ARTICLE

Coastal and Marine Ecology

An underwater Serengeti: Seagrass-mediated effects on intake and cultivation grazing behavior of a marine megaherbivore

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Abstract

Populations of green turtles (*Chelonia mydas*), a megaherbivore that consumes seagrasses via cultivation grazing, are recovering worldwide. Information on plant-mediated effects on herbivore foraging behavior is critical to understanding plant–herbivore interactions and sustainability of grazing as ecosystems continue to change. In a Caribbean seagrass ecosystem, we use stationary cameras and benthic surveys to evaluate the effects of seagrass morphology and leaf nitrogen content on green turtle grazing behavior. *Thalassia testudinum* leaf morphology has significant effects on forage intake (in milligrams of dry mass [DM] per minute) for green turtles, whereas leaf nitrogen content has no effect. Intake increases in grazed areas with shorter leaves and higher leaf biomass concentration (in milligrams of DM per cubic centimeter), indicating more efficient foraging under these conditions. Bite rate (in bites per minute) increases in grazed areas with short leaves, a result of reduced search time. Bite size (in milligrams of DM per bite) increases in grazed areas with short but dense canopies, because a turtle crops more shoots with each bite. Increased foraging efficiency and reduced search time in grazed areas with high biomass concentrations collectively maximize intake. Ingested leaves are shorter than the mean height of all available leaves in grazed areas, indicating herbivore selection for shorter leaves. Our estimate for daily intake is 86.1 g DM day^{-1} 33-kg turtle^{-1}. Our study provides a novel contribution on the effects of plant-level cues on the grazing behavior of a marine megaherbivore, and how cultivation grazing behavior optimizes the green turtle foraging strategy by maximizing foraging efficiency and intake.

INTRODUCTION

Megaherbivore populations are recovering worldwide as a result of long-term conservation efforts, causing dramatic ecosystem-wide changes to terrestrial and aquatic plant communities (e.g., Bakker et al., 2016; Christianen et al., 2021; Gaynor et al., 2020; Gulick et al., 2020) and raising the need to establish natural baselines for megaherbivore biomass (Fløjgaard et al., 2021). Many of these population recoveries are occurring in ecosystems that have been severely degraded by anthropogenic activities, and the plant–herbivore interactions in such systems remain largely understudied. The global recovery of green turtles (*Chelonia mydas*) (Chaloupka et al., 2008; Mazaris et al., 2017; Weber et al., 2014) after centuries of low abundance (Jackson et al., 2001) is emblematic of this phenomenon in marine ecosystems.

Green turtles are the only herbivorous marine turtle, consuming primarily seagrasses throughout much of their global range (Bjorndal, 1980; Esteban et al., 2020). Recovery of green turtle populations offers the opportunity to understand their ecological roles as seagrass meadows are returned to a natural grazed state. Several recent studies have contributed insight into the impacts of increased grazing pressure on seagrasses (e.g., Christianen et al., 2019; Fourqurean et al., 2010; Gulick et al., 2020; Gulick, Johnson, et al., 2021; Hearne et al., 2019; Rodriguez & Heck Jr, 2020; Scott et al., 2020) and their ecosystem services (e.g., James et al., 2020; Johnson et al., 2019, 2020; Scott et al., 2018). However, there is a significant gap in the understanding of plant-mediated effects on green turtle foraging behavior, which is essential to interpreting plant–herbivore interactions and assessing the sustainability of grazing pressure as marine ecosystems continue to be impacted by anthropogenic activities.

Megaherbivore foraging decisions occur along a hierarchical continuum, along which animals respond to cues related to plant and habitat attributes at each decision level (i.e., from the bite/plant scale to ecosystem scale; Launchbaugh, 2020). Plant morphological and nutrient characteristics are important selection cues for herbivores on the bite/plant level. For terrestrial megaherbivores that consume grasses/roughage and rely on efficient fiber digestion for energy acquisition, their grazing strategy is largely driven by the need to maximize rates of intake with minimum energy expenditure (Launchbaugh, 2020; McNaughton, 1984). Plant characteristics and mechanisms for foraging efficiency (i.e., bite rate, bite size, bites per swallow, time spent searching for and/or handling forage) are important factors that can interactively influence megaherbivore grazing behavior and control forage intake on a short-term basis (in milligrams of dry mass [DM] per minute; hereafter referred to as short-term intake) (Chapman et al., 2007; Gross et al., 1993; Launchbaugh, 2020; McNaughton, 1984; Trudell & White, 1981). By contrast, variation in daily intake (in grams of DM per day; hereafter referred to as daily intake) is mostly explained by daily foraging duration and not plant morphology or nutrient content (Launchbaugh, 2020; Trudell & White, 1981). For example, variability in short-term intake by ungulate grazers that maintain grazing lawns is largely explained by forage biomass concentration, or forage DM per unit of volume above the substrate (McNaughton, 1984). Repetitive cropping of forage decreases sward height while stimulating the production of secondary shoots (McIntire & Hik, 2002; McNaughton, 1979), yielding a shorter, but dense, canopy that increases foraging efficiency and reduces search time for grazers (McNaughton, 1984). The effects of plant morphological and nutrient characteristics on foraging behavior and short-term/daily intake is well-studied in terrestrial megaherbivores (see review by Launchbaugh, 2020) but not in their marine counterparts, including green turtles.

