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ORIGINAL PAPER

Role of ingesta particle size in the green turtle grazing strategy, ontogenetic diet shifts, and responses to seagrass declines

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Abstract

Populations of the green turtle (*Chelonia mydas*), a mega-herbivore that consumes seagrasses, are recovering worldwide. Understanding green turtle adaptations to herbivory and responses to changes in seagrass availability will be critical to interpreting plant–herbivore interactions as green turtle populations continue to rebound. Ingesta particle size and diet composition of two green turtle foraging aggregations (Bermuda, 32.3° N, 64.8° W; U.S. Virgin Islands [USVI], 17.8° N, 64.6° W) in the Northwest Atlantic (NWA) were evaluated to assess the prevalence of herbivory across foraging sites and life stages, determine if there is an optimum ingesta particle size, and evaluate green turtle responses to changes in seagrass availability. Both aggregations were herbivorous (> 90% seagrass/algae) across size classes (straight carapace length, SCL). Ingesta particle size (mean ± SD) did not differ between Bermuda (2.6 ± 1.4 cm) and the USVI (2.3 ± 1.2 cm). Of seagrass leaves ingested, 20–30% were 1.7 cm in length, indicating a potential optimum for maximizing digestion rates. Turtle size (SCL) had a significant effect on particle size in Bermuda ($p = 0.01$, $R^2 = 0.16$) (35.1 ± 9.9 cm SCL) but not in the USVI aggregation, which was comprised of larger turtles (49.0 ± 6.1 cm SCL). In Bermuda, there was no apparent response to the declines in seagrass availability. Ingesta particle size and volume of seagrass leaves did not decline from 2015 to 2019, nor was there an increase in volume of seagrass roots and rhizomes. These results indicate herbivory is prevalent across size classes at two NWA foraging sites and ingesta particle size has important implications for optimizing the green turtle grazing strategy and facilitating ontogenetic diet shifts to herbivory in juveniles. Ingesta particle size is a valuable tool for assessing green turtle responses to seagrass declines that should be interpreted within the context of population demographics.

Introduction

Recovery of mega-herbivore populations after decades to centuries of low abundance is occurring across terrestrial and aquatic ecosystems as a result of long-term conservation efforts (e.g. Subalusky et al. 2015; Christianen et al. 2021). For example, this phenomenon is occurring in a hippopotamus (*Hippopotamus amphibius*) population in Maasai Mara National Reserve in Kenya (Subalusky et al. 2015), among large-bodied ungulates in the savannas of Mozambique (Gaynor et al. 2020), and among green turtle (*Chelonia mydas*) populations across their global range (Mazaris et al. 2017; Christianen et al. 2021). Many population recoveries are occurring in ecosystems that have been greatly altered by anthropogenic activity, and plant–herbivore interactions in these degraded systems remain largely understudied.

Marine mega-herbivores, including green turtles and sirenians (Families: Trichechidae and Dugongidae), have been severely overexploited by humans since the fifteenth

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century and were once the primary consumers of seagrass biomass worldwide (Bjorndal 1997; Domning 2001). Green turtle populations in the Caribbean alone are estimated to have been reduced by 97% from historic levels (Jackson et al. 2001), and, until recently, were ecologically extinct throughout much of their global range.

Long-term conservation efforts over the past few decades are resulting in the recovery of many green turtle populations around the world (Chaloupka et al. 2008; Weber et al. 2014; Mazaris et al. 2017) and the return of some seagrass meadows to a natural grazed state. However, seagrasses are rapidly declining globally due to several anthropogenic threats, including eutrophication, climate change, and coastal development (Orth et al. 2006; Waycott et al. 2009; Grech et al. 2012). Rebounding green turtle populations and the return of many seagrass meadows to a natural grazed state have raised concerns that some meadows may become overgrazed (Fourqurean et al. 2010, 2019; Kelkar et al. 2013; Christianen et al. 2014) with concomitant loss of some ecosystems services (Heithaus et al. 2014; Atwood et al. 2015; James et al. 2020). Although recent efforts continue to reveal important insight into seagrass responses to increased grazing pressure by green turtles (e.g. Johnson et al. 2017, 2020; Christianen et al. 2019; Gulick et al. 2020, 2021; Rodriguez and Heck 2020; Scott et al. 2020), an understanding of green turtle adaptations to herbivory and adaptations for maintaining forage will be essential to interpreting green turtle–seagrass interactions as marine ecosystems continue to change.

Green turtles are the only herbivorous marine turtle, consuming mostly seagrasses and algae throughout much of their global range (Mortimer 1981; Esteban et al. 2020). Omnivory in this species can also occur (e.g. Seminoff et al. 2002; Cardona et al. 2009; Williams et al. 2014; Burgett et al. 2018; Howell and Shaver 2021), particularly in foraging aggregations that utilize colder habitats near the limits of their range (Esteban et al. 2020). There is also a shift from omnivory to herbivory (Reich et al. 2007; Jones and Seminoff 2013; Burgett et al. 2018) associated with the ontogenetic habitat shift that occurs when green turtles recruit from oceanic habitats to neritic habitats (Bolten 2003; Reich et al. 2007; Arthur et al. 2008).

In the Northwest Atlantic (NWA), juvenile green turtles recruit to neritic habitats at a body size of 20–25 cm and shift to seagrass-dominated diets (Bjorndal 1997). Green turtles in the NWA consume primarily *Thalassia testudinum* via a cultivation grazing strategy, in which they select distinct areas of seagrass, remove the upper/older portions of the seagrass leaves from the area and allow them to float away, and then repeatedly crop the new growth at the leaf base when it reaches a few centimeters above the substrate (Bjorndal 1980; Williams 1988). Cultivation grazing increases the nitrogen content and reduces lignin of *T. testudinum* leaves, yielding a higher nutrient diet for the turtle (Bjorndal 1980; Moran and Bjorndal 2007). Repetitive cropping should also decrease ingesta particle size (Bjorndal 1980), or the size of *T. testudinum* leaves ingested by green turtles. The ability to reduce ingesta particle size and increase the surface area exposed to microbial activity is critical to maximizing digestive efficiency and rates of fermentation in herbivores (Bjorndal et al. 1990; Lanyon and Sanson 2006), particularly in reptiles that lack the ability to masticate (Fritz et al. 2010). Ingesta particle size and mechanisms for reduction have been overlooked in previous green turtle diet studies. Because of the allometry between body size and head width (a proxy for gape width) in sea turtles (Herrel et al. 2002; Marshall et al. 2014), green turtles should be capable of increasing bite size as they grow, similar to other herbivores (Shipley et al. 1994). Reducing ingesta particle size via small bite size and/or cultivation grazing may optimize the green turtle foraging strategy by allowing energy requirements to be met on a low nutrient diet and may be critical to facilitating the transition to herbivory during the juvenile life stage.

Evaluating temporal and spatial trends in ingesta particle size, in addition to diet composition, may also be a potential tool for assessing green turtle responses to declines in seagrass availability at foraging sites. For example, if seagrass availability is declining and/or overgrazing by green turtles is occurring at a foraging site, the following should be observed in green turtle gut contents over time: (1) a decrease in ingesta particle size as the availability of seagrass tissue becomes limited; (2) a narrower range of values for ingesta particle size; (3) a decline in percent volume of seagrass leaves; (4) an increase in percent volume of seagrass roots and rhizomes (see Christianen et al. 2014) and other food sources. Spatial differences in ingesta particle size and diet composition within a green turtle foraging aggregation may also be useful for detecting changes in seagrass availability at foraging sites.

