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Green Sea Turtles (Chelonia mydas) in Bermuda Exhibit an Ontogenetic Diet Shift despite Overexploitation of Resources in their Developmental Habitat

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FLORIDA INTERNATIONAL UNIVERSITY

Miami, Florida

GREEN SEA TURTLES (CHELONIA MYDAS) IN BERMUDA EXHIBIT AN

ONTOGENETIC DIET SHIFT DESPITE OVEREXPLOITATION OF RESOURCES IN

THEIR DEVELOPMENTAL HABITAT

A thesis submitted in partial fulfillment of

the requirements for the degree of

MASTER OF SCIENCE

in

BIOLOGY

by

Claire Margaret Burgett

2017

To: Dean Michael R. Heithaus
    College of Arts, Sciences and Education

This thesis, written by Claire Margaret Burgett, and entitled Green Sea Turtles (*Chelonia mydas*) in Bermuda Exhibit an Ontogenetic Diet Shift despite Overexploitation of Resources in their Developmental Habitat, having been approved in respect to style and intellectual content, is referred to you for judgment.

We have read this thesis and recommend that it be approved.

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James W. Fourqurean, Major Professor

Date of Defense: March 27, 2017

The thesis of Claire Margaret Burgett is approved.

_____
Dean Michael R. Heithaus
College of Arts, Sciences and Education

_____
Andrés G. Gil
Vice President for Research and Economic Development
and Dean of the University Graduate School

Florida International University, 2017

DEDICATION

This work is dedicated to John Burden, the shiniest of us all.

ACKNOWLEDGMENTS

ABSTRACT OF THE THESIS

GREEN SEA TURTLES (CHELONIA MYDAS) IN BERMUDA EXHIBIT AN

ONTOGENETIC DIET SHIFT DESPITE OVEREXPLOITATION OF RESOURCES IN

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by

Claire Margaret Burgett

Florida International University, 2017

Miami, Florida

Professor James W. Fourqurean, Major Professor

Green sea turtles in Bermuda are overgrazing the seagrasses on which later life

stages are thought to specialize. I hypothesized that larger green turtles in Bermuda

would display individual diet specializations during seagrass scarcity. Stable isotope

methods were used to determine the diet composition of green sea turtles from the

Bermuda Platform as a function of size class and in turtles captured in successive years.

Individual turtles had a wide range of diets, however, the variation in diets was driven by

differences among size class rather than within the size classes of larger turtles, indicating

that green turtles undergo a dietary ontogenetic shift during their residency on the

Bermuda Platform and no clear specialization of diets among late-stage individuals. The

apparent lack of dietary specialization of larger turtles indicates that older turtles are not

diversifying their diets in response to the drastic reductions in seagrass in Bermuda.

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I. INTRODUCTION

Ontogenetic shifts in diet can reduce intraspecific competition, and are shaped by body size, resource availability and size-dependent predation rates; they are a common feature of the life history of many diverse organisms (Werner and Gilliam 1984). Ontogenetic diet shifts are often coupled with changes in both the organism's size and the spatial domain of different life history stages. Theory predicts that if early life stage individuals come from a low-resource environment and subsequent stages recruit to high-resource environments, then the later stages in high-resource environments should not saturate or overexploit the resources in the high-resource habitat (Mittelbach, Osenberg & Liebold 1988; Polis *et al.* 1996).

While ontogenetic shifts in diet can minimize intra-specific competition for food among organisms of different age classes (Werner & Gilliam 1984), extreme population diet specialization makes populations susceptible to declines in the life-stage-specific specialized food choices if all individuals in a population exhibit the same food preferences. Individual diet specialization within a population can arise if 1) cognitive constraints allow individuals to recognize alternate food sources, 2) individuals can only forage efficiently if they specialize in a subset of the potential food resources, 3) different habitats have different resource pools and individuals only inhabit a subset of habitats, 4) ecological tradeoffs (e.g., food for safety) result in variability in the way individuals access food resources, or 5) if food resources are scarce (Estes *et al.* 2003; Svanback & Persson 2004; Araujo *et al.* 2009; Araujo, Bolnick & Layman 2011).