Green turtles utilize a cultivation grazing strategy, in which they select distinct areas of seagrass, remove the upper/older portions of leaves and allow them to float away, and repeatedly crop the new leaf growth once it reaches a few centimeters above the substrate; hereafter referred to as grazed areas (Figure 1a; Bjorndal, 1980; Ogden et al., 1983; Williams, 1988; Zieman et al., 1984). In Caribbean seagrass meadows, repetitive cropping of the dominant seagrass, *Thalassia testudinum*, stimulates leaf growth and turnover (i.e., compensatory growth) (Gulick et al., 2020; Gulick, Johnson, et al., 2021; Moran & Bjorndal, 2005; Ogden et al., 1983; Zieman et al., 1984), and increases leaf nitrogen content while reducing lignin relative to ungrazed leaves, yielding a higher nutrient diet (Bjorndal, 1980; Moran & Bjorndal, 2007). Cultivation grazing also serves as a mechanism for reducing the length of seagrass leaves consumed, which allows green turtles to ingest an optimum ingesta particle size (Gulick,
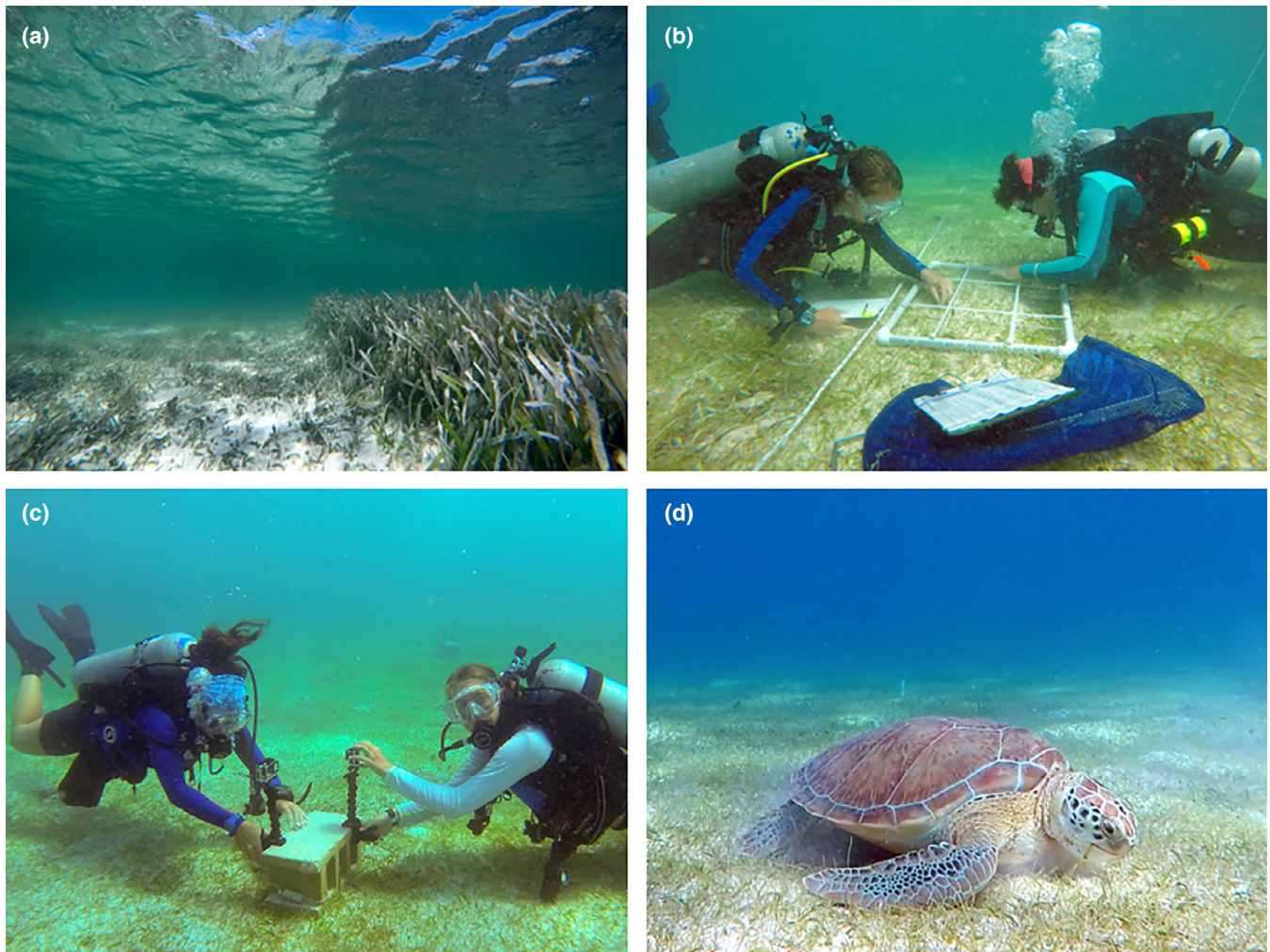
FIGURE 1 (a) A border of a grazed and ungrazed area in a Caribbean seagrass ecosystem; (b) SCUBA divers conduct rapid preliminary surveys across grazed areas to identify gradients in seagrass morphological characteristics; (c) SCUBA divers deploy high-definition video cameras in a grazed area; (d) a snapshot from video footage of a green turtle foraging in a grazed area at our study site. Photos: (a) Modified with permission from Gulick et al. (2020); (b) A. Gulick; (c) L. Palma; (d) A. Gulick.

Meylan, et al., 2021). The ability to reduce ingesta particle size is important for maximizing digestive efficiency and fermentation rates in herbivores (Bjorndal, 1979; Bjorndal et al., 1990; Lanyon & Sanson, 2006), particularly for herbivorous reptiles that lack the ability to masticate (Fritz et al., 2010). Green turtles exhibit high site fidelity to their foraging areas (Bjorndal et al., 2000; Hart et al., 2017) and can maintain grazed areas for at least 2 years (Gulick et al., 2020; Hernández & van Tussenbroek, 2014; Johnson et al., 2017; Ogden et al., 1983). Extended cropping of grazed areas for several months to years distinguishes the cultivation grazing behavior of green turtles from most mammalian megaherbivores, which intensively crop and maintain "grazing lawns" for a few weeks before migrating/moving on to another foraging area (e.g., Bakker et al., 2016; Gaynor et al., 2020; McNaughton, 1984).

The long-term cultivation of grazed areas by green turtles, combined with low metabolic requirements and high foraging site fidelity, is distinct from most terrestrial and aquatic megaherbivores (see Gibson & Hamilton, 1983). In light of green turtle population recovery and the global decline of seagrasses due to anthropogenic threats (e.g., eutrophication, coastal development, and climate change) (Dunic et al., 2021; Orth et al., 2006; Waycott et al., 2009), evaluating plant-mediated effects on foraging behavior and short-term intake of green turtles is needed to understand the impacts of increasing grazing pressure on seagrass ecosystems. Although green turtle foraging behavior has been evaluated on broader scales of home ranges and across foraging areas (e.g., Bjorndal, 1980; Griffin et al., 2020; Hernández & van Tussenbroek, 2014; Thomson et al., 2015), no study has evaluated seagrass-mediated effects on foraging efficiency and intake for green turtles on a bite/plant scale.

In a Caribbean seagrass ecosystem, we use stationary cameras and benthic habitat surveys in grazed areas to explore the effects of *T. testudinum* morphology and leaf nitrogen content on green turtle grazing behavior on a bite/plant scale. We evaluate the following: (1) effects of *T. testudinum* morphology and leaf nitrogen content in grazed areas on bite rate, bite size, and short-term intake; (2) effects of behaviors that may explain variation in bite rate, bite size, and short-term intake (i.e., bites per swallow, search time, and handling time); and (3) role of *T. testudinum* morphology and leaf nitrogen content in determining foraging site selection among established grazed areas. We also use our estimates of short-term intake from the video footage to generate an estimate of daily intake for green turtles on *T. testudinum* diets. Our study provides a novel contribution to understanding how plant-level cues affect grazing behavior and foraging site selection, and the role of long-term cultivation grazing in optimizing the foraging strategy of an ectothermic marine megaherbivore.

METHODS

Study site

This study was conducted in a Caribbean seagrass ecosystem at Buck Island Reef National Monument (BUIS), St. Croix, US Virgin Islands (17°47.4′ N, 64°37.2′ W). Seagrass meadows at this site cover approximately 406 ha across a depth range of 3–10 m (Gulick & Whitman, 2022) and are dominated by *T. testudinum* (Gulick et al., 2020). *Syringodium filiforme* and *Halodule wrightii* are also common. These meadows support a foraging aggregation of juvenile and adult green turtles throughout the year (Griffin et al., 2020; Hart et al., 2017), which has been increasing since the early 2000s (National Park Service, unpublished data). Green turtles at BUIS maintain large grazing areas of *T. testudinum* (>1000 m²) in both shallow (3–4 m) and deep seagrass meadows (9–10 m), many of which have been grazed consistently for at least 2 years (Gulick et al., 2020).

To evaluate the effects of *T. testudinum* morphology and leaf nitrogen content on green turtle grazing behavior, we first conducted rapid preliminary transect surveys (Figure 1b) across established grazed areas to determine if natural gradients in *T. testudinum* morphology existed. We focused our surveys of grazed areas in only shallow meadows (3–4 m), because water depth has a substantial effect on *T. testudinum* morphology in grazed areas (Gulick, Johnson, et al., 2021). The surveys indicated considerable variation in *T. testudinum* morphology

across grazed areas, which informed the placement of camera arrays for sampling grazing behavior along natural gradients of seagrass morphological characteristics. Although it was not logistically feasible to quantify the total nitrogen content of *T. testudinum* leaves at the time of camera placement, we were able to capture considerable variability in leaf nitrogen content across camera viewing areas (Table 1).