In light of green turtle recovery, evaluating ingesta particle size and diet composition of green turtle foraging aggregations will add important context for understanding the prevalence of herbivory across foraging sites and life stages, the implications of ingesta particle size for supporting herbivory and green turtle growth rates, and how green turtles may respond to changes in seagrass availability. Although diet has been described for green turtles in the NWA (e.g. Mortimer 1981; Williams et al. 2014; Stringell et al. 2016; Herren et al. 2018; Burgett et al. 2018; Howell and Shaver 2021) and worldwide (see review by Esteban et al. 2020), no studies have evaluated ingesta particle size, and most have focused on foraging aggregations near the regional limits of the species' range.

In this study, we examined esophagus and stomach contents collected from juvenile green turtles in Bermuda and the U.S. Virgin Islands (USVI) to address the following: (1)

Compare diet composition and ingesta particle size between aggregations in the center (USVI) and northern limit (Bermuda) of the species' range in the NWA; (2) Determine if there is a potential optimum ingesta particle size for green turtles on seagrass diets; (3) Evaluate temporal changes and spatial differences in diet and ingesta particle size to assess green turtle responses to seagrass declines in Bermuda, using the USVI as a reference site.

Methods

Study areas

The Bermuda Platform (32.3° N, 64.8° W) in the Northwest Atlantic (NWA) surrounds the oceanic archipelago of Bermuda, and is approximately 1100 km off the eastern coast of the United States. The shallow platform has a subtropical climate and supports a variety of marine ecosystems, including seagrass meadows (depth range 0–15 m) that are dominated by *Thalassia testudinum* and *Syringodium filiforme*, and also support *Halophila decipiens* and *Halodule* sp. (Murdoch et al. 2007; Manuel et al. 2013). The species of *Halodule* that occurs in Bermuda has not been confirmed (see Manuel et al. 2013). Seagrasses are declining across the Bermuda Platform (Murdoch et al. 2007; Fourqurean et al. 2010), including meadows dominated by *T. testudinum* and *S. filiforme*. The Bermuda Platform provides critical foraging and developmental habitat for juvenile green turtles (Meylan et al. 2011) and is near the northern limit of the species' range. This site is associated with the ontogenetic diet shift that occurs when oceanic juvenile green turtles recruit to neritic foraging grounds (Meylan et al. 2011; Burgett et al. 2018).

Buck Island Reef National Monument (BIRNM) (17.8° N, 64.6° W) is a federal marine protected area off the coast of St. Croix, U.S. Virgin Islands (USVI) in the eastern Caribbean. The monument boundaries encompass an uninhabited island (0.71 km^2) and 76.3 km^2 of tropical marine habitats, including seagrass meadows (Pittman et al. 2008). Seagrass meadows at this site are relatively stable in long-term coverage area (Kendall et al. 2004; Pittman et al. 2008), are distributed across shallow and deep habitats (depth range 3–10 m), and are dominated by *T. testudinum* (Gulick et al. 2020, 2021). *Syringodium filiforme* and *Halodule wrightii* are also common at this site. While seagrass meadows at BIRNM are relatively pristine and do not experience the effects of anthropogenic-driven events such as shoreline erosion, eutrophication, or physical damage (i.e. anchoring), the early presence of an invasive seagrass (*Halophila stipulacea*) was documented during 2017 (National Park Service, unpublished data) at the time of sample collection for this study. BIRNM is an important foraging and nesting site for green turtles and is centrally located within the species' range in the NWA. Seagrass meadows at BIRNM support an increasing foraging aggregation of juvenile and adult green turtles throughout the year (Hart et al. 2017; Griffin et al. 2020; National Park Service, unpublished data). Prior to our study, green turtle diets at BIRNM had not been assessed beyond broad categories and consisted primarily of native seagrasses (Daniels and Hart 2016).

Sample collection

In Bermuda, green turtle esophagus and stomach contents were collected via necropsy from green turtles ($n = 47$) that stranded during 2015–2019. The following parameters were collected for each turtle: straight carapace length (SCL$_{\mathrm{min}}$; cm), mass (kg), sex, stranding location, and turtle condition. SCL$_{\mathrm{min}}$ was measured from the midpoint of the anterior nuchal scute to the midpoint between the last pair of marginal scutes (SCL$_{\mathrm{min}}$ in Bolten 1999). Sex was determined by examination of the gonad; a magnifying lens was used for smaller individuals. Because precise locations of foraging areas for stranded turtles could not be determined, stranding location was binned based on the coastline or sound in which the individual stranded as follows: Castle Harbour, Great Sound, Harrington Sound, Northern Coast, St. Georges Harbour, Western Coast, and undetermined. Stranding location was collected to assess whether spatial differences in diet and ingesta particle size could be a useful tool for evaluating green turtle responses to changes in seagrass availability. Because turtles likely drifted prior to collection (Cook et al. 2021), and stranding locations may not necessarily correspond to an individual's foraging area, we used caution when interpreting our results relating to spatial effects on diet and particle size. Turtle condition at time of stranding was visually classified as alive ($n = 11$), freshly dead ($n = 22$), or moderately decomposed ($n = 14$)—gut content samples were collected postmortem. Individuals found alive at time of stranding died naturally within 1–2 days of the stranding date. Entire contents of the esophagus and stomach were collected during necropsy, as long as both digestive regions were intact (i.e. no damage or severe decomposition). Of the sampled turtles, diet contents were collected from individuals as follows: esophagus and stomach ($n = 32$), esophagus only ($n = 3$), stomach only ($n = 12$). Samples were stored in 95% ethanol. Stranded turtles that had clearly succumbed to chronic health issues were not sampled.

In the USVI, esophagus contents were collected from live-captured green turtles ($n = 31$) via esophageal lavage during 2017–2018. The following parameters were collected from each turtle: SCL$_{n-t}$ (cm), mass (kg), sex, and capture location. Sex and capture location were excluded from our analysis because sex could not be visually determined due to the immature status of most turtles, and the majority of turtles were captured at the same capture location. SCL_{n-t} was measured from the midpoint of the anterior nuchal scute to the tip of the longest posterior marginal scute (SCL_{n-t} in Bolten 1999) and converted to SCL_{min} using the formula provided in Meylan et al. (2011). Esophagus samples ($n=31$) were stored in salt water and frozen the day of collection. Although the collection methods for diet samples differed between Bermuda (entire esophagus and stomach contents from necropsies of stranded turtles) and the USVI (esophageal lavage contents from live turtles), we do not think these differences affect our conclusions.

