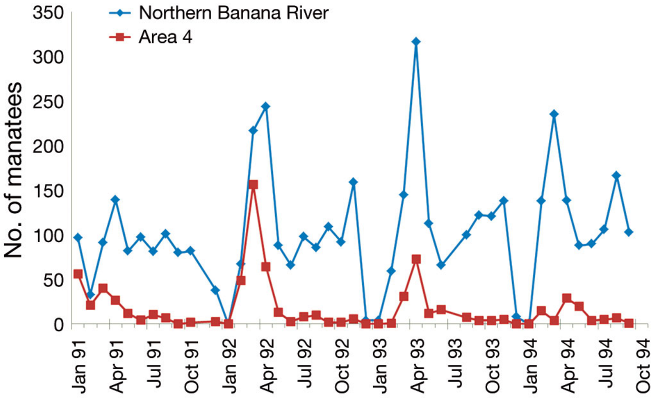

Fig. 3. Total number of manatees sighted in monthly aerial surveys, January 1991–September 1994, in the northern Banana River and in Area 4, where our study site was located. Source: Kennedy Space Center

Between 12 February and 14 May 1991, volunteers spent 104 observation hours (obs h) looking for manatees in the study area. In 1992, volunteers observed the area for 126 h between 16 February and 3 May. Most of the 68 manatee sightings in 1991 occurred between early March and late April, and most of the 108 sightings in 1992 occurred between late February and mid-April. No manatees were observed in Areas A or B Open during February in either year (34.8 obs h in 1991 and 35.0 in 1992), which underscores the unexpected January 1991 observation of feeding manatees.

Manatees were sighted more frequently in Area A than B: 4 times as many in 1991 and 20 times as many in 1992. In March–April 1991, 20 manatee sightings occurred on 8 different days ($\bar{x}$ = 0.30 per obs h) in A Open; in B Open, 5 sightings occurred on 3 days ($\bar{x}$ = 0.07 per obs h). In March–April 1992, 20 manatee sightings occurred on 9 days ($\bar{x}$ = 0.22 per obs h) in A Open and only one sighting occurred in B Open ($\bar{x}$ = 0.01 per obs h). The most commonly observed directional pattern of manatee movement through the study site was from the deeper water north of the shelf across Area A (Fig. 2a).

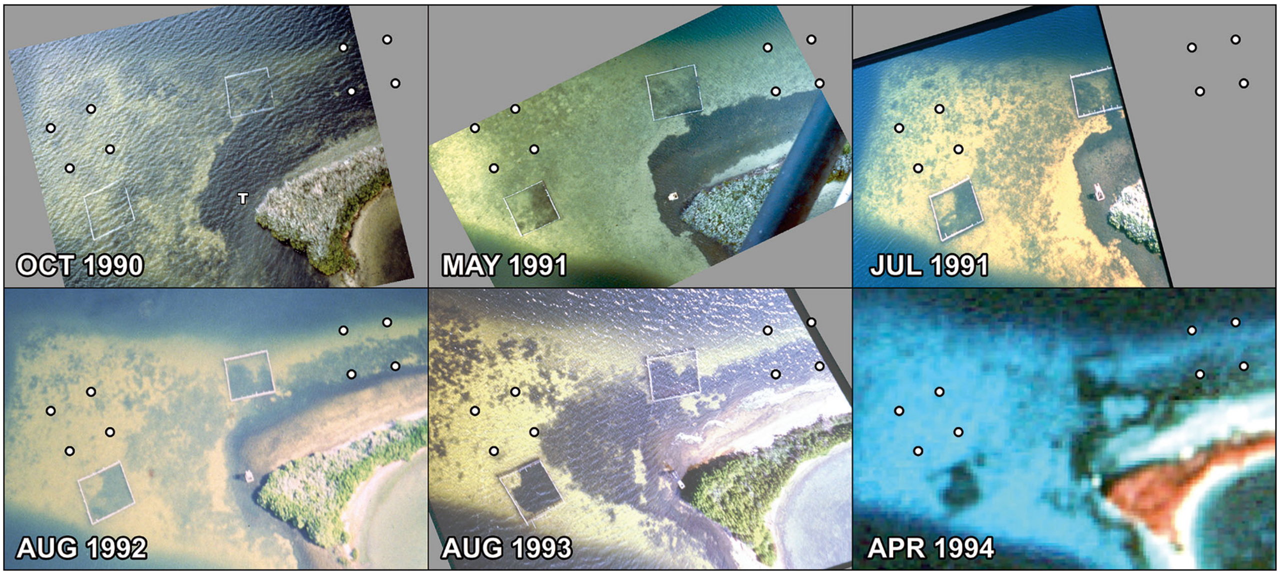

Fig. 4. Aerial images of the study site from October 1990–April 1994. The observation tower can be seen in the photos from July 1991–April 1994; the letter T designates the location of the tower in the October 1990 photo. The white squares are the exclosed plots and the white dots designate the corners of the open plots. B Open is not visible in July 1991. April 1994 is a color infrared satellite image (photo credit: US Geological Survey); all others are georectified oblique photos taken with a hand-held camera during manatee surveys (photo credits: authors; see 'Materials and methods')

Aerial photos

The patchy appearance of the seagrass bed in photos from October 1990 (Fig. 4) was probably the result of recovery following manatee grazing in previous months and years. In April 1991, J. A. Provancha observed a group of manatees feeding between the shore and B Exclosed. The grazing scar is evident in the photos taken from the survey plane in May and July 1991, and the greater density of seagrass inside the exclosures was becoming evident (Fig. 4). Perturbation of the bottom that reduced seagrass coverage was evident by July 1991 in both of the exclosures, particularly in the northwest quadrant of A Exclosed and the northeast quadrant of B Exclosed (Fig. 4). The density of seagrass appeared to be similar in B Open and both A and B Exclosed in the August 1992 photo, whereas A Open appeared almost bare (Fig. 4). By August 1993, seagrass recovery on the outer portion of the shelf, inside the exclosures, and between the exclosures was evident. The April 1994 photo indicates that recent grazing may have occurred on the surrounding shelf (Fig. 4).

Model analysis: *Syringodium filiforme*

Treatment response (Open vs. Exclosed) was significant for *S. filiforme* shoot counts and total biomass, with values in the exclosures exceeding those in the open plots (Table 1). Greater depth negatively

Table 1. Results of model analysis. The fixed effects (model parameters) were Treatment (Open or Exclosed), Area (A or B), Depth, Year, and Season. First-order interactions were Treatment × Area and Treatment × Year vs. 1991, and the second-order interactions were Treatment × Area × Year (1992–1994). Dependent variables were Permanent plot shoot counts and Total biomass (data square-root transformed). Depth shows an inverse relationship with all parameters; greater depth = less seagrass. Syr: *S. filiforme*; Hal: *H. wrightii*; NA: no data; $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$; ns: not significant ($p \geq 0.05$)

Model parameter and interactions	Permanent plot shoot count		Total biomass	
	Syr	Hal	Syr	Hal
Open < Exclosed	***	***	*	ns
Area B < Area A	***	ns	***	***
Depth	***	***	***	***
1992 > 1991	***	***	***	***
1993 > 1991	***	ns	***	***
1994 vs. 1991	94 > 91***	94 < 91***	NA	NA
Summer > Spring	***	***	ns	ns
Fall > Spring	***	ns	*	*
Treat × Area	*	***	ns	*
Treat × 1992	***	**	*	ns
Treat × 1993	***	ns	***	*
Treat × 1994	***	***	NA	NA
Treat × Area × 1992	*	***	ns	ns
Treat × Area × 1993	***	***	***	***
Treat × Area × 1994	***	*	NA	NA