Camera arrays and seagrass surveys

Four camera arrays were established in grazed areas (one array per grazed area) and at separate times throughout the duration of our study (June–August 2017 and November–December 2017). Camera arrays were not established in ungrazed areas. Camera deployments for each array were conducted over a single 5-day period. Because we sampled grazing behavior within each camera viewing area along natural gradients of *T. testudinum* morphology and leaf nitrogen content, our sample size is based on the number of individual camera viewing areas in each array throughout the duration of our study ($n = 48$), and not the number of camera arrays ($n = 4$). All camera arrays were equal in terms of sampling time and area.

Camera arrays were constructed by arranging six concrete cinder blocks 8 m apart along a transect through the center of a grazed area, and mounting two cameras (GoPro Hero 4 Black or Hero 4 Silver fitted with a GoPro Battery BacPac) facing opposite directions on each cinder block (Figure 1c). This arrangement maximized the camera coverage of grazed areas while minimizing the overlap of camera viewing areas between neighboring cinder blocks. The goal of this camera arrangement was not to estimate the abundance or identify the number of individual turtles using each grazed area. Within each camera viewing area, polyvinyl chloride conduit stakes (2 × 25 cm) were established at 2-m intervals along a 6-m transect that extended out perpendicularly from each camera—these markers served as a reference for distance from camera during the video review process.

We quantified seagrass morphology and collected samples for leaf nitrogen analyses within each camera viewing area under SCUBA using 25 × 25 cm quadrats (0.0625-m² area; $n = 3$ quadrats per camera viewing area). *T. testudinum* morphology was evaluated by measuring total shoot density (in shoots per square meter), length (in centimeters), and width (in centimeters) of 15 randomly selected leaves, number of leaves per shoot of 10 randomly selected shoots, and aboveground biomass (in grams of DM per square meter). Shoot/thalli density and aboveground biomass were also quantified

TABLE 1 Summary of *Thalassia testudinum* morphological and nutrient characteristics for camera viewing areas within grazed areas and grazing behavior parameters extracted from video footage.

Parameters	*n*	Mean ± SD	Range	CV
Seagrass				
Aboveground biomass (g DM m^{-2})	48	21.4 ± 14.3	2.8–54.7	0.7
Shoot proportion (% *T. testudinum*)	48	34.1 ± 12.3	12.8–65.3	0.4
Leaf length (cm)	48	5.3 ± 3.1	0.5–17.3	0.6
Total nitrogen content of leaves (% DM)	48	1.8 ± 0.2	1.4–2.2	0.1
Biomass concentration (mg DM 10 cm^{-3})	48	3.8 ± 1.9	0.9–8.4	0.5
Behavior (per bout)				
Bite rate (bites min^{-1})	97	20.7 ± 8.4	1.6–34.6	0.4
Bite size (mg DM bite^{-1})	18	7.9 ± 6.8	2.7–64.5	0.9
Intake (mg DM min^{-1})	18	207.7 ± 114.3	86.3–490.3	0.6
Bites per swallow (no.)	18	21.4 ± 9.5	5.0–58.0	0.4
Handling time (% bout duration)	97	72.4 ± 23.1	4.5–100.0	0.3
Search time (% bout duration)	97	27.8 ± 23.1	0.0–95.5	0.8

Note: Shoot proportion of *T. testudinum* is reported as a proportion of all seagrass shoots and benthic macroalgae thalli present in grazed areas. Aboveground biomass, total nitrogen, biomass concentration, bite size, and intake were evaluated on a dry matter (DM) basis. Seagrass parameters not used in analyses are summarized in Appendix S1: Table S1.

Abbreviation: CV, coefficient of variance.

for other seagrasses (*S. filiforme* and *H. wrightii*) and benthic macroalgae present. For analytical purposes, we accounted for differences in seagrass and macroalgae species composition in each camera viewing area by determining the proportion of *T. testudinum* shoots out of all seagrass shoots and benthic macroalgae thalli present (hereafter referred to as shoot proportion). Aboveground biomass samples of all seagrasses and macroalgae were collected from 10 × 10 cm quadrats (0.01-m^2 area; $n = 3$ quadrats per camera viewing area) by clipping leaves at the leaf-sheath junction (or base of the thallus) using scissors. DM was determined by gently removing epiphytes from leaves with a razor blade, rinsing with fresh water, and drying to a constant mass at 60°C. Biomass concentration is a measure of forage biomass within a unit volume above the substrate, and is a metric used in terrestrial grasslands to quantify the effects of repetitive cropping by megaherbivores (see McNaughton, 1984). Biomass concentration of *T. testudinum* leaves (in milligrams of DM per 10 cubic centimeters) was determined by dividing mean leaf mass (in milligrams; average across three quadrats) by quadrat volume (in cubic centimeters; where height is mean leaf length). Total nitrogen of *T. testudinum* leaf tissue was determined using standard procedures (see Appendix S1).

To minimize disturbance to green turtle behavior, cinder blocks were placed and seagrass surveys were conducted in a grazed area 1 week prior to the 5-day camera deployment period. During the 5-day deployment period, video footage was recorded during the peak morning foraging period of each deployment day (7:00–10:30 AM). Each camera recorded a high-definition video (1080 pixels) for ~3.5 h during each deployment day. All cameras in an array were deployed within a 5-min timeframe on each deployment day, thereby minimizing the gap in recording start time between cameras. The morning peak foraging period for green turtles at this site was determined by conducting visual surveys from a boat from sunrise (7:00 AM) to noon and counting the number of turtles that surfaced to breathe during that period. These surveys were not meant to generate estimates of abundance but allowed us to determine when green turtles were most active in foraging areas—turtles surface to breathe more often when foraging (see Bjorndal, 1980).

Behavioral data extraction from video footage

Videos from each camera viewing area were viewed in their entirety, and all sightings of green turtles were marked for analysis (Figure 1d). Green turtle sightings were selected for behavioral data extraction and classified as a "grazing bout" if a turtle was observed swimming into a grazed area, settling on the substrate to forage, swimming out of the grazed area, and the entire duration of this process was visible within the camera viewing

area. It was not feasible to identify individual turtles observed across all grazing bouts because turtles were sometimes too far from the camera for the post-ocular scute patterns (commonly used to identify individuals) to be visible. Therefore, each grazing bout was assumed to be associated with a "new" individual. In addition, not all parameters (defined below) could be collected for every grazing bout because the ability to extract measurements from the footage was highly dependent upon the distance and orientation of the turtle to the camera.

The following parameters were collected from each grazing bout: grazing bout duration (in minutes), straight carapace length of the turtle (in centimeters; SCL_{n-t}), handling time (in percentages), search time (in percentages), bite rate (in bites per minute), number of bites per swallow, bite size (in milligrams of DM per bite), and short-term intake (in milligrams of DM per minute). Grazing bout duration (in minutes) began with the first bite and ended when the turtle pushed off the substrate and left the grazing area. To standardize when a turtle actively began and stopped the foraging process, bout duration was not based on when the turtle first came in or exited the viewing area. SCL_{n-t} was measured from the midpoint of the anterior nuchal scute to the tip of the longer posterior marginal scute (Bolten, 1999) using ImageJ (version 1.53k) software. Because the width of *T. testudinum* leaves was consistent in grazed areas (Appendix S1: Table S1), distance measurements extracted from the video footage were calibrated based on the leaf width for each camera viewing area. Handling time (in percentages) is the proportion of a grazing bout spent handling/ingesting forage and included all time intervals that began with a bite and ended with a swallow. Search time (in percentages) is the proportion of a grazing bout spent searching for forage and included all time intervals that began with a swallow and ended once the next bite was taken. Bite rate (in bites per minute) for each grazing bout was determined by counting the number of consecutive bites taken over a period of ≥ 1 min. Bites per swallow was determined by counting the number of bites taken prior to each swallow and taking the average of bites across all swallows to represent each grazing bout. The act of swallowing occurred when a turtle would raise its head to swallow a bolus. Bite size (in milligrams of DM per bite) for each grazing bout was determined from the video footage by measuring the length (in centimeters) of *T. testudinum* leaves ingested for up to 30 bites taken during a grazing bout (using ImageJ), and then converting to DM by multiplying the average length of leaves consumed during a grazing bout by the leaf mass per unit centimeter for the corresponding camera viewing area. Only turtles within 4 m of the camera were used to obtain bite size measurements. Short-term intake (in milligrams of DM per minute) for each grazing bout was calculated by multiplying bite rate and bite size.

