Simulated green turtle grazing alters effects of environmental drivers on seagrass growth dynamics across seasons

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Abstract

Seagrasses form productive marine ecosystems that serve as important foraging grounds for grazers. Meadow productivity is vulnerable to environmental change, however, because environmental factors often strongly regulate seagrass growth. Understanding effects of grazing and environmental driver interactions on growth dynamics is therefore needed to ensure the long-term sustainability of seagrass meadow foraging habitats. We simulated natural green turtle (*Chelonia mydas*) grazing by experimentally clipping seagrass for 16 months in a *Thalassia testudinum* meadow and measured how responses in linear growth, production, the production-to-biomass ratio (P : B; compensatory growth), and leaf area index differed between clipped and unclipped seagrass in response to in situ changes in temperature and salinity. While increasing temperature and salinity had positive and negative effects, respectively, on growth rates, clipping did not alter the relationship between these abiotic drivers and seagrass growth. Simulated grazing did, however, alter effects of temperature on seagrass P : B ratio and leaf area index dynamics. Each increased significantly with temperature; however, P : B ratios only increased in experimentally clipped seagrass, whereas leaf area index only increased in unclipped seagrass. These results suggest that, given temperature-stimulated growth, grazed seagrass prioritizes increasing biomass production, whereas ungrazed seagrass prioritizes increasing photosynthetic surface area. In addition, our results demonstrate that the strength of the compensatory growth response to grazing in *T. testudinum* is seasonally dependent, highlighting the importance of biotic-abiotic interactions in driving growth dynamics. In a future with increasing grazer abundance and climate-driven stressors, understanding these types of interactions will be critical for long-term sustainability of seagrass ecosystems.

Seagrasses are highly productive marine plants (Duarte and Chiscano 1999). High productivity is dependent upon high growth rates, however, and these rates are often strongly driven by environmental conditions (e.g., temperature, irradiance, salinity, nutrient availability) (Lee and Dunton 2000; Lee et al. 2007). Environmental factors often co-vary across seasons, but given adequate insolation and nutrient availability, temperature is one of the most important drivers of

seagrass growth (Bulthuis 1987; Lee and Dunton 1996), with many species exhibiting higher rates with warmer water temperatures (albeit up to species-specific thresholds after which detrimental effects occur; Marbà and Duarte 2010; Collier and Waycott 2014; Hammer et al. 2018). Seagrass growth rates are therefore likely to follow climate-driven changes in ocean temperature. With ocean temperatures rising in many locations (Bindoff et al. 2019; Cheng et al. 2020), seagrass meadows are likely to experience not only warmer temperatures within growing seasons, but also longer growing seasons and therefore a greater length of time each year spent within optimal conditions for growth. This will likely result in both increased growth rates and an increase in annual biomass production for many seagrass meadows globally.

Higher rates of production will have numerous benefits for seagrass ecosystems, such as increased metabolic carbon capture (Johnson et al. 2020) and increased grazer carrying capacity (Williams 1988; Moran and Bjorndal 2005). Increased support for grazer populations would be particularly

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important in regions that already host high numbers of grazers or where grazer abundance is increasing, such as the Greater Caribbean (Mazaris et al. 2017). The Caribbean is a globally important foraging region for green turtles (*Chelonia mydas*)—marine megaherbivores that preferentially graze upon turtle grass (*Thalassia testudinum*) (Bjorndal 1997)—where *T. testudinum* is the dominant seagrass in the region (Green and Short 2003) (however, this may change in some areas as the invasive seagrass *Halophila stipulacea* spreads; Willette et al. 2014; Christianen et al. 2019). *T. testudinum* meadows are well-adapted to grazing and can survive in a continually grazed state for years (N. Constant unpubl.) while supporting robust aggregations of green turtles. This is likely due in part to the compensatory growth response in *T. testudinum* following grazing (Valentine et al. 1997; Gulick et al. 2020). Increasing green turtle abundance will lead to higher grazing pressure within meadows with important implications for seagrass growth and production.

While green turtle grazing may stimulate *T. testudinum* growth, how seagrass growth dynamics may be affected by interactions between grazing and other abiotic factors is poorly known. Most previous studies have focused on ungrazed seagrasses (Zieman 1975; Lirman and Cropper 2003; Olsen et al. 2012; Collier and Waycott 2014), resulting in a comparatively poor understanding of growth dynamics within grazed meadows. Few studies have investigated effects of interactions between grazing and abiotic factors on seagrass growth and how responses may differ from those in ungrazed seagrass (Nguyen et al. 2021); however, these interactions are likely to be important. For example, the importance of irradiance in driving production decreases following green turtle grazing (Gulick et al. 2020), while at the same time the change in irradiance created by canopy removal provides a mechanism for the compensatory growth response in *T. testudinum* following grazing (Gulick et al. 2021). In regions such as the Greater Caribbean, significant spatial overlap exists between areas where green turtles graze and where environmental conditions are conducive to high rates of seagrass growth (e.g., high temperatures and insolation, optimal salinity). With tropicalization of temperate areas (Vergés et al. 2014)—already occurring in the northern Gulf of Mexico (Heck et al. 2015)—the spatial extent in the overlap between grazers (as ranges expand into newly-suitable habitats) and seagrass ecosystems in areas with optimal conditions for growth is likely to increase further. As green turtle abundance and grazing pressure increase (Mazaris et al. 2017; Gulick et al. 2020) concomitantly with warming ocean temperatures (Bindoff et al. 2019), it is critical to understand how seagrass growth dynamics are affected by interactions between grazing and changing environmental conditions.

We conducted a long-term manipulative experiment within a *T. testudinum* seagrass meadow in The Bahamas to investigate how green turtle grazing interacts with seasonal changes in temperature and salinity to drive seagrass growth dynamics. Given that seagrass growth rates tend to increase with temperature (Lee et al. 2007) and that *T. testudinum* exhibits

compensatory growth in response to grazing (Valentine et al. 1997; Gulick et al. 2020), we hypothesized that together these drivers would have an additive effect and that grazed seagrass would maintain elevated growth rates relative to ungrazed seagrass across a range of temperatures. We further hypothesized that the compensatory growth response would partially offset negative effects of salinity in grazed seagrass, and thus that growth rates in ungrazed seagrass would be more strongly negatively affected by salinity. To test our hypotheses, we experimentally clipped seagrass to simulate green turtle grazing within a large *T. testudinum* meadow. Simulated grazing was maintained for 16 months—encompassing two summer growing seasons—to measure seagrass growth dynamics across a range of natural environmental conditions occurring over a full annual cycle.

Methods

Study site and experimental design

This experiment was conducted from July 1999 to December 2000 at the Perry Institute of Marine Science's Caribbean Marine Research Center on Lee Stocking Island, Exuma, The Bahamas (23.772963, −73.106910). The study site was a large, monospecific *T. testudinum* seagrass meadow located at a depth of ∼ 3 m (low tide) in an area that typically experiences slow current flow and is dominated by carbonate sediments. Shoot density (560 ± 95 shoots m^{-2}; mean and standard deviation) and height of the ungrazed seagrass canopy (12.7 ± 1.9 cm) at the beginning of the experiment were typical of meadows grazed by green turtles in this region.