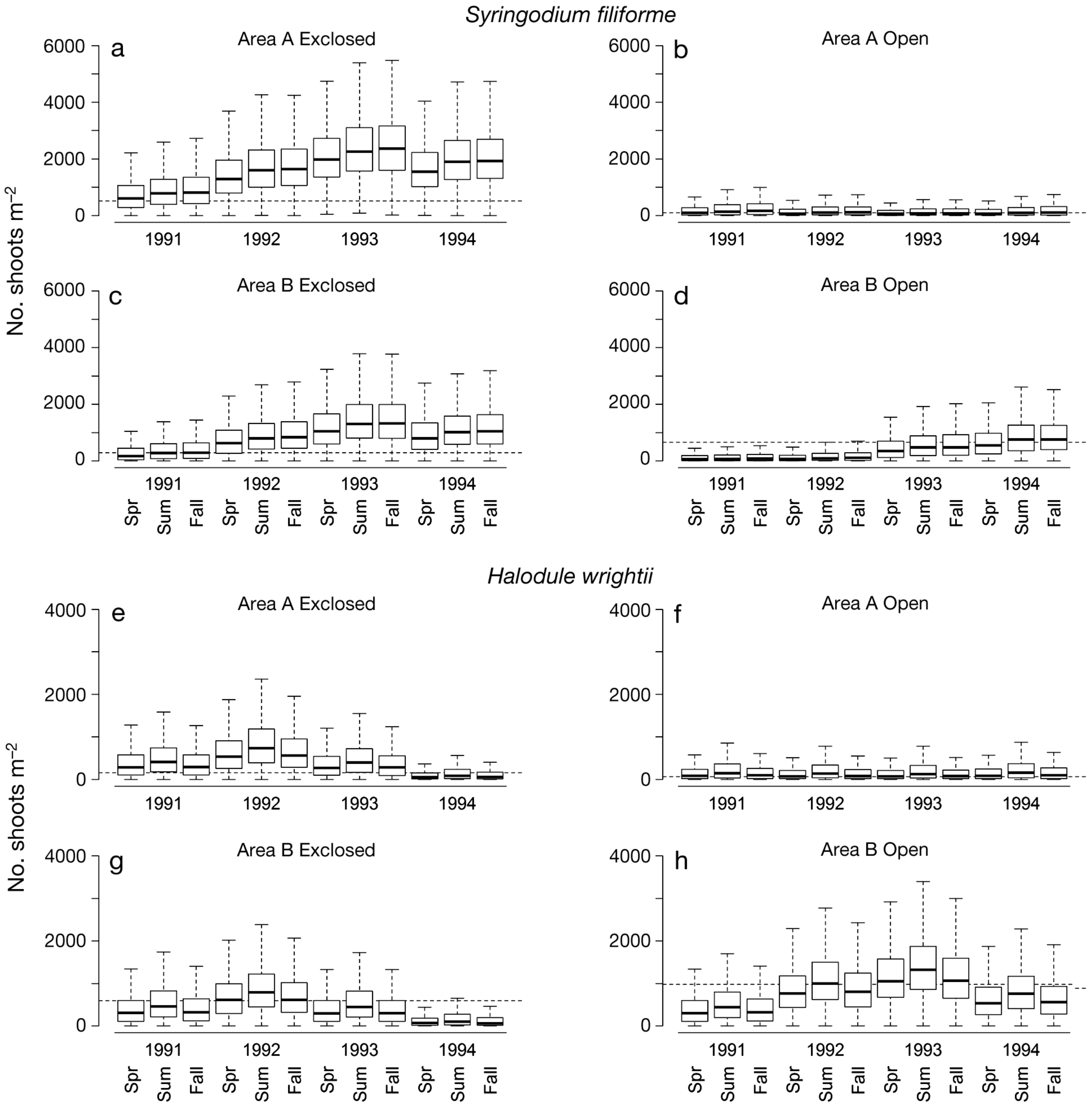

Fig. 5. (a–d) *Syringodium filiforme* and (e–h) *Halodule wrightii* shoot counts in permanent 1 m^2 quadrats by sampling period, treatment (exclosed or open), and area (A or B). Dashed horizontal lines indicate median values at the start of the study in fall 1990. Boxplots show interquartile range and median; whiskers are 1.5× interquartile range

impacted both variables and both were significantly lower overall in Area B than A (Table 1). Shoot counts (1992–1994) and total biomass (1992 and 1993) increased annually in the exclosures and were significantly greater than in 1991 (Table 1, Figs. 5a,c & 6a,c). *S. filiforme* shoot counts were higher in summer and fall than in spring, and biomass was higher in fall than in spring (Table 1, Figs. 5a–d & 6a–d).

The significant Treatment × Year interaction (Table 1) reflects the increasing trend in the response variables in the exclosures through 1993 (Figs. 5a,c & 6a,c). The Treatment × Area × Year interaction was significant for both variables in 1993 and 1994 (Table 1) because their responses were different in the open plots: relatively stable in A Open and upward in B Open (Figs. 5b,d & 6b,d).