Daily intake

Daily intake (in grams of DM per day) for green turtles at our study site was estimated using the mean value of short-term intake across grazing bouts extracted from the video footage assuming a daily grazing duration of 7 h and standardized to a turtle mass of 33.0 kg. We do not evaluate the effects of seagrass morphology or leaf nitrogen content on daily intake because most of the variation in daily intake by megaherbivores grazing on grasses/roughage is explained by daily grazing duration (Launchbaugh, 2020). Turtle mass (in kilograms) was determined by converting the mean SCL_{n-t} of turtles observed in the video footage using the mass of BUIS green turtles for the corresponding size class reported in Gulick, Meylan, et al. (2021). Because variability in daily intake on a mass-specific basis for green turtles across size classes is minimal (Bjorndal, 1980, 1985) and estimating daily intake based on the mean mass of turtles in a foraging aggregation is a standard approach (Bjorndal, 1980, 1982; Williams, 1988), we estimate daily intake for the foraging aggregation at our site based on the average mass of green turtles observed in the video footage. Daily grazing duration was estimated using the duration of the morning peak foraging period (3.5 h) for BUIS green turtles and based on an equivalent amount of time spent foraging during morning and afternoon foraging periods (Gulick et al., unpublished data). This bimodal diurnal foraging pattern with morning and afternoon peaks matches that reported for several green turtle aggregations (e.g., Bjorndal, 1980; Ogden et al., 1983; Williams, 1988). Because variation in grazing bout duration, search time, and handling time for each grazing bout is accounted for when determining the bite rate, it is reasonable to use our values of short-term intake to extrapolate to daily intake.

Analytical methods

Behavior parameters for each grazing bout (extracted from video footage) were matched with *T. testudinum* characteristics (collected via benthic surveys) from the corresponding camera viewing area.

Generalized additive models (GAMs) were used to evaluate the effects of *T. testudinum* morphology on the bite rate ($n = 97$), bite size ($n = 18$), and short-term intake ($n = 18$) for green turtles on a grazing bout basis. In GAM analyses, each covariate is conditioned on all

other covariates. The difference in replicates between models was due to bite rate being feasible to collect from observations where the turtle was too far away from the camera to measure bite size. Models were fit using thin-plate regression splines to evaluate the effects of nonlinear covariates. Model diagnostics and residual plots were checked to ensure that assumptions were not violated. Data were analyzed in R version 4.0.1 (R Core Team, 2020) using the "mgcv" package (Wood, 2011) with smoothness parameters estimated using restricted maximum likelihood (Wood, 2006).

We evaluated three response variables in our models (bite rate, bite size, and short-term intake), with each model including three fixed effects: aboveground biomass, shoot proportion (% *T. testudinum*), and leaf length. Of the seagrass characteristics measured in grazed areas, we selected these three characteristics as covariates because they best captured any variation in seagrass morphology (on a per leaf and per area basis) and species composition. Total nitrogen of *T. testudinum* leaves was not included as a covariate in the GAMs for the following reasons: (1) inclusion of more than three covariates resulted in the over-parameterization of the bite size and short-term intake models; (2) inclusion of leaf N content did not explain any variation in the response variable or improve model fit, regardless of the combination of covariates that were used in the model. However, because it has been suggested in the literature that leaf nitrogen content of seagrasses may drive herbivore foraging site selection and intake (Thayer et al., 1984; Valentine & Heck Jr., 2001; Zieman et al., 1984), we use a separate GAM to assess the relationship between total nitrogen content of *T. testudinum* leaves and short-term intake. Although all camera arrays that were established along natural gradients of seagrass morphology were equivalent in terms of sampling time and area, the sample distribution (rug plots) of the independent variables in each model were based on camera viewing areas within which turtles selected to forage.

We also use a GAM to evaluate the relationship between *T. testudinum* biomass concentration (in milligrams of DM per 10 cubic centimeters) and short-term intake. This analysis improves interpretation of the results from the GAM for bite size and allows comparisons with terrestrial megaherbivores that maintain grazing lawns that increase forage biomass concentration and maximize short-term intake (McNaughton, 1984).

Linear regression models and/or GAMs were used to evaluate behaviors that may affect bite rate, bite size, and short-term intake. The effects of bites per swallow on the three response variables were assessed using linear regression models. Using the same GAM framework described above, we also evaluated the effects of *T. testudinum* morphology on bites per swallow to help interpret our results from the GAM for bite size. Linear regression models were also used to evaluate the effects of handling time and search time on the three response variables. Analyses were performed in R version 4.0.1 (R Core Team, 2020) using the "dplyr" package (Wickham et al., 2020).

To evaluate if leaf length plays a role in selection of foraging sites from established grazed areas, we used a Kolmogorov–Smirnov test to compare the distributions of the length of leaves (in centimeters) ingested by turtles (i.e., bite size; $n = 328$) to the length of leaves available ($n = 705$) in grazed areas.

RESULTS

We reviewed 588 h of video footage and recorded 200 sightings of green turtles grazing within camera viewing areas. Of these observations, we recorded 97 complete grazing bouts from which we could extract behavioral parameters. The duration of grazing bouts averaged 3.4 ± 3.0 min (mean $\pm$ SD; range $= 0.2$–12.4 min; $n = 97$). The mean body size (SCL_{n-t}) of green turtles observed during these bouts was 62.1 ± 18.7 cm (range $= 36.3$–120.3 cm; $n = 43$). Summary statistics of grazing behavior parameters and seagrass characteristics in grazed areas are provided in Table 1 and Appendix S1: Table S1.