Diet composition and ingesta particle size

Each diet sample was rinsed with deionized water through a fine-mesh (1 mm) sieve and the components identified to the lowest possible taxonomic level using a magnifying lamp. Seagrasses were identified to species and included *Thalassia testudinum*, *Syringodium filiforme*, *Halodule wrightii* (*Halodule* sp. for Bermuda), and *Halophila stipulacea* (invasive in USVI). Recovered algae were often broken down and only distinguishable to the phylum level (*Chlorophyta, Rhodophyta*). Animal matter was present in trace amounts (< 0.1 mL) and grouped into Invertebrata (tunicates, sponges, molluscs) and Vertebrata (fish). We did not identify specific taxa for animal matter given its presence in trace amounts—gelatinous invertebrates were not detected. Mangrove tissue (fragments of leaves and propagules) and unidentified tissue (plant and animal combined) were also present in trace amounts. Volume of each sample and its respective diet components were determined via water displacement in graduated cylinders to the nearest 0.1 mL. Percent volume (mean ± standard deviation, coefficient of variation), frequency of occurrence (% frequency), and index of relative importance (IRI) were determined for each diet component. IRI was calculated using the modified formula for herbivores provided by Bjorndal et al. (1997); this index is a reliable measure for ranking relative importance of diet categories because it integrates frequency of occurrence and volume. For Bermuda samples, percent volume of diet components was determined by combining esophagus and stomach samples from each turtle because there was no difference in the percent volume of diet components between the two regions.

Ingesta particle size of ingested *T. testudinum* leaves, if present, was determined by measuring the length (to the nearest 0.1 cm) of up to 30 randomly selected leaves in each esophagus and stomach sample for each turtle. We focused our measurements of particle size on only *T. testudinum* leaves because it is the dominant seagrass species (van Tussenbroek et al. 2014) and primary diet item for green turtles in the NWA (see review by Esteban et al. 2020). All leaves in a sample were measured if fewer than 30 were available. Leaf width (to the nearest 0.1 cm) was also measured (Fig. S2), but because leaf width was relatively constant (range 0.2–1.0 cm) when compared to leaf length, we assumed it was unlikely to affect turtle bite size and thereby simplified “ingesta particle size” to refer to leaf length only. Measurements of ingested *T. testudinum* leaves recovered from the esophagus and stomachs of green turtles is a reliable metric for ingesta particle size. Like all reptiles, green turtles do not masticate (Fritz et al. 2010) and the significant breakdown of cellulose, the major structural carbohydrate in seagrass leaves, does not occur until food items reach the cecum and colon and are digested via microbial hindgut fermentation (Bjorndal 1979). For Bermuda samples, ingesta particle size was determined by combining measurements from the esophagus and stomachs of individuals because there was no difference in *T. testudinum* leaf length or leaf width between digestive regions.

Head width and body size

To aid in the interpretation of our results for the effects of SCL_{min} on ingesta particle size, we used a long-term dataset from a green turtle foraging aggregation in Union Creek, Great Inagua, Bahamas (21.2° N, 73.6° W) to evaluate the relationship between green turtle ($n=616$) head width (cm) and SCL_{min} (cm). Head width is a proxy for gape width (Herrel et al. 2002; Marshall et al. 2014), which is known to affect bite size and ingesta particle size in other herbivores (e.g. Shipley et al. 1994). Head width was measured across the widest part of the head of each turtle. SCL_{min} was measured from the midpoint of the anterior nuchal scute to the midpoint between the last pair of marginal scutes (SCL_{min} in Bolten 1999). Head width was not measured in Bermuda and USVI.

Statistical analysis

Analyses were performed in R version 4.0.1 (R Core Team, 2020) using the ‘dplyr’ package (Wickham et al. 2020). Non-parametric tests of group differences (Mann–Whitney *U* Tests) were used to compare green turtle diet composition (percent volume) and ingesta particle size (*T. testudinum* leaf length) between Bermuda and the USVI. The distributions of particle size at each site were also compared using a Kolmogorov–Smirnov test.

The effects of year, stranding location, sex, and SCL_{min} (5-cm bins) on percent volume of diet items in Bermuda were assessed using nonparametric tests of group differences [Kruskal Wallis Rank Sums with Dunns (posthoc) Tests]. In the USVI, effects of year and SCL_{min} on percent volume of diet items were assessed using Mann–Whitney *U* Tests and Kruskal–Wallis Rank Sums with Dunns Tests, respectively. Similarly, the effects of year and stranding location

(Bermuda only) on ingesta particle size at each site were evaluated using Kruskal Wallis and Mann–Whitney Tests. Effect of SCL_{min} on ingesta particle size was evaluated using linear regression models. Because there was a strong relationship between SCL_{min} and body mass for both aggregations (Fig. S1), the effects of mass on diet composition and ingesta particle size were not assessed. The relationship between maximum head width and SCL_{min} in green turtles from a foraging aggregation in The Bahamas was evaluated using linear regression.

Results

Characterization of green turtles

Green turtle diet in Bermuda was characterized through the analysis of esophagus and stomach contents recovered from stranded turtles. Esophagus and stomach samples were combined for individuals that had both samples because there was no difference in the percent volume of diet components between the two gut regions. Diet samples were collected from 47 individuals during 2015–2019 (2015, $n=5$; 2016, $n=8$; 2017, $n=13$; 2018, $n=14$; 2019, $n=7$), of which, 24 individuals were females, 18 males, and 5 undetermined. Mean (± SD) SCL_{min} of Bermuda green turtles was 35.1 ± 9.9 cm (range 21.4–58.4; median 32.2) (Fig. 1a). Mean turtle mass was 6.1 ± 5.7 kg (range 0.9–20.9; median 3.7). The numbers of individuals sampled by stranding location are as follows: Castle Harbour ($n=4$), Great Sound ($n=16$), Harrington Sound ($n=3$), Northern Coast ($n=6$), St. Georges Harbour ($n=4$), Western Coast ($n=10$), and undetermined ($n=4$).

Green turtle diet in the USVI was evaluated through the analysis of esophagus contents collected by lavage from live-captured turtles. Diet samples were collected from 31 individuals during 2017 ($n=11$) and 2018 ($n=20$). Mean SCL_{min} of USVI green turtles was 49.0 ± 6.1 cm (range 39.2–60.7; median 48.6) (Fig. 1b). Mean turtle mass was 16.8 ± 7.0 kg (range 7.5–33.5; median 15.2).

Diet composition

Diet of Bermuda green turtles is largely herbivorous (94% seagrass and algae) (Table 1). Seagrasses constituted 92 ± 21% volume (100% frequency) of the diet, with *T. testudinum* leaves (41 ± 45% volume; 75% frequency; 53.0 IRI) and *S. filiforme* leaves (35 ± 42% volume; 55% frequency; 33.6 IRI) as the dominant items. Root and rhizome tissue from *T. testudinum* occurred in 26% of Bermuda diet samples, but made up only 8 ± 22% of the volume. Algae comprised 2 ± 14% volume of the diet, with *Chlorophyta* spp. (including *Halimeda* spp.) as the dominant phylum present. Animal matter, primarily invertebrate tissue (tunicates, sponges, molluscs), accounted for 5 ± 17% volume of the diet and was low in relative importance (2.6 IRI). Vertebrate tissue from a single fish was detected in the digestive tract of one turtle. Trace amounts (< 0.1 mL) of mangrove tissue (leaves and propagules) were also detected.

SCL_{min} and sex of green turtles did not affect diet composition (% volume) in Bermuda, and temporal and stranding location effects on diet composition during 2015–2019 were minimal. There was a significant effect of stranding location on percent volume of *Halodule* sp. leaves ($p=0.03$, $df=5$, $\chi^2=12.0$; Kruskal–Wallis) and a marginal year effect on the percent volume of *S. filiforme* leaves ($p=0.05$, $df=4$, $\chi^2=9.3$; Fig. 2c). There were no temporal or stranding location effects on percent volume of the primary diet item, *T. testudinum* leaves (Fig. 2a). In addition, percent volume of *T. testudinum* roots and rhizomes was not significantly affected by year or stranding location, but did exhibit an increasing trend during 2015–2019 ($p=0.08$, $df=4$, $\chi^2=8.5$; Fig. 2b).

