

Recovery of a large herbivore changes regulation of seagrass productivity in a naturally grazed Caribbean ecosystem

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Abstract. What happens in meadows after populations of natural grazers rebound following centuries of low abundance? Many seagrass ecosystems are now experiencing this phenomenon with the recovery of green turtles (*Chelonia mydas*), large-bodied marine herbivores that feed on seagrasses. These seagrass ecosystems provide a rare opportunity to study ecosystem-wide shifts that result from a recovery of herbivores. We evaluate changes in regulation of seagrass productivity in a naturally grazed tropical ecosystem by (1) comparing *Thalassia testudinum* productivity in grazed and ungrazed areas and (2) evaluating potential regulating mechanisms of *T. testudinum* productivity. We established 129 green turtle exclusion cages in grazed and ungrazed areas to quantify *T. testudinum* growth (linear, area, mass, productivity: biomass [P:B]). In each enclosure, we recorded temperature, irradiance, water depth, nitrogen:phosphorus ratio (N:P) of blade tissue, grazing intensity before cage placement, and *T. testudinum* structural and nutrient characteristics. *Thalassia testudinum* exhibited compensatory growth in grazed areas via stimulated blade linear growth, blade area growth, and P:B across seasonal high and low growth periods and in shallow (3–4 m) and deep (9–10 m) seagrass meadows. Irradiance, depth, and N:P ratios had significant roles in regulating mass growth and P:B of *T. testudinum* in ungrazed areas. Depth was a significant regulating factor of mass growth and P:B in grazed areas; rates were higher and more variable in shallow meadows than in deep meadows. Grazing intensity was also a significant regulating factor for P:B, stimulating tissue turnover with increasing grazing pressure. This study provides important insights into how recovery of a large marine herbivore can result in dramatic, sustainable changes in the regulation of seagrass productivity. We also highlight the need for a historical perspective and use of appropriate indicators, including P:B and grazing intensity, when evaluating seagrass response to green turtle grazing as meadows are returned to a natural grazed state. In an age of green turtle recovery and global seagrass decline due to anthropogenic threats, a thorough understanding of green turtle–seagrass interactions at the ecosystem level is critical to ensure the restoration of seagrass ecosystems and continued recovery of green turtle populations.

Key words: *Chelonia mydas*; compensatory growth; grazing intensity; herbivory; productivity; seagrass; *Thalassia testudinum*.

INTRODUCTION

Grazing by large-bodied herbivores is a well-established mechanism for regulating primary productivity in terrestrial ecosystems (McNaughton et al. 1988, de Mazancourt and Loreau 2000, Frank et al. 2002). Productivity of many grasslands, for example, is regulated by a combination of abiotic factors (e.g., seasonal precipitation, nutrient availability) and intensive grazing by

large mammalian herbivores. Such interactions result in stimulated production and turnover of aboveground biomass (Oesterheld and McNaughton 1991, Frank et al. 2002, Schönbach et al. 2011), increased plant nutrient content (McNaughton et al. 1988), successional shifts in plant community composition and diversity (McNaughton 1979, Nickell et al. 2018), and accelerated nutrient cycles (de Mazancourt and Loreau 2000, Wang et al. 2016). In contrast, substantially less is known about the roles of large herbivores in vascular plant-based aquatic ecosystems, including interactions between large herbivores and seagrass meadows (Poore et al. 2012, Bakker et al. 2016, Wood et al. 2016).

Seagrass meadows serve as a foundation for some of the most productive ecosystems on the planet (Duarte and

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Chiscano 1999), but are rapidly declining worldwide due to many anthropogenic factors, including eutrophication, climate change, and coastal development (Orth et al. 2006, Waycott et al. 2009, Grech et al. 2012). Caribbean seagrass meadows are among the most productive systems (Duarte and Chiscano 1999) and are typically dominated by *Thalassia testudinum*, a climax species characterized by long strap-like blades in ungrazed meadows, deep and dense rhizome mats, and high rates of primary production (van Tussenbroek et al. 2014). In the absence of grazing, productivity of *T. testudinum* meadows is primarily regulated by seasonal water temperature, irradiance, and nutrient limitation (van Tussenbroek 1995, Lee and Dunton 1997, Lee et al. 2007), with water depth and sediment characteristics acting as secondary regulating factors (van Tussenbroek et al. 2006). But what happens when conservation efforts are successful and natural grazers return to seagrass meadows after centuries of low abundance due to overexploitation by humans?

Populations of green turtles (*Chelonia mydas*), a large marine herbivore, have been heavily overexploited by humans since the 15th century (Bjorndal and Jackson 2003), and together with large sirenians (Families: Trichechidae and Dugongidae), were once responsible for consuming the majority of seagrass biomass worldwide (Domning 2001, Jackson et al. 2001, Aragones et al. 2012). Populations of Caribbean green turtles alone are estimated to have been reduced by 97% from historic levels (Jackson et al. 2001), rendering studies related to the top-down effects of grazing in seagrass meadows difficult to conduct, and leading to the general assumption that modern seagrass meadows are primarily bottom-up regulated (Burkepile 2013). However, populations of green turtles are now recovering in many areas as a result of long-term conservation efforts (Chaloupka et al. 2008, Weber et al. 2014, Mazaris et al. 2017), offering a unique opportunity to understand the ecological role of these large herbivores and how seagrass ecosystems once functioned under a consistent grazing regime. Green turtle recovery and the return of many seagrass meadows to a natural grazed state have raised concerns that ecosystem services provided by ungrazed seagrasses may be lost (Heithaus et al. 2014, Atwood et al. 2015, Maxwell et al. 2017) and that meadows may become overgrazed (Fourqurean et al. 2010, 2019, Christianen et al. 2014). A historical perspective and an understanding of how green turtle grazing affects the productivity of naturally grazed ecosystems are necessary to evaluate the potential impacts of the current green turtle recovery while avoiding the “shifting-baseline syndrome,” the use of inappropriate baselines to assess population change (Pauly 1995, Pitcher 2001).