Grazing behavior and foraging site selection

Short-term intake ($n = 18$) on a grazing bout basis exhibited positive linear relationships with bite rate (Figure 2a; $R^2 = 0.40$; $p < 0.01$) and bite size (Figure 2b; $R^2 = 0.82$; $p < 0.01$). *T. testudinum* morphology in grazed areas significantly affected bite rate, bite size, and short-term intake (Table 2, Figure 3). The GAM for bite rate explains 33.4% of model deviance, with bite rate significantly decreasing as the length of *T. testudinum* leaves increases (Table 2, Figure 3a). The GAM for bite size explains 98.2% of model deviance (Table 2), with bite size significantly increasing with aboveground biomass (Figure 3b). Bite size also increased once the proportion of *T. testudinum* shoots in grazed areas reached a threshold of ~30%; this proportion is out of all seagrass shoots and benthic macroalgae thalli present (Figure 3c). The GAM for short-term intake explains 89.9% of model deviance (Table 2), with intake increasing with aboveground biomass of *T. testudinum* in grazed areas (similar to bite size) (Figure 3d) but decreasing with leaf
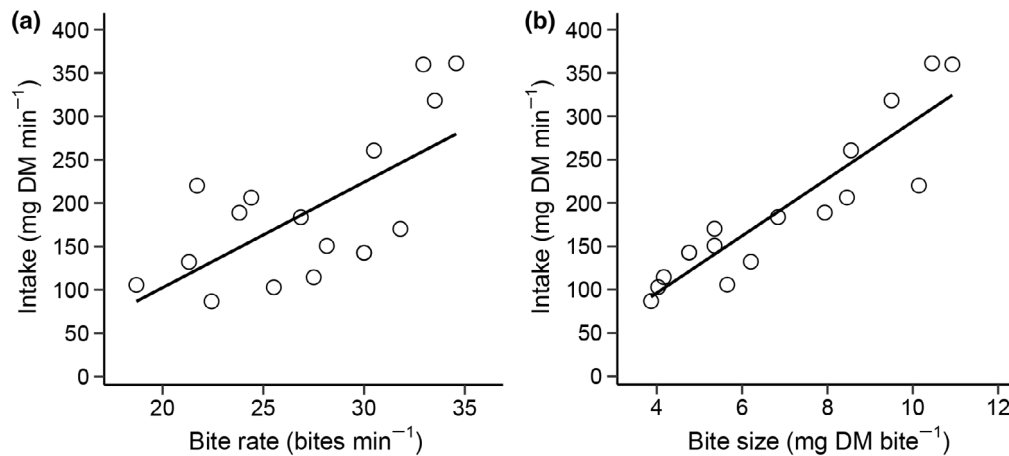
FIGURE 2 Graphical summary of linear regression analyses for evaluating relationships between forage intake on a grazing bout basis ($n = 18$) and (a) bite rate ($p < 0.01$; $R^2 = 0.40$) and (b) bite size ($p < 0.01$; $R^2 = 0.82$). Intake and bite size were evaluated on a dry matter (DM) basis.

TABLE 2 Summary of generalized additive model (GAM) output for evaluating effects of *Thalassia testudinum* morphology on bite rate, bite size, and intake by green turtles on a grazing bout basis.

	Response variable		
Covariate	**Bite rate** (bites min^{-1}; $n = 97$)	**Bite size** (mg DM bite^{-1}; $n = 18$)	**Intake** (mg DM min^{-1}; $n = 18$)
Aboveground biomass (g DM m^{-2})	0.142	**0.030**[a]	**<0.001**[a]
Shoot proportion (% *T. testudinum*)	0.073	**0.002**[a]	0.644
Leaf length (cm)	**0.041**[b]	0.502	**<0.001**[b]
R^2	0.334	0.982	0.899

Note: The *p*-values for significant covariates are indicated in boldface. Models were fit using thin-plate regression splines with smoothness parameters estimated using restricted maximum likelihood. Bite size, intake, and aboveground biomass were evaluated on a dry matter (DM) basis. Raw values for response variables and covariates are summarized in Table 1. Leaf nitrogen content was not included in the GAMs—see text for justification.
[a]Positive relationship.
[b]Negative relationship.

length (similar to bite rate) (Figure 3e). There was no effect of total nitrogen content of *T. testudinum* leaves after short-term intake. Because a wide range of leaf nitrogen values was captured across grazed areas during our study (Table 1), this result indicates that leaf nitrogen content does not affect green turtle foraging site selection among established grazed areas. This result should be distinguished from results of previous studies that found that elevated leaf nitrogen content in grazed areas relative to neighboring ungrazed areas can drive foraging site selection (Bjorndal, 1980; Thayer et al., 1984; Zieman et al., 1984). There is greater variation in leaf nitrogen content between grazed and ungrazed areas (Gulick et al., 2020; Moran & Bjorndal, 2007) than the variation in total nitrogen among established grazed areas in our study.

Short-term intake significantly increased in grazed areas with higher biomass concentrations (Figure 4; $R^2 = 0.66$; $p < 0.01$). Under these conditions where the *T. testudinum* canopy was short and leaf biomass is dense, bites per swallow increased (Appendix S1: Figure S1) and turtles were able to crop more shoots with each bite (Figure 3b), which led to increased bite size (Figure 5a; $R^2 = 0.61$; $p < 0.01$) and short-term intake (Figure 5b; $R^2 = 0.61$; $p < 0.01$).

Handling time and search time also explained some variability in bite rate, bite size, and short-term intake. Bite rate significantly decreased as the proportion of search time increased (Figure 5c) and increased with increasing proportion of handling time (Appendix S1: Figure S2). Bite size and short-term intake exhibited similar trends with search and handling time, but these trends
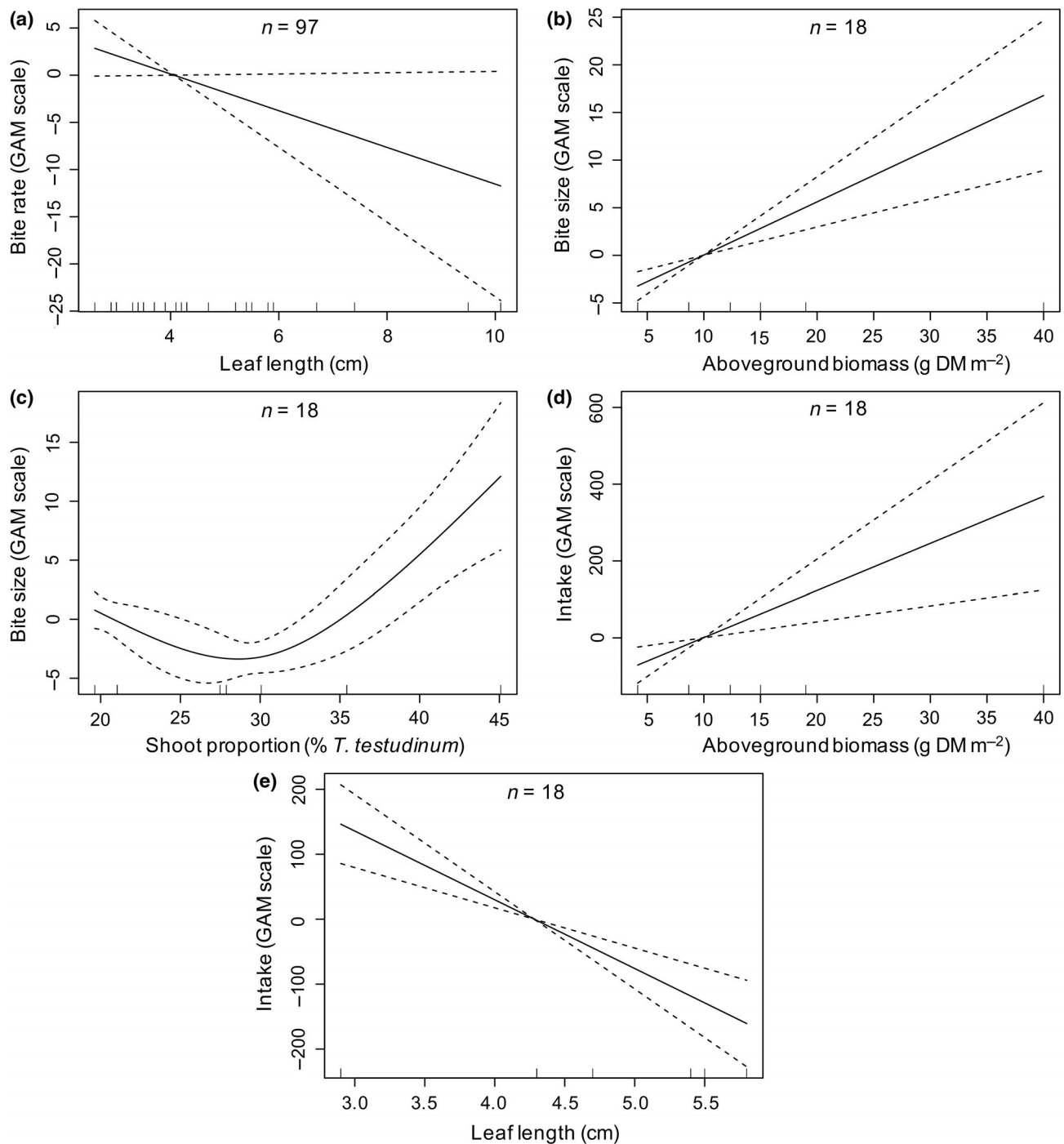
FIGURE 3 Graphical summary of generalized additive model (GAM) analyses for evaluating the effects of *Thalassia testudinum* morphology on the (a) bite rate (in bites per minute; $n = 97$); (b,c) bite size (in milligrams of dry mass [DM] per bite; $n = 18$); and (d,e) intake (in milligrams of DM per minute; $n = 18$) by green turtles on a grazing bout basis. Aboveground biomass, bite size, and intake were evaluated on a DM basis. All covariates were significant fixed effects. The response variable is unitless and shown on the *y*-axis as a centered smooth function scale. Covariates are shown on the *x*-axis with the rug plot corresponding to the sample distribution. Solid curves are smoothing spline fits conditioned on all other covariates and dashed lines are 95% CI. The convergence of 95% CI lines at zero 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). In GAM analyses, each covariate is conditioned on all other covariates.