Green turtle diet in the USVI is also herbivorous (97% seagrass/algae; Table 1). Since green turtle diets prior to 2017 consisted mostly of native seagrasses (Daniels and Hart 2014) and the invasion of *H. stipulacea* was recent (estimated 2017; NPS unpublished data), we first evaluated

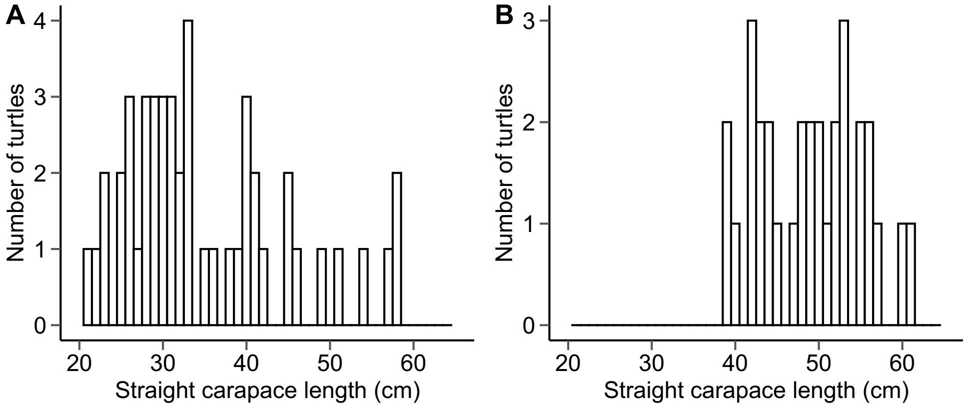

Fig. 1 Size class frequency distribution of green turtles in **A** Bermuda ($n=47$) and **B** Buck Island Reef National Monument, St. Croix, U.S. Virgin Islands ($n=31$). Straight carapace length (SCL_{min}) was measured from the midpoint of the anterior nuchal scute to the midpoint between the last pair of marginal scutes

Table 1 Percent volume (mean ± SD, (coefficient of variance)), frequency of occurrence (% freq), and index of relative importance (IRI) of diet categories for green turtles in Bermuda and U.S. Virgin Islands (USVI)

Diet item	Bermuda ($n=47$)			USVI ($n=31$)			p	**USVI** (n = 29) *H. stipulacea* excluded			p
	% vol	% freq	IRI	% vol	% freq	IRI		% vol	% freq	IRI	
Seagrass											
Thalassia testudinum											
Leaves	41 ± 45 (1.1)	74	53.0	13 ± 26 (2.1)	32	6.2	**< 0.01**	16 ± 30 (1.9)	34	8.9	**< 0.01**
Rhizomes and roots	8 ± 22 (2.7)	26	3.7	0	0	0	**< 0.01**	0	0	0	**< 0.01**
Syringodium filiforme											
Leaves	35 ± 42 (1.2)	55	33.6	18 ± 23 (1.3)	68	18.2	0.61	40 ± 39 (1.0)	72	45.7	0.30
Rhizomes and roots	0.3 ± 1.0 (3.0)	17	0.1	0	0	0	**0.02**	0	0	0	**0.02**
Halodule wrightii (or sp.)											
Leaves	8 ± 24 (3.1)	47	6.3	20 ± 31 (1.5)	74	23.2	**< 0.01**	33 ± 36 (1.1)	79	41.2	**< 0.01**
Rhizomes and roots	0.6 ± 3.0 (5.0)	6	0.1	0	0	0	0.16	0	0	0	0.17
Halophila stipulacea											
Leaves	0	0	0	45 ± 37 (0.8)	74	50.9	**< 0.01**	–	–	–	–
Rhizomes and roots	0	0	0	0	0	0	–	–	–	–	–
Total	92 ± 21 (0.2)	100	–	95 ± 12 (0.1)	100	–	0.96	89 ± 20 (0.2)	100	–	0.59
Algae											
Chlorophyta spp.	2 ± 13 (6.8)	11	–	0.5 ± 1.3 (2.9)	13	–	0.69	1 ± 4 (2.9)	14	–	0.61
Rhodophyta spp.	0.3 ± 1.4 (4.7)	6	–	2 ± 10 (5.6)	3	–	0.57	3 ± 14 (5.4)	3	–	0.62
Total	2 ± 14 (6.4)	15	0.6	2 ± 10 (4.5)	16	0.6	0.78	4 ± 15 (3.7)	17	1.2	0.66
Animal matter											
Invertebrata	5 ± 14 (3.0)	28	–	1 ± 3 (1.9)	29	–	0.79	5 ± 9 (1.9)	31	–	0.60
Vertebrata	0.6 ± 4.3 (6.9)	2	–	0	0	–	0.43	0	0	–	0.45
Total	5 ± 17 (3.1)	28	2.6	1 ± 3 (1.9)	29	0.7	0.79	5 ± 9 (1.9)	31	2.3	0.60
Other											
Mangrove	Trace (3.7)	9	0	0	0	0	–	0	0	0	–
Unidentified	0.2 ± 0.5 (3.3)	21	0.1	1 ± 3 (2.5)	19	0.3	0.85	3 ± 7 (2.6)	21	0.9	0.70

Bold values indicate p-values that are statistically significant ($p < 0.05$)

Animal matter includes invertebrates (tunicates, sponges, molluscs) and vertebrates (fish); unidentified refers to plant and animal matter combined; amounts less than 0.1 mL are classified as "trace"; *H. stipulacea* is invasive to the Caribbean. p values correspond to site comparisons (Mann–Whitney)

the diet of USVI green turtles without considering the presence *H. stipulacea* (Table 1) to facilitate comparison of the primary diet items to Bermuda. Without considering *H. stipulacea* (* denotes units that exclude this species), seagrass leaves from *S. filiforme* (40 ± 39% vol*; 72% freq*; 45.7 IRI*), *H. wrightii* (33 ± 36% vol*; 79% freq*; 41.2 IRI*), and *T. testudinum* (16 ± 30% vol*; 34% freq*; 8.9 IRI*) are the primary diet items. When considering the presence of *H. stipulacea* (Table 1), green turtle diets are dominated by seagrass leaves from *H. stipulacea* (45 ± 37% vol; 74% freq; 50.9 IRI), *H. wrightii* (20 ± 31% vol; 74% freq; 23.2 IRI), *S. filiforme* (18 ± 23% vol; 68% freq; 18.2 IRI), and *T. testudinum* (13 ± 26% vol; 32% freq; 6.2 IRI). Root and rhizome tissue from seagrasses were not found in any of the samples. Algae constituted 2 ± 10% volume of the diet, with *Rhodophyta* spp. as the dominant algae detected (specific taxa were not identified). Animal matter from invertebrates (molluscs only) accounted for 1 ± 3% volume of the diet; vertebrate tissue was not detected. Temporal effects on green turtle diet composition (% vol; *H. stipulacea* included), during 2017–2018 in the USVI were minimal, with a significant effect of year on percent volume of *H. wrightii* leaves ($p=0.03$, $U=162$; Mann–Whitney). $\mathrm{SCL}_{\min}$ did not affect diet composition.

