



Ontogenetic diet shifts of green sea turtles (*Chelonia mydas*) in a mid-ocean developmental habitat

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Abstract

Green sea turtles (*Chelonia mydas*) arrive on the geographically isolated Bermuda platform as small juveniles and remain until they are approaching sexual maturity, at which point individuals depart for distant feeding and nesting sites. It has been reported that younger green turtles generally tend to carnivory or omnivory and that seagrasses become a significant food source as the turtles grow. Evidence indicates that grazing by green sea turtles in Bermuda is negatively impacting seagrass beds, thus understanding their diets is important to both conserving the turtles and their food. Stable isotope methods were used to investigate ontogenetic diet shifts of green sea turtles and to determine reliance on seagrass by larger turtles. Skin samples from 157 individual turtles and samples of known turtle foods, plants and animals, were collected for determination of consumer and food $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. A Bayesian stable isotope mixing model analysis indicated a wide range among individual turtles' diets, with the greatest differences occurring between small and large turtles; larger turtles consumed seagrass almost exclusively. We also examined diet changes in 12 turtles captured in two successive years; these recapture data confirmed the changes in diet suggested by the relationship between size of turtles and diet composition. Very limited evidence was found of any diet variation among larger turtles that would indicate a shift away from declining seagrasses as their major food source.

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Introduction

Through their lives animals may experience profound changes in ecology and biology, among these are fundamental changes in food sources and choices. Ontogenetic shifts in diet are a common feature of the life history of a diverse group of organisms, ranging from arthropods to vertebrates (Werner and Gilliam 1984). Such shifts are frequently coupled with changes in size and habitat. Ontogenetic shifts from carnivorous and omnivorous juveniles to herbivorous adults are common in reptiles, including green sea turtles (Werner and Gilliam 1984; Polis et al. 1996). Stable isotope diet studies have shown such a shift from a macroalgal and animal-based diet in the pelagic environment of very young green turtles to a plant-based diet after the juvenile turtles move into neritic habitats (e.g., Reich et al. 2007; Arthur et al. 2008; Howell et al. 2016).

The availability, quality and kinds of food in different environments may vary widely, and animals must have behaviors that ensure survival across all the conditions encountered in their lifetime. Many marine organisms with ontogenetic diet shifts have larvae and juveniles that feed

in more productive (neritic) habitats with adults feeding in less productive pelagic habitats (e.g., nektonic crustaceans, fish and squid) (Barnes and Hughes 1988; Polis et al. 1996). Green turtles, in contrast, move from less productive pelagic to more productive neritic habitats. While differing predation risks between the two habitats is a major driver of the timing and location of this ontogenetic shift, another factor may have to do with avoiding potential overexploitation of resources. In theory, one benefit of an early life stage in a low abundance or low-quality food resource environment and later stages occupying a higher resource environment is that the later stages will not overexploit the resources of their environment (Mittelbach et al. 1988; Polis et al. 1996). Empirical evidence supporting this theory is largely related to fishes and its relevance to other aquatic animal groups is largely unexplored. The life history of green sea turtles means that they could serve as a test organism for resource exploitation theories for a large-bodied, long-lived marine reptile.

Various benefits to a life history with ontogenetic diet shifts have been proposed. Such shifts could have the benefit of minimizing intraspecific competition for food among different age classes (Werner and Gilliam 1984). But, a population-wide shift from broadly generalized (e.g., omnivory) to highly specialized (e.g., herbivory on marine angiosperms) food choices could instead increase competition within the specialist's age class, if all individuals specialized on a single food. However, specialization might also be based on individual choices, which could distribute the impacts of foraging across a diversity of foods. Factors that could influence the food choices of individuals include, (1) differences among individual preferences; (2) differences among individual foraging behaviors that affect foraging efficiency; (3) differences among individuals in the size and specific locations of feeding ranges; (4) ecological tradeoffs, such as food quality versus safety in the presence of predators, and (5) relative abundance of different foods (Estes et al. 2003; Svanback and Persson 2004; Araujo et al. 2009, 2011).

Studies of the diets of both juveniles and adults indicate that green sea turtles do not consume all potential foods in proportion to their relative availability and that there is a lot of variation among individuals or locations. Various reports indicate that turtles individually specialize on fewer foods than are available (Brand-Gardner et al. 1999; André and Lawler 2003; Fuentes et al. 2006). Where seagrass are scarce, juvenile turtles exploit macroalgae and other foods (Cardona et al. 2009; Carman et al. 2012; Russell and Balazs 2015; Santos et al. 2015; Howell et al. 2016). Even in locations with seagrass, gastric lavage samples of juvenile turtles (Brand-Gardner et al. 1999) show that some individuals specialize on macroalgae while others consume seagrass. Individual adult (sexually mature) green turtles can also show diet specializations on, for

example, cnidarians and ctenophores even where there is abundant seagrass (Brand-Gardner et al. 1999; Burkholder et al. 2011; Shimada et al. 2014). Burkholder et al. (2011) proposed that the turtles may have been making choices that balanced food qualities (abundance, for example) and risk of predation. Vander Zanden et al. (2013) suggested that individual turtles can maintain specialized diets for many years.

Over the last two decades reports of seagrass declines, mostly attributable to declining water quality, have increased (Short and Wyllie-Echeverria 1996; Waycott et al. 2009). Over the same period, the success of conservation measures has resulted in increases in the numbers of green turtles laying eggs on traditional nesting beaches in many areas of the world, including Florida and Costa Rica (Chaloupka et al. 2008). This has been taken as an indication of an overall increase in the total number of turtles in the western North Atlantic. At the same time, reports of overgrazing of seagrass beds by green turtles have increased (e.g., Williams 1988; Fourqurean et al. 2010; Lal et al. 2010; Kelkar et al. 2013; Christianen et al. 2014). Whether green turtles that overgraze their home seagrass beds will switch their diets to consume other food sources, will move to new areas with more seagrass, both, or neither is unknown. Whatever occurs may depend heavily on the over-arching cause of the food shortage. Overgrazing events may be explained partially by the lack of top-down control on green turtle populations due to global overfishing of large sharks (Heithaus et al. 2014). In the continuing absence of these predators, the populations of both seagrass and turtles may ultimately collapse.