were not significant. There was no effect of grazing bout duration or turtle body size (range of 43.1–108.2 cm SCL$_{n-t}$) on bite rate, bite size, and short-term intake on a grazing bout basis. Although green turtles have the capacity to consume larger bite sizes as they grow because of increased gape width (Marshall et al., 2014), there was no
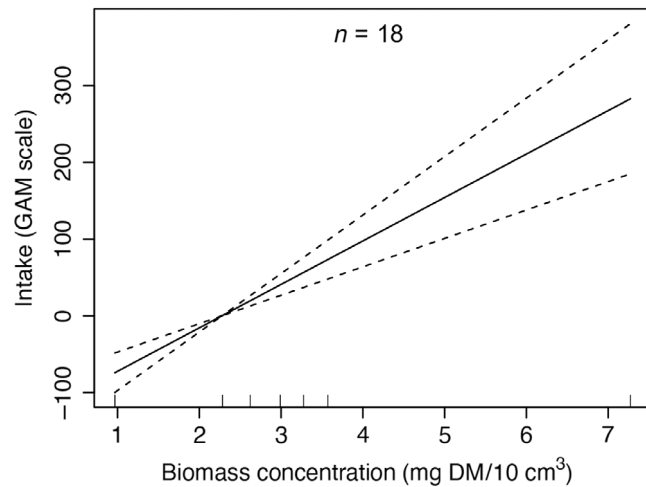
FIGURE 4 Graphical summary of the relationship between *Thalassia testudinum* leaf biomass concentration in grazed areas on forage intake (in milligrams of dry mass [DM] per minute) by green turtles on a grazing bout basis ($n = 18$; $R^2 = 0.66$; $p < 0.01$). Intake and biomass concentration were evaluated on a DM basis. The response variable is unitless and shown on the *y*-axis as a centered smooth function scale. The covariate is shown on the *x*-axis with the rug plot corresponding to the sample distribution. The solid curve is the smoothing spline fit and dashed lines are 95% CI. The convergence of 95% CI lines at zero 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).

relationship between ingesta particle size (equivalent to bite size in terms of leaf length) and body size for green turtles >30.0 cm SCL$_{n-t}$ (range sampled, 21.6–61.5 cm SCL$_{n-t}$; Gulick, Meylan, et al., 2021), suggesting that body size does not regulate ingesta particle size in larger individuals. Therefore, we suspect that any effect of body size on intake would not be captured when measured on a per minute basis (short-term intake), but instead be reflected in daily intake because larger turtles would require longer daily foraging periods to increase their intake and meet energy requirements.

The distribution of leaf lengths consumed by green turtles ($n = 328$; 1.9 ± 0.8 cm; range 0.9–6.5 cm) differed from those available ($n = 705$; 5.3 ± 3.1 cm; range 0.5–17.3 cm) in grazed areas (Figure 6; $p < 0.01$, $D = 0.69$; Kolmogorov–Smirnov), indicating that green turtles select for shorter leaves within grazed areas.

Daily intake

Mean daily intake for BUIS green turtles was estimated to be 86.1 g DM day^{-1} 33-kg turtle^{-1}, which can be extrapolated to an annual intake estimate of 0.95 kg DM [kg green turtle]$^{-1}$ year^{-1}. Our daily and annual
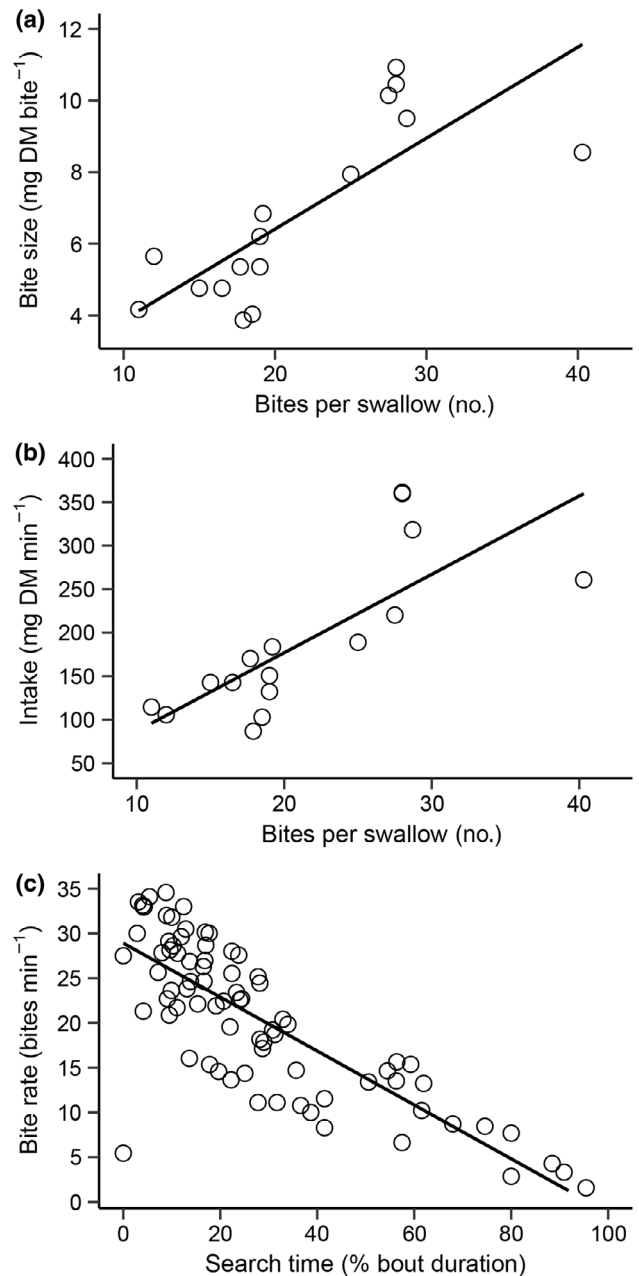