Thirty 3×3 m square plots were established in the seagrass meadow in July 1999. Plots were set up in three blocks of 10 with each block comprised of five experimentally clipped plots to simulate green turtle grazing (hereafter, summer-initiated) and five unclipped plots to serve as an ungrazed reference (hereafter, reference). An additional block of five experimentally clipped plots was established in February 2000 (hereafter, winter-initiated) to test how seagrass responses to grazing may be affected by clipping duration compared to the summer-initiated plots.

Grazing was simulated in experimental plots ($n = 20$; 15 summer- and 5 winter-initiated plots) by clipping all seagrass blades within the plot area at the blade-sheath junction with scissors (Moran and Bjorndal 2005) resulting in shoot heights ∼ 2 cm above the sediment surface. To mimic the natural grazing regime of green turtles in this region, blades were re-clipped each time mean blade length within a plot reached 5 cm (range of 12–37 d depending on growth conditions), and all clipped blades were collected and removed to simulate green turtle consumption and removal of seagrass biomass and nutrients (Bjorndal 1980; Ogden 1980). Rhizomes were severed around the edge of each clipped plot at the beginning of the experiment, and thereafter every 6–8 weeks, to prevent nutrient translocation into the plots as part of a separate experiment (Moran and Bjorndal 2007). To

avoid possible edge effects from the surrounding ungrazed seagrass, all samples were collected from the inner 2 × 2 m area of plots leaving a 0.5 m wide buffer zone on all sides. This experimental regime was maintained for the 16-month duration of the experiment.

Sample and data collection

Environmental temperature (minimum and maximum values) and salinity were measured weekly. Temperatures were recorded from a minimum-maximum thermometer permanently deployed at seagrass canopy height at one location within each block of plots, and thermometers were re-set each week after reading. For analyses, the mean of these minimum and maximum temperatures was used. Salinity values were measured from a water sample collected near each thermometer at seagrass canopy height using a hand-held refractometer calibrated before each use.

Seagrass structural characteristics (blade length, blade width, shoot density, number of blades per shoot) were measured in all plots prior to the initiation of clipping and every 2 weeks thereafter. Shoot density and number of blades per shoot were measured in situ from three randomly placed 25 × 25 cm quadrats (0.0625 m²) in each plot, and blade morphometry (length and width) was measured in situ from 30 randomly selected blades in each plot. Structural characteristics were then used to calculate one-sided leaf area index (often abbreviated as LAI) (Enríquez and Pantoja-Reyes 2005)—a measure of the available photosynthetic leaf area within one square meter of meadow.

Aboveground biomass was measured in all plots prior to the initiation of clipping by collecting all seagrass blades from within three randomly placed 25 × 25 cm quadrats (0.0625 m²). Biomass was measured in this same manner throughout the experiment in reference plots at 2, 6, 11, and 16 months. Following the initiation of clipping, biomass in clipped plots was measured using all blades collected from the inner 4 m² area of each plot at each clipping event (when mean blade length reached 5 cm). For each plot, collected blades were cleaned of epiphytes and rinsed with seawater in the laboratory, and dry mass was measured after drying at 60°C to constant weight.

Seagrass growth rates (linear growth and mass growth) were estimated from measured aboveground seagrass biomass and structural characteristics. Linear growth rates (i.e., vertical blade growth) were measured using different methods for clipped and reference treatments, so as to avoid repeated destructive sampling within reference plots (Moran and Bjorndal 2005). Since all blades in clipped plots were clipped at the blade-sheath junction at each clipping event, linear growth rates (mm d⁻¹) were calculated from the measured blade length of 30 randomly selected blades from each plot at the time of clipping (since all tissue was new growth) divided by the number of days since the previous clipping event. Linear growth in reference plots was estimated using the leaf staple method (Zieman 1974) throughout the experiment at roughly 2-week intervals. A staple was placed just above the

blade-sheath junction in 30 randomly selected blades in each reference plot, and after roughly 2 weeks (mean 13 d) the new growth between the staple and the blade-sheath junction was measured and divided by the number of days since stapling.

Rates of mass growth (hereafter production) were also measured using different methods for clipped and reference treatments. Like linear growth, production (g DM m⁻² d⁻¹) in clipped plots was measured at the time of each clipping event, and the dry mass of all blades collected from the inner 4 m² of each plot (then standardized to 1 m²) was divided by the number of days since the previous clipping event. To avoid repeated destructive sampling in reference plots, rates of production were estimated from other measured metrics using the equation:

$$\frac{(SD \times BPS \times AG \times MPA)}{days},$$

where SD and BPS are shoot density and blades-per-shoot, respectively. AG is blade area growth (mm² blade⁻¹ d⁻¹) and was calculated using the mean linear growth rate and blade width for each plot following each growth interval. MPA is mass per area of blade (g mm⁻²), which is a measure of the mass of one square millimeter of seagrass blade tissue, and can be used to estimate production when blade area growth (AG) is known. MPA was calculated for each clipped plot following clipping events using measured blade length, blade width, blades per shoot, shoot density, and aboveground biomass, and these values of MPA were used to estimate reference plot production assuming MPA to be equivalent for clipped and unclipped blades. This method for calculating reference plot production was first described by Moran and Bjorndal (2005) and has more recently been applied to seagrass meadows naturally grazed by green turtles and shown to produce equivalent estimates of production to those obtained directly via biomass collection (Gulick et al. 2020).

The ratio of production to biomass (P : B ratio) can be used to evaluate compensatory growth in seagrasses—in which production typically scales with biomass across communities (Duarte 1989)—where compensatory growth is signified by a rate of production higher than would be predicted based on available standing biomass (i.e., elevated P : B ratio) (Cebrián et al. 1998). Ratios of production to biomass (also referred to as specific mass growth in some studies) were calculated by dividing rates of production by aboveground biomass and then multiplying by 100 (Moran and Bjorndal 2005; Gulick et al. 2020). Ratios were calculated for both clipped and reference plots for times when measures of both variables were available (i.e., at each clipping event in clipped plots, and at 0, 2, 6, 11, and 16 months in reference plots).

Data analysis

Sampling was interrupted on two occasions (October 1999 and August 2000) when hurricanes passed over the study site.

Data affected by these hurricane events were excluded from analyses (e.g., clipped plot blades that had grown well beyond a mean height of 5 cm, which affected variables such as biomass and growth rates). In addition, one of the summer-initiated clipped plots was covered by sediment following the first hurricane—burying the seagrass blades—and all data from this plot were excluded from analyses.

Effects of clipping on the temporal dynamics in seagrass characteristics and growth rates from this experiment are not presented here, as these have been described previously (Moran and Bjorndal 2005). Effects of clipping duration (i.e., differences between summer- and winter-initiated clipped plots) have not been previously described, however, and these data are presented here with some results modified from Moran and Bjorndal (2005) to demonstrate that environmental variables, rather than grazing duration, drive seagrass growth dynamics.