The green turtle population on the Bermuda Platform (ca. 32.4°N, 64.8°W) provides an ideal system to test general theories about ontogenetic diet shifts and resource exploitation. Compared to the oligotrophic western North Atlantic waters that surround it, the Bermuda Platform is a productive habitat, with seagrass meadows, coral reefs and mangroves (Coates et al. 2013). Bermuda is also an important developmental habitat for green turtles from many nesting populations throughout the Northwest Atlantic. In Bermuda, as at other locations in the Northwest Atlantic, juvenile green turtles recruit to their neritic habitats at sizes of about 20–35 cm straight carapace length (SCL), after spending 3–6 years in pelagic habitats (Carr 1987; Zug and Glor 1998; Reich et al. 2007; Meylan et al. 2011). In the Pacific Ocean, the neritic phase can be longer, resulting in larger size at recruitment to neritic habitats (Limpus and Chaloupka 1997; Balazs and Chaloupka 2004; Hamabata et al. 2015). Green turtles depart the Bermuda Platform as sub-adults, at SCL of 65–75 cm (Meylan et al. 2011). The green turtles leave the platform in order to join breeding populations. Turtles fitted with satellite transmitters have been tracked from Bermuda to the Bahamas and Florida (Meylan et al. 2011; authors' unpubl data) and flipper and pit-tagged turtles from

Bermuda have been recovered in Florida, Cuba, St Lucia, Grenada, Venezuela and Nicaragua (Meylan et al. 2011).

The seagrass resources of Bermuda, *Thalassia testudinum*, *Syringodium filiforme*, *Halophila decipiens* and *Halodule* sp., are in precipitous decline (Murdoch et al. 2007; Fourqurean et al. 2010; Manuel unpubl data) across the entire shallow Bermuda Platform despite high water clarity and generally high water quality (Manuel et al. 2013; Fourqurean et al. 2015). Turtle exclosure experiments undertaken in Bermuda demonstrate that grazing by sea turtles is, at least partly, responsible for the declines (Fourqurean et al. 2010). Seagrass decline, and ultimately complete loss, attributed to turtle grazing was first observed in the late 1990s at offshore beds in the northern parts of the Bermuda Platform (Murdoch et al. 2007; Fourqurean et al. 2010), but this has spread to outer beds on the southwest part of the Platform and, most recently, to several inshore beds (Manuel unpubl data).

Because of the declining abundance of seagrasses, as well as the documented capacity of green turtles to consume foods other than seagrasses in neritic habitats, we predicted that dietary analyses would show diverse diets among individuals rather than a population-wide ontogenetic diet shift to a seagrass-based diet. We posed three specific questions: (1) what is the green turtle diet composition on the Bermuda Platform? (2) How does diet composition differ among green turtle size classes? and (3) How does diet composition vary among sites? We employed stable isotope techniques to address these questions, specifically measuring the ratios of the stable isotopes of carbon and of nitrogen in green turtle skin samples and in potential food sources for the turtles. We used stable isotope mixing models (Parnell et al. 2013) to predict the general composition of the turtles' diets. Mixing model outputs indicated the relative importance of different food sources in the turtles' diets, which we compared to turtle size.

Materials and methods

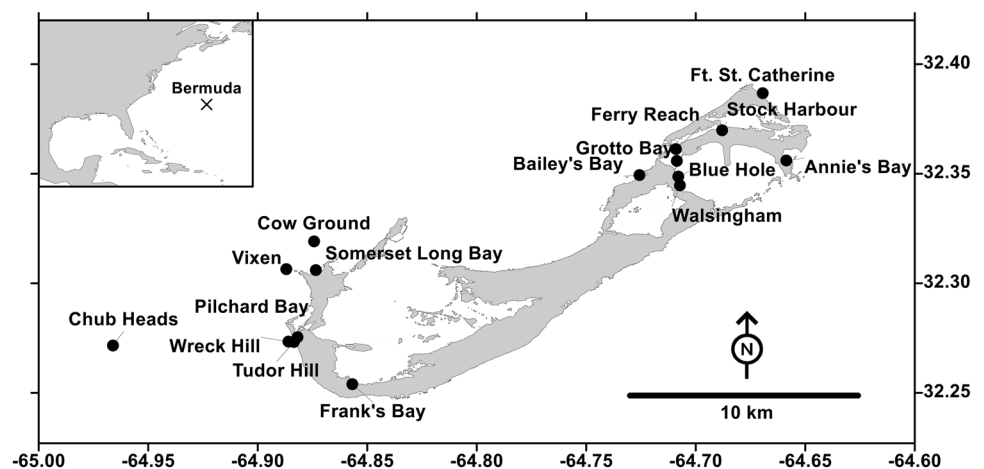
Food sample collection

At our turtle capture locations (Fig. 1), divers haphazardly collected a variety of plants (macroalgae and seagrasses) and animals (including scyphozoans, ctenophores, octocorals, tunicates, sponges, and crustaceans) in groups that have been identified as food items for green turtles in other studies (Mortimer 1981; Mendonça 1983; Burkholder et al. 2011). We augmented our collections with seagrass samples collected at many more sites across the Bermuda Platform as part of a previous study (Fourqurean et al. 2015). Non-seagrass food samples were each discrete individuals or clonal groups (such as octocorals or some tunicates). Each seagrass sample was a composite of 5–40 shoots, depending on the seagrass species (see Fourqurean et al. 2015), collected from a 3 × 3 m area. Samples were stored on ice in the field and then frozen at –20 °C until processing.

Turtle tissue collection

Green sea turtles were captured at 12 locations (Fig. 1) using the entrapment net procedure described by Meylan et al. (2011). Turtles were captured at two periods: in 23 net sets from July 30 to August 17, 2012 and in 7 net sets on August 6 and 16, 2013. Captured turtles were transferred to a nearby vessel for measurement and tissue sampling. All turtles were measured for SCL with calipers and tagged following BTP procedures (Meylan et al. 2011), allowing 12 recaptures in 2013 to be recognized. Skin samples from the turtles were taken from a standardized location on the trailing edge of the rear flippers. The area was swabbed with ethanol and then samples were extracted using a stainless steel 5 or 8 mm biopsy punch. These samples were placed immediately on

Fig. 1 Capture locations of turtles on the Bermuda Platform. Inset shows location of Bermuda in the western North Atlantic Ocean



ice, and stored frozen ($-20\text{ }^{\circ}\text{C}$) until processed for stable isotope analysis.