Ontogenetic shifts from carnivorous and omnivorous juveniles to herbivorous adults are common in reptiles, including turtles (Werner & Gilliam 1984; Polis *et al.*

1996), and the ontogenetic diet shift often seen in green sea turtles (*Chelonia mydas*) is particularly well-studied. While most marine organisms that exhibit ontogenetic diet shifts have young that feed in more productive (littoral) habitats with adults feeding in less productive pelagic habitats (Barnes & Hughes 1988; Polis *et al.* 1996), green turtles display the opposite pattern. Juvenile green turtles recruit to productive, neritic, nearshore habitats at a size of about 25 cm – 35 cm straight carapace length (SCL) after spending 3-6 years in unproductive, oceanic, pelagic habitats (Carr 1987; Zug & Glor 1998; Reich, Bjorndal & Bolten 2007), and stable isotope diet studies show an ontogenetic shift from a pelagic to a neritic, often seagrass-based, diet after the juveniles arrive in the neritic habitats (Reich, Bjorndal & Bolten 2007; Arthur, Boyle & Limpus 2008; Howell *et al.* 2016). But, evidence from areas with few seagrass resources suggest that subadult green turtles can and do exploit non-seagrass resources when seagrasses are not available (Cardona, Aguilar & Pazos 2009; Carman *et al.* 2012; Russell & Balazs 2015; Santos *et al.* 2015; Howell *et al.* 2016). Substantial individual specialization in the diets of adult green turtles, including specialization on animal food resources, from a habitat with abundant seagrass resources and very high predation rates on turtles suggest that individual green turtles can make different choices that balance food abundance and risk (Burkholder *et al.* 2011). Individual turtles with specialized diets remain specialized over many years (Vander Zanden, Bjorndal & Bolten 2013).

While green turtles remain a CITES-listed protected species (Cheloniidae, Appendix 1) (https://cites.org/eng/app/appendices.php, 2017), the successes of conservation measures has resulted in rapid increases in the number of nesting turtles laying eggs on nesting beaches in many areas of the world, including Florida and

Tortuguero, Costa Rica in the Western North Atlantic (Chaloupka *et al.* 2008).

Concomitant with these population increases, the number of reports of overgrazing of

seagrasses 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). Such overgrazing events may

be partially explained by the lack of top-down control on green turtle populations because

of global overfishing of their predators, large sharks (Heithaus *et al.* 2014).

The green turtle population on the Bermuda Platform (ca. 32.4ºN, 64.8ºW)

provides an ideal system to test general theories about ontogenetic diet shifts and dietary

specialization. Compared to the oligotrophic western North Atlantic waters that surround

the islands, Bermuda is a productive neritic 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 NW Atlantic. The turtles

arrive as juveniles on the Platform at about 22 cm Straight Carapace Length (SCL), and

depart the Platform many years later when they are 65-75 cm sub-adults (Meylan,

Meylan & Gray 2011). The seagrass resources on which they may depend are in

precipitous decline (Murdoch *et al.* 2007), and it has been experimentally demonstrated

that overgrazing by sea turtles is at least partly responsible for these declines (Fourqurean

et al. 2010). Because of the declining abundance of seagrasses, as well as the documented

capacity of green turtles to consume foods other than seagrasses after their settling in

neritic habitats, we expected that dietary analyses would illuminate a diversity of diet

strategies among individuals within the green turtle population rather than a population-

wide ontogenetic diet shift to a seagrass-based diet. Specifically, we posed these three

questions: 1) What is the green turtle diet composition in the neritic developmental

habitat on the Bermuda Platform? 2) How does diet composition differ across green turtle size classes? 3) How do sites with potentially different resource availability or resource quality affect green turtle diet composition? We employed stable isotope techniques to address these questions, specifically measuring $\delta^{13}C$ and $\delta^{15}N$ composition of green turtles and potential food sources. We then used isotope mixing models (Parnell *et al.* 2013) to determine turtle diets. Mixing model outputs were used to indicate the importance of different potential food sources in the turtles' diets as a function of their size class. Marked gradients in the stable isotopic composition of seagrasses across the Platform (Fourqurean *et al.* 2015) also provided the potential to refine stable-isotope-derived diet composition measurements using site-specific values of these food sources.

II. MATERIALS AND METHODS

A. FOOD WEB SAMPLE COLLECTION

In order to establish the stable carbon and nitrogen isotopic composition of potential food for green turtles, samples of a variety of primary producers (macroalgae and seagrasses) and animals (scyphozoans, ctenophores, octocorals, tunicates, sponges, and crustaceans) that had been identified as prey in other studies (Burkholder *et al.* 2011) were haphazardly collected by divers during turtle capturing sessions. Seagrasses were sampled across the entire Platform as part of another contemporaneous study (Fourqurean *et al.* 2015). Each seagrass sample was a composite of 5-20 shoots collected from a 3×3 m area. Seagrass species found at our sampling sites included *Thalassia testudinum*, *Syringodium filiforme*, and *Halodule* sp. (the taxonomic identity of the *Halodule* encountered is an unresolved question). Samples were stored on ice in the field and then

frozen at -20°C until processing. Prior to isotope analyses epiphytes were removed from