The responses of seagrass growth variables (i.e., rates of linear growth and production, P : B ratio) and physical characteristics (i.e., leaf area index) to simulated grazing and environmental drivers (i.e., temperature, salinity) were evaluated using linear mixed effects models. Leaf area index was
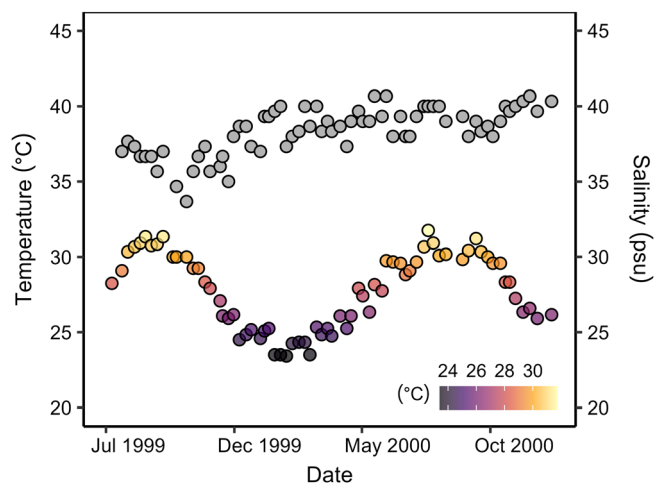

Fig. 1. Environmental temperature (colored points) and salinity (gray points) measured weekly at seagrass canopy height. Data points are means from the three blocks of summer-initiated plots. Color of temperature data points is also mapped to temperature value for ease of comparison across figures. This figure is borrowed and modified with permission from Moran and Bjorndal (2005).

Table 1. Model comparisons and AIC values for identifying the best-fit model for each seagrass response variable. Models are presented in order of most to least complex for each response. An "*" between fixed effects signifies an interaction between the terms. A "—" signifies that a component was not included in the model. The selected best-fit model (*see* "Data analysis" section) for each response variable is in bold text.

Response	Fixed effects	Random	Correlation	DF	AIC
Linear growth	Treatment * (temperature + salinity)	1|plot	AR(1)	12	862.8
	Treatment * (temperature + salinity)	1|plot	—	11	861.1
	Treatment * (temperature + salinity)	—	—	10	897.3
	Treatment + temperature + salinity	**1|plot**	**—**	**7**	**862.0**
	Treatment + temperature	1|plot	—	6	996.9
	Treatment + salinity	1|plot	—	6	1460.5
Production	Treatment * (temperature + salinity)	1|plot	AR(1)	12	−405.9
	Treatment * (temperature + salinity)	1|plot	—	11	−386.4
	Treatment * (temperature + salinity)	—	AR(1)	11	−349.4
	Treatment + temperature + salinity	1|plot	AR(1)	8	−407.3
	Treatment + temperature	**1|plot**	**AR(1)**	**7**	**−408.0**
	Treatment + salinity	1|plot	AR(1)	7	−215.9
P : B ratio	**Treatment * (temperature + salinity)**	**1|plot**	**AR(1)**	**12**	**957.4**
	Treatment * (temperature + salinity)	1|plot	—	11	986.0
	Treatment * (temperature + salinity)	—	AR(1)	11	955.4
	Treatment + temperature + salinity	1|plot	AR(1)	8	1033.9
	Treatment * temperature	1|plot	AR(1)	9	1019.1
	Treatment * salinity	1|plot	AR(1)	9	1158.5
Leaf area index	Treatment * (temperature + salinity)	1|plot	AR(1)	12	498.0
	Treatment * (temperature + salinity)	1|plot	—	11	505.8
	Treatment * (temperature + salinity)	—	AR(1)	11	644.6
	Treatment * temperature + salinity	**1|plot**	**AR(1)**	**10**	**498.2**
	Treatment + temperature + salinity	1|plot	AR(1)	8	520.1
	Treatment * temperature	1|plot	AR(1)	9	501.8
	Treatment + salinity	1|plot	AR(1)	7	549.9

DF, degrees of freedom.

used as a representative metric of seagrass physical structure, as it integrates measures of blade morphometry with meadow structure and thus represents an areal measure of photosynthetic leaf area. For each seagrass response variable, a model that included temperature, salinity, and treatment (with interaction terms) as fixed effects was fit using maximum likelihood. Full models also allowed for a random intercept for individual plots to account for the repeated measures sampling design and a lag-1 autoregressive (AR(1)) correlation structure to account for temporal autocorrelation in the temperature and salinity data. Model components were then iteratively removed to evaluate significance, and the best model was selected based on Akaike's information criterion (AIC) following a likelihood ratio test and re-fit using restricted maximum likelihood for the final model output. If models were within two AIC units of each other (i.e., $\Delta AIC \leq 2$), the less complex model was selected (except for the P : B ratio model,

for which model estimates were identical whether random effects were included or not) (Table 1).

Analyses were conducted in R 4.1.3 (R Core Team 2021). Linear mixed effects models were run using the lme() function from the "nlme" package (Pinheiro et al. 2021). Generalized least squares models (i.e., fixed effects only) were used to test significance of random effects in the mixed models and were run using the gls() function from the "nlme" package. Significance for all statistical tests was evaluated at an alpha value of 0.05. Data and code supporting the findings of the present study are openly available via the Environmental Data Initiative repository (Johnson et al. 2022) and Zenodo, respectively (*see* Data Availability).