Diet composition of green turtle foraging aggregations in Bermuda and USVI was very similar when assessed by broad diet categories (herbivorous; > 90% seagrass and algae). Although the use of two sample collection methods (gut contents collected from necropsies of stranded turtles versus esophageal lavage from live turtles) could have affected prey diversity, this would not have affected our overall conclusion that both aggregations are herbivorous because the breakdown of plant matter does not occur until food items reach the cecum and colon (Bjorndal 1979).

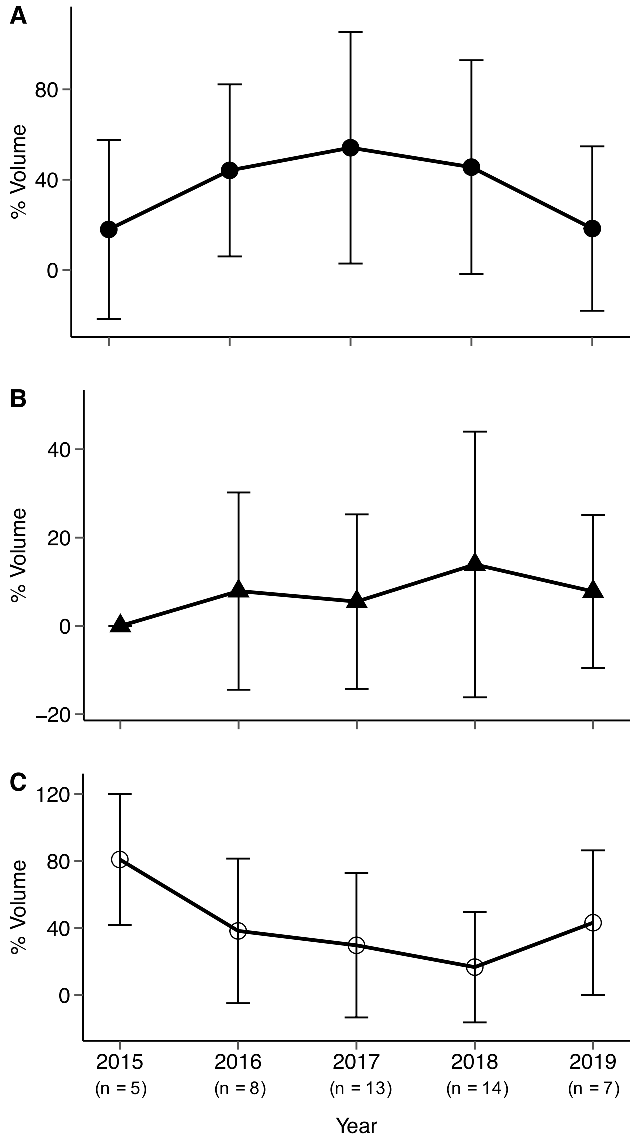

Fig. 2 Mean (± SD) percent volume by year of **A** *Thalassia testudinum* leaves, **B** *T. testudinum* rhizomes/roots, and **C** *Syringodium filiforme* leaves consumed by green turtles ($n=47$) in Bermuda. Esophagus and stomach contents were combined to determine percent volume of each diet component. There was no effect of year on percent volume of *T. testudinum* leaves ($p=0.15$, $df=4$, $\chi^2=6.8$) or rhizomes/roots ($p=0.08$, $df=4$, $\chi^2=8.5$), and a marginally significant effect on *S. filiforme* leaves ($p=0.05$, $df=4$, $\chi^2=9.3$). Year effects were evaluated by Kruskal Wallis Rank Sums tests

Significant differences in diet composition were found when comparing the % volume of specific diet items between sites, particularly at the species level for ingested seagrasses (Table 1). *Thalassia testudinum* leaves was a major item in Bermuda green turtle diets when compared to USVI green turtles ($p<0.01$; Table 1), whereas *H. wrightii* leaves* was the most prevalent native seagrass species in USVI green turtles when compared to Bermuda ($p<0.01$; Table 1). Seagrass root and rhizome tissue was only present in green turtle diets in Bermuda, and not in the USVI. Because there was no effect of $\mathrm{SCL}_{\mathrm{min}}$ on percent volume of seagrass root and rhizome tissue consumed by turtles in Bermuda, and the distribution of percent volume was evenly distributed across size classes, we do not believe the presence (or absence in the USVI) of belowground tissue in green turtle diets is a result of body size.

Ingesta particle size

Ingesta particle size of *T. testudinum* leaves averaged 2.6 ± 1.4 cm ($n=1045$ particles collected from 33 turtles; range 0.1–10.0; median 2.2; mode 1.7) for Bermuda green turtles (Fig. 3a). Measurements for ingesta particle size collected from the esophagus and stomachs of individual turtles were combined because there was no difference in *T. testudinum* leaf length ($p=0.35$; $U=162$; Mann–Whitney) between the two regions. There was a significant effect of $\mathrm{SCL}_{\mathrm{min}}$ ($p=0.01$, $R^2=0.16$; Fig. 3c), year ($p<0.01$, $df=4$; $\chi^2=22.3$; Kruskal–Wallis; Fig. 3d), and stranding location ($p<0.01$, $df=5$, $\chi^2=48.4$; Fig. 3e) on ingesta particle size in Bermuda. Despite the significant year effect, there was no apparent trend in particle size over time (Fig. 3d). And while there was a significant effect of stranding location on ingesta particle size, this effect seems to be driven by the greater variation in ingesta particle size in Great Sound relative to other locations (Fig. 3e).

Mean ingesta particle size for USVI green turtles was 2.3 ± 1.2 cm ($n=89$ particles collected from nine turtles; range 0.5–6.6; median 2.0; mode 1.7; Fig. 3b). There was no effect of year or $\mathrm{SCL}_{\mathrm{min}}$ on ingesta particle size in the USVI.

There was no difference in ingesta particle size between green turtle foraging aggregations in Bermuda and the USVI ($p=0.14$, $D=0.13$; Kolmogorov–Smirnov; Fig. 3a, b). The mode for ingesta particle size was 1.7 cm for both aggregations, accounting for 20–30% of ingested leaves, indicating a potential optimum particle size for maximizing digestive efficiency for green turtles on seagrass diets. There was a significant linear effect of $\mathrm{SCL}_{\mathrm{min}}$ on ingesta particle size in Bermuda (Fig. 3c), but not in the USVI. This is likely due to the greater range in $\mathrm{SCL}_{\mathrm{min}}$ values for Bermuda (Fig. 1a) than the USVI (Fig. 1b). When size range of Bermuda green turtles was limited to that of the USVI (> 39 cm $\mathrm{SCL}_{\mathrm{min}}$), there was no effect of $\mathrm{SCL}_{\mathrm{min}}$ on particle size in Bermuda ($p=0.84$, $R^2=0.01$). There was no difference in leaf width (Fig. S2) of ingested leaves between Bermuda (0.5 ± 0.2; range 0.2–1.0) and the USVI (0.5 ± 0.1; range 0.3–0.8) ($p=0.72$, $W=146$; Mann–Whitney).