seagrass leaves by scraping them with a razor blade.
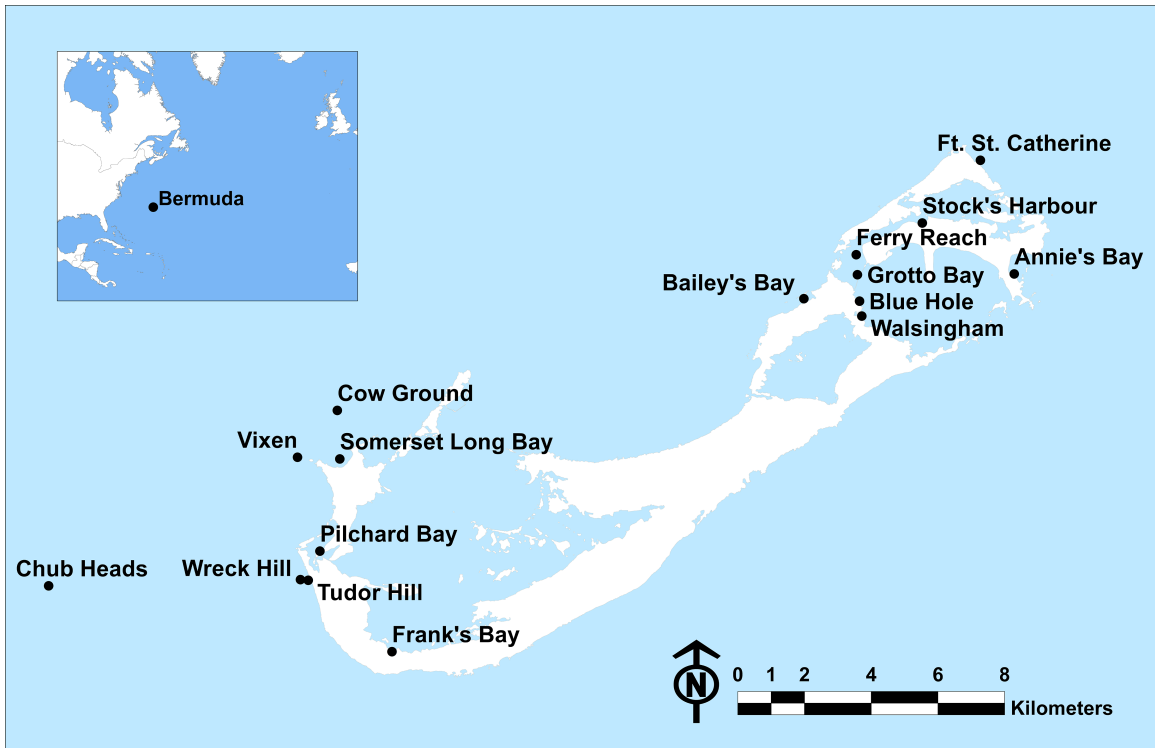
Figure 1. Capture Locations of Green Turtles (*Chelonia mydas*) on the Bermuda
Platform. Inset shows location of Bermuda within the Atlantic Ocean.

B. TURTLE TISSUE COLLECTION

Green turtles were captured from 12 locations on the Bermuda Platform by the

Bermuda Turtle Project (BTP) and at an additional four locations by the Department of

Environment and Natural Resources using the entrapment net procedure described by

Meylan et al. (2011, Figure 1). Captured turtles were transferred to a nearby vessel for

measurement and tissue sampling. Individual net sets produced between 1 and 20 turtles.

One of the capture locations was Chub Heads, an intensely grazed site at which a turtle

grazing exclosure experiment was conducted (Fourqurean *et al.* 2010). Epidermal tissue

samples were collected from a total of 159 individual turtles captured in 23 net sets over the period July 30 to August 17, 2012 and in 7 net sets between August 6 and 16, 2013. All turtles were tagged following Bermuda Turtle Project procedures (Meylan, Meylan & Gray 2011), allowing recaptures in 2013 of turtles caught in 2012 to be recognized. All turtles were measured for straight carapace length (SCL) with calipers. Skin samples from the turtles were collected from a standardized location on the trailing edge of the rear flippers, which had been swabbed with ethanol. Skin samples were collected using a stainless steel 5 or 8 mm biopsy punch, placed on ice in the field, and transported to the lab, where they were frozen (-20°C) until processed.

C. STABLE ISOTOPE ANALYSIS

All samples (seagrass, macroalgal, potential animal prey, and turtle tissue) were dried at 50°C to constant weight and each sample was ground for homogenization. Macroalgal and animal prey samples were decalcified by placing moistened, powdered samples in a sealed chamber over concentrated hydrochloric acid until they reached constant weights. Variation in lipid concentrations of organisms and tissue types has been shown to bias stable isotope analyses (Post *et al.* 2007). Nonetheless, lipids were not extracted from any samples as our previous work with green turtle stable isotope ratios concluded lipid extraction was not necessary for this tissue type (Burkholder *et al.* 2011). Samples were analyzed for stable isotopic content of C and N using standard EA-IRMS techniques at the Florida International University Stable Isotope Laboratory. Analytical reproducibility of the reported δ values, using sample replicates, was better than ±0.2‰ for δ15N and ±0.08‰ for δ^{13}C.

