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# Green turtle herbivory and its effects on the warm, temperate seagrass meadows of St. Joseph Bay, Florida (USA)

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ABSTRACT: Green turtles *Chelonia mydas* occur sporadically in tropical and subtropical latitudes, but effective conservation efforts are leading to increasing abundances at higher latitudes. One consequence of increased green turtle abundance in some locations has been the overgrazing of seagrasses, their preferred food item. Recent, large increases in juvenile green turtle abundance in the warm temperate northern Gulf of Mexico, especially in the clear waters of St Joseph Bay, FL, make this a prime location to study effects of their feeding activities on the extensive turtlegrass *Thalassia testudinum*-dominated meadows. Using caging and simulated grazing to quantify green turtle effects, we found that excluding green turtles led to increased *Thalassia* shoot density, and that simulating turtle grazing resulted in narrowed leaves and decreased turtlegrass productivity. Naturally grazed areas protected from further turtle grazing did not recover after 14 wk of protection. Two years following relaxation of simulated grazing, turtlegrass continued to show residual stress symptoms, with narrower and fewer leaves per shoot than control areas. The future success of sea turtle conservation efforts is critically linked, and dependent on, the protection and sustainability of globally decreasing sea turtle feeding grounds. Thus, continued study of how increasing green turtle populations affect warm temperate turtlegrass meadows will provide important information on how best to manage both turtle and seagrass resources.

KEY WORDS: *Chelonia mydas* · Plant–herbivore interactions · Megaherbivore · Turtlegrass · *Thalassia testudinum*



## 1. INTRODUCTION

The world's warming oceans are restructuring marine communities and altering their productivity (Mooney et al. 2009). A consequence of warming ocean temperatures is poleward shifts in species distributions, and range expansions of tropical species have been documented in most of the world's oceans (Fodrie et al. 2010, Comeaux et al. 2012, Pike 2013, Vergés et al. 2014a, Wernberg et al. 2016). In several locations, poleward-flowing boundary currents are creating global ocean warming hotspots, enabling the range expansion of many tropical herbivores that feed extensively on temperate algae, effectively turning algal forests into 'barrens' (Vergés et al. 2014a,b).

Green turtles *Chelonia mydas* occur in tropical and subtropical regions of the world's oceans. Effective conservation efforts have led to increased abundances and poleward range expansions in many locations worldwide (Foley et al. 2007, Fourqurean et al. 2010, Lal et al. 2010). Like most sea turtle species, green turtles undergo habitat shifts during ontogeny (Hirth 1997). After hatching, green sea turtles actively swim to the open ocean (Carr 1987). Between 1 and 7 yr later, juvenile green turtles will recruit to neritic,

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coastal waters (Musick & Limpus 1997, Reich et al. 2007, Goshe et al. 2010). Juvenile, subadult, and adult *C. mydas* are predominantly herbivorous, with diet composition varying among feeding areas. For example, Bjorndal (1980), Mortimer (1981), and Mendonça (1983) reported seagrass as the major food item of juvenile green turtles, while in the eastern Gulf of Mexico, juvenile green sea turtles feed primarily on turtlegrass *Thalassia testudinum* (Foley et al. 2007).

An immediate effect of the green turtles' range expansion is increased grazing of seagrass meadows in areas with low grazing pressure. Seagrass grazers exhibit a variety of foraging techniques, and their influences on the morphology and productivity of seagrasses vary (Thayer et al. 1984). For instance, dugong feeding produces trenches, leaving bare areas and often removing aboveground biomass as well as roots and rhizomes (Aragones & Marsh 1999), while fish grazing is characterized by semicircular patches of tissue removed from the grass. Overgrazing, i.e. when grazing rates exceed production rates, may occur depending on the intensity and frequency of grazing, as well as seagrass recovery capability. In conjunction with other stressors, overgrazing can severely stress these vital and globally threatened foundation species and lead to their collapse (Thayer et al. 1984, Williams 1988, Valentine & Heck 1991, Cebrián & Duarte 1998, Christianen et al. 2014, Fourqurean et al. 2019).

Green turtles have been increasing over the last 2 to 3 decades worldwide (Chaloupka et al. 2008, Seminoff et al. 2015, Mazaris et al. 2017), and it is unknown whether seagrass ecosystems can continue to sustain this increase in turtle numbers. Thayer et al. (1984) hypothesized that repeated grazing events would stress seagrasses, leading to decreased leaf widths and declining shoot density and leaf production. While herbivory has historically had a major seagrass-structuring influence, and some have argued that the expansion of *C. mydas* populations may simply increase their numbers to levels prior to human exploitation (Moran & Bjorndal 2005), their foraging grounds have been reduced and are under additional anthropogenically induced stress. Globally, the areal extent of seagrass beds has declined at an average of about 1.8%, or about 110 km$^2$, per year since 1980, and 7% since 1990 (Orth et al. 2006, Waycott et al. 2009). Additionally, overfishing of large sharks, the primary predators of green sea turtles (Heithaus et al. 2008), may permit the growth of turtle populations beyond their historic numbers (Heithaus et al. 2014).

Green turtle grazing can produce severe impacts on seagrass meadows; for example, Lal et al. (2010) reported that *C. mydas* grazing in tropical Indian Ocean seagrass meadows substantially changed meadow structure, reduced flowering, and caused shifts in seagrass species composition. The Lakshadweep archipelago studied by Lal et al. (2010) has reported particularly high green turtle densities, and using megaherbivore exclusion cages, Kelkar et al. (2013b) determined that the sustained turtle grazing caused a clear shift in seagrass species dominance from the longer-lived, larger *T. hemprichii* to the relatively short-lived, pioneering species *Cymodocea rotundata*. While it is possible that this may be a change to a more historically natural system, as pioneering species typically support higher grazing pressure (Cebrián & Duarte 1998), long-lived seagrass species have morphological traits, such as wide leaves and thick belowground rhizomes, that provide greater resistance to disturbances (Congdon et al. 2019). A decrease in long-lived seagrass species would maintain an early successional stage, possibly decreasing nutrient storage potential (Duarte 2000), which could be problematic under conditions of changing climate and increased anthropogenic stressors.

Achieving a balance where ecosystem services of both herbivores and seagrasses are maximized (Scott et al. 2018) may prove challenging in oligotrophic, temperate systems, as it has been hypothesized that tropical seagrass species may be more susceptible to top-down stress at higher latitudes given the seasonality of light (Manuel et al. 2013) and P-limitation (Holzer & McGlathery 2016). For example, an expanding green turtle population in Bermuda produced an overall decrease in shelf-wide turtlegrass biomass, mean leaf length and width, and areal primary productivity, which ultimately led to the collapse of some meadows (Fourqurean et al. 2019). Similarly, Ibarra-Obando et al. (2004) found that in the northern Gulf of Mexico, turtlegrass grew slower and could not exhibit compensatory growth following simulated grazing under low light conditions.

Increasing numbers of juvenile turtles now inhabit the northern Gulf of Mexico (Foley et al. 2007, Avens et al. 2012, Fish and Wildlife Research Institute 2018), yet there remains a severe lack of data on their foraging ecology in this area, as existing information regarding feeding behavior is limited to diet studies of stranded individuals (Foley et al. 2007, Williams et al. 2014). Understanding how increasing green turtle populations and grazing pressure structures temperate seagrass ecosystems is fundamental to the management and conservation of both turtles and globally declining seagrass meadows (Heithaus et al. 2014). In this study, we quantified current green turtle grazing effects and estimated their future impacts on turtlegrass meadows of St. Joseph Bay, Florida (USA) and add to the much-needed literature regarding how temperate turtlegrass meadows respond to and possibly recover from both natural and simulated grazing.