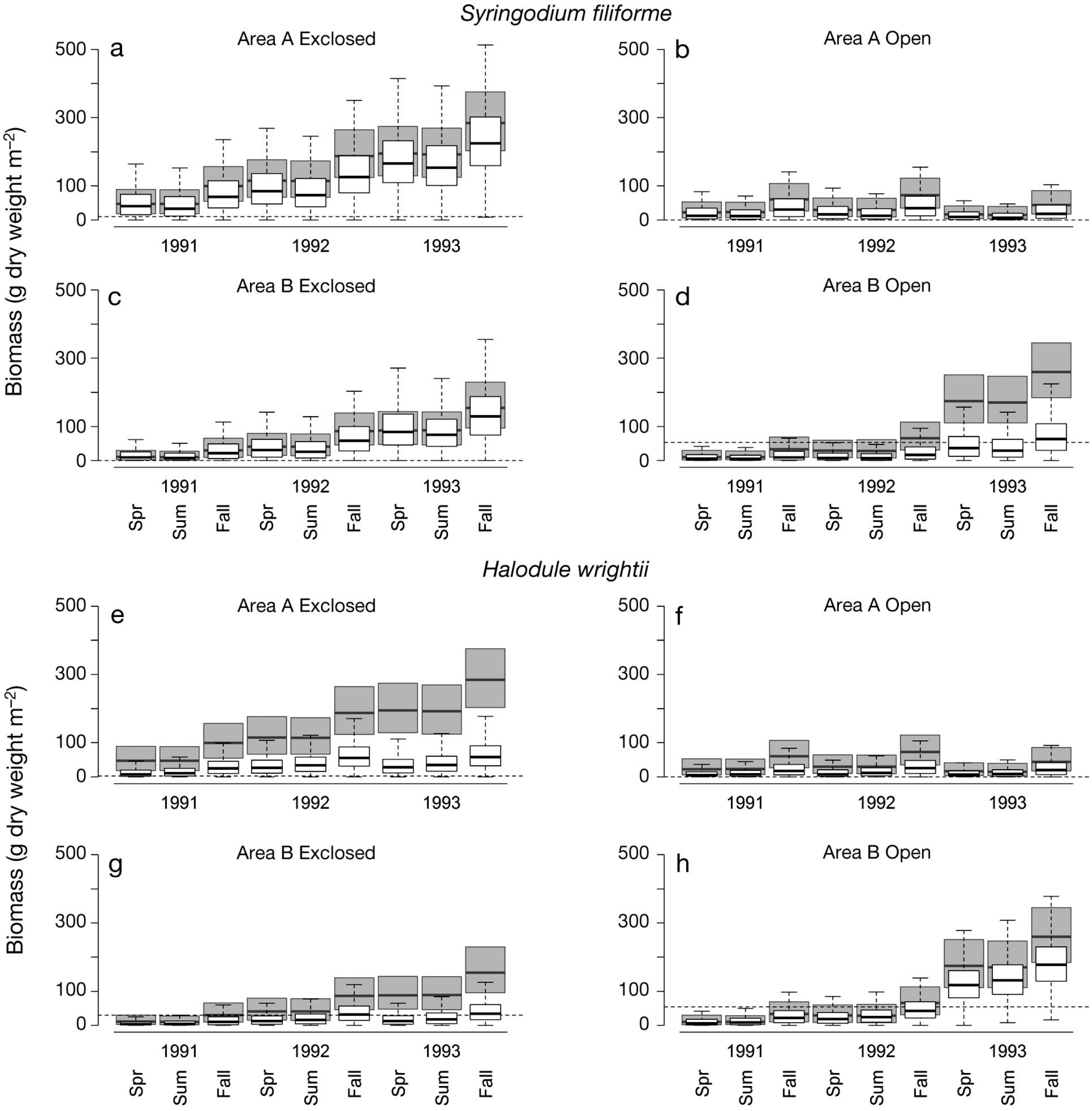

Fig. 6. (a−d) *Syringodium filiforme* and (e−h) *Halodule wrightii* biomass (shoots + rhizomes) by sampling period, treatment (exclosed or open), and area (A or B). Dashed horizontal lines indicate median values at the start of the study in fall 1990. Boxplots show interquartile range and median; whiskers are 1.5× interquartile range. White boxes and whiskers show *S. filiforme* or *H. wrightii* values and gray boxes show total seagrass biomass (*S. filiforme* + *H. wrightii*)

Model analysis: *Halodule wrightii*

Model results for *H. wrightii* differed from those for *S. filiforme*. Overall, *H. wrightii* biomass was not significantly different between the exclosed and open plots, as it was for *S. filiforme* (Table 1). Like *S. filiforme*, treatment response was significant for *H. wrightii* shoot counts and depth had a significant negative impact on all *H. wrightii* variables. However, the pattern of interannual differences for *H. wrightii* variables contrasted with the pattern for *S. filiforme* in the exclosures (Table 1, Figs. 5 & 6).

Halodule wrightii shoot counts in the exclosures were significantly higher in 1992 than in 1991, not significantly different or lower in 1993 than in 1991, and significantly lower in 1994 than in 1991 (Table 1, Fig. 5e,g). *H. wrightii* biomass was higher in 1993 than in 1991; however, Treatment × Area × 1993 was

Table 2. Means of Permanent plot shoot counts, Total biomass by species, Total seagrass biomass, and Occupied subquadrats, by Year and Treatment (EX = exclosed, OP = open) and Species. Fall 1990 values represent conditions at the start of the study; 1991–1993 values were from summer sample periods; 1994 values were from the spring sample period (sampling was not conducted in summer 1994). Total biomass = shoots + rhizomes + roots; Total seagrass biomass = *Syringodium filiforme* + *Halodule wrightii*. NA: no data; Syr: *S. filiforme*; Hal: *H. wrightii*

Season	Year	Treatment	Perm plot shoot count (shoots m^{-2})		Total biomass (g dry wt m^{-2})		Total seagrass biomass (g dry wt m^{-2})	Occupied subquadrats (out of 16)	
			Syr	Hal	Syr	Hal	Syr + Hal	Syr	Hal
Fall	1990	EX	470.7	455.4	25.6	17.7	43.3	11.4	12.8
Fall	1990	OP	454.4	536.0	28.1	32.4	60.4	12.1	11.9
Summer	1991	EX	788.5	636.5	27.1	21.7	48.7	13.1	12.3
Summer	1991	OP	108.2	338.6	9.3	10.7	20.0	8.6	10.0
Summer	1992	EX	1353.9	1247.7	76.6	54.0	130.7	13.2	13.2
Summer	1992	OP	78.1	512.6	8.8	22.4	31.2	6.7	10.0
Summer	1993	EX	2581.3	873.7	166.6	53.4	220.1	12.8	11.4
Summer	1993	OP	453.1	1294.1	28.2	92.3	120.4	7.2	9.6
Spring	1994	EX	2158.1	97.2	NA	NA	NA	12.5	8.6
Spring	1994	OP	304.6	394.2	NA	NA	NA	7.5	11.8

also significant (Table 1). In both the exclosures and in A Open, the biomass response curve flattened in 1992 (Fig. 6e,f,g), whereas *H. wrightii* biomass in B Open trended strongly upward in 1993 (Fig. 6h). B Open was primarily responsible for the greater density (1993 and 1994) and biomass (1993) of *H. wrightii* in the open than in the exclosed plots (Figs. 5h & 6h).

Total biomass was significantly lower overall in Area B than A (Table 1). The Treatment × Area interaction was significant for both *H. wrightii* variables (Table 1), because B Open values tended to trend upward and were higher than in the other 3 plots (Figs. 5e–h & 6e–h). There were no consistent seasonal trends for *H. wrightii,* possibly because the treatment (exclosure) response changed over time (first upward, then downward) and masked seasonal influences (Table 1). The higher fall biomass and higher spring occurrence of *H. wrightii* in our study may reflect cumulative recovery from manatee grazing in the previous spring.

Mean seagrass values

We present variable means by treatment and year (Table 2) to show initial experimental conditions and to more readily compare our results with those of other studies. At the start of the study in fall 1990, *S. filiforme* and *H. wrightii* mean shoot densities, total biomass (by species and combined), and number of occupied subquadrats were similar (Table 2). By summer 1992, *S. filiforme* in the exclosures was 17.3× denser in the permanent plots and 8.7× greater in biomass than in the open plots (Table 2). Total seagrass biomass (*S. filiforme* + *H. wrightii*) was 4× greater in the exclosures than the in the open plots (Table 2). By July 1993, mean *S. filiforme* biomass values in the exclosures (167 g dry wt m^{-2}) was 6× greater than in the open plots (28 g dry wt m^{-2}); however total seagrass biomass was only 1.8× higher in the exclosures (220 g dry wt m^{-2}) than in open plots (120 g dry wt m^{-2}) because of the relatively high *H. wrightii* biomass in the open plots (almost 3× the *H. wrightii* biomass in fall 1990) (Table 2). *H. wrightii* density and biomass tended to be higher in the exclosures relative to the open plots in 1991 and 1992, but lower in 1993 and 1994 (no data for biomass in 1994) (Table 2).

Mean number of subquadrats with *S. filiforme* and *H. wrightii* started at similar levels (11.4 and 12.8, respectively) in both the exclosed and open plots (Table 2). *S. filiforme* occurred in a relatively large number of subquadrats (range 13.1–12.5 between summer 1991 and spring 1994) in the exclosed plots, and declined in the open plots (to 6.7 subquadrats by summer 1992) (Table 2). Mean number of subquadrats occupied by *H. wrightii* in the exclosed plots was relatively high in 1991 and 1992 (12.3 and 13.2, respectively) and declined in 1993 and 1994 (11.4 and 8.6, respectively). *H. wrightii* occurrence in the open plots was relatively stable, ending in 1994 with almost the same mean value as at the start (11.9 and 11.8, respectively) (Table 2).