Results

Temperature and salinity dynamics

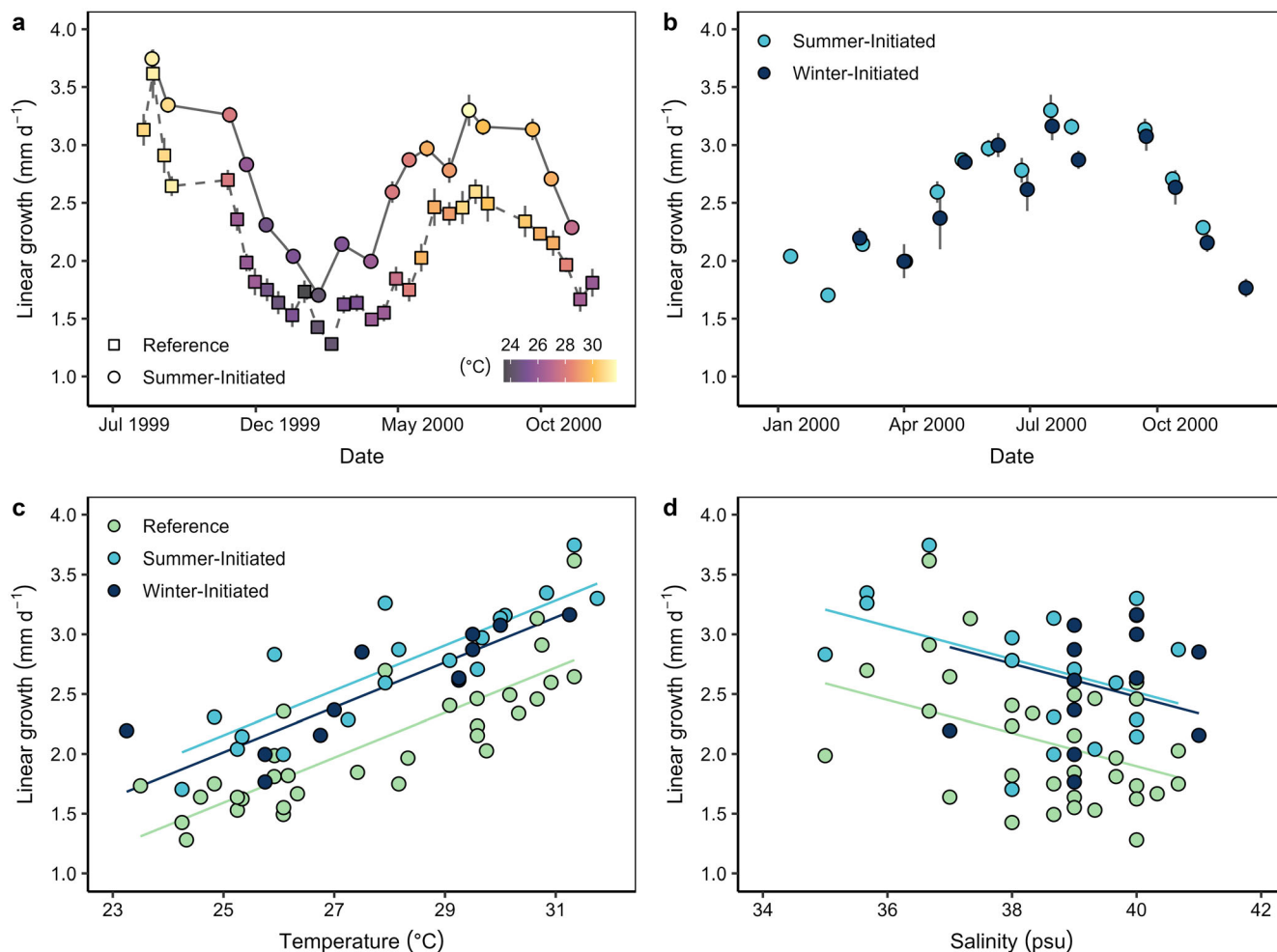Water temperature and salinity varied within the seagrass meadow over the course of the 16-month simulated grazing

Fig. 2. Linear growth rates of *Thalassia testudinum*. (**a**) In the reference and summer-initiated clipped treatments during the experiment, with the color of data points mapped to temperature, (**b**) in the two clipped treatments (clipping began in February 2000 for the winter-initiated clipped treatment), (**c**) vs. temperature, and (**d**) vs. salinity. Data points are treatment means. Error bars in (**a**) and (**b**) are standard error (small error bars are covered by data points). Solid lines in (**c**) and (**d**) show the significant relationships between linear growth and temperature and salinity, respectively, with significant differences among treatments (Table 2). (**a**) Is borrowed and modified with permission from Moran and Bjorndal (2005).

experiment, which encompassed two summer growing seasons and captured the full range in values naturally occurring at the site over an annual cycle. Temperature was seasonally variable, with maximum water temperatures in late summer ($\sim 31.5°C$, July–September) and minimum water temperatures in late winter ($\sim 23.5°C$, January–February; Fig. 1). Salinity did not vary with season and generally increased throughout the experiment, from 37.3 psu (practical salinity units) in July 1999 to 40.2 psu in November 2000. A temporary decrease in salinity occurred near the beginning of the experiment when a hurricane passed over the study site (October 1999; Fig. 1).

Effects of temperature, salinity, and simulated grazing

Linear growth rates of *T. testudinum* blades (i.e., blade vertical growth; mm d^{-1}) followed a similar temporal trend to that of water temperature (Fig. 2a) and increased significantly with increasing temperature (0.18 mm $d^{-1}°C^{-1}$) across all treatments (Table 2; Fig. 2c). Salinity had the opposite effect, and rates of linear growth decreased significantly (-0.12 mm d^{-1} psu^{-1}) across all treatments as salinity increased (Table 2; Fig. 2d). Though experimental clipping had a positive effect on linear growth—rates were significantly higher in both clipped treatments compared to the unclipped reference treatment (Table 2; Fig. 2)—simulated grazing did not alter the relationship between linear growth and either temperature or salinity (i.e., no significant interaction between treatment and temperature or salinity; Table 2). In addition, linear growth rates did not differ between the two clipped treatments (Table 2; Fig. 2b), even though summer-initiated plots had been clipped 6 months longer than winter-initiated plots.

Rates of seagrass production (i.e., mass growth; g DM m^{-2} d^{-1}) also followed a similar temporal trend to that of water temperature (Fig. 3a), and, like linear growth, increased significantly with increasing temperature (0.07 g DM m^{-2} d^{-1} °C^{-1}; Table 2; Fig. 3c). Unlike linear growth, however, there was not a significant relationship between production and salinity during the experiment (Fig. 3d), and salinity was not included in the best-fit model (Table 1). In addition, rates of seagrass production did not differ across treatments (Table 2; Fig. 3)—perhaps a result of wider blades or slightly higher shoot densities in the reference treatment (*see* Moran and Bjorndal 2005) offsetting the advantage of higher linear growth rates in the clipped treatments—and simulated grazing therefore did not alter the relationship between production and temperature. As a result, rates of production were not affected by clipping duration either (Table 2; Fig. 3b).

Table 2. Results from the best-fit linear mixed effects model for each seagrass response variable.

Response	Fixed effect	Estimate ± SE	DF	t	p
Linear growth	(Intercept)	1.61 ± 0.42	756	3.81	< 0.01
(n = 792)	Temperature	0.18 ± 0.01	756	30.15	< 0.01
	Salinity	−0.12 ± 0.01	756	−12.22	< 0.01
	Treatment (summer)	0.55 ± 0.06	31	9.88	< 0.01
	Treatment (winter)	0.52 ± 0.08	31	6.18	< 0.01
Production	(Intercept)	−1.07 ± 0.09	757	−11.59	< 0.01
(n = 792)	Temperature	0.07 ± 0.00	757	21.20	< 0.01
	Treatment (summer)	−0.04 ± 0.04	31	−1.09	0.29
	Treatment (winter)	−0.06 ± 0.06	31	−0.98	0.33
P : B ratio	(Intercept)	−3.76 ± 4.08	347	−0.92	0.36
(n = 387)	Temperature	0.09 ± 0.07	347	1.35	0.18
	Salinity	0.07 ± 0.07	347	1.12	0.26
	Treatment (summer)	9.70 ± 4.24	31	2.29	0.03
	Treatment (winter)	3.18 ± 5.64	31	0.56	0.58
	Temp × treatment (summer)	0.23 ± 0.07	347	3.29	< 0.01
	Temp × treatment (winter)	0.24 ± 0.08	347	2.97	< 0.01
	Salinity × treatment (summer)	−0.33 ± 0.07	347	−4.62	< 0.01
	Salinity × treatment (winter)	−0.17 ± 0.13	347	−1.36	0.18
Leaf area index	(Intercept)	−0.39 ± 0.36	967	−1.10	0.27
(n = 1005)	Temperature	0.05 ± 0.01	967	8.14	< 0.01
	Salinity	0.02 ± 0.01	967	2.44	0.01
	Treatment (summer)	−0.01 ± 0.26	31	−0.03	0.97
	Treatment (winter)	−0.32 ± 0.43	31	−0.75	0.46
	Temp × treatment (summer)	−0.05 ± 0.01	967	−5.19	< 0.01
	Temp × treatment (winter)	−0.03 ± 0.02	967	−2.12	0.03