Stable isotope analysis

Before any other processing, epiphytes were removed from seagrass leaves by gently scraping the leaves with a razor blade. Epiphyte communities had low biomass and appeared typical of relatively low-nutrient regions of the Caribbean, dominated calcareous red encrusting algae and attached sessile invertebrates; these were not included in the stable isotope analysis as a group but representatives of these taxa were included in the analyses. All samples (seagrass, macroalgae, potential prey animal, and turtle tissue) were dried at $50\text{ }^{\circ}\text{C}$ and each sample was ground separately to a powder for homogenization. Macroalgal and prey animal samples were decalcified following the procedure outlined in Burkholder et al. (2011). Our previous work with green turtle stable isotope ratios indicated that lipid extraction was not necessary for green turtle skin in order to use stable isotope assessments of diet (Burkholder et al. 2011; Post et al. 2007). Lipids were not extracted from food samples since we assumed that any lipids present in the foods would be incorporated into the tissues of the turtles. Samples were analyzed to determine stable isotope ratios for C ($^{13}\text{C}:^{12}\text{C}$ expressed as $\delta^{13}\text{C}$) and N ($^{15}\text{N}:^{14}\text{N}$ as $\delta^{15}\text{N}$) using standard EA-IRMS techniques at the Florida International University Stable Isotope Laboratory. Analytical reproducibility of the reported δ values, based on sample replicates, was better than $\pm 0.2\text{‰}$ for $\delta^{15}\text{N}$ and $\pm 0.08\text{‰}$ for $\delta^{13}\text{C}$.

Statistical analyses

Throughout the paper, we report central tendencies and error estimates as means ± 1 standard deviation, unless otherwise indicated. Potential foods were separated into isotopically indistinguishable groups (which we call food groups) by first pooling all observations within 10 broad taxonomic categories of foods (detailed in supplemental Table S1). As an analysis of the QQ-plot indicated that the data were normally distributed and Levine's test indicated equality of variances, we used ANOVA with Tukey post hoc tests to define homogenous subsets of the broad categories. The earlier seagrass samples used in this study, spanning the whole Bermuda Platform (Fourqurean et al. 2015), revealed marked spatial gradients in nitrogen stable isotopic values, but not carbon isotopic values, across the Bermuda platform. Generally, ^{15}N enrichment occurred at sites nearer the islands and in enclosed sounds, and was progressively more depleted with distance from shore. However, the overall spatial pattern was much more complex than a simple distance from shore gradient (Fourqurean et al. 2015, Fig. 6). Our sampling of other

potential foods present, which occurred at turtle sampling sites visited by the BTP in summer 2012, was not as spatially extensive as for seagrasses (see Fig. 1, compared to Manuel et al. 2013, Fig. 9), nor were all potential foods sampled at all capture sites. Thus, we explored the relationships between seagrass isotope values (independent variable) with the stable isotope values of other food sources from the BTP sites (dependent variables) using a simple linear regression analysis to determine if we could extrapolate the seagrass spatial patterns in isotope values into isoscapes (Bowen 2010) for other food groups.

For population-level analysis of the variability among turtles in isotopic values and in the relationship between size (SCL) and isotope values, data were grouped by turtle size class. Size classes were defined by 10 cm increments in SCL. Differences in turtle isotope ratios between the size classes were determined using ANOVA. Any recaptures in 2013 were excluded from these analyses.

Diet mixing models

Diet composition was determined using the SIAR Bayesian diet mixing model program package in R (Parnell et al. 2008, 2013) using an average of published discrimination factors of epidermal tissues from diet $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for juvenile green turtles [Seminoff et al. 2006; $\delta^{15}\text{N} = 2.80 \pm 0.11\text{‰}$ (\pm SE, $n = 8$), $\delta^{13}\text{C} = 0.17 \pm 0.03\text{‰}$ (\pm SE, $n = 8$) and Vander Zanden et al. 2012: $\delta^{15}\text{N} = 3.77 \pm 0.40\text{‰}$ (\pm SD, $n = 40$), $\delta^{13}\text{C} = 1.87 \pm 0.56\text{‰}$ (\pm SD, $n = 40$)]. The average discrimination values were used because we had no a priori reason to weight one of these literature values more than the other. Diet composition mixing models were performed on the population as a whole, for each size class, and for each individual. Site-specific seagrass isotope values for the large seagrass species (average values for the three species *Thalassia testudinum*, *Syringodium filiforme*, *Halodule* sp.) were determined using interpolated seagrass $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values from the results presented in Fourqurean et al. (2015) because there is non-random, high variability in seagrass stable isotopes across the Bermuda Platform. Mixing models were run twice for each individual turtle using the seagrass isotope values associated with the site at which the turtle was collected, as well as using the average from the entire Bermuda Platform. The diet compositions indicated by the site-specific values and the Platform average were compared to determine if knowledge of small-scale spatial variability in seagrass isotopic values could improve diet composition analyses. We analyzed the ontogenetic diet shifts as a function of turtle size by a series of model fitting exercises using regressions and Akaike's information criterion to describe the relationship between the amount of seagrass in each turtle's diet and SCL.

Results

Potential turtle food sources

Five hundred and sixty-seven samples of 32 different taxa of potential turtle-food items were analyzed, including four genera of seagrasses, 13 genera of macroalgae, and 15 taxa of animals (see Table S1 in Supporting Information). Based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, we assigned the potential foods to three isotopically distinct food groups: seagrasses, macroalgae, and animals and the differences among the three groups were significant (ANOVA, $\delta^{15}\text{N}$: $F(2, 564) = 918.3$, $P < 0.001$; $\delta^{13}\text{C}$: $F(2, 564) = 38.8$, $P < 0.001$). These food groups had considerable variability in their stable isotopic compositions (Fig. 2). In general, the seagrass group had the lowest $\delta^{15}\text{N}$ ($1.7 \pm 3.5\text{‰}$, $n = 455$) and the animal group had the highest ($5.4 \pm 2.1\text{‰}$, $n = 52$; Table 1). Conversely, seagrasses had the highest average $\delta^{13}\text{C}$ ($-7.4 \pm 1.9\text{‰}$, $n = 455$) and animals had the lowest ($-17.9 \pm 1.4\text{‰}$, $n = 52$; Table 1). Seagrasses from the Platform-wide survey (Fourqurean et al. 2015) had a very broad range in $\delta^{15}\text{N}$,

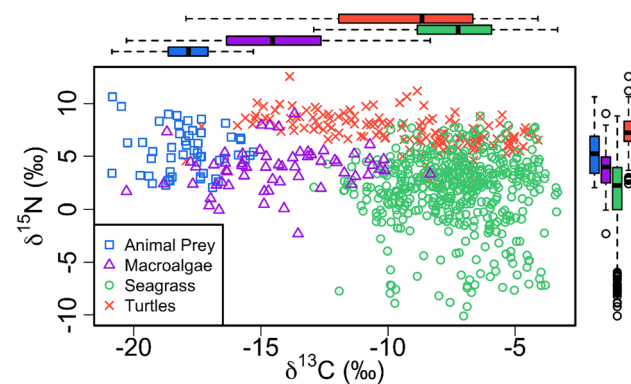


Fig. 2 Nitrogen and carbon stable isotope ratios (in standard δ notation in ‰) for all green turtles (*Chelonia mydas*, $n = 157$) and potential food groups (macroalgae, $n = 60$; animals, $n = 52$; and seagrass, $n = 455$) on the Bermuda Platform. Descriptive box-and-whisker plots in the margins show the distribution of the values for each group, with median at the central line, first to third quartile in the boxes (IQR), and the whiskers indicate $1.5 \times \text{IQR}$. Open circles in the box-and-whiskers plots indicate data outside $1.5 \times$ the IQR