Seagrass frequency

S. filiforme frequency in A Exclosed increased from an average of 12 to 20 quadrats with 16 vegetated subquadrats (the maximum possible) between fall

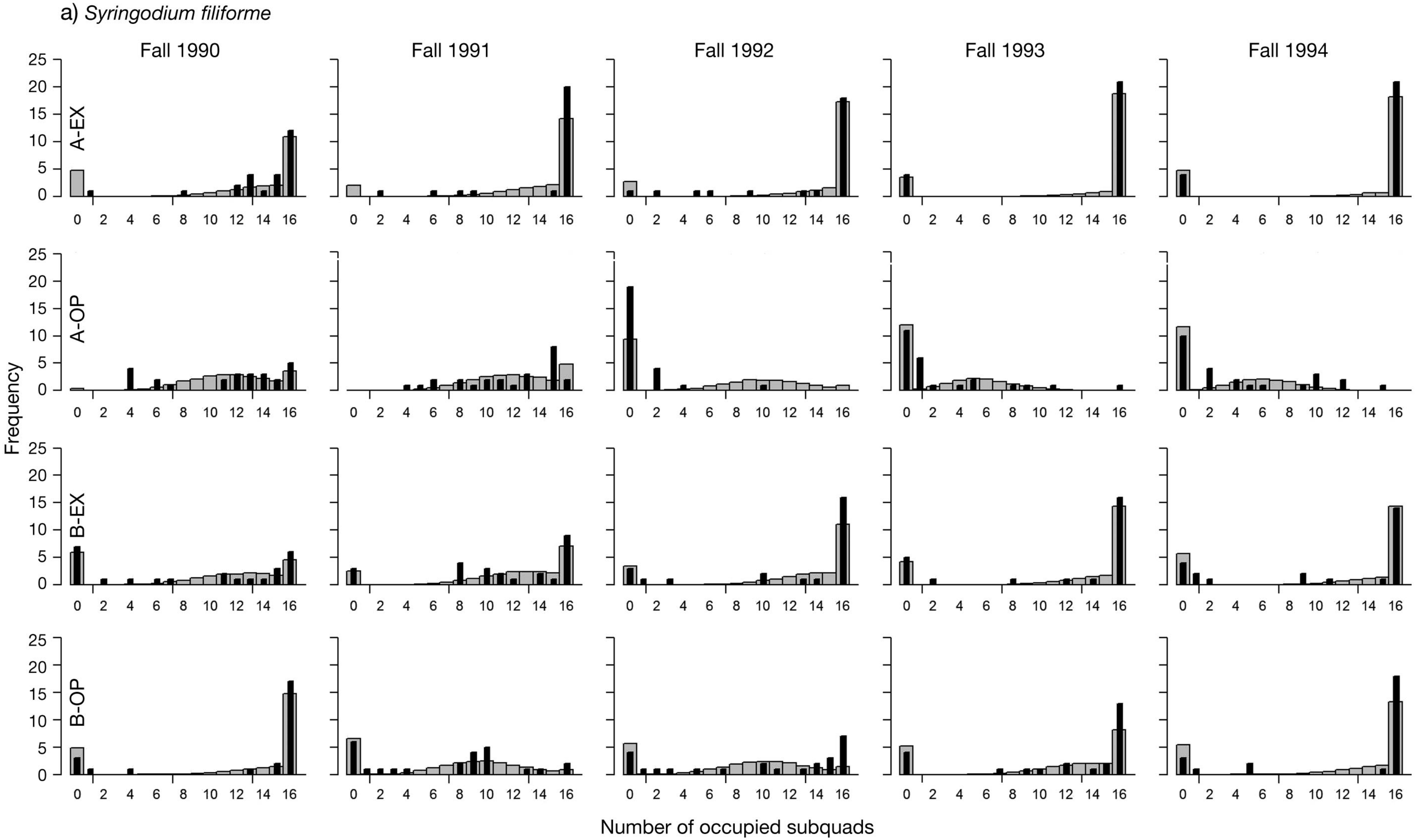

Fig. 7. Frequency of quadrats (total of twenty-five 1 m^2 quadrats per plot, with 0–16 subquadrats per quadrat) occupied by (a) *Syringodium filiforme* and (b) *Halodule wrightii*. The graphs show trends in seagrass coverage both over time (left to right) and among plots (top to bottom). Fall sample periods were used to represent the patterns in the 4 study plots: A Exclosed (A-EX), A Open (A-OP), B Exclosed (B-EX), B Open (B-OP). Black bars represent actual data and gray bars are model estimates

(Fig. continued on next page)

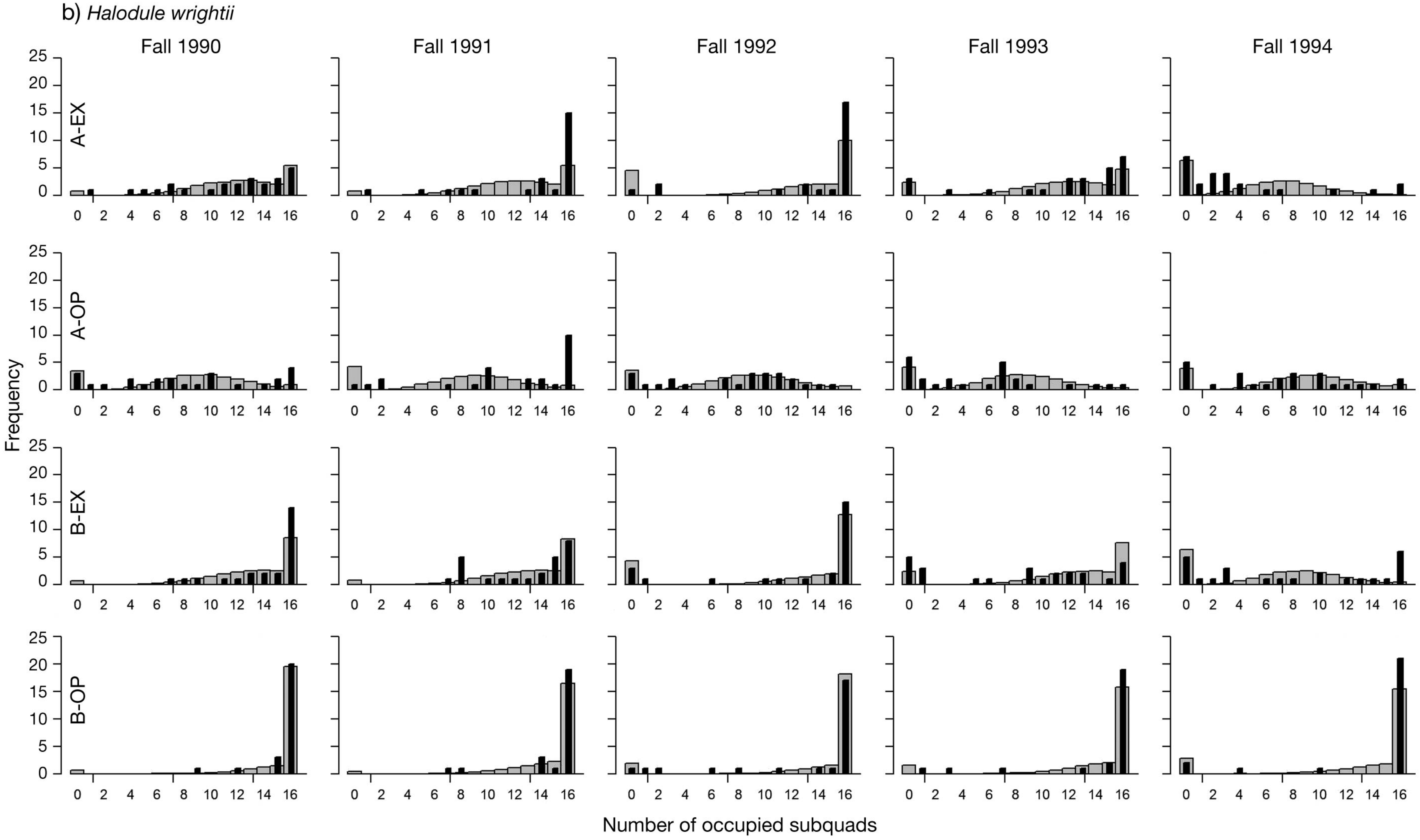

Fig. 7 (continued)