Head width and body size

Measurements ($n=616$) of maximum head width and $\mathrm{SCL}_{\mathrm{min}}$ were obtained from 442 green turtles during 1986–2008 in

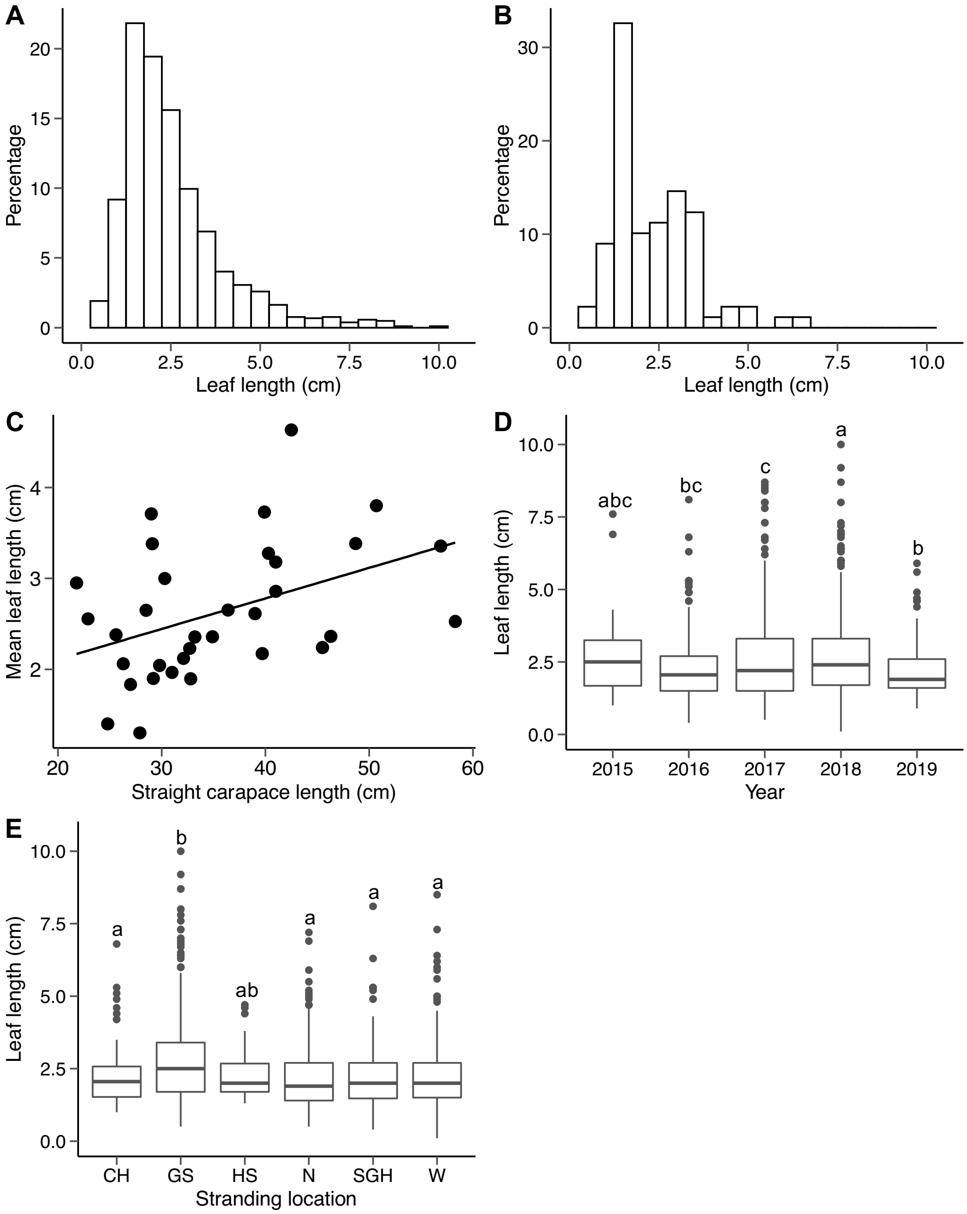

Fig. 3 Ingesta particle size of *Thalassia testudinum* leaves (length in cm) consumed by green turtles from **A** Bermuda ($n = 1045$ particles, collected from 33 turtles) and **B** U.S. Virgin Islands (USVI) ($n = 89$ particles, collected from 9 turtles). When available, the length of up to 30 T. *testudinum* leaves were measured in each esophagus and stomach sample. Ingesta particle size did not differ between the two sites ($p = 0.14$, $D = 0.13$; Kolmogorov–Smirnov). There was a significant effect of **C** straight carapace length ($\mathrm{SCL}_{\mathrm{min}}$) ($p = 0.01$, $R^2 = 0.16$), **D** year ($p < 0.01$, $df = 4$; $\chi^2 = 22.3$), and **E** stranding location ($p < 0.01$, $df = 5$, $\chi^2 = 48.4$) on ingesta particle size in Bermuda. These factors did not affect ingesta particle size in the USVI. Effects of $\mathrm{SCL}_{\mathrm{min}}$ on the mean particle size for each turtle were assessed with linear regression. Year and stranding location effects were assessed by Kruskal Wallis and Dunns posthoc tests; letters above error bars denote differences among years or locations. Abbreviations for stranding location in Bermuda are as follows: *CH* Castle Harbour, *GS* Great Sound, *HS* Harrington Sound, *N* Northern Coast, *SGH* St. Georges Harbour, *W* Western Coast

Union Creek, Great Inagua, Bahamas. Mean maximum head width was 7.5 ± 1.2 cm (range 4.6–10.7; median 7.6) and mean $\mathrm{SCL}_{\mathrm{min}}$ was 47.6 ± 9.3 cm (range 24.8–73.8; median 48.0). There was a positive linear relationship between maximum head width and $\mathrm{SCL}_{\mathrm{min}}$ ($p < 0.01$, $R^2 = 0.96$; Fig. 4). Because head width is a proxy for gape width (Herrel et al. 2002; Marshall et al. 2014), this result indicates that green turtles are capable of increasing bite size with body size.

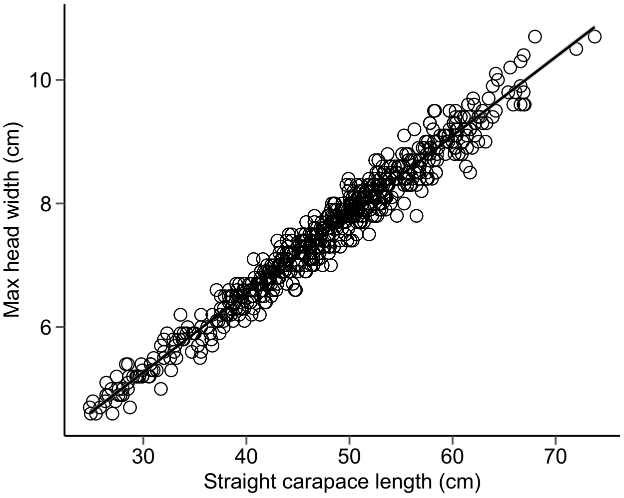

Fig. 4 Graphical summary of the relationship between maximum head width and straight carapace length (SCL_{min}) of green turtles in Union Creek, Great Inagua, Bahamas ($n=616$; $p<0.01$, $R^2=0.96$). SCL_{min} was measured from the midpoint of the anterior nuchal scute to the midpoint between the last pair of marginal scutes