## 2. MATERIALS AND METHODS

### 2.1. Study area

Located in the northeastern Gulf of Mexico (30° N, 85.5° W), St. Joseph Bay is a protected, semi-enclosed bay ca. 21 km long with a maximum width of 8 km (Fig. 1). Depth ranges to 13.3 m (McMichael et al. 2008), and the bay encompasses just under 30 000 ha (FL DEP 2008). The bay has a tidal range of approximately 0.47 m, a very low current flow, and highly organic sediments (Stewart & Gorsline 1962). St. Joseph Bay is the only large body of water in the eastern Gulf of Mexico with little freshwater input. Average salinities range from 30–36, while water temperature varies annually from 8–30°C (Valentine & Heck 1993).

In St. Joseph Bay, dense monospecific turtlegrass *Thalassia testudinum* meadows are dominant, although manatee grass *Syringodium filiforme* and shoal grass *Halodule wrightii* are also present. Seagrasses cover about 2899 ha (7166 acres) and are most abundant in the southern portion of St. Joseph Bay (Fig. 1, Yarbro & Carlson 2016). Manatee grass often occurs with turtlegrass and is located predominantly along the eastern shore of the bay; shoal grass occurs sporadically along the eastern and western shorelines and can occur in monospecific or mixed beds (Yarbro & Carlson 2016). Our efforts were focused in the southern portion of the bay, which contains shallow, dense turtlegrass beds separated by 5 deeper channels, and which supports the greatest number of juvenile green turtles (Lamont et al. 2015).

### 2.2. Green turtles in St. Joseph Bay

Green turtles *Chelonia mydas* are present in St. Joseph Bay year-round (McMichael 2005, Lamont & Iverson 2018). Neritic juvenile green turtles are the life stage primarily found in St. Joseph Bay. Although loggerhead *Caretta caretta* and Kemp's ridley turtles *Lepidochelys kempii* are present, Foley et al. (2007) found that green turtles comprised >96% of the turtles collected in St. Joseph Bay during a 2001 cold-stunning event. Avens et al. (2012) saw similar proportions of green sea turtles during the 2010 cold stunning (>95%), and the most recent cold stunning in 2018 continued this trend, with >95% of the ~1250 turtles stunned being juvenile green turtles (M. Lamont pers. comm.). Given that the smaller body size of juveniles might make them more vulnerable to cold stunning, it is possible that larger individuals do frequent the bay, although no significant differences were reported in the size ranges of the turtles in the 2001 and 2010 cold stun events and mark-recapture sampling efforts in this area from 2001 to 2004 (McMichael et al. 2008, Avens et al. 2012). In addition, green turtles are known to leave their neritic juvenile feeding grounds as they become sexually mature (Musick & Limpus 1997).

After examining gastrointestinal (GI) tracts of cold-stunned turtles, Foley et al. (2007) confirmed that turtlegrass was a major diet component of the juvenile green turtles in St. Joseph Bay, and *T. testudinum* was present in the GI tract of all examined turtles. Williams et al. (2014) also found turtlegrass to be a major diet item in juvenile *C. mydas* in St. Joseph Bay, but the authors also identified tunicates (*Pyrosoma* sp. and *Botrylloides* sp.) as important prey. *Botrylloides* sp. grows epiphytically on turtlegrass leaves and appears as water temperature decreases in the fall.


Fig. 1. St. Joseph Bay, Florida (USA). Yellow dots indicate site locations of the 2016 exclusion cage experiment, the red dot is the simulated grazing plot site, and the blue dot is the 2017 turtlegrass recovery exclusion cage site. Yellow star in inset shows the location of St. Joseph Bay in the northeastern Gulf of Mexico

### 2.3. Exclusion cages

Exclusion cages were used to directly estimate green turtle grazing effects on turtlegrass from June to October 2016, which includes the majority of the *T. testudinum* growing season. Four sites with replicated sets of control and cage plots (n = 3) were established across the southern portion of the bay in seagrass beds with no signs of prior grazing. The cages were arranged in 6 m intervals, with 4 m between each cage and its uncaged control. Control areas were delineated with PVC poles 1.5 × 1.5 m apart. The cages were also 1.5 × 1.5 m (2.25 $m^2$) wide with a height of 50 cm above the sediment surface and were constructed of PVC and covered with 5.08 × 5.08 cm flexible nylon bird netting (MTN Gearsmith, ASIN B00O24L392). The bottom 20.32 cm of bird netting were cut to 10.16 × 10.16 cm squares to ensure that only green turtles, but not other grazers such as purple sea urchins *Lytechinus variegatus*, which are abundant in St. Joseph Bay (Valentine & Heck 1991), were excluded. While emerald parrotfish *Nicholsina usta* can be found north and south of St. Joseph Bay, they do not frequent the bay (Fodrie et al. 2010). Cages were checked every 2–3 wk and were cleaned of drifting debris and fouling as needed, but fouling was limited by the small diameter of the bird netting. Exclusion cages have been successfully used before in several studies, but we investigated potential shading impacts to turtlegrass by measuring photosynthetic active radiation (PAR) (4μA Underwater QuantumSensor; LI-COR) in cages and control plots at the mid-point and conclusion of the experiment to ensure that the turtlegrass received adequate irradiance, even with some inevitable algal fouling on cages.

Changes in turtlegrass morphology and biomass were measured by taking 2 cores (10 cm deep × 7.62 cm diameter) in each cage and uncaged replicate at the initiation (Day 0), mid-point (Day 81), and conclusion (Day 144) of the experiment. Cores were placed in a 500 μm sieve to separate plant material from the sediments. Plant material was frozen and returned to the laboratory for analysis. Once in the lab, samples were thawed, and all epiphytes were scraped from the leaves with a razorblade. From these samples, we recorded mean leaf length/width (cm), mean number of leaves per shoot, shoot density (shoots $m^{-2}$), aboveground turtlegrass biomass (g dry weight [DW] $m^{-2}$), and belowground turtlegrass biomass (g DW $m^{-2}$). Each sample was separated into aboveground and belowground biomass beginning at the base of the sheath (i.e. where the rhizome begins). Leaf length and width were measured by separating leaves of each *T. testudinum* shoot from youngest to oldest and measuring lengths and widths to the nearest centimeter. Aboveground and belowground *T. testudinum* biomass was dried at 60°C for at least 48 h before recording weights.

### 2.4. Simulated grazing plots

To demonstrate how simulated regrazing affects turtlegrass, during June to October 2016, a series of 1 $m^2$ plots was established with leaf clipping done at 3 and 6 wk intervals with four 3 wk clippings and three 6 wk clippings, along with unclipped control plots. Each of the treatments and the control had 3 randomly positioned replicates for a total of 9 plots. Although green turtle feeding plots have been described as being 10–100 $m^2$ in size (Bjorndal 1980, Williams 1988), the feeding plots we have seen in St. Joseph Bay are often <0.1 $m^2$. Plots of this size have also been reported in Australia (Kuiper-Linley et al. 2007) and Bermuda (Holzer & McGlathery 2016), indicating that a wide range of feeding plot sizes occurs. Our treatments were scaled to those of Kuiper-Linley et al. (2007), who tested 2 and 4 wk clipping intervals for 3.5 mo in a sub-tropical climate.

Our plots were established along the St. Joseph Bay peninsula where there was no evidence of *L. variegatus* grazing at the time of initiation and green turtles are less frequent (Lamont et al. 2015, Lamont & Iverson 2018) to minimize the likelihood of natural grazing in simulated grazing plots. To simulate *C. mydas* grazing (Bjorndal 1980), all leaves in each clipped plot were severed at the leaf/sheath junction (~1–2 cm above the sediment) with scissors. Corners of the 1 $m^2$ areas were marked with PVC pipe and zip ties to identify treatment level (Fig. 2). The sampling regime was the same as described in Section 2.3.