1990 and fall 1991, and continued to maintain a high frequency throughout the study (Fig. 7a). *S. filiforme* frequency in B Exclosed increased more gradually than in A Exclosed (Fig. 7a). A Open had a low frequency of sparsely (0–5 subquadrats) vegetated quadrats in fall 1990; however, by fall 1992, the number of 0 subquadrats was much greater than the number of vegetated subquadrats, and this pattern continued in A Open through fall 1994, i.e. there was no apparent recovery of *S. filiforme* (Fig. 7a). In contrast, B Open had a high frequency of quadrats with 16 vegetated subquadrats in fall 1990 which declined by fall 1991 (the decline occurred between fall 1990 and spring 1991). *S. filiforme* frequency remained relatively low in B Open until fall 1993, and appeared to recover to fall 1990 frequencies by fall 1994 (Fig. 7a).

H. wrightii frequency in both exclosed and open plots started at a lower level in Area A than in B, possibly reflecting a difference in manatee grazing pressure on these 2 areas in previous years (Fig. 7b). However, by fall 1992, the number of quadrats with 16 vegetated subquadrats increased in both exclosures to 17 (A exclosed) and 15 (B exclosed), and then declined in both through the end of the study (Fig. 7b). Unlike A Open, B Open consistently had a high number of quadrats with 16 subquadrats vegetated by *H. wrightii* (Fig. 7b). A Open consistently had a wider range in the number of vegetated subquadrats and more 0's than B Open (Fig. 7b). *H. wrightii* frequency initially increased in A Open between fall 1990 and fall 1991, and then declined. By fall 1994, *H. wrightii* frequency in A Open resembled that in A and B Exclosed (Fig. 7b).

Differences in grazing pressure between A Open and B Open plots

Manatee grazing within the study site was not evenly distributed, as shown by our observations of manatee distribution, seagrass model, and seagrass frequency results. Direct observation from the tower in 1991 and 1992 showed more manatees in Area A than in Area B. Even in 1992, when the highest density of manatees was documented in the study area by aerial surveys and telemetry, far fewer manatees were observed in the seagrass bed in Area B, northeast of the observation tower, than the area between the 2 exclosures, including A Open (Fig. 2a). Protection from the easterly wind by Cape Canaveral and the proximity of the deep basin may attract manatees to this particular location in Area 4 of the NBR. The basin borders 3 sides of Area A and only the offshore side of Area B; thus, greater accessibility by manatees may explain the differences in observed manatee occurrence and grazing pressure between the 2 open plots (A > B).

S. filiforme shoot counts and biomass showed little (B Open) or no (A Open) recovery from prior grazing (Figs. 5b,d & 6b,d), whereas frequency of occurrence increased gradually in B Open following grazing in 1991 (Fig. 7a). *H. wrightii* appeared to respond more positively to grazing pressure than *S. filiforme*, particularly in B Open, with greater *H. wrightii* shoot counts, biomass, and frequency in B Open than in A Open (Figs. 5f,h, 6f,h& 7b).

DISCUSSION

Grazing promotes co-dominance of *Syringodium filiforme* and *Halodule wrightii*

Aerial surveys, direct observations, and satellite telemetry confirmed that our study area was regularly used by manatees. The time series of aerial photographs and the results of excluding manatees from two 169 m^2 seagrass plots also indicated that seagrasses in the open plots were periodically grazed by manatees. Initially, the species composition and abundance of seagrasses in our study plots were similar to each other and comparable to reported values for mixed *S. filiforme* and *H. wrightii* meadows in the IRL (see (a) in Supplement 4; Dawes et al. 1995, Gallegos & Kenworthy 1996). Following installation of exclosures, both *S. filiforme* and *H. wrightii* initially responded positively to release from manatee grazing pressure, as evidenced by their increased density and biomass between 1991 and 1992. This initial response was consistent with what we generally know about the growth dynamics of these 2 species. *H. wrightii* and *S. filiforme* are relatively fast growing, opportunistic species (den Hartog 1971, Williams 1990, Gallegos et al. 1994) and are often observed as the first species to reoccupy suitable seagrass habitat and disturbance sites in the tropical Atlantic and Caribbean (Zieman 1982, Kenworthy et al. 2002). In the exclosures, however, *S. filiforme* continued to increase in shoot density, total biomass, and frequency, and gradually replaced *H. wrightii* to become the dominant species.

An earlier study of manatee grazing impacts in the southern IRL showed that *Halodule wrightii* recovered at twice the rate of *Syringodium filiforme* in 16 grazed 1 m^2 quadrats (Lefebvre et al. 1999). In the current study, our results indicated that it took several years of protection from grazing before *S. filiforme* dominated biomass and species composition in the exclosures, suggesting that *S. filiforme* is likely to have a longer period of recovery than *H. wrightii* in areas where manatees feed. If manatees do not respond to seagrass declines in this coastal region of Florida by shifting their feeding activities from seagrasses to other food resources or other regions, one might predict that *H. wrightii* will dominate in coverage and biomass in the NBR for perhaps years.

H. wrightii biomass was higher in the open plots in 1993 than in 1990 and 1991, indicating that it was recovering from prior and more recent grazing pressure, or even benefitted from grazing. However, as indicated by direct observations from the tower in 1991 and 1992, manatees were not uniformly distributed across our study site. Many more manatees were observed in and near A Open than B Open; presumably, grazing pressure was also not uniform. All metrics of *H. wrightii* abundance were greater in B Open than in A Open. Assuming relatively different levels of grazing pressure between A Open and B Open, the study results could be summarized as a continuum: from *S. filiforme* dominance in the absence of grazing in both exclosure plots, to *H. wrightii* dominance with relatively moderate grazing pressure in B Open, to *S. filiforme*/*H. wrightii* co-dominance under relatively heavy grazing pressure in A Open (Fig. 8). Manatee grazing and subsequent perturbation by other organisms (see (b) in Supplement 4) may minimize or prevent dominance by *S. filiforme*, resulting in a mixed community with similar abundance of both species. Such was the case for our study site in 1990, where all 4 experimental plots had been exposed to manatee grazing prior to the study. Likewise, Slone et al. (2013) noted that higher seagrass species diversity corresponded with areas of relatively higher manatee use in the Ten Thousand Islands, southwest Florida. These observations and the results of our exclosure study provide empirical evidence for the important functional role that manatees and other large marine herbivores may play in affecting the diversity of seagrass ecosystems. Because grazer populations have been depleted, some have argued that the structure of contemporary seagrass ecosystems are likely to be much different from that in historical populations that would have experienced higher rates of grazing (Jackson 1997, Domning 2001, Valentine & Duffy 2006). The results of our experiment support the suggestion that, historically, the diversity of tropical seagrass meadows in the western hemisphere may have been higher when grazers were more abundant (Domning 2001).