Caribbean green turtles consume the dominant seagrass, *Thalassia testudinum*, and exhibit a cultivation grazing strategy in which they select and repeatedly crop distinct areas of seagrass (Fig. 1; Bjorndal 1980, Odgen et al. 1983, Williams 1988). This grazing strategy increases blade nitrogen content and decreases lignin,

yielding a higher nutrient diet (Bjorndal 1980, Moran and Bjorndal 2007). Grazed areas within a naturally grazed ecosystem are typically observed in shallow habitats (likely due to increased accessibility by human observers), range in area from 10 to several hundred square meters, and may be maintained for periods of at least 1 yr (Odgen et al. 1983, Williams 1988, Hernández and van Tussenbroek 2014). Recent satellite tracking studies have revealed that green turtles also use deeper seagrass habitats (Hart et al. 2017, Esteban et al. 2018), but the effects of grazing have not been evaluated in *T. testudinum* meadows deeper than 6 m.

Results from *in situ* studies and simulated grazing experiments in shallow, tropical areas have shown that repetitive cropping of *T. testudinum* by green turtles reduces aboveground biomass and blade width (Odgen et al. 1983, Williams 1988, Moran and Bjorndal 2005), stimulates compensatory growth (Moran and Bjorndal 2005), accelerates nutrient recycling via short-circuiting the detritus cycle (Thayer et al. 1982), and facilitates succession of seagrass and benthic macro-algal communities (Hernández and van Tussenbroek 2014, Hearne et al. 2019, López et al. 2019). Recent studies have also shown that removal of biomass via grazing may not result in the loss of some ecosystem services (Christianen et al. 2012, Johnson et al. 2017, 2019) as anticipated (Heithaus et al. 2014, Atwood et al. 2015, Maxwell et al. 2017), and does not affect the reproductive success of *T. testudinum* (van Tussenbroek and Morales 2017). Given that *T. testudinum* shares many morphological, growth, and life history traits with terrestrial grasses that are considered adaptations to herbivory (McNaughton 1984, Valentine and Heck 1999), including compensatory growth, it is likely that *T. testudinum* coevolved with green turtles, as well as large sirenians, under consistent grazing pressure (Domning 2001, Jackson et al. 2001, Aragones et al. 2012). As green turtle populations recover and seagrass meadows are returned to a natural grazed state, an understanding of how increased grazing pressure affects meadow productivity throughout the growth cycle and across gradients of water depth is essential for assessing the sustainability of grazing and understanding green-turtle–seagrass interactions at an ecosystem level.

We evaluate the changes in regulation of productivity in a naturally grazed tropical ecosystem by (1) comparing *T. testudinum* productivity in grazed and ungrazed areas and (2) evaluating grazing intensity, in addition to abiotic factors, as potential regulating mechanisms of *T. testudinum* productivity. This study provides critical insights into the role of a recovering large-bodied marine herbivore in regulating the productivity of seagrass ecosystems.

METHODS

Study design and data collection

This study was conducted in a naturally grazed Caribbean seagrass ecosystem at Buck Island Reef National

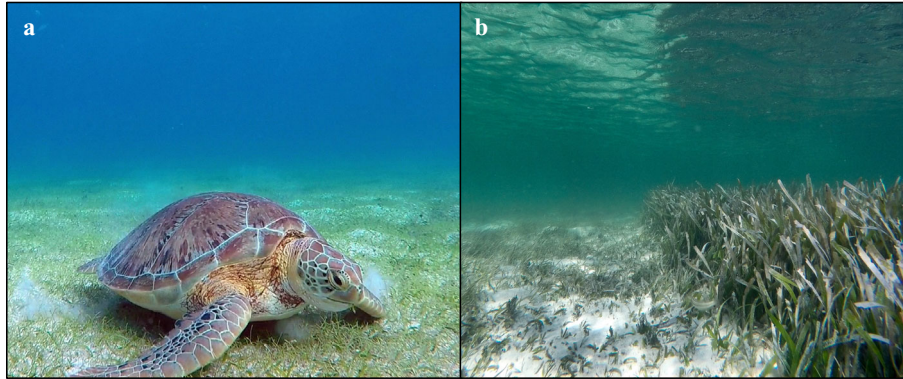


FIG. 1. (a) A green turtle forages in a grazed area at Buck Island Reef National Monument; (b) A border of a grazed (left) and ungrazed (right) area in a naturally grazed Caribbean seagrass ecosystem. Photos: A. Gulick.

Monument (BIRNM), St. Croix, U.S. Virgin Islands (17°47.4' N, 64° 37.2' W). Seagrass meadows at BIRNM are dominated by *Thalassia testudinum* and support an increasing foraging aggregation of green turtles (juvenile and adult) throughout the year (Hart et al. 2017; National Park Service, *unpublished data*). Green turtles at BIRNM maintain large grazing areas (>1,000 m²) within this naturally grazed ecosystem (Fig. 1), of which many have been grazed consistently for at least two years (A. Gulick, *personal observation*).

All seagrass meadows at this study site (depth range, 3–10 m) were surveyed, and grazed areas were found primarily in shallow (3–4 m) and deep (9–10 m) habitats. Grazed and ungrazed study sites were selected at both depths, and *T. testudinum* growth was measured during August–October 2017 (shallow and deep) and January–February 2018 (deep). These sampling periods correspond to the Caribbean summer and winter at this site (NOAA Coral Reef Watch 2018); a 3°C difference in sea-floor water temperature between seasons was recorded. Due to time and resource limitations, winter measurements of *T. testudinum* productivity in deep meadows were given higher priority over shallow meadows because of the paucity of research at those depths.

Green turtle exclosures ($n = 129$ total; 0.5 × 0.5 × 0.3 m; mesh size 2.5 cm; see Appendix S1) were deployed for 7–10 d intervals in grazed and ungrazed areas throughout the duration of this study. Each exclosure was fitted with a HOBO Pendant Logger (Model UA-002-08, Onset Computer Corporation, Bourne, Massachusetts, USA) that recorded hourly temperature (°C) and irradiance (lx) at canopy height for the duration of the growth period. Mean temperature and irradiance were determined for each exclosure. Because the hourly reading interval did not sufficiently capture the change in irradiance associated with sunrise and sunset, we only used irradiance values collected between 08:00 and 16:00 (period of peak irradiance) to calculate the mean for the growth period. Water depth (m) was recorded at each exclosure location using a

SCUBA diver's depth gauge. Grazing intensity was calculated at time of exclosure placement using the following index (range from 0 to 1; i.e., from 0% to 100% blade biomass removal)

$$\left(\frac{\text{No. grazed shoots m}^{-2}}{\text{No. total shoots m}^{-2}} \right) \times \left(\frac{\text{Ungrazed blade length} - \text{Grazed blade length}}{\text{Ungrazed blade length}} \right) \quad (1)$$

This index accounted for differences in seagrass structural complexity, particularly between shallow and deep meadows, and how recently a meadow may have been grazed.