FIGURE 5 Graphical summary of behaviors that explain variability in bite rate, bite size, and intake on a grazing bout basis. (a) Bite size ($n = 18$; $p < 0.01$; $R^2 = 0.61$) and (b) intake ($n = 18$; $p < 0.01$; $R^2 = 0.56$) significantly increased with the number of bites per swallow. (c) Bite rate significantly decreased with search time ($n = 97$; $p < 0.01$; $R^2 = 0.68$), or the proportion of a grazing bout spent searching for forage in a grazed area. Bite size and intake also exhibited a decreasing trend with search time, but these trends were not significant. Intake and bite size were evaluated on a dry matter (DM) basis.

intake values fall within the range of estimates reported by three other studies that used three different methodologies (daily range: 24–218 g DM day^{-1}; annual range: 0.74–1.77 kg DM [kg green turtle]$^{-1}$ year^{-1}) (Bjorndal, 1980,
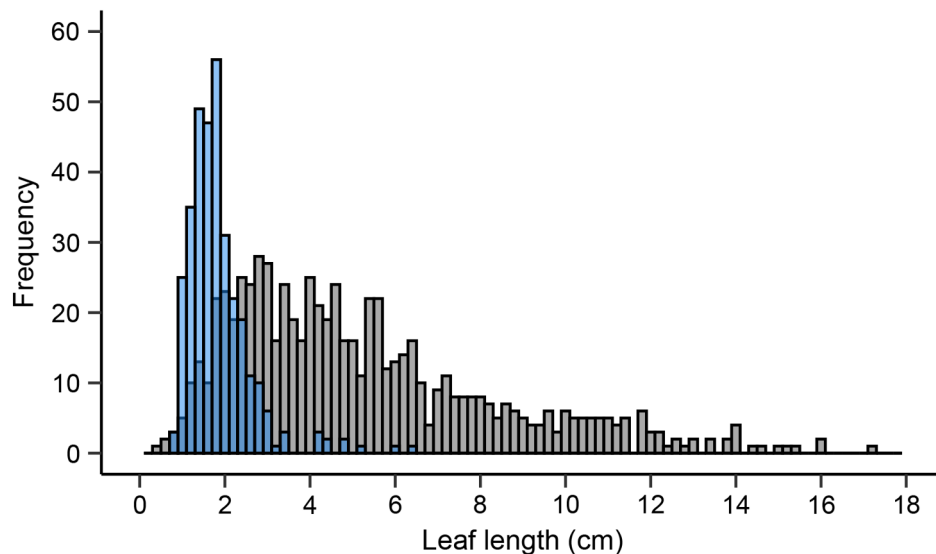
FIGURE 6 Frequency distribution of the length of *Thalassia testudinum* leaves consumed by green turtles (shown in blue; $n = 328$) versus the length of leaves available in grazed areas (shown in gray; $n = 705$). The distribution of the length of leaves consumed differed from those available in grazed areas ($p < 0.01$, $D = 0.69$; Kolmogorov–Smirnov).

1982; Williams, 1988), thereby providing support for the accuracy of the extraction of intake measurements based on video footage.

DISCUSSION

Plant-mediated effects on foraging efficiency, intake, and site selection

T. testudinum morphological characteristics in naturally grazed areas have significant effects on short-term intake by green turtles, while leaf nitrogen content has no effect. Short-term intake is highest in grazed areas with short leaves (Figure 3e), high levels of aboveground biomass (Figure 3d), and high biomass concentrations (Figure 4), which is a function of efficient foraging under these conditions. Bite rate increases in grazed areas with shorter leaves (Figure 3a), because of reduced search time (Figure 5a). Bite size increases in grazed areas with short but dense leaf canopies (Figure 3b), because the turtle crops more shoots with each bite (Figure 5b). The high forage yield per bite and minimal time spent searching for forage in grazed areas with high biomass concentrations collectively result in increased short-term intake. Cultivation grazing behavior clearly plays an important role in optimizing the green turtle foraging strategy not only by increasing leaf nutrient quality (Bjorndal, 1980; Moran & Bjorndal, 2007) but also by maximizing foraging efficiency and short-term intake.

Most aquatic turtles prehend forage via a quick acceleration of the head toward the food item, severing the selected item, followed by a strong suction that is induced by oropharyngeal volume expansion (Natchev et al., 2015). In contrast to mammalian herbivores, green turtles lack the ability to masticate (Fritz et al., 2010), which has important implications for digestive efficiency (Bjorndal et al., 1990; Lanyon & Sanson, 2006). Green turtles also do not appear to utilize lingual protrusion (based on our video footage), which is important in terrestrial turtles and tortoises (Natchev et al., 2015) and mammalian herbivores (Hofmann, 1989; Launchbaugh, 2020) for forage retention in the mouth prior to swallowing. Small bite size is a mechanism previously documented in herbivorous freshwater turtles, that reduces ingesta particle size, and thereby increases intake (Bjorndal & Bolten, 1992). It is important to distinguish between bite size and ingesta particle size because these metrics are not always directly related, particularly for megaherbivores that masticate and breakdown large bite sizes. Maintenance of grazed areas with shorter leaves reduces ingesta particle size for green turtles via small bite size (Gulick, Meylan, et al., 2021). Small bite size (in terms of leaf length), combined with increased bite rate and bites per swallow in grazed areas with short leaves (Figures 3a and 5a), would allow a turtle to retain more forage in its mouth while actively foraging. Increased intake per swallow could reduce the ingestion of seawater, although because much of the seawater entering the turtle's mouth during the foraging process is expelled through the nasal cavity before swallowing (White, 1994), intake per swallow should not greatly affect seawater intake. Therefore, the maintenance of grazed areas with shorter leaves and high leaf biomass concentrations via cultivation grazing is an important mechanism for

maximizing foraging efficiency and short-term intake for green turtles. We expect that cultivation grazing by green turtles also plays a role in maximizing daily intake while minimizing daily grazing duration and energy expenditure, given that most of the variability in daily intake by terrestrial megaherbivores (specifically grass and roughage grazers) is explained by the time devoted to grazing on a daily basis (Launchbaugh, 2020; Trudell & White, 1981).

Cultivation grazing behavior also provides valuable insight into foraging site selection among established grazed areas. Green turtles select shorter leaves within grazed areas (Figure 6), thereby maximizing foraging efficiency and short-term intake (Figures 3–5). Green turtles also select for a more digestible diet through the repetitive cropping of seagrasses, which yields younger and more nutritious leaves with higher nitrogen content and lower lignin content (Bjorndal, 1980; Moran & Bjorndal, 2007) and reduces ingesta particle size (Gulick, Meylan, et al., 2021). However, short-term intake was not affected by leaf nitrogen content in our study. Although cultivation grazing increases leaf nitrogen content in grazed areas when compared with neighboring ungrazed areas (Bjorndal, 1980; Moran & Bjorndal, 2007; Zieman et al., 1984), our result indicates that the nitrogen content of leaves does not affect green turtle selection of grazed areas across those that have been already established. Plant characteristics are important factors that affect foraging efficiency and short-term intake for megaherbivores (e.g., Chapman et al., 2007; Gross et al., 1993; Launchbaugh, 2020), but other factors, such as digestive physiology constraints, also affect forage intake.

Digestive physiology constraints to forage intake by green turtles

Much of the literature that evaluates the effects of plant morphological and nutrient characteristics on foraging behavior and short-term intake for megaherbivores is based on ruminants that rely on foregut fermentation to digest cellulose (Chapman et al., 2007; Launchbaugh, 2020; Trudell & White, 1981). Our study provides novel insight into how plant morphology affects foraging behavior of an herbivorous reptilian megaherbivore that utilizes hindgut fermentation.