At the conclusion of the experiment (October 2016), we also measured turtlegrass areal net aboveground primary production (NAPP) and leaf C:N ratios in all 9 plots. To estimate NAPP in *T. testudinum*, we used a modified hole-punch technique (Zieman 1974) in 3 replicate 7.62 cm diameter PVC rings haphazardly arranged in each plot. C and N content (wt/wt) were determined using a C/N/S analyzer (COSTECH elemental combustion system). Nutrient ratios were calculated on a mol:mol basis for C and N.

Fig. 2. Example of a simulated, recently clipped green sea turtle grazing plot

### 2.5. Turtlegrass recovery

Following the discovery of the first natural green turtle feeding plot recorded in St. Joseph Bay (Fig. 3), we evaluated whether and how *T. testudinum* might recover from grazing in both natural and simulated grazing plots after grazing was halted. In a natural setting, 6 exclusion cages were set up in the feeding area and 6 uncaged controls were established in the adjacent, ungrazed *T. testudinum* bed. This experiment was set up on 24 March 2017, when salinity was 31.1 and temperature was 21.9°C. The experiment concluded on 28 June 2017, when salinity was 30.6 and temperature was 28.6°C. Cages were the same as those previously described in Section 2.3, and control plots were once again marked with PVC poles. The sampling regime and methods also remained the same as described above.

Turtlegrass in the simulated grazing plots was allowed to regrow without further clipping from October 2016 to May 2017 (194 d, ca. 28 wk), and again until December 2018 (770 d, 110 wk). The sampling regime used the methods described in Section 2.3, and we recorded the same parameters (mean leaf length and width, mean number of leaves per shoot, shoot density, and aboveground and belowground turtlegrass biomass).

### 2.6. Statistical analysis

#### 2.6.1. Exclusion cages

The exclusion cage experiment employed a before-after-control-impact (BACI) design. Replicate seagrass cores in each treatment were averaged. Start values were subtracted from the End values for all the turtlegrass response variables (mean leaf length, mean leaf width, shoot density, mean number of leaves per shoot, and above- and belowground turtlegrass biomass) and a *t*-test was used to compare treatment means. If there were significant differences between the caged and control End–Start response variables, this would suggest that *C. mydas* grazing had produced a

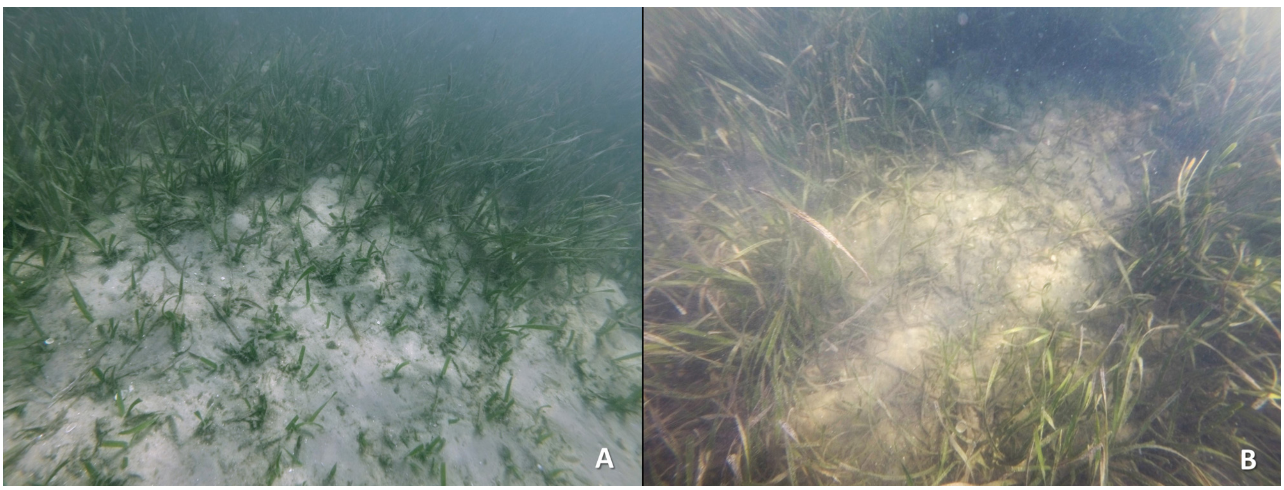


Fig. 3. Naturally grazed green turtle feeding plot (A) adjacent to and (B) inside a dense *Thalassia testudinum* bed

detectable impact. Shoot densities were transformed taking the square root to meet homogeneity of variance assumptions. Additionally, *t*-tests were used to compare treatment End data means. To test whether there was a significant reduction of light in caged areas, light availability measured as PAR by a 4μA Underwater Quantum-Sensor (LI-COR) at the seagrass canopy height was compared between caged and control treatments with *t*-tests at the midpoint and conclusion of the experiment.

#### 2.6.2. Simulated grazing plots

The simulated grazing experiment also used a BACI design. Start values were subtracted from End values to evaluate differences among treatments. The response variables were *T. testudinum* mean leaf width, shoot density, mean number of leaves per shoot, and belowground biomass (aboveground biomass and leaf length were not measured because clipping alters these variables and cannot indicate a response). Turtlegrass areal NAPP and C:N ratios were measured at the conclusion of the experiment, after 21 wk. A 1-way ANOVA was used with Student-Newman-Keuls (SNK) post hoc comparisons between treatments for both BACI (Start–End) response variables and End data response variables. Normality was tested using a Shapiro-Wilk test, and Levene's test of equality was used to check data for homogeneity of variance.

#### 2.6.3. Turtlegrass recovery

The exclusion cage experiment also employed a BACI design. Replicate seagrass cores in each treatment were averaged. Start values were subtracted from the End values for all turtlegrass response variable means (mean leaf length, mean leaf width, shoot density, mean number of leaves per shoot, and above- and belowground turtlegrass biomass), and a *t*-test was used to compare treatment means to determine if *T. testudinum* had recovered. If no differences were detected between cage and control values, *T. testudinum* was considered recovered. Aboveground biomass required a square root transformation to achieve homogeneity of variance. Additionally, *t*-tests were used to compare treatment End data means. Belowground biomass values at the conclusion of the experiment were square root transformed to achieve homogeneity of variance.

The 28 and 110 wk simulated grazing recovery cores were analyzed using a 1-way ANOVA for each sampling period. In addition, a BACI design (Sampling date data – Experiment conclusion data) was used to determine differences between treatment means with SNK post hoc comparisons. While the ANOVA on the recovery cores tested whether turtlegrass response variables (mean leaf length, mean leaf width, shoot density, mean number of leaves per shoot, and above- and belowground turtlegrass biomass) in the previously clipped plots resemble the control plots, thus showing recovery, the BACI results indicated whether or not variables showed trends of recovery since the simulated clipping events.

All *F*-values in the main text will be presented with the degrees of freedom (df) both between and within groups, whereas the ANOVA result tables will present the sum of the df. All statistical analyses were performed using SigmaPlot™ 12.3 and the associated statistical package SigmaStat™.

## 3. RESULTS

### 3.1. Exclusion cages

There were no detectable differences in light levels between caged (918.44 ± 82.1 μE $m^{-2}$ $s^{-1}$) and control (821.39 ± 92.2 μE $m^{-2}$ $s^{-1}$) treatments at the mid-point ($t_{12}$ = 0.786, p = 0.44) or at the conclusion of the experiment (caged: 650.67 ± 49.6 μE $m^{-2}$ $s^{-1}$ and control: 643.35 ± 50.5 μE $m^{-2}$ $s^{-1}$; $t_{12}$ = 0.103, p = 0.92). Because mean PAR measurements were all above the reported saturation levels for turtlegrass (357–438 μE $m^{-2}$ $s^{-1}$; Fourqurean & Zieman 1991), it is very unlikely that light reduction caused by cage netting and/or biofouling negatively affected turtlegrass growth.