Thalassia testudinum structural characteristics, nutrient composition, and growth were also measured in each exclosure (0.25 m²). Structural complexity was evaluated by measuring total shoot density (shoots/m²), grazed shoot density (grazed shoots/m²), length and width of 30 randomly selected blades, number of blades per shoot of 10 randomly selected shoots, and above-ground biomass (g dry mass [DM]/m²). Belowground biomass (g DM/m²), consisting of *T. testudinum* roots and rhizomes, was determined from a single 1,140-cm³ core (7.62 cm inner diameter, 25 cm depth) taken from inside each exclosure.

At the time of exclosure establishment, *T. testudinum* blades in grazed exclosures were trimmed to the blade–sheath junction to provide a consistent initial blade length and the small amount of trimmed blade biomass was removed. This initial trimming did not affect growth or tissue nutrient content in grazed exclosures because these areas were already maintained via natural grazing (Moran and Bjorndal 2005, 2007). In ungrazed exclosures, *T. testudinum* blades were left intact and marked at the blade–sheath junction using the needle-point method (Zieman 1974, Fourqurean et al. 2001). Upon removal of exclosures (both grazed and ungrazed), all

blades inside were collected by clipping at the blade–sheath junction for growth, biomass, and nutrient analyses. Aboveground and belowground biomass samples were rinsed with fresh water and dried to a constant mass at 60°C. Standard procedures were used to determine dry matter, nitrogen, and phosphorus content of blade tissue and soluble carbohydrate content of rhizome tissue (see Appendix S1). Molar ratios of nitrogen (N) to phosphorus (P) in *T. testudinum* blade tissues in grazed and ungrazed areas were determined as an indicator of nutrient availability and whether N or P was the limiting nutrient (Gerloff and Kromholz 1966, Fourqurean et al. 1992). Limitation was inferred using a ratio of 30:1 N:P as a threshold, which represents a critical balance of N and P availability known as the seagrass Redfield Ratio (Atkinson and Smith 1983, Fourqurean and Zieman 2002). Root uptake of nutrients from sediment pore water is considered the most important nutrient source for seagrasses (see review by Short [1987]), and *T. testudinum* meadows in the Caribbean region are typically P limited (Fourqurean and Zieman 2002, Gras et al. 2003), as reflected by N:P values exceeding 30:1. Green turtle grazing initially increases N content of *T. testudinum* blades (Bjorndal 1980), but the N content stabilizes after 4–6 months of consistent cropping (Moran and Bjorndal 2007). Because grazed areas at this study site have been maintained by natural grazing for at least two years, the N content of blades has likely stabilized. Although higher N content in grazed areas affects N:P, this ratio still represents nutrient availability.

Thalassia testudinum growth (per blade and per area) in each enclosure was quantified as blade linear growth ($\text{mm}\cdot\text{blade}^{-1}\cdot\text{d}^{-1}$), blade area growth ($\text{mm}^2\cdot\text{blade}^{-1}\cdot\text{d}^{-1}$), mass growth ($\text{g DM}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$), and the ratio of mass growth to aboveground biomass ($\% \text{d}^{-1}$), hereafter referred to as P:B). Linear growth ($\text{mm}\cdot\text{blade}^{-1}\cdot\text{d}^{-1}$) was determined in grazed areas by measuring the length of growth above the blade/sheath junction of 30 random blades from the interior of each enclosure. Linear growth in ungrazed areas was determined by measuring the vertical movement of the needle mark relative to the blade/sheath junction of 30 random blades from the interior of each enclosure (Zieman 1974, Fourqurean et al. 2001). Blades were selected randomly, rather than in specific age ranks. Because blade length growth was used to determine blade area growth in grazed and ungrazed enclosures and mass growth in ungrazed enclosures, the accuracy of estimated mean growth in each enclosure was more important than the precision in estimating the linear growth in a given blade age rank (see Moran and Bjorndal 2005). Because blade width differed between grazed and ungrazed areas, rates of area growth ($\text{mm}^2\cdot\text{blade}^{-1}\cdot\text{d}^{-1}$) were calculated for each enclosure using linear growth and average blade width. Mass growth ($\text{g DM}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) of blades was measured for enclosures in grazed areas by dividing the dry mass of blades collected by the number of days in the growth period. Mass growth of blades in ungrazed enclosures

was calculated using the equation provided by Moran and Bjorndal (2005)

$$(\text{AG} \times \text{MPA} \times \text{BPS} \times \text{SD}) / \text{growth period}$$

Abbreviations denote the following: blade area growth (AG, $\text{mm}^2\cdot\text{blade}^{-1}\cdot\text{d}^{-1}$), mass per area of blade (MPA, g/mm^2), blades per shoot (BPS), and total shoot density (SD, shoots/ m^2). Using data from the grazed enclosures, this mass growth equation generated values equivalent to the known rates of mass growth (from measured biomass production). We are therefore confident that this equation provides an accurate estimate of mass growth and that the growth rates estimated from ungrazed enclosures (using the needle-point method) are comparable to those from the grazed enclosures. P:B in grazed and ungrazed enclosures was determined by dividing mass growth ($\text{g DM}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) by aboveground biomass ($\text{g DM}/\text{m}^2$) and multiplying by 100. P:B is equivalent to measures of specific mass growth and relative growth reported in other studies.

Statistical analyses

Comparisons of *Thalassia testudinum* growth in grazed and ungrazed areas across depth (shallow, deep) and season (summer, winter) were conducted using three-way ANOVA and Tukey's post-hoc tests. Data were analyzed in R version 3.3.3 (R Core Team 2017) using the dplyr package (Wickham et al. 2017).

Generalized additive models (GAM) were used to explore the regulating mechanisms of *T. testudinum* growth in grazed and ungrazed areas of a naturally grazed tropical ecosystem. All models were fitted using thin-plate regression splines to evaluate the effects of nonlinear covariates. Analyses were performed using the mgcv package (Wood 2011) with smoothness parameters estimated using REML (Wood 2006); model statements are provided in Appendix S1.