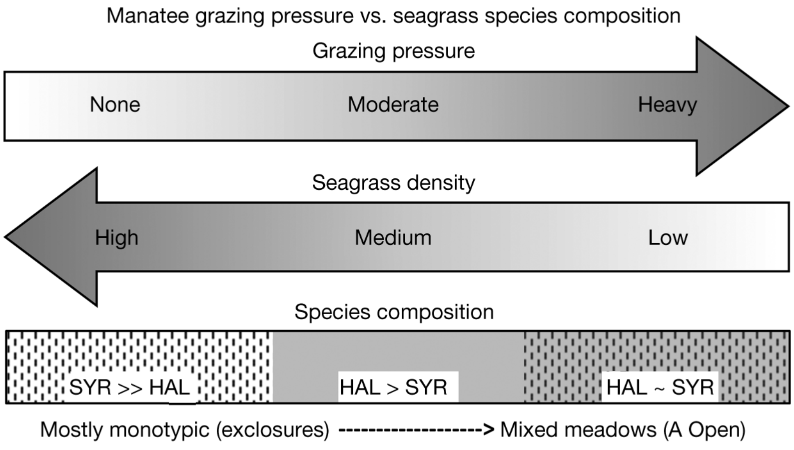

Fig. 8. Schematic summary of how manatee grazing pressure affected seagrass composition, density, and biomass (reflected in Figs. 5–7) in our study plots. By the end of the study, the exclosures were dominated by high-density *Syringodium filiforme* (SYR), whereas the open plots had mixed *Halodule wrightii* (HAL) and SYR meadows. The less-grazed B Open plot had medium density and more HAL than SYR, and the heavily-grazed A Open had a low density of each species

Several processes could contribute to *S. filiforme*'s dominance over *H. wrightii* when a mixed community is protected from grazing. Generally, *S. filiforme* is a morphologically larger plant with taller leaves and larger rhizome and root structure than *H. wrightii* (Duarte 1991). Kenworthy & Schwarzschild (1998) noted that the ' … capability of *S. filiforme* to proliferate vertically enables this species to form populations of multi-layered canopies…' which can reduce light penetration for competing species, while minimizing the effects of self-shading. Grazing would crop the canopies of both species equally and prevent *S. filiforme* from gaining this advantage. However, in the absence of grazing in the exclosures, we theorize that the advantage of a taller canopy could partly explain the eventual dominance of *S. filiforme*. In addition, the seagrass canopy is the primary source of carbon fixation, and, once *S. filiforme* gains this advantage over *H. wrightii*, it is likely to be translated into higher rates of production, lateral branching, and space occupation, that would improve *S. filiforme's* competitive superiority over *H. wrightii* for acquisition of nutrients, occupation of space, and anchorage in the sediments.

Another way that seagrasses expand their spatial coverage is by

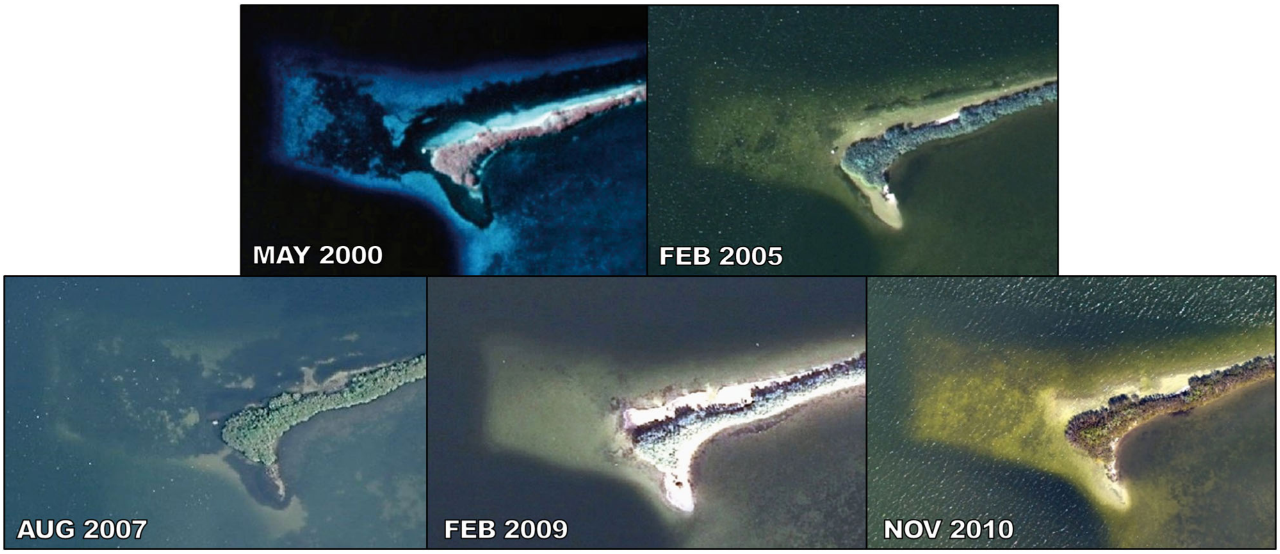

Fig. 9. Aerial images of the study site 6, 11, 13, 15, and 16 yr after the study was completed in Oct 1994. The observation tower can still be seen in the May 2000, Feb 2005, and Aug 2007 photos. Seagrass coverage, as shown by the dark green patches, goes from relatively dense with grazed areas in 2000, to sparse in 2005, to dense in 2007, very sparse in 2009, and recovering in 2010 (photo credits: May 2000 US Geological Survey; all others St. Johns River Water Management District)

clonal growth (Tomlinson 1974, Kendrick et al. 2012). Clonal fragments of seagrasses are viable natural propagules (di Carlo et al. 2005, Hall et al. 2006, Kendrick et al. 2012) and have been used for transplanting seagrasses (Fonseca et al. 1998). Manatees have been observed uprooting seagrasses and producing clonal fragments (L. W. Lefebvre, W. J. Kenworthy, J. Reid, all pers. obs.) that can naturally disperse, settle, and establish new patches of seagrass (Hall et al. 2006, Kendrick et al. 2012). This may have been one of the processes that facilitated rapid recovery of *H. wrightii* in the northern IRL following complete loss of an existing seagrass bed (Morris & Virnstein 2004). It is reasonable to assume that clonal fragments might partially explain how, even under intense manatee grazing pressure demonstrated by A Open, both species of seagrass persisted, albeit at lower levels than ungrazed or moderately grazed sites.

Although we did not measure any aspects of sexual reproduction (flowering, seed production, and seed recruitment), future grazing studies would benefit from consideration given to examining the effects of grazing on this aspect of seagrass life history. *H. wrightii* and *S. filiforme* have distinctly different reproductive architectures; flowers and fruits of *H. wrightii* are located at the base of the shoot beneath the leaf canopy near and in the sediment while *S. filiforme* flowers are elevated high up in the canopy and thus are more directly exposed to grazing. It is reasonable to hypothesize that leaf canopy grazing would have a greater impact on *S. filiforme* flowers and seed production than *H. wrightii*. If this were true, the exclusion of grazing pressure over time might provide *S. filiforme* with a recruitment advantage that may partially explain its eventual dominance over *H. wrightii*.