Table 1 Descriptive statistics of the carbon and nitrogen isotope values for the green sea turtles and the three isotopically distinct food groups (animals, seagrass, and macroalgae)

	n	$\delta^{15}\text{N}$				$\delta^{13}\text{C}$			
		Mean	Min	Max	SD	Mean	Min	Max	SD
Turtles	157	7.3	2.4	12.6	1.6	-9.3	-17.3	-4.1	3.1
Animals	52	5.5 ^a	2.0	10.6	2.1	-17.9 ^a	-20.9	-15.3	1.4
Seagrass	455	1.7 ^b	-10.1	8.8	3.5	-7.4 ^b	-12.9	-3.3	1.9
Macroalgae	60	3.8 ^c	-2.3	9.0	2.1	-14.3 ^c	-20.3	-8.3	2.5

Letter superscripts for food group means indicate homogenous subsets (Tukey post hoc test, $P < 0.01$)

from -10.1 to 8.8‰ ($n = 380$, for four species of seagrass), but the range at nearshore sites was much less than the total range. Similarly, the $\delta^{15}\text{N}$ of seagrasses from turtle capture sites sampled in 2012 and 2013, which were generally shallow and close to shore, had a much narrower range ($2.9 \pm 1.6\text{‰}$, $n = 75$; range 0.1 – 6.3‰). For food items collected at the turtle capture sites, there were no significant relationships between site-specific $\delta^{15}\text{N}$ of seagrass and $\delta^{15}\text{N}$ of macroalgae and animals, as assessed by linear regression [macroalgae: $r^2 = 0.00$, $F(1, 58) = 0.2$, $P = 0.624$; animals: $r^2 = 0.01$, $F(1, 50) = 0.5$, $P = 0.461$]. Macroalgae and animal foods did not display the same spatial pattern in nitrogen isotope values as seagrasses (Fourqurean et al. 2015) at nearshore sites on the Bermuda Platform.

Size distribution and stable isotope ratios of captured turtles

Each net-set produced between 1 and 20 turtles. One hundred fifty-seven turtles captured and sampled in 2012 and 2013 ranged in size from 25.1 to 68.9 cm SCL (see Table S2 in Supporting Information for details of turtle captures). The size distribution was positively skewed toward larger turtles (Fig. 3). Mean SCL was 38.4 ± 10.5 cm, $n = 157$ and the median was 35.0 cm. Skin samples from the captured turtles had $\delta^{15}\text{N}$ of $7.3 \pm 1.6\text{‰}$, $n = 157$ and $\delta^{13}\text{C}$ of $-9.3 \pm 3.1\text{‰}$, $n = 157$ (Table 1), but there was considerable variation in both isotope ratios (Fig. 2). Plotted as a function of the size of individual turtles, a trend of increasing $\delta^{13}\text{C}$ with increasing size was evident. No similar trend was evident for $\delta^{15}\text{N}$ with size but the scatter in $\delta^{15}\text{N}$ was especially large for smaller turtles (Figure S1 in Supporting Information). When analyzed using 10-cm size classes as groups (Fig. 4), there were significant differences among size classes in $\delta^{13}\text{C}$ [ANOVA, $F(4, 152) = 35.6$, $P < 0.001$], but no significant differences in $\delta^{15}\text{N}$ [ANOVA, $F(4, 152) = 1.6$, $P = 0.173$].

We recaptured 12 turtles in 2013 that were initially caught in 2012. Eleven out of those 12 were captured at the same site in 2013 as in 2012; the other turtle was recaptured at a site 1 km away from the site of the 2012 capture. All recaptured turtles had longer SCL in 2013 than in 2012, but growth was not a linear function of initial SCL for these turtles. Recaptured turtles ranged from 27.2 to 51.9 cm SCL

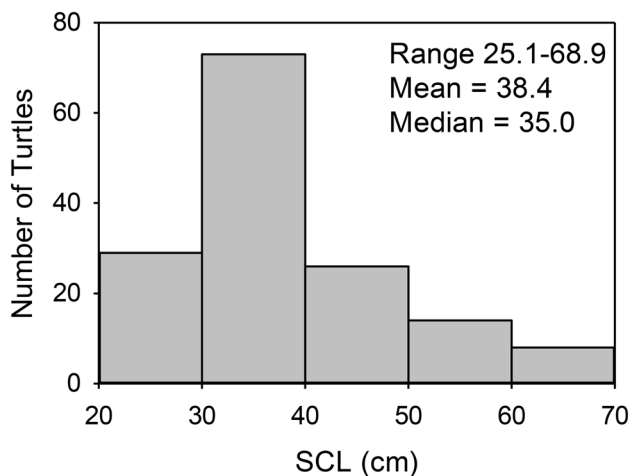


Fig. 3 Size distribution of the green sea turtles (*Chelonia mydas*) captured in 2012, given in the frequency of observations within 10 cm categories of SCL

at initial capture (2012), and were $6.4 \pm 2.6\%$ greater at recapture (2013), with annual growth increments ranging from 1.6 to 9.2% year⁻¹ (0.5–2.8 cm year⁻¹). Smaller turtles had large changes in $\delta^{13}\text{C}$ from 2012 to 2013, while the two turtles above 40 cm SCL showed no change over the year. Inter-annual changes in $\delta^{15}\text{N}$ were small in magnitude ($0.20 \pm 0.60\text{‰}$), variable, and not a function of the size of the turtles in 2012 (Fig. 5).

Diet mixing models

Averaged across all size classes and using Platform-wide averages of the isotopic composition of the groups of potential food sources, the isotope mixing model indicated that seagrasses were the most important component of the diet of the Bermudian green turtle population. For all the turtles we sampled, 55% of the C and N assimilated came from seagrasses, 22% came from macroalgae, and 24% came from animal sources. A clear ontogenetic diet shift was apparent when the mixing model was applied to turtles grouped by size class. The diets of the turtles with SCL > 40 cm were dominated by seagrass, and animal prey were the largest contributors to the diet of the smallest turtles (Fig. 6). Using seagrass data from each site in our mixing models, rather than the Platform averages, led to predictions of lower proportions of seagrass in turtle diets. The range in seagrass proportions in turtle diets calculated for individual turtles using site-specific data was 5–80% with an average of 47% while the range was 7–83% (average 51%), using the Platform average data. There was no clear pattern in the differences driven by size class (Figure S3 in Supporting Information). We used results from models employing the site-specific seagrass isotope values in subsequent analyses.