To evaluate regulation of seagrass productivity, we assessed five fixed effects on two response variables, mass growth and P:B. Response variables were evaluated in separate models for grazed and ungrazed areas. Of the five fixed effects, temperature (summer, winter) and depth (shallow, deep) were assigned as two-level factors given the bimodal distribution of both variables (Appendix S1: Figs. S1, S2). The remaining fixed effects included irradiance, N:P, and grazing intensity as continuous parameters with smoothers applied. Grazing intensity was not included as a covariate in models for ungrazed areas since grazing did not occur. We conducted GAM analyses for only mass growth and P:B since these growth metrics are commonly reported in other aquatic and terrestrial-based studies and when presented together, are functionally important growth metrics for quantifying plant response to grazing (Oosterheld and McNaughton 1991, Cebrián and Duarte 1998, Ramula et al. 2019).

RESULTS

Overall, *Thalassia testudinum* growth in grazed areas exhibited a trend for compensatory growth. Blade linear growth ($\text{mm}\cdot\text{blade}^{-1}\cdot\text{d}^{-1}$), blade area growth ($\text{mm}^2\cdot\text{blade}^{-1}\cdot\text{d}^{-1}$), and P:B (with the exception of deep meadows during summer) was elevated when compared to ungrazed areas, although significance level changed with depth and temperature (Table 1, Appendix S1: Table S1). Mass growth ($\text{g DM}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) was significantly lower in all grazed areas when compared to ungrazed areas, with the exception of deep meadows during winter. Although many structural characteristics differed between grazed and ungrazed areas (Table 2), storage of rhizome soluble carbohydrates was maintained. Because variation in *T. testudinum* growth in grazed areas across depth and temperature may be due to differences in seagrass structural characteristics (Table 2, Appendix S1: Table S2) and grazing pressure, we developed an index of grazing intensity (Eq. 1, Table 3) to evaluate the role of grazing in regulating productivity of *T. testudinum* meadows.

The GAM for mass growth of *T. testudinum* in ungrazed areas explains 64.3% of model deviance with depth ($P < 0.001$, Fig. 2a) as the only significant fixed effect. Mass growth was greater in shallow meadows than in deep meadows, which may be due to the greater shoot density at shallow depths (Table 2). Temperature ($P = 0.196$), irradiance ($P = 0.821$), and N:P ($P = 0.514$) did not significantly affect mass growth in ungrazed areas. The model for P:B in ungrazed areas explains 60.9% of model deviance with three significant fixed effects: depth ($P < 0.001$, Fig. 2b), irradiance ($P < 0.004$, Fig. 2c), and N:P ($P < 0.001$, Fig. 2d). Temperature did not have a significant effect ($P = 0.974$). Thus, in ungrazed areas, water depth had a significant effect on both mass growth and P:B, but irradiance and N:P only had a significant effect on P:B. P:B increased with increasing N:P until N:P reached a value of ~55 (Fig. 2d).

The model for mass growth of *T. testudinum* in grazed areas explains 47.8% of model deviance. Depth is the

only significant fixed effect ($P = 0.002$, Fig. 3a), similar to the model for ungrazed areas. Mass growth in grazed areas was significantly higher in shallow meadows than in deep meadows. Temperature ($P = 0.061$), irradiance ($P = 0.747$), N:P ($P = 0.112$), and grazing intensity ($P = 0.320$, Fig. 3b) did not significantly affect mass growth in grazed areas. The model for P:B in grazed areas explained 65.4% of model deviance with depth ($P = 0.003$, Fig. 3c) and grazing intensity ($P = 0.030$, Fig. 3d) as significant effects. Similar to the model for mass growth, P:B was greater and more variable in shallow meadows than in deep meadows. P:B was also stimulated by increased grazing intensity (Fig. 3d). Temperature ($P = 0.999$), irradiance ($P = 0.493$), and N:P ($P = 0.875$) did not significantly affect P:B.

DISCUSSION

Regulation of seagrass productivity in a naturally grazed ecosystem

Our results from ungrazed areas were consistent with previous studies of seagrass meadows conducted in the tropical Caribbean: irradiance, N:P, and depth were important factors regulating *Thalassia testudinum* growth whereas the small change in seasonal water temperature (3°C) played a lesser role (e.g., van Tussenbroek 1995). In contrast, there was a dramatic shift in the relative importance of regulating factors of growth in areas grazed by green turtles. Growth of *T. testudinum* in grazed areas was significantly regulated by grazing intensity and water depth, with higher and more variable rates in shallow meadows than in deep meadows. Irradiance, temperature, and N:P did not play a significant role in regulating growth in this tropical grazed area.

High levels of aboveground biomass and low rates of tissue turnover (i.e., low P:B) are characteristic of terrestrial plant communities at the climax of the succession cycle (Woodwell and Whittaker 1968, McNaughton et al. 1988). Introducing herbivory into terrestrial systems can facilitate dramatic changes in the composition of the plant community via removal of aboveground

TABLE 1. Summary of *Thalassia testudinum* growth in grazed and ungrazed meadows across water depth and season (mean \pm SD).

Parameter	Shallow (3–4 m) Summer (28.9–29.2°C)			Deep (9–10 m) Summer (29.0–29.6°C)			Deep (9–10 m) Winter (26.6–26.8°C)		
	Grazed, <i>n</i> = 25	Ungrazed, <i>n</i> = 25	<i>p</i>	Grazed, <i>n</i> = 25	Ungrazed, <i>n</i> = 24	<i>P</i>	Grazed, <i>n</i> = 15	Ungrazed, <i>n</i> = 15	<i>P</i>
Linear ($\text{mm}\cdot\text{blade}^{-1}\cdot\text{d}^{-1}$)	5.7 \pm 1.0	3.5 \pm 0.3	<0.001	5.2 \pm 0.8	4.7 \pm 0.6	0.296	4.9 \pm 0.4	3.9 \pm 0.4	0.003
Area ($\text{mm}^2\cdot\text{blade}^{-1}\cdot\text{d}^{-1}$)	32.8 \pm 5.9	21.9 \pm 2.7	<0.001	37.2 \pm 8.4	34.4 \pm 6.6	0.663	32.3 \pm 4.0	25.0 \pm 3.2	0.016
Mass ($\text{g DM}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$)	0.7 \pm 0.2	4.0 \pm 1.4	<0.001	0.4 \pm 0.2	1.3 \pm 0.9	0.003	0.3 \pm 0.1	0.9 \pm 0.4	0.472
P:B (% d ⁻¹)	39.1 \pm 15.4	16.4 \pm 2.1	<0.001	11.0 \pm 3.1	11.4 \pm 3.4	0.999	13.2 \pm 4.1	12.5 \pm 0.1	0.999

Notes: Comparisons were made using three-way ANOVAs (Appendix S1: Table S1) and Tukey's post hoc tests; *P* values from Tukey's tests for grazed and ungrazed comparisons are reported (significant results in boldface type). Mass growth was determined on a dry matter (DM) basis. P:B is the ratio of mass growth to aboveground (standing crop) biomass.