Over the 20 wk experiment, 144 seagrass cores were collected and analyzed. When the turtle exclusion cages were established in June 2016, no response variables showed significant differences between caged and control areas. After excluding green turtles from the caged *Thalassia testudinum* for 20 wk, BACI analysis showed a lower shoot density in controls than cages ($t_{22}$ = 2.160, p = 0.04; Table 1). When comparing the caged and control means at the end of the experiment, there were fewer shoots in the control area than in the excluded area ($t_{22}$ = 3.201, p = 0.004), and controls tended to have less aboveground biomass than cages ($t_{22}$ = 2.008, p = 0.06; Table 2).

Table 1. Results of the cage/control before-after-control-impact (BACI) analysis for all *Thalassia testudinum* response variables at the end of the 20 wk exclusion cage experiment (n = 12). Control and Cage values represent the mean ± SE End–Start response variable. **Bold** indicates significance (p < 0.05). AG: aboveground; BG: belowground; DW: dry weight

| Response variable | Control | Cage | df | *t* | p |
|---|---|---|---|---|---|
| AG biomass (g DW $m^{-2}$) | −20.01 ± 222.0 | 496.49 ± 210.7 | 22 | 1.475 | 0.15 |
| BG biomass (g DW $m^{-2}$) | 892.39 ± 2142.8 | 1140.00 ± 911.2 | 22 | 0.106 | 0.92 |
| Shoot density (shoots $m^{-2}$) | −319.81 ± 69.4 | 91.37 ± 143.4 | 22 | 2.160 | **0.04** |
| Mean number leaves $shoot^{-1}$ | −0.64 ± 0.09 | −0.62 ± 0.18 | 22 | 0.120 | 0.91 |
| Mean leaf length (cm) | 5.53 ± 1.6 | 2.78 ± 1.41 | 22 | 1.495 | 0.15 |
| Mean leaf width (cm) | 0.035 ± 0.03 | 10.73 ± 3.53 | 22 | 0.441 | 0.66 |

Table 2. Results of *t*-tests to determine whether *Thalassia testudinum* response variables were statistically different at the end of the 20 wk exclusion cage experiment (n = 12). Control and cage values represent mean ± SE End response variables. **Bold** indicates significance (p < 0.05). AG: aboveground; BG: belowground; DW: dry weight

| Response variable | Control | Cage | df | *t* | p |
|---|---|---|---|---|---|
| AG biomass (g DW $m^{-2}$) | 853.93 ± 171.0 | 1368.59 ± 191.0 | 22 | 2.008 | 0.06 |
| BG biomass (g DW $m^{-2}$) | 6332.36 ± 1895.5 | 7355.27 ± 1214.4 | 22 | 0.454 | 0.65 |
| Shoot density (shoots $m^{-2}$) | 548.25 ± 61.9 | 1005.12 ± 128.6 | 22 | 3.201 | **0.004** |
| Mean number leaves $shoot^{-1}$ | 2.74 ± 0.10 | 2.64 ± 0.09 | 22 | −0.788 | 0.44 |
| Mean leaf length (cm) | 13.97 ± 0.74 | 15.22 ± 0.67 | 22 | 1.253 | 0.22 |
| Mean leaf width (cm) | 0.66 ± 0.02 | 0.67 ± .01 | 22 | 0.558 | 0.58 |

### 3.2. Simulated grazing plots

At the initiation of the experiment, there were no detectable differences in response variables between the randomly assigned experimental plots. Turtlegrass aboveground biomass and mean leaf length were clearly much lower in clipped plots because of the clipping treatment, so those data are not presented. Results from the BACI analysis indicated that turtlegrass belowground biomass, shoot density, and mean number of leaves per shoot were not affected by repeated simulated grazing on short temporal scales (Table 3). Leaves grew wider over time in the control, suggesting that these leaves were responding to increased temperatures and light levels during the growing season, but leaves in the reclipped plots did not widen, presumably due to the added stress ($F_{2,15}$ = 4.950, p = 0.02; Fig. 4).

End data results (Table 4) showed that mean leaf width was significantly narrower following repeated regrazing, although there were no differences between 6 and 3 wk clipping levels, only between clipped and control treatments ($F_{2,24}$ = 24.385, p < 0.001), and that there tended to be higher shoot densities in the clipped treatments than in control treatment ($F_{2,24}$ = 2.957, p = 0.07; Fig. 5). Additionally, NAPP was significantly lower in clipped than in unclipped treatments ($F_{2,24}$ = 8.165, p = 0.002; Fig. 6). C:N molar ratio (wt/wt) was not significantly different between treatments and controls ($F_{2,6}$ = 0.535, p = 0.61).

### 3.3. Turtlegrass recovery

Of the 6 exclusion cages set up in March 2017 on the naturally grazed feeding plots, only 4 cages remained at the conclusion of the experiment due to boat propeller damage. Light data analysis failed to detect differences between caged (1371.03 ± 141.2 µE $m^{-2}$ $s^{-1}$) and control (1443.88 ± 99.3 µE $m^{-2}$ $s^{-1}$)

Table 3. Results of BACI analysis between simulated grazing treatments on *Thalassia testudinum* response variables (n = 6). Control, 6 wk, and 3 wk clipping values represent mean ± SE End–Start response variables of all treatments. **Bold** indicates significance (p < 0.05). BG: belowground; DW: dry weight

| Response variable | Control | 6 wk | 3 wk | df | *F* | p |
|---|---|---|---|---|---|---|
| BG biomass (g DW $m^{-2}$) | 220.00 ± 158.7 | 439.16 ± 109.1 | −155.81 ± 190.0 | 17 | 3.204 | 0.07 |
| Shoot density (shoots $m^{-2}$) | −365.50 ± 238.0 | −36.55 ± 454.45 | 292.40 ± 414.8 | 17 | 0.746 | 0.49 |
| Mean number leaves $shoot^{-1}$ | −0.63 ± 0.14 | −0.72 ± 0.16 | −0.55 ± 0.29 | 17 | 0.169 | 0.85 |
| Mean leaf width (cm) | 0.10 ± 0.03 | −0.03 ± 0.04 | −0.02 ± 0.04 | 17 | 4.950 | **0.02** |

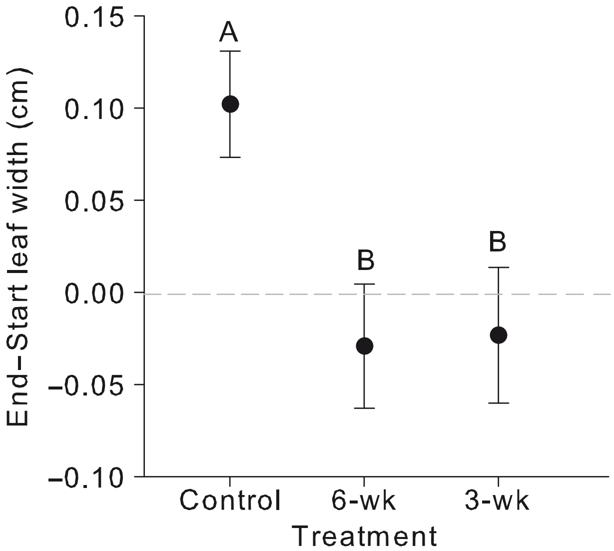


Fig. 4. Mean differences (±SE) in *Thalassia testudinum* leaf width in the BACI analysis between simulated clipping treatment levels (control, 6 wk clipping, 3 wk clipping). Letters indicate Student-Newman-Keuls post hoc results (different letters indicate $p < 0.05$) ($F_{2,15} = 4.95$, $p = 0.02$)

treatments at the mid-point of the experiment ($t_4$ = −0.422, p = 0.69), or between caged (917.88 ± 20.3 µE $m^{-2}$ $s^{-1}$) and control (936.11 ± 20.4 µE $m^{-2}$ $s^{-1}$) plots at the conclusion ($t_{12}$ = −0.0633, p = 0.55) of the experiment. Mean PAR measurements were again above the reported light saturation levels for *T. testudinum* of 357–438 µE $m^{-2}$ $s^{-1}$ (Fourqurean & Zieman 1991), so it is unlikely that light reduction caused by the cage netting and/or biofouling negatively affected turtlegrass growth or other parameters.