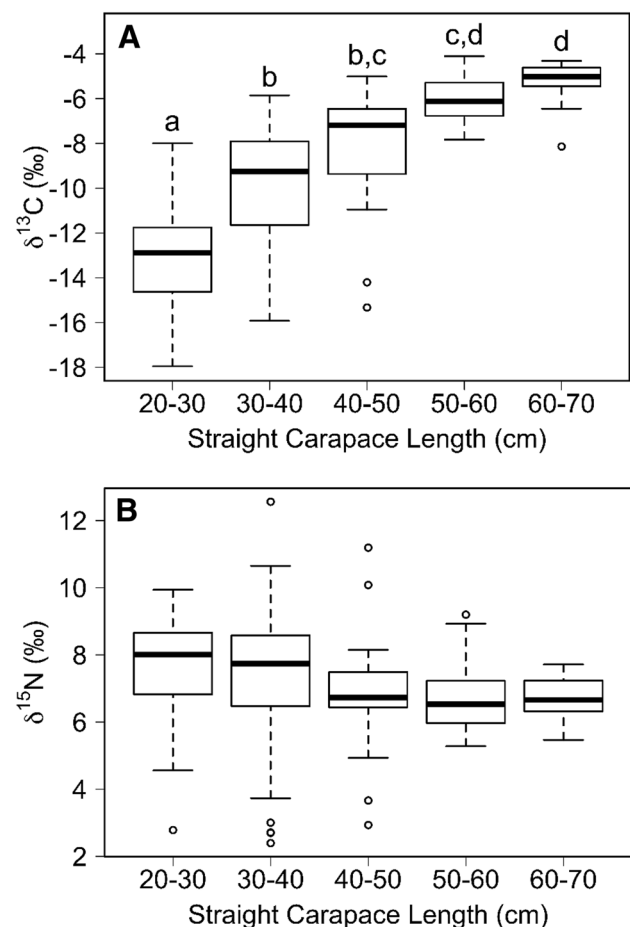


Fig. 4 Variation in stable isotope ratios (A: $\delta^{13}\text{C}$, B: $\delta^{15}\text{N}$, in ‰) of skin samples as a function of size class for captured green turtles (*Chelonia mydas*). There were significant differences among size classes in $\delta^{13}\text{C}$ [ANOVA, $F(4, 152) = 35.6$, $P < 0.001$], but no significant differences in $\delta^{15}\text{N}$ [ANOVA, $F(4, 152) = 1.6$, $P = 0.173$]. Letters denote homogenous subsets of the data (Tukey post hoc test). N by size class: 20–30 cm = 28; 30–40 cm = 73; 40–50 cm = 29; 50–60 cm = 16; 60–70 cm = 11

When plotted as a function of SCL, the fraction of seagrasses in the diets of turtles increased with size, asymptotically approaching a maximum value (Fig. 7). We determined the rational function with the formula $S_i = 1 + S_{\max} - (SCL_i / (SCL_i - V))$, which best described our data (see Table S3 and Figure S4 in Supporting Information for details of candidate models), where S_i was the proportion of seagrass consumed for an individual i , S_{\max} was the horizontal asymptote which represents the average highest fraction of seagrasses in the diet of individuals, SCL_i is the SCL or size of the individual i , and V is the vertical asymptote for the relationship necessary to shift the line away from zero as these individuals have no access to seagrass during their pelagic life phase. The x-intercept represents the size of turtles when entering the Bermuda Platform. The model described 40% of the variation (R^2_{adj}) in S_i . We found $S_{\max} = 0.9$ and $V = 10.7$,

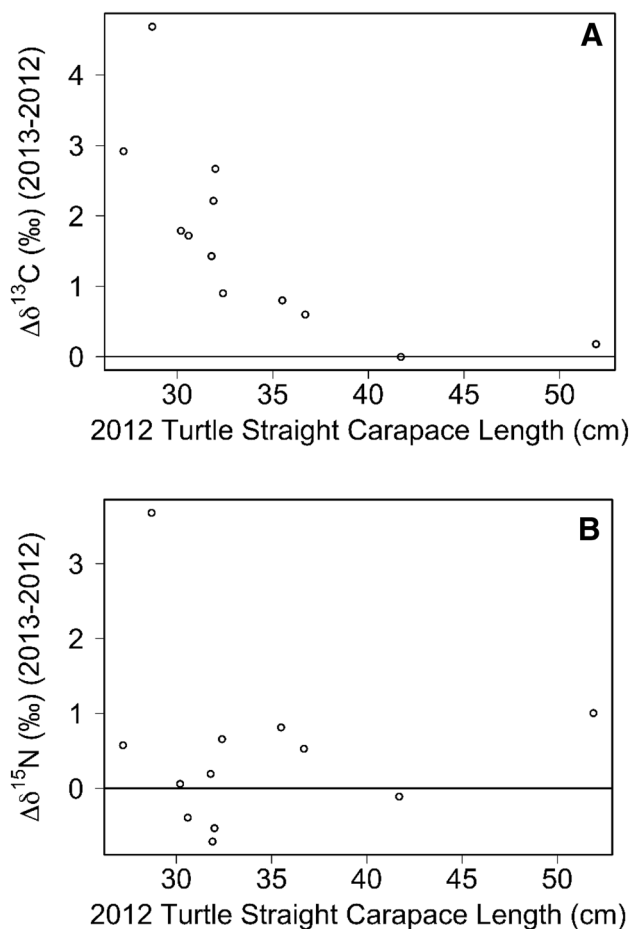


Fig. 5 **a** Absolute change in $\delta^{13}\text{C}$ as a function of straight carapace length for all recaptured green turtles (*Chelonia mydas*) from Bermuda. **b** Absolute change in $\delta^{15}\text{N}$ as a function of straight carapace length for all recaptured turtles from Bermuda. Y-axes indicate difference in stable isotope ratios between years for each individual

which solves for an x-intercept of 22.6 cm SCL. The S_{max} of 0.9 indicates that the percentage of seagrass in the diet of our largest turtles was likely to be increasing still, albeit slowly. The largest turtle we sampled (68.9 cm SCL) was predicted by this model to consume 71% seagrass, and the actual C and N values for this turtle, when applied to the mixing model, was estimated at 76% seagrass consumption. The average-sized turtle in our sample (39.0 cm SCL) was predicted to consume 52% seagrass by this relationship. The halfway point between the effective maximum of the relationship for our population (71%) and the minimum (0%) was reached at 30.5 cm SCL, reflecting the decrease in the rate of diet change during the time an individual turtle is on the Platform, i.e., the small turtles quickly transition to seagrass eaters once they come onto the Platform.