TABLE 2. Structural characteristics and rhizome soluble carbohydrate content of *Thalassia testudinum* in grazed and ungrazed areas (mean \pm SD).

Parameter	Shallow (3–4 m) Summer (28.9–29.2°C)			Deep (9–10 m) Summer (29.0–29.6°C)			Deep (9–10 m) Winter (26.6–26.8°C)		
	Grazed, <i>n</i> = 25	Ungrazed, <i>n</i> = 25	<i>P</i>	Grazed, <i>n</i> = 25	Ungrazed, <i>n</i> = 24	<i>P</i>	Grazed, <i>n</i> = 15	Ungrazed, <i>n</i> = 15	<i>P</i>
Blade length (mm)	31.0 \pm 8.3	80.9 \pm 27.5	<0.001	45.2 \pm 18.4	84.0 \pm 54.0	<0.001	39.3 \pm 8.7	113.3 \pm 42.8	<0.001
Blade width (mm)	5.7 \pm 0.9	6.2 \pm 0.8	0.176	7.2 \pm 2.3	7.3 \pm 1.6	0.999	6.6 \pm 1.0	6.4 \pm 1.0	0.863
Blades per shoot	1.9 \pm 0.6	2.1 \pm 0.6	0.051	2.3 \pm 0.6	2.4 \pm 0.1	0.963	2.0 \pm 0.5	2.2 \pm 0.5	0.575
Shoot density (shoots/m ²)	505.3 \pm 150.9	791.7 \pm 137.7	<0.001	242.9 \pm 84.6	154.0 \pm 60.2	0.075	215.5 \pm 62.9	172.5 \pm 70.4	0.954
Aboveground biomass (g DM/m ²)	3.8 \pm 1.3	24.2 \pm 6.5	<0.001	4.0 \pm 2.0	10.6 \pm 6.2	<0.001	2.4 \pm 0.7	6.8 \pm 3.4	0.115
Belowground biomass (g DM/m ²)	32.5 \pm 11.4	50.9 \pm 19.3	<0.001	22.8 \pm 12.3	24.6 \pm 8.8	0.999	16.7 \pm 7.9	14.9 \pm 9.6	0.999
Rhizome soluble carbohydrates (mg C/g DM)	96.1 \pm 15.2	109.1 \pm 34.3	0.974	109.0 \pm 29.9	137.4 \pm 61.3	0.513	75.8 \pm 10.6	80.1 \pm 9.0	0.999

Notes: Comparisons were made using three-way ANOVAs (Appendix S1: Table S2) and Tukey's post hoc tests; *P* values from Tukey's tests for grazed and ungrazed comparisons are reported (significant results in boldface type). Biomass and carbohydrate content were evaluated on a dry matter (DM) basis.

TABLE 3. Summary of environmental conditions in grazed and ungrazed areas and the grazing intensity index for grazed areas across depth and season (mean \pm SD).

Parameter	Shallow (3–4 m) Summer (28.9–29.2°C)		Deep (9–10 m) Summer (29.0–29.6°C)		Deep (9–10 m) Winter (26.6–26.8°C)	
	Grazed, <i>n</i> = 25	Ungrazed, <i>n</i> = 25	Grazed, <i>n</i> = 25	Ungrazed, <i>n</i> = 24	Grazed, <i>n</i> = 15	Ungrazed, <i>n</i> = 15
Temperature (°C)	29.1 \pm 0.5	29.1 \pm 0.4	29.3 \pm 0.3	29.3 \pm 0.3	26.7 \pm 0.4	26.7 \pm 0.3
Irradiance \times 10 ³ (lx)	11.4 \pm 10.4	8.8 \pm 6.8	8.7 \pm 6.1	7.6 \pm 5.6	6.6 \pm 5.2	6.4 \pm 4.5
N:P	26.6 \pm 3.9	39.0 \pm 9.1	41.6 \pm 18.3	43.9 \pm 12.5	39.0 \pm 5.1	45.9 \pm 10.6
Water depth (m)	3.9 \pm 0.3	4.2 \pm 0.3	8.7 \pm 0.2	9.4 \pm 0.6	8.5 \pm 0.0	8.9 \pm 0.3
Grazing intensity	0.5 \pm 0.1	NA	0.1 \pm 0.1	NA	0.2 \pm 0.6	NA

Notes: A molar ratio of 30:1 for nitrogen (N) to phosphorus (P) in *Thalassia testudinum* blade tissue is the threshold used to indicate which element may be limiting productivity.

biomass, which stimulates production of photosynthetic tissue and increases P:B (McNaughton 1979, Frank et al. 2002). Production of aboveground biomass in terrestrial plant communities is strongly driven by multiple abiotic factors (e.g., seasonal rainfall, nutrient availability), but grazing intensity by large herbivores also plays an important role in regulating plant productivity (McNaughton et al. 1988, Schönbach et al. 2011). Similar dynamics have been reported in aquatic vascular plant systems, where biotic (i.e., grazing) and abiotic factors can individually, additively, and interactively affect productivity (Wood et al. 2012, Bakker et al. 2016).

In the absence of grazing, *T. testudinum* exhibits growth patterns characteristic of a plant community at its climax: high levels of aboveground biomass and low P:B. Productivity of these ungrazed systems is regulated

by seasonal temperature, irradiance, and nutrient limitation, with factors such as water depth acting as secondary mechanisms (van Tussenbroek 1995, Lee and Dunton 1997, Lee et al. 2007). Although these abiotic factors, with the exception of temperature, played a significant role in regulating mass growth or P:B of *T. testudinum* in ungrazed areas at our study site, the relative importance of these factors changed dramatically in areas grazed by green turtles. With the exception of depth, most abiotic factors known to regulate mass growth and P:B in ungrazed *T. testudinum* meadows had less of a role in grazed areas in our study, including temperature, irradiance, and N:P.