At the start of this experiment, all *T. testudinum* response variables were significantly different between caged and control plots, except for the mean number of leaves per shoot. After 14 wk of protection from natural turtle grazing, both BACI (Table 5) and End (Table 6) results indicated that all of the same response variables remained significantly different, thus showing no signs of recovery.

After turtlegrass in the simulated grazing plots regrew for 28 wk, *T. testudinum* mean leaf width ($F_{2,15}$ = 10.541, p < 0.001) was the only response variable to show significant differences between treatments (Table 7). At the conclusion of the simulated grazing experiment, leaf width was narrower in clipped vs. unclipped plots (Table 2; $F_{2,24}$ = 4.950, p = 0.02), and after 28 wk of recovery time, *T. testudinum* leaf width in the control plots remained significantly wider than leaves that had previously been grazed every 6 or every 3 wk (Fig. 7). BACI results (Table 8) indicated an increase in aboveground biomass (Fig. 8) and mean leaf length (Fig. 9) in clipped plots, suggesting that after 28 wk, *T. testudinum* recovered aboveground biomass and leaf length after repeated regrazing. Post hoc analysis indicated that the turtlegrass clipped every 3 wk did not recover leaf length as quickly as turtlegrass clipped every 6 wk.

After 110 wk of recovery, leaves remained narrower in clipped vs. unclipped plots ($F_{2,15}$ = 6.976, p = 0.01; Table 9, Fig. 7). Additionally, there were fewer leaves per shoot in the 3 wk than in the 6 wk clipped plots. which were also significantly less than control plots ($F_{2,15}$ = 18.108, p < 0.001; Fig. 10). This was the only variable that showed significant differences between clipping treatments. Also, there was more aboveground biomass in control than in clipped plots, likely as a result of differences in the number of leaves per shoot ($F_{2,15}$ = 4.826, p = 0.02). BACI results are similar to data presented after 28 wk of recovery (Table 8): while aboveground biomass and leaf length recovered, leaf width remained significantly narrower.

## 4. DISCUSSION

We found that excluding *Chelonia mydas* led to more *Thalassia testudinum* shoots and higher aboveground biomass in the grazed control versus the ungrazed turtle exclusion caged area. Simulat-

Table 4. Results of 1-way ANOVA between simulated grazing treatments on *Thalassia testudinum* response variables (n = 6). Control, 6 wk, and 3 wk clipping values represent mean ± SE End response variables of all treatments. **Bold** indicates significance (p < 0.05). BG: belowground; DW: dry weight

| Response variable | Control | 6 wk | 3 wk | df | *F* | p |
|---|---|---|---|---|---|---|
| BG biomass (g DW $m^{-2}$) | 170.36 ± 288.4 | 1412.80 ± 1068.8 | 1068.82 ± 319.0 | 26 | 0.944 | 0.40 |
| Shoot density (shoots $m^{-2}$) | 1364.52 ± 166.6 | 2119.88 ± 258.4 | 1876.22 ± 237.2 | 26 | 2.957 | 0.07 |
| Mean number leaves $shoot^{-1}$ | 2.18 ± 0.13 | 2.09 ± 0.09 | 1.97 ± 0.07 | 26 | 1.143 | 0.34 |
| Mean leaf width (cm) | 0.77 ± 0.03 | 0.57 ± 0.03 | 0.56 ± 0.01 | 26 | 24.385 | **<0.001** |
| Primary productivity (g DW $m^{-2}$ $d^{-1}$) | 1.55 ± 0.2 | 0.85 ± 0.1 | 0.93 ± 0.1 | 26 | 7.333 | **0.003** |
| Carbon nitrogen ratio (wt/wt) | 24.76 ± 0.8 | 22.61 ± 2.1 | 23.91 ± 1.2 | 8 | 0.535 | 0.61 |

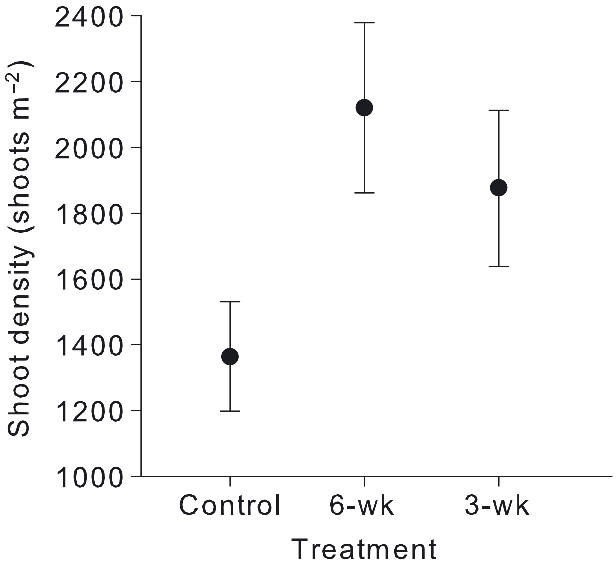


Fig. 5. *Thalassia testudinum* shoot density (±SE) after a 21 wk simulated green turtle grazing experiment ($F_{2,24}$ = 2.957, p = 0.07)

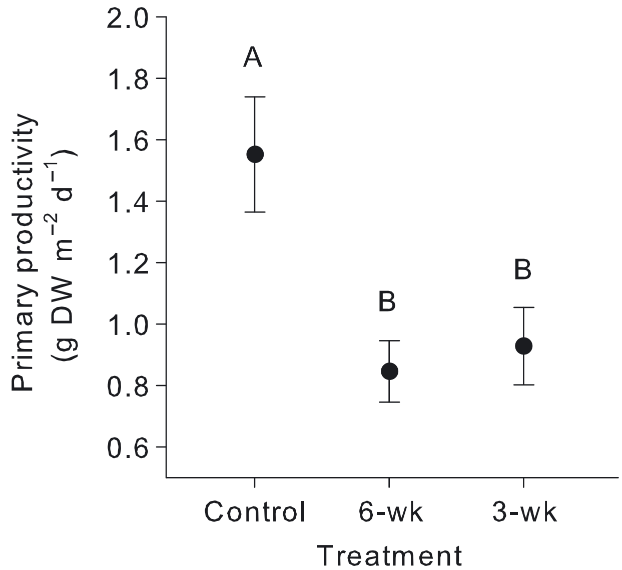


Fig. 6. *Thalassia testudinum* net aboveground primary productivity (±SE) after a 21 wk simulated green turtle grazing experiment. Letters indicate Student-Newman-Keuls post hoc results (different letters indicate p < 0.05) ($F_{2,24}$ = 8.165, p = 0.002). DW: dry weight

ing *C. mydas* grazing for 3 mo produced narrower turtlegrass leaves and lowered productivity in clipped plots when compared to unclipped controls. Turtlegrass did not recover from natural turtle grazing after 14 wk of protection from green turtles and did not completely recover following simulated turtle grazing, as it continued to show signs of stress 2 yr following a relaxation of simulated grazing, with leaves narrower and fewer leaves per shoot depending on grazing intensity.