Mixing model outputs for diet compositions showed large variations in diets of turtles captured within sites and indicated that there were differences in foraging preferences

based on site (See Figure S2 in Supporting Information). However, there were differences in the distribution of size classes among sites, and the size classes had different diet compositions (Fig. 6). Plots of the average seagrass percentage in the diet versus the average size of the turtles captured at a site (Fig. 8) followed the general relationship already described between individual turtle diets and size. The most obvious site-wise deviation from this relationship was seen at Chub Heads, a site described in Fourqurean et al. (2010) where seagrasses have been lost due to overgrazing.

Discussion

Because there were isotopically distinct food groups available to green turtles on the Bermuda Platform, we were able to use stable isotope mixing models to determine that individual turtles had different diets that gave rise to broad ranges in the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of turtle skin. However, the greatest amount of diet variation was due to differences among size classes of turtles and diets were relatively consistent within a size class. Thus, there is clearly an ontogenetic shift in the diets of green sea turtles during their residency on the Bermuda Platform. As the turtles got larger (and presumably older) seagrass became the largest component of their diets. Even though seagrass abundance is declining in Bermuda (Murdoch et al. 2007; Fourqurean et al. 2010; Manuel et al. unpubl data), there was little deviation among the larger turtles from this progression to seagrass specialization, with the possible exception of turtles collected from one location (Chub Heads).

In Bermuda, the older turtles seem to be depleting an important food resource of their neritic habitat. Mittelbach et al. (1988) and Polis et al. (1996) have presented theories that such resource depletion should not occur. Are there reasons that such theories might not be relevant to the current situation or to the general conditions on the Bermuda Platform? There is an enormous disparity in the total area of the pelagic habitat of the young turtles compared to the very small, neritic, habitat of the turtles on the Bermuda Platform. The Sargasso Sea, where small turtles congregate, has a surface area about $2.8 \times 10^6 \text{ km}^2$, whereas the Platform has an area of about $5.0 \times 10^2 \text{ km}^2$ and seagrass meadows cover less than 24% of that area (Manuel et al. 2013). Related to these enormous differences of available habitat size, the population density of turtles is likely much higher on the Bermuda Platform than in the open ocean, hence both total and per capita resources could be lower in the neritic habitat than in the pelagic habitat. However, evidence suggests that the per capita food availability was ample to support the populations of turtles seen in Bermuda in the recent past. About 20 years ago, Vierros et al. (2002) (also see Vierros 1999) estimated both the area of turtle foraging habitat and, very roughly,

Fig. 6 Diet composition across green turtle (*Chelonia mydas*) size classes in the Bermuda Platform. The gray stacked boxes represent 50, 75, and 95% credibility intervals for the mixing model outputs of the turtle diet proportions. The thick black line represents the mean, the dotted line represents the median, and the dot represents the mode of the mixing model iterations for each group. *N* by size class: 20–30 cm = 28; 30–40 cm = 73; 40–50 cm = 29; 50–60 cm = 16; 60–70 cm = 11

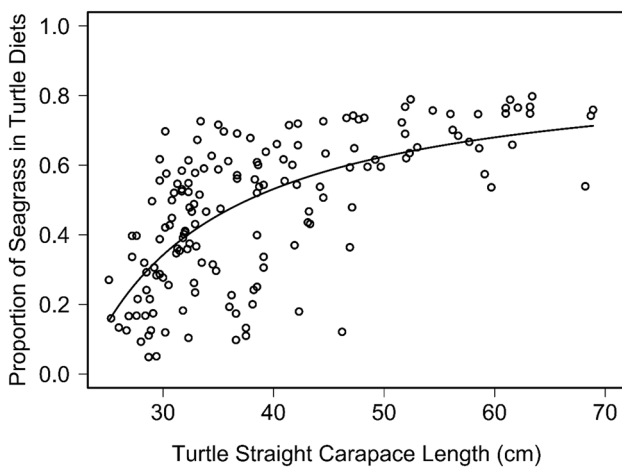
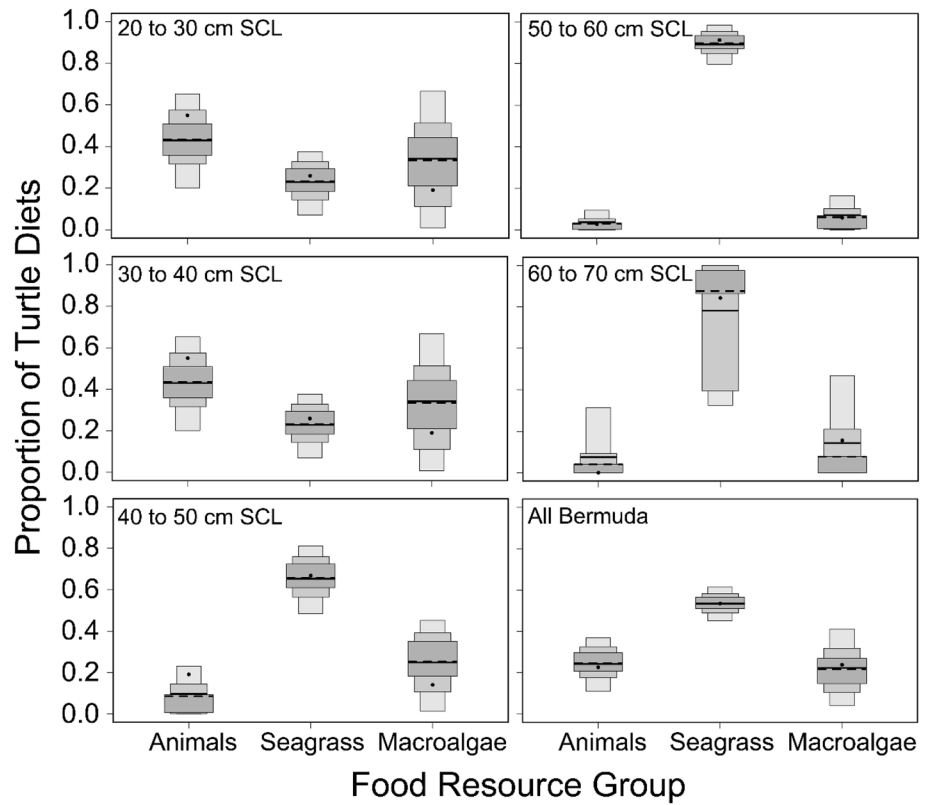