Discussion

Ontogenetic diet shifts and prevalence of herbivory across foraging sites

Juvenile green turtles in the Northwest Atlantic (NWA) recruit from oceanic habitats to neritic foraging grounds at 20–25 cm (Bjorndal 1997), and transition to primarily herbivorous diets (Reich et al. 2007; Jones and Seminoff 2013; Burgett et al. 2018). Green turtles will then move among neritic foraging grounds as they grow to maturity (Bolten 2003; Meylan et al. 2011). The green turtle foraging aggregation at Buck Island Reef National Monument in the USVI has a predominantly herbivorous diet, consisting mostly of seagrasses (Table 1). This result is not surprising considering green turtles sampled in our study were > 39 cm SCL_{min} (Fig. 1b), and these individuals likely used other developmental habitats and completed the transition to herbivory prior to arriving at foraging grounds in the USVI. In addition, an herbivorous diet was expected for this foraging aggregation (see Daniels and Hart 2014) because of the central locale of this site within the range for green turtles in the NWA, which are typically associated with herbivory (Mortimer 1981; Esteban et al. 2020).

The Bermuda Platform is at the northern limit of the green turtle range in the NWA. Green turtles recruit to neritic foraging areas on the Bermuda Platform directly from oceanic environments, arriving at sizes comparable to other foraging grounds in the NWA (Meylan et al. 2011). Bermuda green turtles exhibit strong site fidelity to neritic foraging grounds, sometimes for several years (Meylan et al. 2011). For example, five turtles examined during this study had originally been live-captured and tagged by the Bermuda Turtle Project up to 10 years before they stranded (Bermuda Turtle Project, unpublished data). Using stable isotope analysis, Burgett et al. (2018) showed strong variability in green turtle diets across size classes (SCL_{min}) in Bermuda (mean ± SD, 38.4 ± 10.5 cm; range 25.1–68.9 cm), but larger turtles consumed mostly seagrass. Because our study sampled green turtles within a similar SCL_{min} range (Fig. 1a) as that in Burgett et al. (2018) and peripheral, cooler foraging sites are typically associated with omnivory, one might have expected to find that diets of Bermuda green turtles would be more omnivorous when compared to the USVI, and that SCL_{min} would have an effect on diet composition. However, diets of Bermuda green turtles in our study were largely herbivorous (> 90% seagrass and algae; Table 1), and there was no effect of SCL_{min} on diet composition. The disparity in results between the two studies is likely due to use of stable isotopes (Burgett et al. 2018) versus gut contents to assess diet—the former measuring diet components incorporated into the tissue and the latter measuring those ingested. Both approaches come with limitations (see Esteban et al. 2020). For example, a green turtle foraging aggregation can appear to be omnivorous based on stable isotope composition, when in fact, the composition is attributable to variation in primary production and nutrient cycling rather than prey consumption (Vander Zanden et al. 2013). In addition, stable isotope composition of Bermuda turtles may still reflect the more omnivorous diet from their oceanic habitats even after individuals have started consuming plant matter, because isotope signatures in the epidermal tissue can reflect a previous diet within 1 year (Seminoff et al. 2006). While gut content analyses offer an opportunity to assess diet on a fine-scale, samples only represent the diets of individuals over a short time frame. However, gut content analyses do have a distinct advantage for assessing important metrics for digestive processes, including ingesta particle size.

Optimal ingesta particle size for herbivory in green turtles

The ability to reduce food particle size is critical to maximizing digestive efficiency and rates of fermentation in herbivores (Bjorndal et al. 1990; Lanyon and Sanson 2006), particularly for reptiles that lack the ability to masticate (Fritz et al. 2010). Green turtles have at least two adaptations to their herbivorous diet. First, their gut microflora digests ~ 90% of cellulose in the diet and produces short–chain fatty acids, an important energy source for turtles (Bjorndal 1979). Second, they select a more digestible diet by repetitively cropping seagrasses, yielding younger and more nutritious leaves (Bjorndal 1980) and smaller particle sizes. Reduction of ingesta particle size in green turtles has important implications for maximizing digestive efficiency, supporting higher growth rates, and facilitating the transition from omnivory to herbivory in juveniles.

Ingesta particle size (mean ± SD) did not differ between green turtle foraging aggregations in Bermuda (2.6 ± 1.4 cm) and the USVI (2.3 ± 1.2 cm), and both aggregations had the same mode (1.7 cm; 20–30% of ingested leaves) for the length of ingested *T. testudinum* leaves (Fig. 3a, b). Because this similarity occurs in foraging aggregations from two geographically distinct areas and green turtles are capable of increasing bite size with body size (discussed below), this result may be indicative of an optimal ingesta particle size for maximizing intake of digestible matter, digestive efficiency, and fermentation rates in green turtles on seagrass diets.

The positive linear relationship between head width (a proxy for gape width) and body size (SCL_{min}) in green turtles (Fig. 4) clearly indicates that they are capable of increasing bite size with growth, similar to other herbivores (e.g. Shipley et al. 1994). Because green turtles lack the ability to masticate (Fritz et al. 2010) and the breakdown of cellulose in seagrass leaves does not occur until food items reach the cecum and colon (Bjorndal 1979), ingesta particle size of seagrass leaves recovered from the esophagus and stomach region should exhibit a relationship with body size that is comparable to that of bite size and body size. Similar to other reptilian herbivores (e.g. Bjorndal and Bolten 1992), there was a positive linear effect of green turtle body size (SCL_{min}) on ingesta particle size in Bermuda (Fig. 3c), but not in the USVI. Because the USVI foraging aggregation is comprised of larger turtles (> 39 cm) over a narrower range of SCL_{min} (Fig. 1), and there was no effect of SCL_{min} on particle size in Bermuda for turtles > 39 cm, the ability to consume an optimal particle size is not regulated by body size in larger individuals—although, these patterns should be evaluated for adults. The ability to reduce and consume an optimal ingesta particle size would have important implications for green turtle growth, especially for juveniles undergoing an ontogenetic diet shift. Mechanisms for reducing ingesta particle size for green turtles on seagrass diets include small bite size and cultivation grazing behavior.

Small bite size is a mechanism that enables small-bodied herbivores to meet mass-specific nutrient requirements by improving the physical structure and nutrient quality of the diet. During the juvenile life stage of a herbivorous freshwater turtle, small bite size allows for increased intake and digestive processing, yielding rates of digestive efficiency comparable to adults (Bjorndal and Bolten 1992). Small bite size decreases ingesta particle size (Bjorndal and Bolten 1992), which increases the surface-to-volume ratio that is exposed to microbial attack and promotes rapid digestion (Bjorndal et al. 1990). High mortality is associated with juvenile green turtles undergoing the ontogenetic diet shift (Meylan et al. 2011), during which the composition of gut microbiota slowly changes to support an herbivorous diet (Campos et al. 2018). Small bite size may play a critical role in facilitating an efficient transition of gut microbiota to support herbivory through achieving an optimum ingesta particle size (1.7 cm) that promotes rapid digestion via microbial hindgut fermentation and stimulates growth rates.