### 4.1. Exclusion cages

We expected to find a relatively small green turtle population in St. Joseph Bay, given their recent expansion into the northern Gulf of Mexico, and hypothesized that the short-term exclusion of turtles would not produce significant differences between grazed and ungrazed areas. However, excluding green turtles decreased turtlegrass aboveground biomass and shoot density in grazed areas. Grazing did not clearly affect belowground biomass, number of leaves per shoot, or their mean length or width.

While reduced light availability was ruled out as an experimental artefact, the cage structure may have produced an unwanted effect. Other researchers have observed that structure can attract juvenile green turtles (P. Carlson pers. comm.), and, anecdotally, we observed more turtles

Table 5. Results of the End–Start BACI analysis for all response variables in the 14 wk *Thalassia testudinum* recovery exclusion cage experiment (n = 4). Control and Cage values represent the mean ± SE End–Start response variable. **Bold** indicates significance (p < 0.05). AG: aboveground; BG: belowground; DW: dry weight

| Response variable | Control | Cage | df | *t* | p |
|---|---|---|---|---|---|
| AG biomass (g DW m$^{-2}$) | 682.07 ± 138.6 | 89.78 ± 60.8 | 14 | −16.637 | **<0.0001** |
| BG biomass (g DW m$^{-2}$) | 83.56 ± 10.8 | 30.66 ± 5.2 | 14 | −52.902 | **0.001** |
| Mean number leaves shoot$^{-1}$ | 0.75 ± 0.27 | 0.66 ± 0.25 | 14 | 0.241 | 0.81 |
| Mean leaf length (cm) | 8.40 ± 1.4 | 4.00 ± 1.4 | 14 | −2.231 | **0.04** |
| Mean leaf width (cm) | −0.061 ± 0.04 | 0.098 ± 0.04 | 14 | 2.603 | **0.03** |

Table 6. Results of the *t*-test to determine whether *Thalassia testudinum* response variable means were able to recover following a 14 wk long exclusion cage experiment (n = 4). Control and Cage values represent the mean ± SE End response variable. **Bold** indicates significance (p < 0.05). AG: aboveground, BG: belowground; DW: dry weight

| Response variable | Control | Cage | df | *t* | p |
|---|---|---|---|---|---|
| AG biomass (g DW m$^{-2}$) | 1078.60 ± 130.8 | 162.66 ± 55.6 | 14 | −6.445 | **<0.001** |
| BG biomass (g DW m$^{-2}$) | 9927.7 ± 2049.3 | 914.33 ± 216.26 | 14 | −6.369 | **<0.001** |
| Shoot density (shoots m$^{-2}$) | 959.43 ± 130.6 | 411.18 ± 133.9 | 14 | −2.931 | **0.01** |
| Mean number leaves shoot$^{-1}$ | 3.05 ± 0.17 | 3.06 ± 0.27 | 14 | 0.049 | 0.96 |
| Mean leaf length (cm) | 14.55 ± 1.50 | 8.28 ± 1.45 | 14 | −3.001 | **0.01** |
| Mean leaf width (cm) | 0.60 ± 0.03 | 0.47 ± 0.04 | 14 | −2.862 | **0.01** |

Table 7. One-way ANOVA results between simulated grazing treatments on *Thalassia testudinum* response variables after 28 wk of recovery. Control, 6 wk, and 3 wk clipping values represent mean ± SE End response variables of all treatments. **Bold** indicates significance (p < 0.05). AG: aboveground, BG: belowground; DW: dry weight

| Response variable | Control | 6 wk | 3 wk | df | *F* | p |
|---|---|---|---|---|---|---|
| AG biomass (g DW $m^{-2}$) | 116.47 ± 25.3 | 98.68 ± 16.9 | 70.60 ± 18.9 | 17 | 1.252 | 0.31 |
| BG biomass (g DW $m^{-2}$) | 1517.7 ± 198.1 | 1138.0 ± 191.8 | 924.1 ± 145.8 | 17 | 2.787 | 0.09 |
| Shoot density (shoots $m^{-2}$) | 1498.5 ± 279.8 | 1644.7 ± 231.7 | 1279.2 ± 191.3 | 17 | 0.602 | 0.56 |
| Mean number leaves $shoot^{-1}$ | 3.18 ± 0.17 | 3.65 ± 0.17 | 3.23 ± 0.11 | 17 | 2.864 | 0.09 |
| Mean leaf length (cm) | 8.60 ± 0.57 | 6.84 ± 0.56 | 7.44 ± 0.60 | 17 | 2.361 | 0.13 |
| Mean leaf width (cm) | 0.64 ± 0.03 | 0.50 ± 0.02 | 0.51 ± 0.02 | 17 | 10.541 | **0.001** |

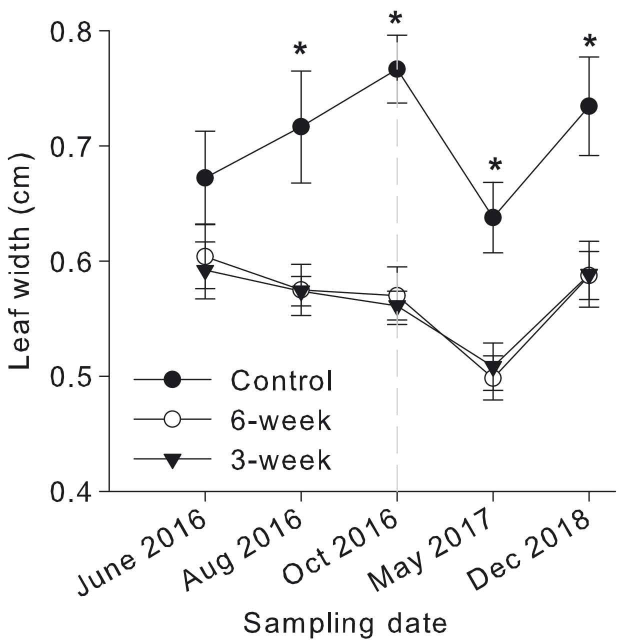


Fig. 7. *Thalassia testudinum* leaf width (±SE) throughout the simulated grazing experiment and following recovery sampling. Grey dashed line indicates experiment conclusion date (asterisks indicate p < 0.05)

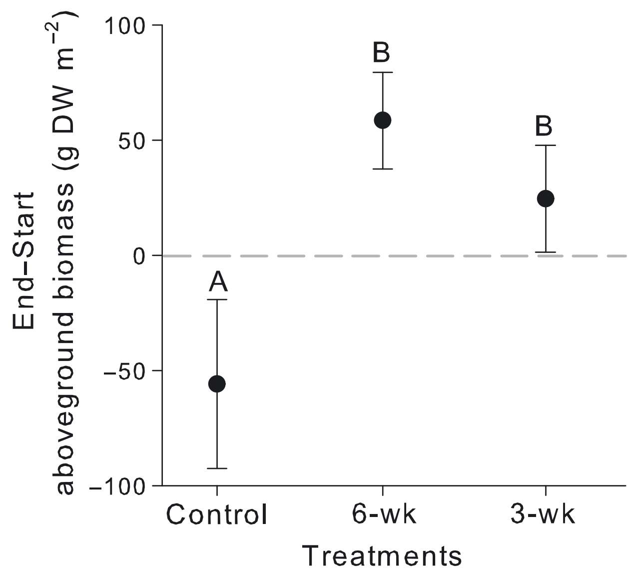


Fig. 8. Mean differences (±SE) in *Thalassia testudinum* aboveground biomass in the 28 wk turtlegrass recovery BACI analysis between simulated clipping treatment levels (control, 6 wk clipping, 3 wk clipping). Letters indicate Student-Newman-Keuls post hoc results (different letters indicate p < 0.05) ($F_{2,15}$ = 5.587, p = 0.02). DW: dry weight

around cages than elsewhere. It is therefore possible that the *C. mydas* grazing effects we measured are exaggerated because turtle densities may have been artificially elevated in the vicinity of the cages. Results remain pertinent because given that green turtle abundances are increasing in the northern Gulf of Mexico, they reflect how increased green turtle grazing will affect *T. testudinum* in a temperate bay.