An adaptation of green turtles to their herbivorous diet is the ability of their gut microflora to digest ~90% of the cellulose in their diet and produce short-chain fatty acids as an important energy source (Bjorndal, 1979). The hindgut fermentation process in green turtles on seagrass diets is distinctive from other reptilian herbivores that consume different diets (e.g., land iguanas and tortoises). Microbes in the green turtle gut rapidly reduce the ingesta particle size of seagrass tissue in the initial portion of the hindgut by quickly breaking down cellulose, the primary structural carbohydrate in seagrass, via hindgut fermentation (Bjorndal, 1979). Smaller particles have greater surface area exposed to microbial activity, which increases fermentation rates and allows particles to pass through the digestive system more quickly (Bjorndal, 1979). Consumption of a non-seagrass or larger particle size diet by green turtles could result in decreased efficiency or particle breakdown in the initial portion of the hindgut. The gut microflora required to breakdown other food items like algae (that are low in cellulose) may differ from the cellulolytic gut microflora in green turtles on seagrass-dominated diets (Bjorndal, 1985). This may lead to the gut filling quickly with larger particle sizes and may increase passage time for digesta, while physically limiting additional intake of forage.

Short-term intake by green turtles significantly decreases in grazed areas with longer leaves (Figure 3e), reflecting reduced foraging efficiency via a decrease in bite rate. However, consumption of longer leaves would also fill the gut rapidly with more lignified forage (Moran & Bjorndal, 2007) and larger particle sizes. The maintenance of grazed areas with short nutritious leaves likely releases green turtles from the physical constraints to forage intake by decreasing bite size (in terms of leaf length) and ingesta particle size (Gulick, Meylan, et al., 2021), yielding a more nutritious and less lignified diet (Bjorndal, 1980).

Cultivation grazing behavior in an ecological context

Cultivation grazing behavior by green turtles has been primarily documented in seagrass meadows of the Greater Caribbean (e.g., Bjorndal, 1980; Hernández & van Tussenbroek, 2014; Ogden et al., 1983; Williams, 1988; Zieman et al., 1984) and Western Atlantic (Holzer & McGlathery, 2016). As green turtle populations rebound and the number of studies conducted in grazed areas become more widespread, this behavior is now being documented in other regions (i.e., Australia; Scott et al., 2020). Because variation in green turtle grazing behavior remains largely understudied, this raises the question: When is cultivation grazing behavior advantageous for green turtles?

In terrestrial grasslands, repetitive cropping of grazing lawns by megaherbivores stimulates leaf growth and production of secondary shoots (McIntire & Hik, 2002; McNaughton, 1979), which maintains high concentrations of leaf biomass (McNaughton, 1984). Most of the variability in short-term intake by herbivores in these systems is

explained by forage biomass concentration, indicating that the maintenance of grazing lawns is advantageous to herbivores when the productivity of the forage can support current levels of grazing intensity (McNaughton, 1984). Long-term cultivation grazing by green turtles can also result in seagrass compensatory growth responses (Gulick et al., 2020; Moran & Bjorndal, 2005; Ogden et al., 1983; Zieman et al., 1984), despite the initial reduction in leaf biomass and leaf mass growth (in grams of DM per square meter per day) relative to ungrazed areas (Gulick et al., 2020). This compensatory growth response is supported by increased production of secondary shoots, which allows leaf surface area and canopy light harvesting potential to be maintained as grazing intensity increases (Gulick, Johnson, et al., 2021), and results in higher leaf biomass concentration. Analogous to grazing lawns in the African savanna, the increase in short-term intake by green turtles with biomass concentration (Figure 4) reflects the advantage of cultivation grazing in stimulating plant responses to maintain high biomass concentrations in grazed areas to maximize short-term intake. Further research on the plasticity of foraging behavior in green turtles, while accounting for the capacity of turtles to adjust intake and metabolic rates based on forage productivity, is needed. The capacity for *T. testudinum* compensatory growth responses to grazing probably changes with latitude (Rodriguez & Heck Jr, 2020), grazing intensity (Gulick et al., 2020; Williams, 1988), habitat characteristics of grazed areas (e.g., water depth; Gulick et al., 2020), and density dependent effects in green turtle foraging aggregations (Bjorndal et al., 2000). Additional mechanisms for seagrass compensatory growth responses to grazing also need to be explored (see summary in Gulick, Johnson, et al., 2021).

The video footage of green turtles foraging in the multi-species seagrass meadows at our study site showed that more seagrass biomass is removed by grazing than is ingested. Although green turtles target *T. testudinum* shoots at our study site, some incidental breakage of other seagrass shoots in the process of consuming *T. testudinum* did occur. Breakage without consumption of seagrasses other than *T. testudinum* and macroalgae may be a greater proportion of their biomass than it is for *T. testudinum*, and further research is needed on this topic. Although we are not able to provide a quantitative estimate of the biomass not consumed on a per bite basis, the combination of ingestion and "breakage without consumption" of seagrass biomass from meadows by green turtles may affect the composition of seagrass communities in grazed areas (Hearne et al., 2019; Hernández & van Tussenbroek, 2014) and has important implications for the sustainability of grazing and the capacity of meadows to support green turtles.

Our estimates of daily and annual intake by green turtles are within the range of those previously reported (Bjorndal, 1980, 1982; Williams, 1988). Similar to our study, Williams (1988) estimated intake via bite counts and bite size, but collected measurements during snorkel surveys and assumed a constant bite size of 11 mg bite^{-1} when calculating daily intake. That study was conducted in a heavily grazed area with very short leaves and low rates of compensatory growth. Therefore, an estimate of constant bite size of 11 mg bite^{-1}, which was considerably greater than that measured in our study (7 mg bite^{-1}; Table 1), may have inflated the estimate of daily intake. Our results reflect the advantage of using remote video methods to capture the variability in bite size (Table 1), which is important for accurate assessment of forage intake across gradients of habitat characteristics and estimation of natural baselines for green turtle biomass in seagrass ecosystems (see Fløjgaard et al., 2021).

Our study provides a novel contribution to the understanding of plant-mediated effects on the grazing behavior and foraging site selection of a reptilian marine megaherbivore. Maintenance of grazed areas via cultivation grazing optimizes the green turtle foraging strategy by stimulating plant responses that allow meadows to support grazing pressure (i.e., compensatory growth), while maximizing foraging efficiency and intake. Evaluating megaherbivore behavioral processes is critical to understanding the functioning of seagrass ecosystems under natural grazing regimes, and the sustainability of grazing by a recovering megaherbivore that is reassuming its historical ecological role.

AUTHOR CONTRIBUTIONS

Alexandra G. Gulick, Alan B. Bolten, and Karen A. Bjorndal conceived and designed the study. Alexandra G. Gulick, Alan B. Bolten, Karen A. Bjorndal, Clayton G. Pollock, and Zandy Hillis-Starr contributed to the planning and implementation of the study. Alexandra G. Gulick, Robert A. Johnson, Laura A. Palma, Ashley M. Kusel, and Clayton G. Pollock collected the data. Alexandra G. Gulick and Karen A. Bjorndal analyzed the data. Alexandra G. Gulick wrote the manuscript with contributions and final approval from all authors.

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CONFLICT OF INTEREST
The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT
Data (Gulick et al., 2022) are available from Dryad: https://doi.org/10.5061/dryad.g4f4qrfsx.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.