Based on the results of our study, we hypothesize that manatee grazing can help maintain more diverse, mixed species seagrass meadows. Moderate grazing pressure, exemplified by B Open, may have little impact or even be beneficial to *H. wrightii*, and allow recovery of *S. filiforme* over several years. The differences we found between A Open and B Open in manatee activity and grazing impacts suggest that manatees shifted their grazing activity among different locations, both intra- and inter-annually. This was confirmed by a series of satellite images of our site showing alternating levels of seagrass grazing impact and recovery over a 10 yr period (Fig. 9). Local and regional shifts in the intensity of grazing activity may occur in response to changing seagrass quantity and quality. Packard (1981) suggested that there may be a point where the energetic return becomes insufficient in a heavily grazed bed, and manatees may then move on to feed in other areas. Consequently, periods of diminished grazing can result in greater abundance of *S. filiforme*, and periods of intense grazing can modify the relative species composition and biomass without complete destruction of the seagrass meadow. Despite the repeated annual presence of 100s of manatees in Area 4 of the Banana River in the spring, seagrass was not removed to a degree such that it could not recover, even in a highly favored location such as our study site. Valentine & Heck (1999) argued that seagrasses persist in the face of grazing pressure because of their ability to increase aboveground primary production in response to grazing and because of the belowground location of much of their biomass. The timing of grazing is also likely to be important (Aragones & Marsh 1999). By feeding intensively on seagrass in late winter/early spring, before the seagrasses have reached peak productivity, the seagrass beds have the maximum opportunity to recover before manatees revisit the same sites the following spring.

Conservation and management implications

For the western hemisphere tropics it has been argued that large marine grazers were more abundant before Europeans arrived and populations of manatees and green sea turtles were depleted by overharvesting and habitat alteration (Jackson 1977, Lefebvre et al. 2001, Bjorndal & Jackson 2003). However, recent evidence suggests that conservation programs directed at protecting grazer populations are leading to noticeable increases in some regions (Langtimm et al. 1998, Chaloupka et al. 2008, Heithaus et al. 2014, Kleen & Breland 2014, Martin et al. 2015), accompanied by significant grazing impacts on seagrasses (Fourqurean et al. 2010, Heithaus et al. 2014, Molina Hernández & van Tussenbroek 2014, Bakker et al. 2016). In addition to this study, we are aware of several other examples of seagrass grazing by local manatee aggregations which may have both short- and long-term implications for local seagrass resources (Packard 1984, Lefebvre et al. 1999, Deutsch et al. 2003, Castelblanco-Martínez et al. 2012, Slone et al. 2013).

Our results should be of special interest to resource managers, considering the documented global (Waycott et al. 2009) and local (Phlips et al. 2015) declines of seagrasses. The recent catastrophic loss of 31 900 acres (12 900 ha) of seagrasses associated with a 'superbloom' of phytoplankton in coastal lagoons of northeast Florida (Morris et al. 2015, Phlips et al. 2015) included the region of our exclosure study site and highlights the need to better understand the role manatees may have in the seagrass recovery process. Before the extensive loss of seagrass in the region, many scientists and managers considered the northern IRL and the Banana River ideal habitat for sustaining large numbers of manatees, even in winter, because of the proximity of warm water produced by the Florida Power and Light (FPL) Co.'s Canaveral power plant. As long as this winter warm-water refuge remains operating in the region and manatees continue their seasonal use of the Indian and Banana Rivers, it appears likely that manatee grazing will continue to be a factor in seagrass recovery and species composition.

The long-term spatial and temporal changes we documented in response to manatee grazing could have important conservation implications for both manatees and seagrass meadows. The number of manatees using the NBR has grown over the past 3 decades; however, this does not mean their future survival is secure. In addition to the possible loss of this region's principal winter warm water source (FPL power plant effluent) sometime in the future, manatees may lose critical food resources because of phytoplankton blooms or other causes. Manatees are adaptable and capable of moving large distances (100s of km) in response to changing environmental conditions (Deutsch et al. 2003); however, they must find needed resources along travel routes and at their destination sites. Our findings demonstrate that a relatively small (<1 ha) seagrass meadow can sustain intense, seasonal manatee grazing, suggesting that a series of small manatee sanctuaries located within seagrass beds along the intracoastal waterway might help to protect manatees migrating between Brevard County and south Florida. Seagrass communities could be protected by shifting or rotating protected sites if overgrazing occurs in the vicinity of sanctuaries. Conservation of coastal seagrass communities will be essential for the recovery of manatees and other marine megaherbivores.

Acknowledgments. We thank Merritt Island National Wildlife Refuge personnel who built and deployed the observation platform and coordinated volunteers to observe manatees at the study site in 1991 and 1992. L. Morris at the St Johns River Water Management District provided us with aerial imagery and made several insightful comments on the study area. Discussions with T. O'Shea helped in the conceptual phase of the study. D. Easton, R. Lowers, and D. Scheidt assisted in the collection of seagrass data. Numerous students assisted in sorting, drying, and weighing of seagrass biomass samples. P. Ryan assisted with data entry and C. Langtimm with preliminary data analysis. Several anonymous reviewers provided numerous improvements to the manuscript. The project was funded by the National Biological Service, the US Geological Survey, and the Biomedical Office at NASA's Kennedy Space Center. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the US Government.

LITERATURE CITED

Aragones L, Marsh H (1999) Impact of dugong grazing and turtle cropping on tropical seagrass communities. Pac Conserv Biol 5:277–288

Bakker ES, Wood KA, Pagès JF, Veen GF and others (2016) Herbivory on freshwater and marine macrophytes: A review and perspective. Aquat Bot 135:18–36

Bjorndal KA, Jackson JBC (2003) Roles of sea turtles in marine ecosystems: reconstructing the past. In: Lutz PL, Musick J, Wyneken J (eds) Biology of sea turtles, Vol 2. CRC Press, Boca Raton, FL, p 259–273

Castelblanco-Martínez DN, Everardo B, Schmitter-Soto JJ, Hernández-Arana HA, Morales-Vela B (2012) The trophic role of the endangered Caribbean manatee *Trichechus manatus* in an estuary with low abundance of seagrass. Estuar Coasts 35:60–77

Chaloupka M, Bjorndal KA, Balazs GH, Bolten AB and others (2008) Encouraging outlook for recovery of a once severely exploited marine herbivore. Glob Ecol Biogeogr 17:297–304

Dawes CD, Hanisak D, Kenworthy WJ (1995) Seagrass biodiversity in the Indian River Lagoon. Bull Mar Sci 57: 59–66

den Hartog C (1971) The dynamic aspect in the ecology of seagrass communities. Thalassia Jugosl 7:101–112

Deutsch CJ, Reid JP, Bonde RK, Easton DE, Kochman HI, O'Shea TJ (2003) Seasonal movements, migratory behavior, and site fidelity of West Indian manatees along the Atlantic coast of the United States. Wildl Monogr No 151

di Carlo G, Badalamenti F, Jensen A, Koch E, Riggio S (2005) Colonisation process of vegetative fragments of *Posidonia oceanica* (L) Delile on rubble mounds. Mar Biol 147:1261–1270

Domning DP (1981) Sea cows and sea grasses. Paleobiology 7:417–420

Domning DP (2001) Sirenians, seagrasses, and Cenozoic ecological change in the Caribbean. Palaeogeogr Palaeoclimatol Palaeoecol 166:27–50

Duarte CM (1991) Allometric scaling of seagrass form and productivity. Mar Ecol Prog Ser 77:289–300

Fonseca MS, Kenworthy WJ, Thayer GW (1998) Guidelines for the conservation and restoration of seagrasses in the United States and adjacent waters. NOAA Coastal Ocean Program, Decision Analysis Series No 12. US Department of Commerce, NOAA, Coastal Ocean Office, Silver Spring, MD

Fourqurean JW, Manuel S, Coates CA, Kenworthy WJ, Smith SR (2010) Effects of excluding sea turtle herbivores from a seagrass bed: overgrazing may have led to loss of seagrass meadows in Bermuda. Mar Ecol Prog Ser 419:223–232

Gallegos ME, Kenworthy WJ (1996) Seagrass depth limits in the Indian River Lagoon (Florida USA): application of an optimal water quality model. Estuar Coast Shelf Sci 42: 267–288