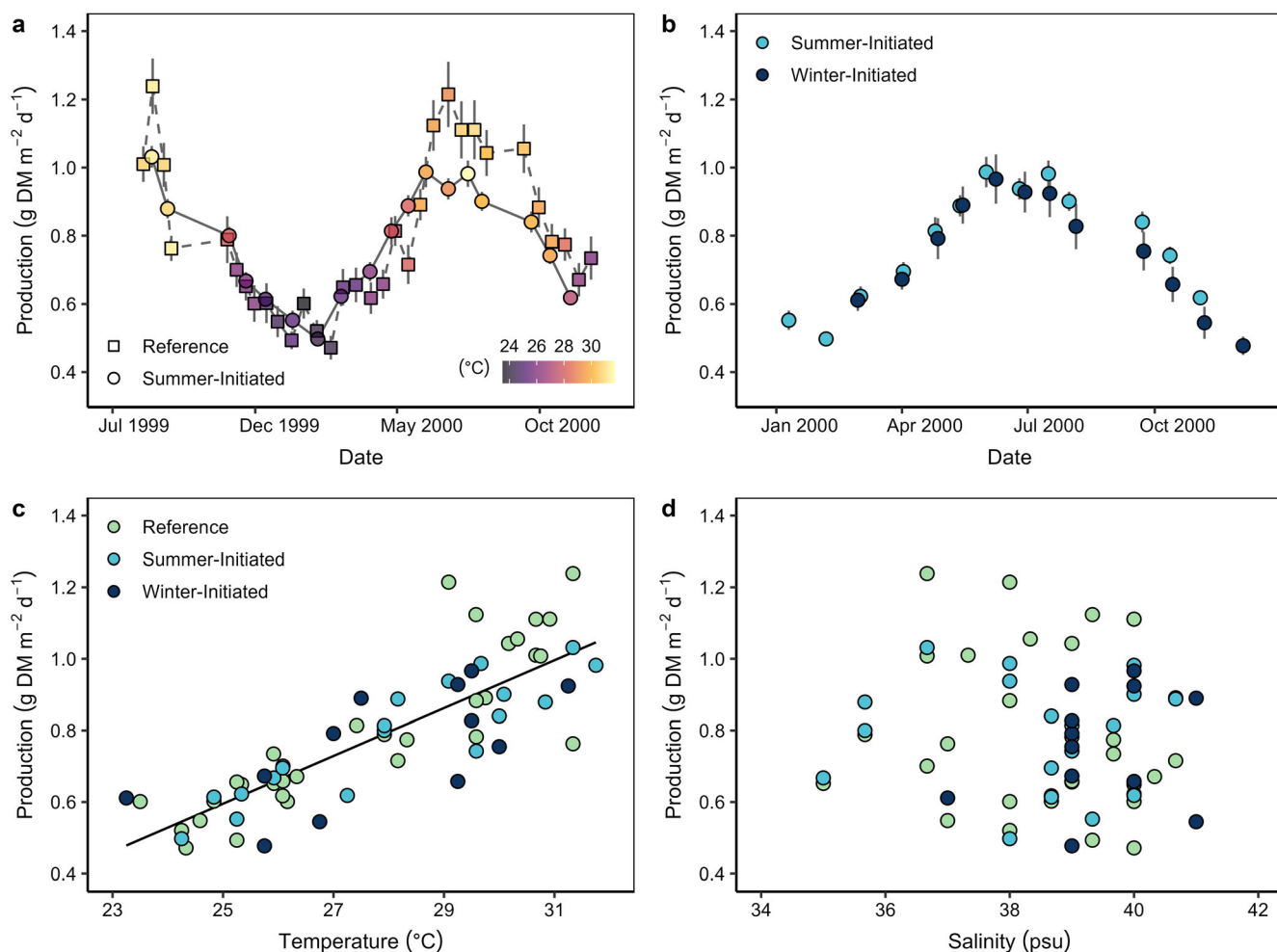DF, degrees of freedom; SE, standard error.

Fig. 3. Rates of production of *Thalassia testudinum*. (**a**) In the reference and summer-initiated clipped treatments during the experiment, with the color of data points mapped to temperature, (**b**) in the two clipped treatments (clipping began in February 2000 for the winter-initiated clipped treatment), (**c**) vs. temperature, and (**d**) vs. salinity. Data points are treatment means. Error bars in (**a**) and (**b**) are standard error (small error bars are covered by data points). Solid line in (**c**) shows the significant relationship between production and temperature (no difference among treatments; Table 2). (**a**) Is borrowed and modified with permission from Moran and Bjorndal (2005).

Given that simulated grazing directly reduced aboveground seagrass biomass, the lack of an effect on rates of production, and therefore an elevated P : B ratio, was indicative of a compensatory growth response in both the summer- and winter-initiated clipped treatments throughout the experiment (Fig. 4a). In contrast to linear growth and production, the relationship between the P : B ratio and temperature was dependent upon whether the seagrass was clipped or not. The P : B ratio increased significantly with temperature in both the summer-initiated ($0.32°C^{-1}$) and winter-initiated ($0.33°C^{-1}$) clipped treatments (Table 2; Fig. 4b), whereas the ratio of production to biomass in the unclipped reference treatment was relatively stable throughout the experiment (Fig. 4a) and did not vary with temperature (Table 2; Fig. 4b). Similarly, the effect of salinity varied across treatments. The P : B ratio decreased significantly with salinity in the summer-initiated

clipped treatment (-0.26 psu^{-1}), whereas trends were not significant in either the winter-initiated clipped treatment or the reference treatment (Table 2; Fig. 4c).