Cultivation grazing of seagrasses is also likely to fulfill an important role in reducing ingesta particle size in green turtles, in addition to increasing the nutrient quality of seagrass leaves (Bjorndal 1980; Moran and Bjorndal 2007) and stimulating leaf growth (Gulick et al. 2020, 2021). Repetitive cropping reduces the length of leaves relative to neighboring ungrazed areas, which should allow turtles to select for and maintain an optimum leaf length. However, the effects of seagrass morphological characteristics on the bite size and intake of green turtles must be evaluated to further understand how green turtles use cultivation grazing to optimize their foraging strategy (Gulick et al. In prep).

Use of ingesta particle size to assess green turtle responses to seagrass declines

As seagrass meadows continue to decline globally due to several anthropogenic threats (e.g. climate change, eutrophication) (Orth et al. 2006; Waycott et al. 2009; Grech et al. 2012), concerns for overgrazing by recovering green turtle populations continue to be raised (Fourqurean et al. 2010, 2019; Kelkar et al. 2013; Christianen et al. 2014). Bermuda is emblematic of this issue (Fourqurean et al. 2010, 2019) because of the declines in seagrasses across the Bermuda Platform (Murdoch et al. 2007; Fourqurean et al. 2010; Manuel et al. 2013) and the increase in green turtle abundance since their near extirpation in the 1700s (Parsons 1962; Jackson et al. 2001). Green turtle gut contents from Bermuda and a reference site in the USVI where seagrasses are not in decline (Kendall et al. 2004; Pittman et al. 2008), offered an opportunity to evaluate ingesta particle size and diet composition as potential tools for assessing green turtle dietary responses to declines in forage availability.

We hypothesized that the following temporal trends would be observed in green turtle gut contents if seagrass availability and/or overgrazing is occurring at a foraging site: (1) a decrease in ingesta particle size; (2) a narrower range of values for ingesta particle size; (3) a decline in percent volume of seagrass leaves; and (4) an increase in percent volume of seagrass roots and rhizomes (see Christianen et al. 2014) and other food sources. During the time frame of our study in Bermuda (2015–2019), there were minimal temporal and stranding location effects on ingesta particle size and diet composition (Figs. 2, 3c, d). Although seagrass root and rhizome tissue was detected in Bermuda green turtle diets and not in the USVI (Table 1), it constituted only 8% volume of the diet and there was no temporal trend (Fig. 2b) to suggest increased consumption or destructive grazing behavior due to lack of forage resources (see Christianen et al. 2014). We did not expect these results because gut contents were sampled over a 5-year time frame that overlaps with known declines of seagrass in the area (Bermuda Department of Environment and Natural Resources, unpublished data). In addition, Burgett et al. (2018) found little diet variation among larger turtles during 2012–2013 that would indicate a shift away from seagrasses. Because these two studies span almost 7 consecutive years, one might conclude that the declines in seagrass availability in Bermuda had yet to be reflected in green turtle diets or that green turtles were foraging in seagrass meadows that had not been documented. Since the latter is unlikely because of extensive seagrass mapping efforts in Bermuda (Murdoch et al. 2007; Manuel et al. 2013), population demographics of the Bermuda foraging aggregation should be considered when interpreting the lack of a dietary response to seagrass declines based on stable isotope and gut content analyses.

Green turtles are capable of reducing their metabolism in response to changes in environmental conditions, and degradation of foraging habitats has been linked to regional declines in green turtle growth rates in the NWA (Bjorndal et al. 2017) and may affect recruitment and emigration rates in neritic foraging grounds (Chaloupka and Limpus 2001; Bjorndal et al. 2019; Christianen et al. 2019). There is no trend in density (turtle captures ha^{-1}), biomass (kg ha^{-1}), or average SCL$_{\text{min}}$ of live-captured green turtles in Bermuda during 2015–2019, but average body mass significantly decreased during this period (Bermuda Turtle Project, unpublished data). Although the impact of seagrass declines in Bermuda is not reflected in green turtle gut contents from this time period, the decline in green turtle body mass potentially indicates reduced intake and decreasing mass-growth rates of turtles in this foraging aggregation as a result of degrading foraging habitats. Therefore, we propose that ingesta particle size and diet composition can be valuable indicators for green turtle responses to declines in forage availability, when interpreted within the context of demographic parameters.

As green turtle populations continue to recover and some foraging aggregations rely on degraded foraging habitats, it will be critical to evaluate the interactive effects of natural stressors (e.g., grazing) and anthropogenic-driven stressors on seagrasses (e.g. eutrophication, shoreline runoff, introduction of invasive species, climate change). This is particularly true for Bermuda, where the combined effects of green turtle grazing and other stressors could be driving seagrass declines. The potential consequences of degraded seagrass habitats on the productivity of green turtle populations should also be considered. Although the invasion of *H. stipulacea* at the USVI site is very recent (est. 2017; National Park Service, unpublished data), this seagrass was present in the diets of green turtles sampled during our study (Table 1). Because *H. stipulacea* is lower in nutrient concentrations (%N and %P) compared to native seagrasses (Christianen et al. 2019), the invasion of the USVI site may eventually impact green turtle habitat-use (see Christianen et al. 2019) and growth rates. Intake and digestibility trials will be required to assess the nutritional value and associated impact of this invasive seagrass on green turtle productivity.

Recovery of the green turtle, after centuries of low abundance and ecological extinction (Jackson et al. 2001), is resulting in dramatic ecosystem-wide shifts in the productivity and functioning of seagrass ecosystems (e.g. Johnson et al. 2017, 2020; Gulick et al. 2020, 2021; Christianen et al. 2021). A historical perspective, an ecosystem-based approach to conservation, and recognition of the potential impacts of increased grazing pressure in degraded foraging habitats will be essential for correct interpretation of ecosystem changes as this marine mega-herbivore reassumes its ecological role in seagrass ecosystems.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00227-021-03965-1.

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Author contributions AGG, ABB, and KAB conceived and designed the study. AGG, ABM, PAM, KMH, JAG, GR, ABB, and KAB collected the data and contributed to the planning and implementation

of the study. AGG, ABB, and KAB analyzed the data. AGG wrote the manuscript with contributions and final approval from all authors.

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Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request, and in Griffin et al. (2020).

Declarations

Conflict of interest The authors declare no conflicts or competing interests.

Ethics approval Sampling in Bermuda for this project was permitted by the Government of Bermuda Department of Conservation Services (License 15-07-27-28) and the Bermuda Department of Natural and Environmental Resources (Licenses 16-07-27-54, 17071007, 2018071309, and 2019061105). International transportation of diet samples from Bermuda to the United States was carried out under CITES export permits from the Bermuda Department of Natural and Environmental Resources (16BM0008, 18BM0002, 18BM0005, 19BM0009) and CITES import permits from the U.S. Fish and Wildlife Service to the Florida Fish and Wildlife Conservation Commission (16US758093/9, 18US48288C/9) and the University of Florida Archie Carr Center for Sea Turtle Research (19US724540/9). Sampling in the USVI was permitted by the National Marine Fisheries Service (Permits 16146 and 20315, issued to K. Hart), National Park Service IACUC (USGS-SESC2014-02), U.S. Geological Survey IACUC (WARC\GNV 2017-04), and the National Park Service at Buck Island Reef National Monument (BUIS-2011-SCI-0012, BUIS-2014SCI-0009, BUIS-2016-SCI-0009, issued to K. Hart). The long-term study in Union Creek, Great Inagua, Bahamas was conducted under permits issued by the Bahamas Department of Marine Resources.

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