Thalassia testudinum meadows in tropical locations do not experience dramatic shifts in productivity with seasonal changes in water temperature (van Tussenbroek

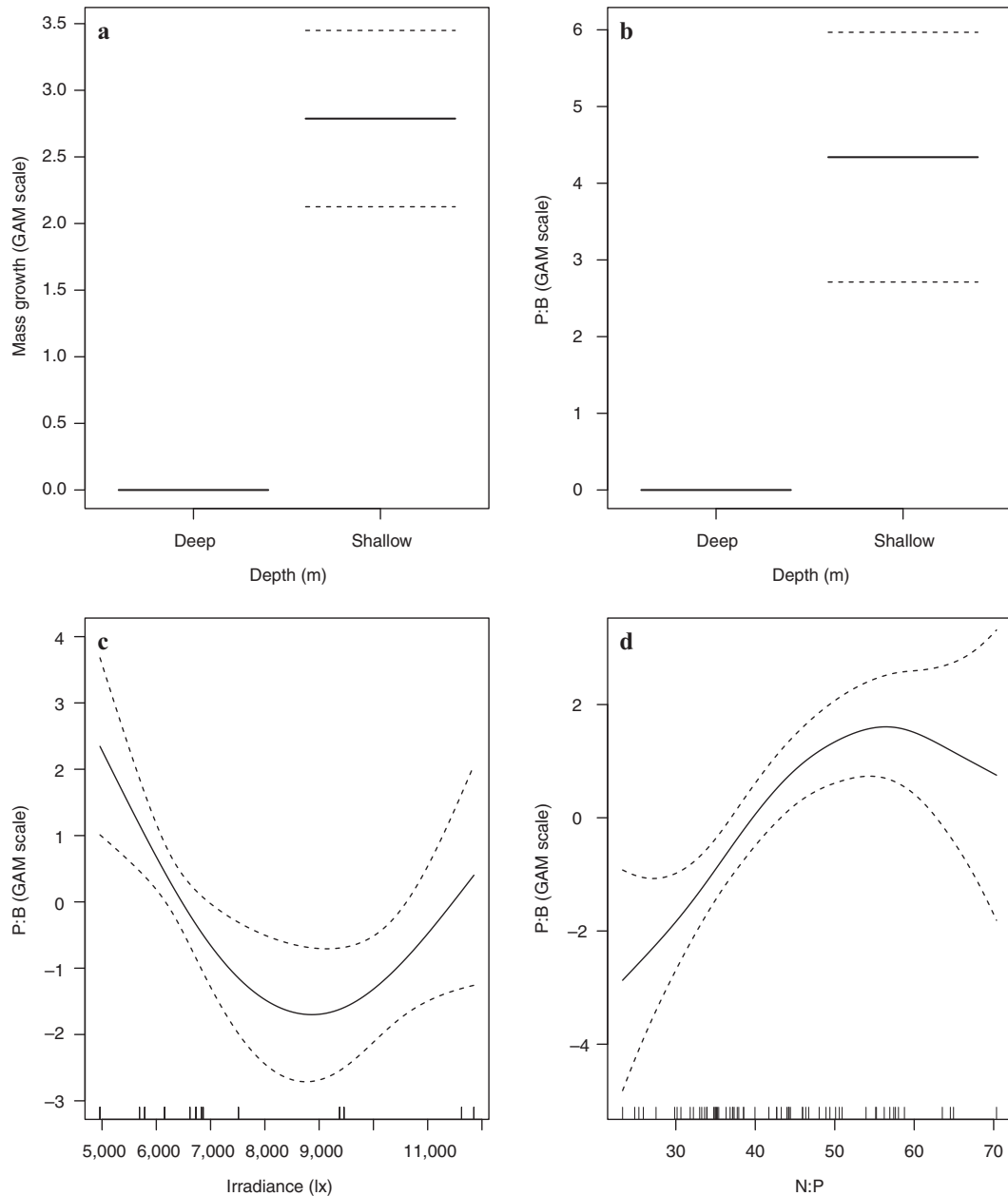


FIG. 2. Graphical summary of generalized additive models (GAM) analysis for evaluating the regulating factors of (a) mass growth and (b–d) P:B in ungrazed *Thalassia testudinum* meadows. Only significant covariates from each model are shown. P:B is the ratio of mass productivity to aboveground (standing crop) biomass. Response variables (mass growth, P:B) are shown on the y-axis as a centered smooth function scale, and are unitless. Covariates are shown on the x-axis with the rug plot corresponding to the sample distribution. Solid lines (horizontal [a, b], curves [c, d]) are smoothing spline fits conditioned on all other covariates and dashed lines are 95% CI.

1995) because the consistently warm waters are typically optimal for photosynthesis and growth (Bulthuis 1987). Therefore, we did not anticipate a significant effect of seasonal water temperature on growth in grazed areas at our study site given the tropical location and minimal change in temperature (3°C). However, grazed *T. testudinum* meadows in temperate regions that experience

greater fluctuations in seasonal water temperature warrant further study.

The combination of clear water at deeper depths and reduced aboveground biomass, and thus reduced self-shading, in grazed areas could explain why irradiance was not a significant factor regulating growth at our study site. Aboveground biomass and mass growth of *T.*