Seagrass leaf area index (i.e., areal photosynthetic leaf area) was reduced as a direct effect of experimental clipping (i.e., shortened blade lengths; though clipped blade widths also narrowed over time; *see* Moran and Bjorndal 2005). Like with P : B ratios, the relationship between seagrass leaf area index and temperature was dependent upon whether seagrass was clipped or unclipped. There was a distinct seasonal trend in leaf area index within the reference treatment (Fig. 5a), and the leaf area index of unclipped seagrass increased significantly with temperature ($0.05°C^{-1}$) during the experiment (Fig. 5b). Conversely, seasonal trends were absent following simulated grazing, and leaf area index did not vary with temperature in either the summer-initiated or winter-initiated
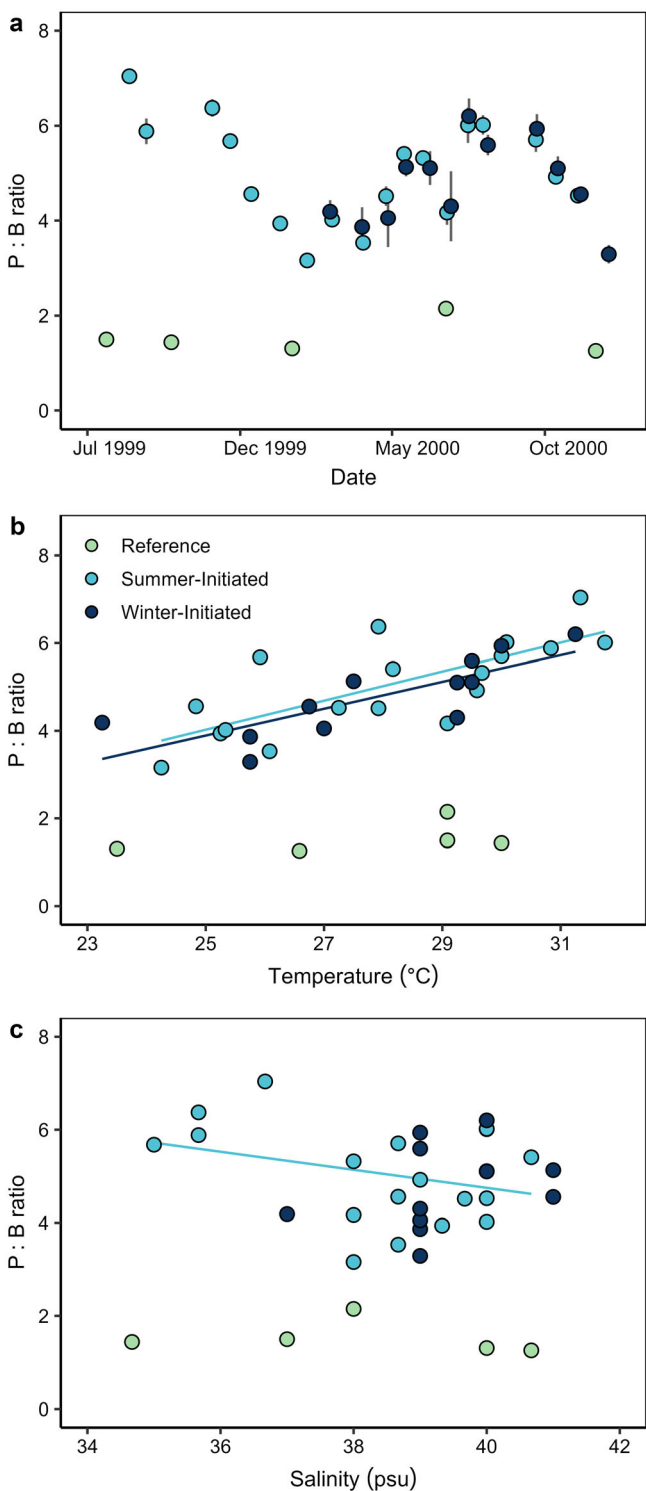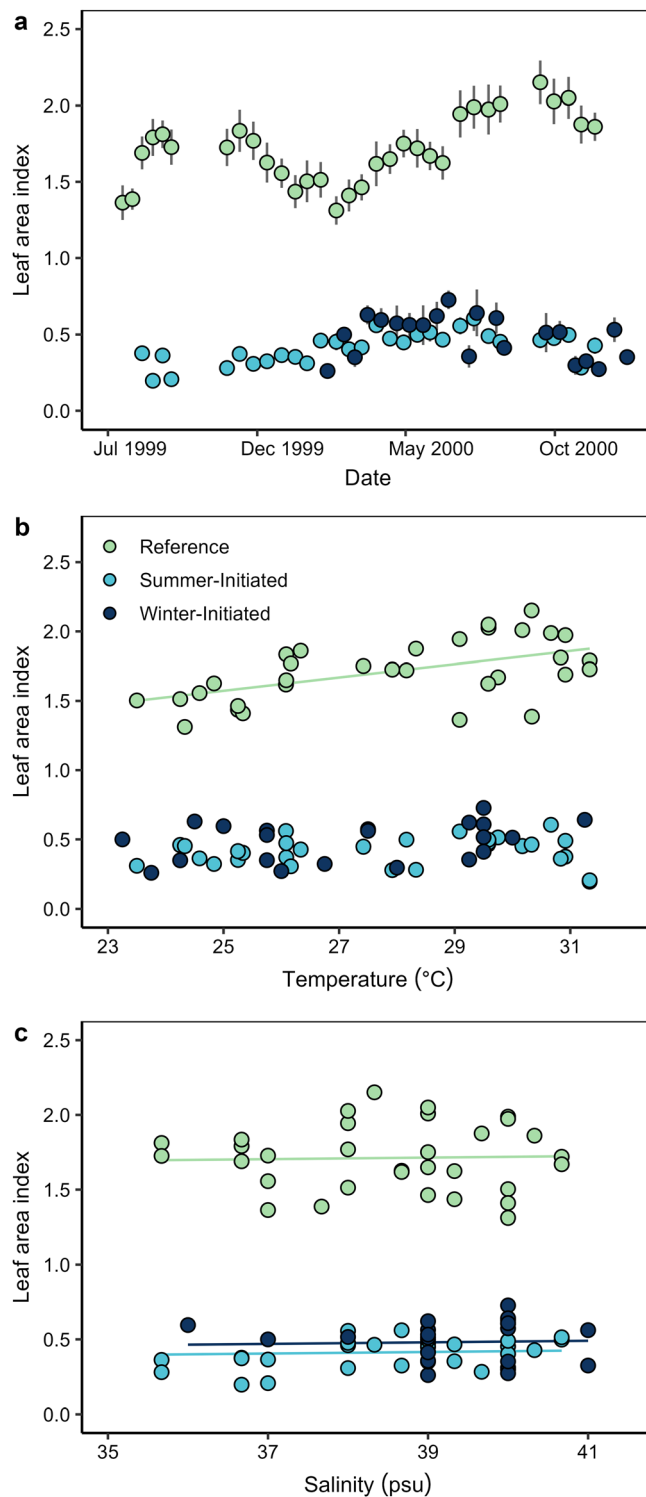
Fig. 4. Production-to-biomass ratios of *Thalassia testudinum*. (**a**) Throughout the experiment, (**b**) vs. temperature, and (**c**) vs. salinity. Data points are treatment means. Error bars in (**a**) are standard error (small error bars are covered by data points). Solid lines show the significant relationships between the P : B ratio and (**b**) temperature in the two clipped treatments, and (**c**) salinity in the summer-initiated treatment only (Table 2). (**a**) Is borrowed and modified with permission from Moran and Bjorndal (2005).