Gallegos ME, Merino M, Rodriguez A, Marba N, Duarte CM (1994) Growth patterns and demography of pioneer Caribbean seagrasses (*H. wrightii* and *S. filiforme*). Mar Ecol Prog Ser 109:99–104

Hall LM, Hanisak MD, Virnstein RW (2006) Fragments of the seagrasses *Halodule wrightii* and *Halophila johnsonii* as potential recruits in Indian River Lagoon, Florida. Mar Ecol Prog Ser 310:109–117

Hartman DS (1979) Ecology and behavior of the manatee (*Trichechus manatus*) in Florida. Am Soc Mamm Spec Publ 5:1–153

Heithaus MR, Alcoverro T, Arthur R, Burkholder DA and others (2014) Seagrasses in the age of sea turtle conservation and shark overfishing. Front Mar Sci 1:28

Jackson JBC (1997) Reefs since Columbus. Coral Reefs 16: S23–S32

Kendrick GA, Waycott M, Carruthers TJB, Cambridge ML and others (2012) The central role of dispersal in the maintenance and persistence of seagrass populations. BioSci 62:56–65

Kenworthy WJ, Schwarzschild AC (1998) Vertical growth and short-shoot demography of *S. filiforme* in outer Florida Bay, USA. Mar Ecol Prog Ser 173:25–37

Kenworthy WJ, Fonseca MS, Whitfield PE, Hammerstrom K (2002) Analysis of seagrass recovery in experimental excavations and propeller-scar disturbances in the Florida Keys National Marine Sanctuary. J Coast Res 37: 75–85

Kleen JM, Breland AD (2014) Increases in seasonal manatee (*Trichechus manatus latirostris*) abundance within Citrus County, Florida. Aquat Mamm 40:69–80

Langtimm CA, O'Shea TJ, Pradel R, and Beck CA (1998) Estimates of annual survival probabilities for adult Florida manatees (*Trichechus manatus latirostris*). Ecology 79:981–997

Ledder DA (1986) Food habits of the West Indian manatee, *Trichechus manatus latirostris*, in South Florida. MS thesis, University of Miami, Coral Gables, FL

Lefebvre LW, Reid JP, Kenworthy WJ, Powell JA (1999) Characterizing manatee habitat use and seagrass grazing in Florida and Puerto Rico: implications for conservation and management. Pac Conserv Biol 5:289–298

Lefebvre LW, Marmontel M, Reid JP, Rathbun GB, Domning DP (2001) Status and biogeography of the West Indian manatee In: Woods CA, Sergile FE (eds) Biogeography of the West Indies: patterns and perspectives. CRC Press, Boca Raton, FL, p 425–474

Lunn D, Spiegelhalter D, Thomas A, Best N (2009) The BUGS project: evolution, critique and future directions. Stat Med 28:3049–3082

Lunn D, Jackson C, Best N, Thomas A, Spiegelhalter D (2012) The BUGS book: A practical introduction to Bayesian analysis. Chapman & Hall/CRC, Boca Raton, FL, p 185–193

Marsh H, O'Shea TJ, Reynolds JE III (2012) Ecology and conservation of the Sirenia: dugongs and manatees. Cambridge University Press, New York, NY

Martin J, Edwards HH, Fonnesbeck CJ, Koslovsky SM, Harmak CW, Dane TM (2015) Combining information for monitoring at large spatial scales: first statewide abundance estimate of the Florida manatee. Biol Conserv 186: 44–51

Molina Hernández AL, van Tussenbroek BI (2014) Patch dynamics and species shift in seagrass communities under moderate and high grazing pressure by green sea turtles. Mar Ecol Prog Ser 517:143–157

Morris LJ, Virnstein RW (2004) The demise and recovery of seagrass in the northern Indian River Lagoon, Florida. Estuaries 27:915–922

Morris LJ, Chamberlain RC, Jacoby CA (2015) Summary report for the northern Indian River Lagoon. In: Yarbro LA, Carlson PR Jr (eds) Seagrass integrated mapping and monitoring report No. 2. Fish and Wildlife Research

Institute Technical Report TR-17B, St. Petersburg, FL p 122–126

Packard JM (1981) Abundance, distribution, and feeding habits of manatees (*Trichechus manatus*) wintering between St. Lucie and Palm Beach Inlets, Florida. USFWS Contract Report No 14-16-0004-80-105

Packard JM (1984) Impact of manatees (*Trichechus manatus*) on seagrass communities in eastern Florida. Acta Zool Fenn 172:21–22

Phlips EJ, Badylak S, Lasi MA, Chamberlain R and others (2015) From red tides to green and brown tides: bloom dynamics in a restricted subtropical lagoon under shifting climatic conditions. Estuar Coasts 38:886–904

Provancha JA, Hall C (1991) Observations of associations between seagrass beds and manatees in East Central Florida. Fla Sci 54:87–98

Provancha JA, Provancha MJ (1988) Long-term trends in abundance and distribution of manatees (*Trichechus manatus*) in the NBR, Brevard County, Florida. Mar Mamm Sci 4:323–338

Provancha JA, Scheidt DM (2000) Long-term trends in seagrass beds in the Mosquito Lagoon and NBR, Florida. In: Bertone, SA (ed) Seagrasses: monitoring, ecology, physiology, and management. CRC Press, Boca Raton, FL, p 177–193

R Core Team (2015) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. www.R-project.org/

Reynolds JE III, Wilcox JR (1994) Observations of Florida manatees (*Trichechus manatus latirostris*) around selected power plants in winter. Mar Mamm Sci 10:163–177

Rubin DB (1976) Inference and missing data. Biometrika 63: 581–592

Shane S (1984) Manatee use of power plant effluents in Brevard County, FL. Fla Sci 47:180–187

Slone DH, Reid JP, Kenworthy WJ (2013) Mapping spatial resources with GPS animal telemetry: foraging manatees locate seagrass beds in the Ten Thousand Islands, Florida, USA. Mar Ecol Prog Ser 476:285–299

St Johns River Water Management District, Bethune-Cookman University, Florida Atlantic University – Harbor Branch Oceanographic Institution, Florida Fish and Wildlife Conservation Commission and others (2012) Indian River Lagoon 2011 superbloom: plan of investigation. St. Johns River Water Management District, Palatka, FL

Thayer GW, Bjorndal KA, Ogden JC, Williams SL, Zieman JC (1984) Role of larger herbivores in seagrass communities. Estuaries 7:351–376

Thomas A, O'Hara B, Ligges U, Sturtz S (2006) Making BUGS open. R News 6:12–17

Tomlinson PB (1974) Vegetative morphology and meristem dependence — the foundation of productivity in seagrasses. Aquaculture 4:107–130

Valentine JF, Duffy E (2006) The central role of grazing in seagrass ecology. In: Larkum AW, Duarte CM, Orth R (eds) Seagrass biology. Springer, Dordrecht, p 463–501

Valentine JF, Heck KL Jr (1999) Seagrass herbivory: evidence for the continued grazing of marine grasses. Mar Ecol Prog Ser 176:291–302

Waycott M, Duarte CM, Carruthers TJB, Orth RG and others (2009) Accelerating loss of seagrasses across the globe threatens coastal ecosystems. Proc Natl Acad Sci USA 106:12377–12381

Williams SL (1990) Experimental studies of Caribbean seagrass bed development. Ecol Monogr 60:449–469

Zieman JC (1982) The ecology of the seagrasses of south Florida: a community profile. US Fish and Wildlife Service, FWS/OBS82/25, Washington, DC

Editorial responsibility: Just Cebrian,
Dauphin Island, Alabama, USA

Submitted: April 18, 2016; Accepted: November 14, 2016
Proofs received from author(s): January 17, 2017