Fig. 7 Relationship between green turtle (*Chelonia mydas*) size and seagrass consumption for all individuals. The line was determined using non-linear regression in SPSS using the relationship $S_i = 1 + S_{max} - (SCL_i / (SCL_i - V))$ where S_i is the proportion of seagrass consumed for individual i , S_{max} is the horizontal asymptote which represents the average highest seagrass consumption by individuals, SCL_i is the straight carapace length or size of the individual i , and V is the vertical asymptote for the relationship necessary to shift the line away from zero as these individuals have no access to seagrass during their pelagic life phase. The resulting equation was $S_i = 1 + 0.886 - (SCL_i / (SCL_i - 10.548))$, $R^2_{adj} = 0.40$

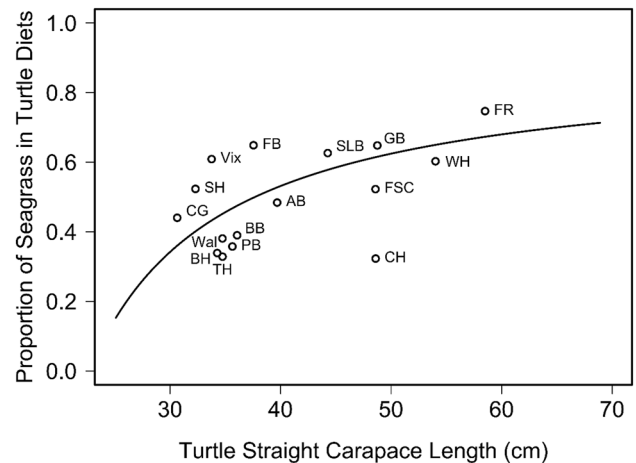


Fig. 8 Relationship between green turtle (*Chelonia mydas*) size and the proportion of seagrass in diet, by capture site. The line plotted represents the relationship between straight carapace length and proportion of turtle diet that comprised seagrass determined using seagrass isotope values for the individual sites. The means of the turtle size and the seagrass consumption data were calculated in order to visualize how each site varied from this relationship. *AB* Annie’s Bay, *BB* Bailey’s Bay, *BH* Blue Hole, *CH* Chub Heads, *CG* Cow Ground, *FR* Ferry Reach, *FB* Frank’s Bay, *FSC* Fort Saint Catherine’s, *GB* Grotto Bay, *PB* Pilchard Bay, *SLB* Somerset Long Bay, *SH* Stock’s Harbour, *TH* Tudor Hill, *Vix* Vixen, *Wal* Walsingham, and *WH* Wreck Hill

the number of turtles on the Bermuda Platform, (between about 1900 and 7500 individuals). They predicted that this number of turtles was well below the carrying capacity (as per Bjorndal 1985) of the Platform, suggesting that, at that time, there was abundant plant food available for the turtles. Unfortunately, good data on recent changes in population sizes of the green turtles in Bermuda are not available to allow a reassessment of the carrying capacity of the Bermuda Platform using similar methodology. Information on turtle population trends in Bermuda are very limited and frequently anecdotal (Godley et al. 2004). The lack of reliable estimates of numbers of turtles on the Bermuda Platform and of trends in these numbers since about the mid-1990s, when declines in seagrass beds due to overgrazing were first noted in Bermuda (Fourqurean et al. 2010), make it extremely difficult to relate definitively numbers of turtles to overgrazing.

Outside Bermuda, in specific locations where seagrass is scarce, juvenile and adult turtles incorporate high proportions of macroalgal and animal food in their diets (Hatase et al. 2006; Cardona et al. 2009; Shimada et al. 2014; Santos et al. 2015; Howell et al. 2016). Site-specific analysis of our turtle diet data showed that at one of the better-studied sites, Chub Heads, seagrass represented less of the total diet of green turtles than would be predicted based on size. Declines in the seagrasses of this site led to the experiments that implicated turtle grazing as the driver of decline (Fourqurean et al. 2010). Perhaps the deviation from the general ontogenetic shift to reliance on seagrass in larger turtles we documented at Chub Heads is an indicator that the larger turtles from this site are relying less on seagrasses for food as seagrasses become less available.

It seems possible that turtles whose home feeding grounds decline could move to less exploited seagrass beds, if any are close enough, instead of shifting diets. In general, green sea turtles establish strong site fidelity at their neritic foraging grounds (Reich et al. 2007; Arthur et al. 2008; Howell et al. 2016; Shimada et al. 2016) and data from Bermuda corroborate this (Meylan et al. 2011). Preliminary data from satellite-tagged turtles suggest home ranges of Bermuda turtles are on the scale of 1 km² (Manuel, unpub. Data). Inshore in Bermuda, seagrass beds are closer together than further offshore (Manuel et al. 2013) and one or more inshore beds may fall within a single home range so that turtles might regularly move among beds. However, if and when all the seagrass is depleted on the Bermuda Platform, it will be a long swim to other seagrass habitats in the western North Atlantic—at least 1000 km. Whether this is something that can be accomplished by juveniles at the size they would normally switch to a primarily seagrass diet is not known.

Food availability is not the sole factor driving the foraging behaviors of animals (Werner and Gilliam 1984); resource supply and predation risk interact to determine food choices throughout the life of an animal. The non-lethal

effects of predators create landscapes of risk that can have marked influences over feeding behaviors and food selection (Estes et al. 2011). Green sea turtles avoid high-risk, high-quality seagrasses and forage in lower quality habitat in the face of predation risk (Heithaus et al. 2007) and it is likely that the high risk of foraging in seagrass meadows drives some green turtles to specialize on non-seagrass foods (Burkholder et al. 2011). Tiger sharks are the primary predator of large green turtles (Heithaus et al. 2008) and their populations near Bermuda have apparently declined drastically since the 1980s (Baum et al. 2005). Thus, in Bermuda, the benefits of vigilance may be so low that no meaningful food resource giving-up-densities (GUD) are instilled in the turtle population. GUD is defined as the critical resource density where costs of continued grazing are higher than the derived benefit (Brown 1988) and turtles should abandon a food or feeding site when biomass falls below GUD (Lacey et al. 2014). Lack of top-down pressure on rebounding sea turtle populations may be contributing to ecosystem crashes in some of the world's seagrass meadows, including in Bermuda (Heithaus et al. 2014).