Fig. 5. Leaf area index of *Thalassia testudinum*. (**a**) Throughout the experiment, (**b**) vs. temperature, and (**c**) vs. salinity. Data points are treatment means. Error bars in (**a**) are standard error (small error bars are covered by data points). Solid lines show the significant relationship between leaf area index and (**b**) temperature in the reference treatment and (**c**) salinity across treatments (Table 2).

clipped treatments (Table 2; Fig. 5b). Leaf area index also increased significantly with salinity ($0.02 \, \text{psu}^{-1}$) during the experiment (Table 2). However, this response was consistent across treatments (Fig. 5c), and simulated grazing did not affect the relationship between leaf area index and salinity. In addition, the effect of salinity was rather small, and the best-fit model was only marginally better ($\Delta \text{AIC} = 3.6$; Table 1) than the model in which temperature was the sole environmental variable (temperature and salinity, $R_m^2 = 0.761$; temperature only, $R_m^2 = 0.759$).

Discussion

Our study demonstrates that herbivory by green turtles can alter the growth response of seagrass to changes in environmental conditions. Through a long-term simulated grazing experiment in a shallow *T. testudinum*-dominated meadow, we show that growth dynamics in response to environmental drivers differ between grazed and ungrazed seagrass. Though seagrass growth was stimulated by experimental clipping—linear growth rates remained elevated in clipped treatments compared to the reference treatment—simulated grazing did not change the relationship between rates of seagrass linear growth or production and the measured environmental drivers (temperature and salinity) across seasons (Figs. 2, 3). While growth rates increased with temperature irrespective of simulated grazing status, responses in other growth metrics to seasonal changes in temperature were dependent upon whether the seagrass was clipped or not. Compensatory growth (P : B ratio) increased with temperature across seasons, but only in the two clipped treatments (Fig. 4). Conversely, seagrass physical size and structure (i.e., leaf area index) also increased with temperature across seasons, but only in the unclipped reference treatment (Fig. 5). Together, our results demonstrate an important interaction between green turtle grazing and temperature as drivers of *T. testudinum* growth: that is, as temperatures warm, grazed seagrass prioritizes increasing biomass production whereas ungrazed seagrass prioritizes increasing photosynthetic surface area.

A combination of *T. testudinum* physiology and the grazing strategy used by green turtles across the Greater Caribbean may explain these differences in growth prioritization between grazed and ungrazed seagrass. Aboveground biomass is a strong driver of seagrass metabolism (production and respiration) in *T. testudinum*-dominated meadows across this region (Johnson et al. 2020). By prioritizing biomass over photosynthetic surface area, grazed seagrass may benefit from an increase in metabolic potential. Increasing the P : B ratio with temperature may therefore be a mechanism by which grazed seagrass can maintain a high production-to-respiration ratio (Johnson et al. 2017) and counteract higher metabolic demands induced by warmer temperatures (Marsh et al. 1986; Egea et al. 2019; Rasmusson et al. 2020). In the current study, the P : B ratio (compensatory growth) within experimentally

clipped plots was largely driven by rates of production. This is partially a result of the typical green turtle grazing strategy in the Caribbean (Bjorndal 1980), whereby re-grazing keeps aboveground biomass relatively stable over time. Temporal stability in biomass within clipped treatments, as opposed to the slight seasonal trend within the reference treatment (Supporting Information Fig. S1), likely contributed to the differing relationships between temperature and P : B ratios among treatments (Fig. 4b). While it is known that *T. testudinum* exhibits compensatory growth (i.e., elevated P : B ratio) in response to grazing (Valentine et al. 1997; Gulick et al. 2020), our results show, for the first time, the positive relationship between this response and temperature. Additional environmental growth drivers (e.g., irradiance, precipitation) often co-vary with temperature across seasons, and our results therefore suggest that the strength of this compensatory response is seasonally dependent.

Ungrazed seagrass blades, which do not exhibit a similar form of compensatory growth, are subject to other factors, such as self-shading, which can drive changes in growth and physical structure. Ungrazed *T. testudinum* blades in tropical meadows are typically ca. 10–20 cm in height (Fourqurean et al. 2010; Enríquez et al. 2019; Johnson et al. 2020) (though blades can reach 40–50 cm under warm, nutrient-rich conditions; Lee and Dunton 2000; R. A. Johnson unpubl.) and become prone to self-shading as they grow (Enríquez and Pantoja-Reyes 2005). By prioritizing an increase in leaf area index, unclipped seagrass in the reference treatment maximized the amount of photosynthetic leaf area available to capture incident sunlight as warming temperatures stimulated growth (Fig. 5b). Increasing photosynthetic surface area to capture more light may be a mechanism by which ungrazed seagrass counteracts a reduction in photosynthetic potential—a result of reduced irradiance received by the basal portions of blades—that occurs with self-shading (Enríquez et al. 2002). Grazed seagrass is unlikely to be similarly affected by self-shading, however. In the Greater Caribbean, green turtles create grazing areas in which blades are cropped (Bjorndal 1980), which results in both higher light availability and lower within-canopy light attenuation compared to adjacent ungrazed areas (Gulick et al. 2021). A difference in self-shading, induced by the change in blade morphometry, could explain why leaf area index was affected by temperature in the reference treatment, but not in the clipped treatments.

These differing growth dynamics between grazed and ungrazed *T. testudinum* demonstrate the existence of a tradeoff in prioritization between biomass and surface area when increasing growth in response to temperature. It is likely such a tradeoff exists along a continuum, and our results suggest the possibility of an inflection point at which, following a cessation of grazing, seagrass would switch from prioritizing increasing biomass to prioritizing increasing photosynthetic surface area (i.e., leaf area index) as it re-grows. Though we are not able to evaluate the presence of such an inflection point

from our current experiment, we hypothesize that this point would occur when seagrass shoots reach a sufficient height, size, or density to begin self-shading, as would be predicted under the leaf "self-thinning rule" (Westoby 1984; Enríquez et al. 2019; Gulick et al. 2021). Future research within grazing patches following green turtle abandonment will be particularly beneficial for increasing our understanding of how seagrass growth is driven by interactions between biotic and abiotic factors.

While our results suggest that growth dynamics were strongly driven by temperature, other environmental characteristics, such as water column salinity and incident sunlight, are also important in regulating seagrass growth. Though we did not measure underwater irradiance, it is likely that any growth responses to irradiance would have been similar to those for temperature, as temperature and irradiance are typically correlated in shallow, clear-water systems such as our study site. Effects of these variables are also not easily decoupled in situ. While either temperature or irradiance can become the dominant driver (i.e., limiting factor) at very high or low values in a system, previous research has suggested that temperature is likely a more important driver than irradiance for seagrass growth when neither factor is limiting (Bulthuis 1987; Lee and Dunton 1996; Lee et al. 2007).