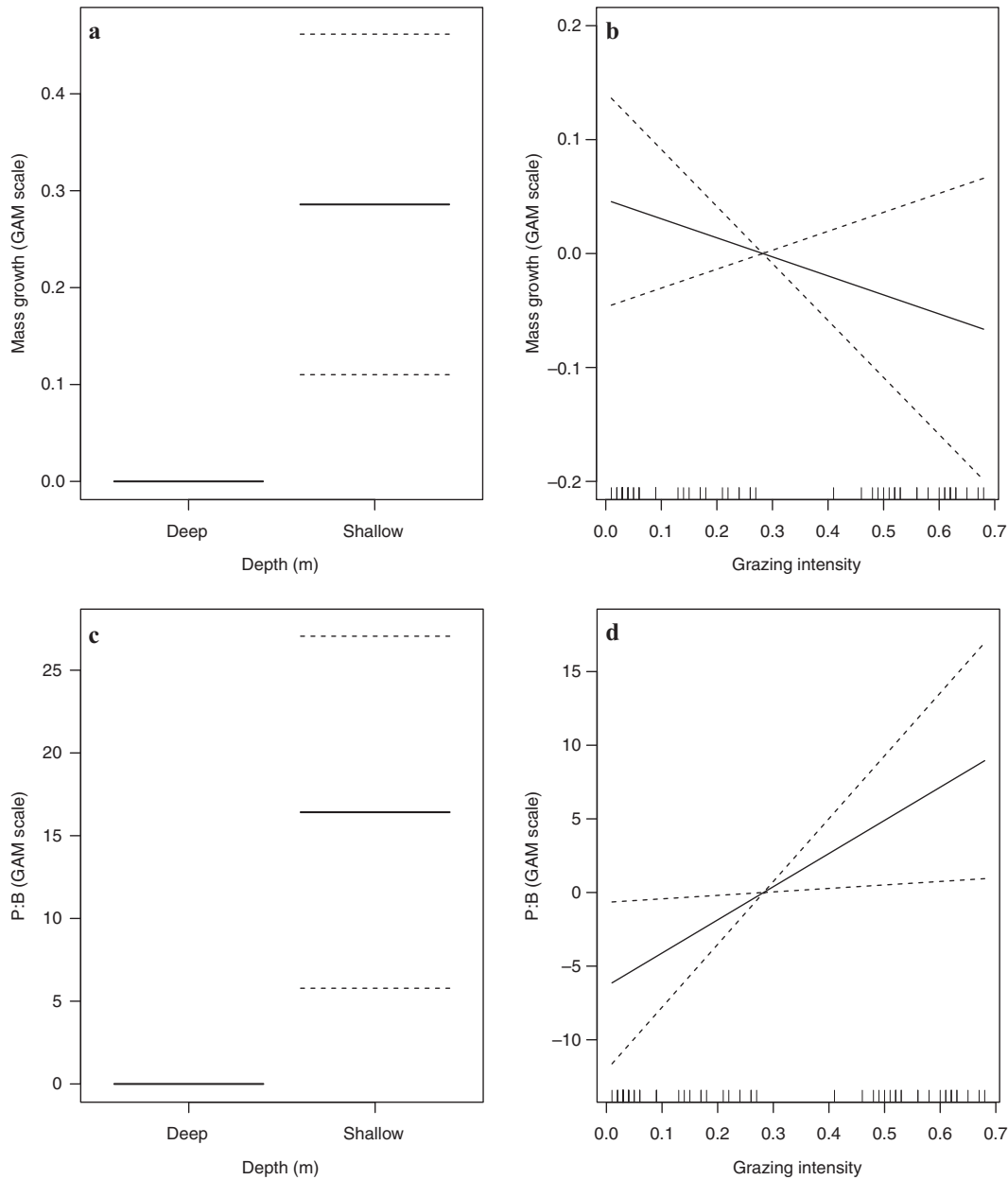


FIG. 3. Graphical summary of GAM analysis for evaluating the regulating factors of (a, b) mass growth and (c, d) P:B in grazed *Thalassia testudinum* meadows. All covariates shown are significant except for (b) grazing intensity (Eq. 1) in the mass growth model. P:B is the ratio of mass productivity to aboveground (standing crop) biomass. Response variables (mass growth, P:B) are shown on the y-axis as a centered smooth function scale, and are unitless. Covariates are shown on the x-axis with the rug plot corresponding to the sample distribution. Solid lines (horizontal [a, b], curves [c, d]) are smoothing spline fits conditioned on all other covariates and dashed lines are 95% CI. The convergence of 95% CI lines at zero (b, d) is a result of the identifiability constraint applied to the smooth terms and indicates that there is no uncertainty about this point (see Wood 2006).

testudinum typically decrease with increasing water depth as light becomes limited (Dawes and Tomasko 1988, Lee and Dunton 1997, Dawes 1998, Enriquez et al. 2019). However, this response is less pronounced in clear, tropical waters where *T. testudinum* can grow at depths up to 10 m (van Tussenbroek et al. 2006), similar to our study site. The percentage of photosynthetically active radiation (PAR) absorbed by seagrasses increases

non-linearly with aboveground biomass, stimulating growth until self-shading occurs (Zimmerman 2006, Enriquez et al. 2019). Irradiance likely fulfills a lesser role in the regulation of growth in grazed meadows because the lower levels of aboveground biomass would be less limited by access to PAR. The increased scattering of PAR that is not absorbed by the seagrass canopy may also explain the higher and more variable irradiance

observed in grazed areas (Zieman et al. 1984, Zimmerman 2006). Therefore, we propose that irradiance may not significantly regulate productivity in grazed areas, particularly in tropical habitats with clear water at depths less than 10 m, until sufficient seagrass biomass has accumulated.

Changes in seagrass structural complexity can also lead to shifts in nutrient allocation (Medina-Gómez et al. 2016, Enriquez et al. 2019). Grazing substantially reduces aboveground biomass, which can affect the production of above- vs. belowground tissues (see Table 2) (Thayer et al. 1984, Hernández and van Tussenbroek 2014). Most grazed and ungrazed areas at our study site were P limited as reflected by N:P values exceeding 30:1, which represents a critical balance of N and P availability (Atkinson and Smith 1983, Fourqurean and Zieman 2002). Although N:P did not regulate mass growth or P:B in grazed areas, it did significantly stimulate P:B in ungrazed areas until reaching a threshold value of ~55 (Fig. 2d), which suggests that biomass removal via grazing affects how nutrient availability drives seagrass productivity. Holzer and McGlathery (2016) proposed that P-limited *T. testudinum* meadows may not be able to support extended grazing by green turtles, based on low rates of mass growth and N:P values that exceeded 30:1 in their unfertilized, simulated grazing treatments in Bermuda. However, N:P also exceeded 30:1 in most naturally grazed areas in St. Croix (Table 3), but did not significantly affect mass growth or P:B. Because the calcium carbonate substrate is responsible for significantly limiting the phosphorus available to seagrass meadows at both study sites, and throughout the Caribbean (Short 1987, Gras et al. 2003), we recommend exercising caution applying this P-limited hypothesis at larger scales.