Table 8. End–Start BACI results between simulated grazing treatments on *Thalassia testudinum* response variables after 28 wk of recovery. Control, 6 wk, and 3 wk clipping values represent mean ± SE response variables of all treatments. **Bold** indicates significance (p < 0.05). AG: aboveground, BG: Belowground; DW: dry weight

| Response variable | Control | 6 wk | 3 wk | df | *F* | p |
|---|---|---|---|---|---|---|
| AG biomass (g DW $m^{-2}$) | −55.84 ± 39.7 | 58.51 ± 21.0 | 24.59 ± 21.1 | 17 | 5.587 | **0.02** |
| BG biomass (g DW $m^{-2}$) | 336.2 ± 282.3 | −270.8 ± 254.6 | −102.8 ± 246.9 | 17 | 1.434 | 0.27 |
| Shoot density (shoots $m^{-2}$) | 0 ± 315.3 | −475.1 ± 377.4 | −584.8 ± 489.3 | 17 | 0.602 | 0.56 |
| Mean number leaves $shoot^{-1}$ | 1.05 ± 0.18 | 1.54 ± 0.20 | 1.21 ± 0.09 | 17 | 2.352 | 0.13 |
| Mean leaf length (cm) | 18.67 ± 5.50 | 164.00 ± 11.88 | 135.96 ± 5.79 | 17 | 87.027 | **<0.001** |
| Mean leaf width (cm) | −0.14 ± 0.03 | −0.08 ± 0.02 | −0.06 ± 0.02 | 17 | 2.360 | 0.13 |

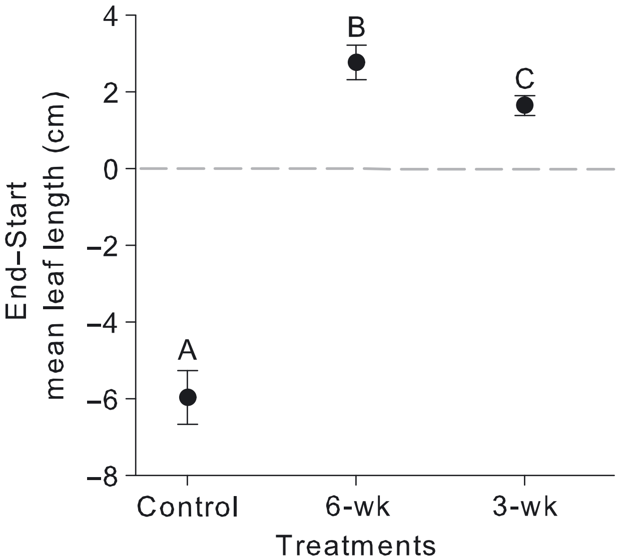


Fig. 9. Mean differences (±SE) in *Thalassia testudinum* mean leaf length in the 28 wk turtlegrass recovery BACI analysis between simulated clipping treatment levels (control, 6 wk clipping, 3 wk clipping). Letters indicate Student-Newman-Keuls post hoc results (different letters indicate $p < 0.05$) ($F_{2,15} = 87.027$, $p < 0.001$)

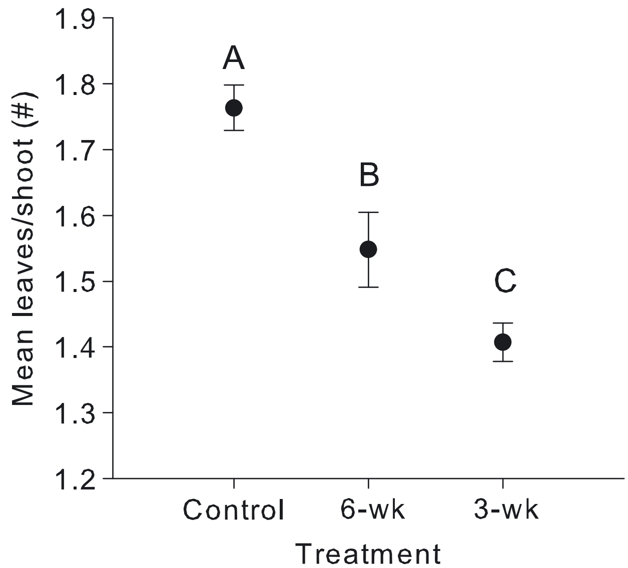


Fig. 10. Number of *Thalassia testudinum* leaves per shoot (±SE) between simulated clipping treatment levels (control, 6 wk clipping, 3 wk clipping) after 110 wk of recovery. Letters indicate Student-Newman-Keuls post hoc results (different letters indicate $p < 0.05$) ($F_{2,15} = 18.108$, $p < 0.001$)

To our knowledge, cages have not been tested to evaluate their effects on turtle behavior. One approach would be to use a partial cage that allows turtles to forage in its interior and then compare results with those of a nearby uncaged area. Alternatively, uncaged controls some distance away from the experimental array would also allow an evaluation of this potential artefact. Future studies should consider employing these procedures to account for potential cage effects.

### 4.2. Simulated grazing plots

Repeated regrazing can influence the morphology (Thayer et al. 1984, Ibarra-Obando et al. 2004, Moran & Bjorndal 2005, Kuiper-Linley et al. 2007, Christianen et al. 2012), productivity (Aragones & Marsh 1999, Moran & Bjorndal 2005, Kuiper-Linley et al. 2007, Christianen et al. 2012), biomass (Aragones & Marsh 1999, Kuiper-Linley et al. 2007), tissue chemistry (Moran & Bjorndal 2005, Kuiper-Linley et al. 2007), biogeochemical cycling (Aragones & Marsh 1999, Moran & Bjorndal 2005, 2007), and community composition of seagrasses (Zieman 1974, Thayer et al. 1984, Aragones & Marsh 1999, Moran & Bjorndal 2007). Our repeated simulated turtle grazing for 3 mo produced significantly narrower turtlegrass leaves, which is a stress symptom consistent with simulated grazing elsewhere in the northern Gulf of Mexico (Ibarra-Obando et al. 2004), the Bahamas (Moran & Bjorndal 2005), and natural grazing in Mexico (Molina Hernández & van Tussenbroek 2014). Primary pro-