The small foraging ranges of green sea turtles makes understanding the spatial variation in their potential food sources significant to the development of diet mixing models. Steep spatial gradients in seagrass $\delta^{15}\text{N}$ are present on the Bermuda Platform, with $\delta^{15}\text{N}$ ranging from -10.1 to 8.8‰ over a linear distance of only 8 km (Fourqurean et al. 2015). We used the measured $\delta^{15}\text{N}$ fractionation during assimilation by green turtles of $2.8\text{--}3.8\text{‰}$ (Seminoff et al. 2006; Vander Zanden et al. 2012) in our mixing models. Therefore, using values of seagrass $\delta^{15}\text{N}$ from an inappropriate location on the Bermuda Platform, compared to a turtle's actual small home range, could lead to an apparent change of 3 trophic levels for the green turtle's diet and to the under- or overestimation of the importance of animal foods in their diet. When we used Platform-average seagrass isotope values in mixing models we got different predictions of the proportion of seagrass consumed than when site-specific values were used. Nevertheless, in our study, these differences were small because all the turtles we captured were from sites where the $\delta^{15}\text{N}$ of seagrasses ($0.1\text{--}6.3\text{‰}$) fell in the middle of the total range for Bermuda. Spatial patterns in stable isotopic composition of primary producers are common in widespread locations (e.g., south Florida (Fourqurean et al. 2005), the Mediterranean Sea (Fourqurean et al. 2007)) and they should be considered when designing stable isotope food web investigations.

Stable isotope mixing model analyses of animals and their foods cannot detect all of the variation in organisms' diets or in food web structure (see review by Layman et al. 2012). We were limited in our analyses by the lack of significant differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ content of many of the potential food sources for green sea turtles. We could

only resolve three isotopically distinct groupings of potential foods (seagrasses, macroalgae, and animal prey). Populations of green sea turtles have been shown to prefer some species of seagrass over others in some locations (André and Lawler 2003; Fuentes et al. 2006) and individual turtles to prefer some macroalgae over others (Brand-Gardner et al. 1999); thus, our analyses could have missed within-food group specialization by individual turtles. Further, potentially important foods could have been eaten by our sea turtles that we did not collect. Investigating such specializations, within isotopically indistinct food groups, would require different techniques such as direct observations of feeding in the wild, manipulative feeding experiments, gastric lavage, or gut content analyses.

Interestingly, we saw a clear pattern in the $\delta^{13}\text{C}$ of skin of Bermuda turtles that is consistent with an ontogenetic change from an early omnivorous diet to a later sub-adult seagrass-based diet, but no consistent pattern of decreasing $\delta^{15}\text{N}$ as their diets become more seagrass-based. Mixing models consistently predicted a high probability that animal foods persist in green sea turtle diets, both in our study and in other locations (e.g., Hatase et al. 2006; Cardona et al. 2009; Shimada et al. 2014; Santos et al. 2015; Howell et al. 2016). Perhaps the lack of a trend in $\delta^{15}\text{N}$ with size is driven by more variability in $\delta^{15}\text{N}$ in the diets of early life stage omnivores than in the later life-stage, predominantly seagrass grazing, juveniles, or by as-yet unknown regional variation in the $\delta^{15}\text{N}$ of the foods preferred by smaller green turtles.

The $\delta^{13}\text{C}$ versus SCL relationship for Bermuda's green sea turtles is remarkably similar in shape to the relationship found in the western Gulf of Mexico where seagrass meadows were abundant (Howell et al. 2016). However, along the northern part of that coastline, Howell et al. (2016) found that turtles in 30 to 60 cm SCL size classes had isotopic values indicative of a variety of diet specializations, from macroalgal- to seagrass-based. They hypothesized this difference was caused by decreased seagrass abundance and faunal diversity in the northern part of their sampling range. We found only scant evidence that older Bermuda turtles have responded to declines in seagrass abundance in a similar manner.

The epidermal tissue of green turtles reflects new diets within 371 days of a diet change (Seminoff et al. 2006), thus the patterns we have seen in the variation in stable isotopes of turtle tissues as a function of age are not solely a function of time since recruitment to the neritic habitat because the observed change in the $\delta^{13}\text{C}$ of their skin tissue plays out over many years. Individual turtles are resident in Bermuda for as long as 20 years (Meylan et al. 2011). The derived parameters of our rational function model of the $\delta^{13}\text{C}$ to SCL relationship suggests that for most of their residency on the Bermuda Platform, most of the diet of green

turtles is composed of seagrasses. Our model indicates that new recruits arrive on the Bermuda Platform at an SCL of 22.6 cm; this is similar to the minimum SCL of sea turtles captured in the BTP (22.3 cm; Meylan et al. 2011) and to the smallest recorded neritic green turtle reported (20.8 cm SCL; Bressette et al. 1998). Both the relationship between $\delta^{13}\text{C}$ and SCL for the population and the change in $\delta^{13}\text{C}$ with size in our recaptured turtles suggest that an ontogenetic diet shift occurs when turtles reach about 40 cm SCL. Based on the average growth rates of our 12 recaptured turtles of $6.4\% \text{ year}^{-1}$, turtles would converge on a consistent, seagrass-dominated diet $\delta^{13}\text{C}$ signature by 9 years after they arrived on the platform. Based on an average growth rate of Bermuda turtles of about $2.5 \text{ cm SCL year}^{-1}$, reported by Meylan et al. (2011), a seagrass-dominated diet would occur about 7 years following arrival. These are in the range of the timing of ontogenetic diet changes estimated for other green turtle populations, for example, green turtles from Australia exhibit changes in $\delta^{13}\text{C}$ for 4 years following recruitment to neritic habitats and their $\delta^{15}\text{N}$ stabilizes at an herbivorous signal after 6 years (Arthur et al. 2008).

The sustainability of Bermuda as a developmental habitat for green sea turtles may be at risk, since the older turtles do not seem to be responding to a decline in the seagrass food resource by switching their diets. The green sea turtles of Bermuda are a mixed stock of individuals from nesting beaches throughout the North Atlantic and Caribbean (Meylan et al. 2011) and collapse of the benthic habitats of the Bermuda Platform could have wide ranging effects in the North Atlantic. Going forward, our results can stand as a baseline for "normal" turtle-by-size diets on the Bermuda Platform. Future work should be designed to answer questions about how turtles are responding to changes in seagrass abundance. Important questions include: will larger turtles eventually begin to shift to non-seagrass foods? If not, will larger turtles become a smaller part of the total population? Will the size of the whole population decrease? and Will overall turtle health decline?

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Compliance with ethical standards

Research involving human/animal participants This work complied with all applicable national and international standards for the care and

use of animals. Research was conducted with authorization from FIU's IACUC #11-019, and importing and exporting of turtle samples was done under CITES permits 12BM0025 and 12US88774A/9.

Conflict of interest The authors declare that they have no conflicts of interest.

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