Grazing intensity regulates seagrass productivity

Grazing intensity (Eq. 1) was a significant regulating factor for P:B in grazed areas. P:B is an important measure of plant response to grazing and is one of the most functionally appropriate metrics for this purpose (Hilbert et al. 1981, Oosterheld and McNaughton 1991, Cebrián and Duarte 1998, Schönbach et al. 2011, Ramula et al. 2019). An increase in P:B after defoliation is indicative of a compensatory growth response, even if accompanied by a decrease in mass growth (Ferraro and Oosterheld 2002, Schönbach et al. 2011). Stimulated production of photosynthetic tissue (i.e., compensatory growth) following grazing indicates a plant's ability to partially or fully compensate for the removal of biomass. Grazing intensity, time of recovery from a grazing event, and other stress factors (i.e., temperature, light, nutrients) can all affect the degree of the compensatory response (Oosterheld and McNaughton 1991). However, a decline in P:B under increasing grazing intensity could indicate overgrazing, or that the plant's maximum P:B had been reached and could no longer support the level of tissue regrowth needed to reach compensatory growth

(Belsky 1986, Oosterheld and McNaughton 1991). In our study, P:B of *T. testudinum* in grazed areas was stimulated by increased grazing intensity (Fig. 3d), even though mass growth declined (Fig. 3b) and aboveground biomass was lower in grazed areas (Table 2). Linear and area growth of blades was stimulated in grazed areas relative to ungrazed areas, providing further support of the observed compensatory growth response. Stores of rhizome soluble carbohydrates were also maintained in grazed areas (Table 2), indicating that depleted stores in response to defoliation may not be a uniform response and mechanism of decline in grazed seagrass meadows as previously hypothesized (Fourqurean et al. 2010). Given that many grazed areas at this study site have been maintained for at least 2 yr (A. Gulick, *personal observation*), this compensatory growth response indicates that *T. testudinum* is capable of sustaining levels of grazing greater than what we observed in our study site, an ability that likely stems from its co-evolution with green turtles and other large herbivores (Domning 2001, Jackson et al. 2001, Aragones et al. 2012).

Similar compensatory growth responses of P:B to grazing intensity have been observed in terrestrial grasslands (McNaughton 1979, Oosterheld and McNaughton 1991, Schönbach et al. 2011, Ramula et al. 2019) that have coevolved with large vertebrate herbivores (McNaughton 1984). Terrestrial grasses that evolved under intensive grazing regimes exhibit several traits indicative of herbivore tolerance and the ability to support a compensatory growth response. These traits include proliferation of belowground basal meristems, clonal propagation, rapid regrowth of photosynthetic tissue, reduced rates of leaf senescence, and high tolerance to defoliation (McNaughton 1984, Ramula et al. 2019). Although seagrasses evolved independently of terrestrial grasses, many seagrass species, including *T. testudinum*, have developed similar morphological and growth traits indicative of adaptation to intensive grazing, including deep belowground networks of basal meristems and rhizomes, rapid regrowth of defoliated tissue, and high densities of short shoots (Valentine and Heck 1999). *Thalassia testudinum* in grazed areas reduces the height of its flowers and fruits, thereby reducing consumption by green turtles and limiting the impacts of grazing on reproductive success (van Tussenbroek and Morales 2017). *Thalassia testudinum* blades also contain silica and oxalate crystals (Dobbs et al. 2004) that are known anti-herbivore compounds in terrestrial plants (Franceschi and Nakata 2005, Ramula et al. 2019), and oxalate crystals have been linked to renal oxalosis in green turtles (Stacy et al. 2008).

These characteristics and the sustained levels of rhizome soluble carbohydrates under the long-term, relatively high levels of grazing intensity (Fig. 3d) observed at our study site provide compelling evidence that *T. testudinum* coevolved with green turtles under a consistent grazing regime and can sustain increases in grazing pressure by recovering green turtle populations. *Thalassia*

testudinum in shallow habitats has been shown to exhibit decreased blade width, aboveground biomass, and shoot density under consistent grazing pressure by green turtles (Williams 1988, Moran and Bjorndal 2005, Fourqurean et al. 2010, Hernández and van Tussenbroek 2014, Holzer and McGlathery 2016, Fourqurean et al. 2019). However, these responses may not be consistent across all seagrass meadows, particularly over gradients of depth and grazing intensity as demonstrated by our study (Tables 2, 3). Also, typical stress responses such as decreased blade width and shoot density are not necessarily indicative of meadow decline as a result of grazing, especially when accompanied by a compensatory growth response like stimulated blade growth (linear and area) and P:B (Table 1). Although blade width was significantly reduced after one month of clipping, consistent clipping of *T. testudinum* plots did not affect mass growth rates during the 16-month clipping trial (Moran and Bjorndal 2005).

Our results emphasize the need for caution when interpreting seagrass response to grazing based primarily on measures of mass growth or blade morphology (e.g., Hernández and van Tussenbroek 2014, Fourqurean et al. 2019). Use of P:B and measures of in situ grazing intensity, in addition to mass growth, are critical to understanding effects of green turtle grazing as meadows are returned to a natural grazed state.

As demonstrated by this study, green turtle grazing is a regulating mechanism of productivity of naturally grazed Caribbean seagrass meadows. However, the importance of grazing as a regulating factor may vary at a regional scale (Wood et al. 2012), because ungrazed *T. testudinum* exhibits spatial and temporal gradients in productivity across regions (van Tussenbroek et al. 2014). Seasonal migrations of terrestrial herbivores coinciding with primary production cycles (e.g., McNaughton et al. 1988, Wood et al. 2012) may provide context for seasonal changes in foraging habitat-use patterns by green turtles and the respective impacts of grazing in temperate vs. tropical locales. Additional studies that evaluate grazing dynamics in deeper seagrass ecosystems will also improve understanding of green-turtle-seagrass interactions, particularly because depth was an important parameter in the growth models from this study and green turtles are known to access deep foraging habitats (Hart et al. 2017, Esteban et al. 2018). Individual and interactive effects of anthropogenic threats and grazing on seagrass productivity will also be important to consider as green turtles continue to recover and utilize degraded foraging habitats (e.g., Christianen et al. 2012, 2014, Tomas et al. 2015).

Populations of large marine herbivores have severely declined due to overharvesting since the 15th century, with most species experiencing ecological or global extinction (Domning 2001, Jackson et al. 2001, Aragones et al. 2012). Green turtles once fulfilled a critical role as major consumers in seagrass ecosystems (Bjorndal and Jackson 2003). In the near-absence of green

turtles over the last few centuries, their ecological role and the functioning of seagrass meadows under natural grazing have been greatly altered. Lack of historical context and reliable baselines for population assessments have resulted in green turtles, as well as seagrass ecosystems, falling victim to the shifting-baseline syndrome (Pauly 1995, Pitcher 2001). Now, pristine seagrass meadows are often envisioned as having dense, tall canopies with high levels of biomass. However, this “shifted baseline” fails to reflect how seagrass meadows would have appeared and functioned in a natural grazed state when supporting large populations of green turtles. In an age of green turtle recovery and the global decline of seagrasses due to anthropogenic threats, a historical perspective and an integrated approach to conservation (Sievers et al. 2019, Unsworth et al. 2019) will be essential to ensure both the restoration of seagrass ecosystems and the continued recovery of green turtles.

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