Table 9. One-way ANOVA results between simulated grazing treatments on *Thalassia testudinum* response variables after 110 wk of recovery. Control, 6 wk, and 3 wk clipping values represent mean ± SE End response variables of all treatments. **Bold** indicates significance ($p < 0.05$). AG: aboveground, BG: belowground; DW: dry weight

| Response variable | Control | 6 wk | 3 wk | df | *F* | p |
|---|---|---|---|---|---|---|
| AG biomass (g DW $m^{-2}$) | 155.7 ± 13.3 | 105.2 ± 13.7 | 108.3 ± 11.6 | 17 | 4.826 | **0.02** |
| BG biomass (g DW $m^{-2}$) | 1217.8 ± 73.6 | 1119.2 ± 61.0 | 1223.8 ± 149.3 | 17 | 0.0157 | 0.98 |
| Shoot density (shoots $m^{-2}$) | 1973.7 ± 217.6 | 2485.4 ± 386.8 | 2229.5 ± 249.5 | 17 | 0.688 | 0.52 |
| Mean number leaves $shoot^{-1}$ | 1.76 ± 0.03 | 1.55 ± 0.06 | 1.40 ± 0.03 | 17 | 18.108 | **<0.001** |
| Mean leaf length (cm) | 12.85 ± 1.48 | 12.99 ± 1.19 | 13.69 ± 1.29 | 17 | 0.116 | 0.89 |
| Mean leaf width (cm) | 0.73 ± 0.04 | 0.59 ± 0.02 | 0.59 ± 0.03 | 17 | 6.976 | **0.01** |

ductivity was lower in the clipped turtlegrass plots than in the ungrazed, control plots, comparable to results in natural grazing plots in Puerto Morelos, Mexico, where grazed turtlegrass showed decreased foliar productivity compared to adjacent, ungrazed turtlegrass (Molina Hernández & van Tussenbroek 2014). However, neither *T. testudinum* productivity (Moran & Bjorndal 2005), nor nutrient content (Moran & Bjorndal 2007) declined after 16 mo of simulated turtle grazing in the Bahamas, where turtlegrass exhibited compensatory growth and sustained prolonged grazing with minimal negative effects. However, in Perdido Bay, Florida (northern Gulf of Mexico), Ibarra-Obando et al. (2004) found that after simulating grazing, turtlegrass under low light conditions had lower primary production and did not exhibit compensatory growth. This suggests either that over a longer period of sustained simulated grazing, our turtlegrass plots would have eventually also exhibited compensatory growth, or that warm, temperate turtlegrass meadows respond differently to repeated regrazing, likely due to limited light availability during winter months. It has also been suggested that in P-limited turtlegrass meadows such as St. Joseph Bay (Fourqurean & Cai 2001), regrazing is not sustainable (Holzer & McGlathery 2016).

### 4.3. Turtlegrass recovery

During the field experiment, we discovered the first natural juvenile green sea turtle feeding plots reported in the northern Gulf of Mexico (29.70° N, 85.35° W; Fig. 3A), confirming that green turtles produce distinct feeding plots near the northern limit of their range in the Gulf. The feeding plots originated from an unvegetated sand flat to about a 1.5 m wide section of naturally grazed turtlegrass, along the edge of a large expanse of ungrazed turtlegrass (Fig. 3). The feeding plots continued for at least 10 m along the margin of the turtlegrass meadow, with at least 3 separate plots observed. Although there were many turtles in the area, it is not known for certain whether one or more turtles regrazed these plots. We also encountered small (~0.5 × 0.5 m), roughly circular areas that remained ungrazed within the presumed feeding plots (visible in Fig. 3A). Additionally, there were several small (~1 × 1 m), distinct grazed plots within the dense, mostly ungrazed bed that connected to the larger grazed area (Fig. 3B). Perhaps turtles selectively grazed shoots containing the ascidian *Botrylloides* sp., as suggested by Williams et al. (2014) to be a major food source in St. Joseph Bay. Nearby along the same sand flat, we discovered the only mixed seagrass bed seen in the southern part of St. Joseph Bay. Turtlegrass was mixed with shoal grass *Halodule wrightii*, a pioneering seagrass species, along the border of a dense turtlegrass bed. It is possible that the site was previously a green turtle grazing plot, and that shoal grass colonized what was formerly a monospecific turtlegrass meadow, similar to results reported by Kelkar et al. (2013b) in the Lakshadweep Archipelago, where sustained turtle grazing caused a seagrass species composition shift from a long-lived to a short-lived, pioneering species.

Following the discovery of these natural green turtle feeding plots, we evaluated turtlegrass recovery from natural and simulated green turtle grazing. After protecting naturally grazed turtlegrass, no response variable showed recovery from repeated regrazing after 14 wk of protection, suggesting that turtlegrass requires more time left undisturbed to completely recover from green turtle grazing in St. Joseph Bay. In the clipping experiment, after 28 wk, *T. testudinum* aboveground biomass and leaf length had recovered, but leaves remained narrower in the simulated grazing plots. The plots continued to show residual stress symptoms 110 wk after simulated grazing concluded: leaves remained thinner and there were fewer average leaves per shoot, depending on clipping intensity. While average leaves per shoot showed marginal differences between clipping treatments after 28 wk of recovery in May 2017, in December 2018 after 110 wk of recovery, average leaves per shoot were much lower in clipped plots. Because samples were taken in December, it is possible that the cold weather exacerbated the stress and created synergistic effects, not only resulting in fewer leaves per shoot, but also in lower aboveground biomass in grazed plots than in the control plots.

In Bailey's Bay, Bermuda, at least 2 yr after simulated grazing, *T. testudinum* stress symptoms persisted in the form of narrow leaves and low shoot density, but only in P-limited areas (Holzer & McGlathery 2016). After 1 yr of protection from *C. mydas* grazing in offshore Bermuda, *T. testudinum* leaf width was similar to ungrazed controls, and leaf length, biomass, and productivity — while not completely recovered — had increased (Fourqurean et al. 2010), whereas the leaves in St. Joseph Bay remained narrower and showed no signs of recovery 2 yr after halting simulated grazing.

However, Fourqurean et al. (2019) found that after 11 yr of monitoring, turtle grazing resulted in seagrass leaves that had become narrower and shorter in Bermuda. While *C. mydas* grazing has been destructive in certain areas (Williams 1988, Fourqurean et al. 2010, 2019, Kelkar et al. 2013a), some researchers have seen sustained positive effects of grazing in seagrass species (Moran & Bjorndal 2007, Christianen et al. 2012). Evidence suggests that either seagrass nutrient status (Holzer & McGlathery 2016), seasonality of light availability (Manuel et al. 2013), or some combination thereof may be the key to understanding when sustained long-term turtle grazing is possible, with oligotrophic and/or temperate waters unable to sustain prolonged turtle grazing.

## 5. CONCLUSIONS

The continuing increase of green turtle numbers has led to a need to determine the long-term consequences for their *Thalassia testudinum* feeding grounds. In some locations, green turtles have had little impact on turtlegrass communities (e.g. Moran & Bjorndal 2005, van Tussenbroek & Morales 2017), while in other locations, especially those burdened by other stressors, including seasonality of light, there have been severe impacts to seagrass meadows that include their complete collapse (Christianen et al. 2014, Fourqurean et al. 2019). In some locations, turtlegrass was able to recover following natural or simulated grazing events, such as in the Bahamas (Moran & Bjorndal 2005), whereas in other locations, including the northern Gulf of Mexico, it was not (Williams 1988, Ibarra-Obando et al. 2004, Fourqurean et al. 2010, Holzer & McGlathery 2016). In the present study in the northern Gulf of Mexico, we found that excluding green turtles from turtlegrass led to an increase in *T. testudinum* shoot density and that simulated turtle grazing altered *T. testudinum* morphology by producing narrower leaves and decreasing productivity. Naturally grazed turtlegrass beds protected from further turtle grazing did not recover after 14 wk of protection, and 2 yr following the relaxation of simulated turtle grazing pressure, turtlegrass continued to show residual stress symptoms: leaves remained thinner, and there were fewer average leaves per shoot, depending on clipping intensity. Given that achieving a balanced ecosystem where ecosystem services of both herbivores and seagrasses are maximized (Scott et al. 2018) may prove challenging in temperate, oligotrophic ecosystems, it is vital that we continue studying the effects that increasing green turtle populations are having on seagrass meadows across different latitudes in the world's oceans.

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