Salinity can have strong detrimental effects on seagrasses (Zieman et al. 1999; Fernández-Torquemada and Sánchez-Lizaso 2005; Herbert and Fourqurean 2009). Unlike temperature, however, effects mostly occur under atypical conditions, such as a rapid change in salinity (Koch et al. 2007) or sustained exposure to high or low salinity outside a species' optimal range (Lirman and Cropper 2003). Optimal salinity for *T. testudinum* growth in the Greater Caribbean is ca. 20–40 psu (Kahn and Durako 2006; Herbert and Fourqurean 2009), which may explain why relationships between seagrass growth responses and salinity were not strongly affected by simulated grazing in our experiment—salinity was within this optimal range, albeit at the high end, for nearly the entire duration (Fig. 1). Had there been a greater range in salinity or seasonal variability, it is possible that simulated grazing may have had stronger effects on these relationships. Given the increasing trend throughout the experiment, the observed negative effects of salinity on some growth metrics are not surprising (e.g., linear growth; Fig. 2d). However, relationships between seagrass growth and salinity did not always mirror those observed with temperature. While compensatory growth increased with temperature in both clipped treatments, a decrease in the P : B ratio with salinity was only observed in the summer-initiated treatment (Fig. 4)—possibly a result of the greater total change in salinity experienced by the seagrass following clipping compared to the winter-initiated treatment. In addition, though simulated grazing drove differences among treatments in the response of leaf area index to temperature, there was not a similar interaction between simulated grazing and salinity (Fig. 5; Table 2).

Effects of salinity have not been well studied in seagrasses following herbivory, and it is possible that differences in physiological response to changes in temperature vs. salinity in *T. testudinum* could account for differences observed in our study. Further research in grazed seagrass meadows is needed, and investigations into mechanisms underlying growth dynamics will be particularly beneficial to furthering our understanding of seagrass responses to future increases in grazing pressure.

An increase in the duration of grazing patch maintenance will likely accompany increases in grazing pressure as green turtle numbers rise (Mazaris et al. 2017) and more individuals begin to rely on the same areas within meadows as grazing sites. This could be cause for concern if productivity declines over time with continued grazing, which could lead to earlier patch abandonment (Lacey et al. 2014) and/or necessitate the establishment of additional grazing patches to support the grazer population (Hernández and van Tussenbroek 2014). To evaluate how grazing duration may affect seagrass growth in our experiment, we established a second clipped treatment (winter-initiated) 6 months after the first (summer-initiated). Temporal growth dynamics were not affected by the season in which clipping was initiated (Moran and Bjorndal 2005), and there was no difference in linear growth (Fig. 2b) or production (Fig. 3b) between the two clipped treatments. In addition, growth rates had not appreciably declined after 1 yr within the summer-initiated treatment and were similar across both summer seasons during which growth was measured (Figs. 2a, 3a), demonstrating that, at least over a 16-month period, growth was not strongly influenced by grazing duration. Environmental conditions, and temperature in particular, were the strongest drivers of growth dynamics—a conclusion further strengthened by the visible correlation between growth rates and temperature across seasons (Figs. 2a, 3a). That prolonged maintenance of simulated grazing was not a strong control on seagrass growth dynamics in our study has important implications for the long-term sustainability of seagrass meadows that support grazing green turtle populations.

Long-term grazing may not always be sustainable, however, and high grazing pressure may have detrimental effects or lead to overgrazing under certain circumstances. Periods of sustained overgrazing may ultimately lead to meadow-scale seagrass loss as has been recently documented across *T. testudinum* meadows in Bermuda (Fourqurean et al. 2019). In contrast, green turtle grazing in Lac Bay, Bonaire has not directly caused a decline in *T. testudinum*, but rather has facilitated the expansion of the invasive seagrass *Halophila stipulacea*—which can rapidly colonize grazing patches to the detriment of native seagrass regrowth—following its establishment in the bay (Christianen et al. 2019). High grazing pressure does not always lead to seagrass decline, however. Green turtles have been found to continuously maintain grazing areas for at least 2 yr in the U.S. Virgin Islands (Gulick et al. 2020) and for well over 2 yr at sites in The Bahamas

(N. Constant unpubl.). The sustainability of high grazing pressure thus appears to vary across locations, and it may be that dynamics in belowground seagrass biomass (e.g., carbohydrate reserves) are an important driver in seagrass meadow responses to changes in grazing pressure (Fourquean et al. 2010; Dahl et al. 2016; Johnson et al. 2017). Given expected climate-driven changes along with increases in green turtle abundance, our results highlight the need to better understand how grazing and environmental conditions interact to regulate seagrass growth and meadow sustainability.

Interestingly, our results suggest that seagrass may benefit more than expected from future climate-driven warming under a typical green turtle grazing regime. Many seagrasses are already expected to benefit from increasingly warm and/or acidic ocean conditions (Garrard and Beaumont 2014; Zimmerman et al. 2017; Zimmerman 2021). Given the ability to maintain elevated linear growth rates (Fig. 2a) and increasing compensatory growth with seasonal warming (Fig. 4b), grazed *T. testudinum* may show an even stronger positive response to future warming than ungrazed conspecifics. Temperature-driven responses are also likely to be spatially heterogeneous, with more pronounced effects occurring in areas experiencing greater changes (e.g., those at higher latitudes), whether due to seasonal variability or long-term warming. For example, temperature was not a strong driver of *T. testudinum* P : B ratios in the U.S. Virgin Islands, where annual temperature fluctuations were less than $3°C$, and differences were instead regulated by green turtle grazing pressure (Gulick et al. 2020). In contrast, temperature was a strong driver of compensatory growth at our study site in The Bahamas—where temperature varied by more than $8°C$ across seasons—demonstrating the importance of both grazing pressure and environmental conditions in driving seagrass growth dynamics. Seasonally dependent compensatory growth may therefore be especially important within meadows in which a simultaneous increase in grazing pressure occurs with warming. Under typical green turtle grazing in the Greater Caribbean, seagrass aboveground biomass remains relatively stable over time within grazing patches, as new growth is continually removed via re-grazing (Christianen et al. 2012; Gulick et al. 2020). Provided that overgrazing does not occur (e.g., Fourquean et al. 2019), increasing compensatory growth with warming may help *T. testudinum* seagrass to offset an increase in biomass consumption and thereby sustain a larger grazer population.

Our study highlights the importance of understanding how grazing and abiotic drivers interact to alter seagrass responses to changing environmental conditions. Given ongoing tropicalization of temperate ecosystems (Vergés et al. 2014; Heck et al. 2015), along with increasing green turtle abundance, grazing pressure is likely to increase across many seagrass habitats. At the same time, seagrasses are under threat from a multitude of anthropogenic- and climate-driven stressors (Orth et al. 2006). Especially in regions such as the Greater Caribbean, which host both increasing grazer populations (Mazaris et al. 2017) and extensive seagrass meadows (Green and Short 2003; Wabnitz et al. 2008), a better understanding of biotic-abiotic interactions will be particularly critical for successful management and the long-term sustainability of these important coastal ecosystems.

Data availability statement

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Acknowledgments

Conflict of interest

None declared.