D. STATISTICAL ANALYSES

Potential food species were pooled into isotopically indistinguishable groups (which we call food groups) by pooling all observations within 10 broad categories and then using ANOVA (SPSS 23) to define homogenous subsets of the broad categories. We tested for relationships between the haphazardly-collected non-seagrass potential foods and the more dense and spatially comprehensive data on spatial patterns in seagrass stable isotopic signatures (Fourqurean *et al.* 2015) by comparing non-seagrass food signatures to the seagrass signatures by site with linear regression. For analysis of population-level descriptions of the variability among turtles in isotopic signatures and the relationship between SCL and isotope values, data from the second observation of recaptured turtles in 2013 were excluded. Turtle size classes were defined by 10 cm increments in SCL in order to maintain an adequate sample size in the groups of our larger turtles and to facilitate direct comparisons to other studies. Differences in turtle isotope ratios between size classes of turtles were determined using ANOVA (SPSS 23).

E. DIET MIXING MODELS

Diet composition was determined using the SIAR Bayesian diet mixing model program package in R (Parnell *et al.* 2008; Parnell *et al.* 2013) using an average of published discrimination of epidermal tissues from diet values for juvenile green turtles ((Seminoff *et al.* 2006); $\delta^{15}N = 2.80 \pm 0.11‰$, $\delta^{13}C = 0.17 \pm 0.03‰$ and (Vander Zanden *et al.* 2013); $\delta^{15}N = 3.77 \pm 0.40‰$, $\delta^{13}C = 1.87 \pm 0.56‰$). 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 (*Thalassia*

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testudinum, *Syringodium filiforme*, *Halodule* sp.) were determined using interpolated seagrass $\delta^{15}N$ and $\delta^{13}C$ values from the results presented in (Fourqurean *et al.* 2015) because of high variation between sites for seagrass stable isotopes. 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 determined using 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 form of the ontogenetic diet shift 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.

III. RESULTS

A. POTENTIAL TURTLE FOOD SOURCES

Samples of 21 different taxa of potential turtle food items were collected, including four genera of seagrasses, 13 genera of macroalgae, and 15 taxa of animals (see Table S1 in Supporting Information). The potential foods grouped into three isotopically-distinct food groups: seagrasses, macroalgae, and animals (ANOVA results for differences among groups: $\delta^{15}N$: F=25.16, p<0.001, $\delta^{13}C$: F=211.8, p<0.001). These food groups had considerable variability in their stable isotopic compositions (Figure 2), In general, seagrasses had the lowest $\delta^{15}N$ (1.7 ± 3.5 ‰, confidence intervals associated with means expressed as one standard deviation throughout the paper) and animals had the highest (5.5 ± 2.1 ‰, Table 1). Conversely, seagrasses had the highest average $\delta^{13}C$ (-

7.4 ± 1.9 ‰) and animals had the lowest (−17.9 ± 1.4 ‰, Table 1). Note that seagrasses

from the Platform-wide survey (Fourqurean *et al.* 2015) reported in Table 1 had a very

broad range in δ^{15}N, from -10.1 ‰ to 8.8 ‰. However, the δ^{15}N of seagrasses from turtle

capture sites had a much narrower range ($\overline{X}$ = 2.9 ± 1.6 ‰, with a range of 0.1 − 6.3 ‰)

since the capture sites were generally close to shore where δ^{15}N of seagrasses varied less

than they do across the whole Platform. There were no significant relationships between

seagrass δ^{15}N and the δ^{15}N of macroalgae and animals across sites as assessed by linear

regression, indicating that macroalgae and animal prey did not have the same spatial

pattern in nitrogen isotope values as documented for seagrasses across the Bermuda

Platform (Fourqurean *et al.* 2015).

Table 1: Descriptive statistics of the carbon and nitrogen isotope values for the focal
consumers (turtles) and the three food groups (animals, seagrass, and macroalgae).

	δ^{15}N				δ^{13}C			
	Mean	Min	Max	SD	Mean	Min	Max	SD
Turtles	7.2	2.4	12.6	1.7	-9.5	-17.9	-4.1	3.2
Animals	5.5	2.0	10.6	2.1	-17.9	-20.9	-15.3	1.4
Seagrass	1.7	-10.1	8.8	3.5	-7.4	-12.9	-3.3	1.9
Macroalgae	3.8	-2.3	9.0	2.1	-14.3	-20.3	-8.3	2.5
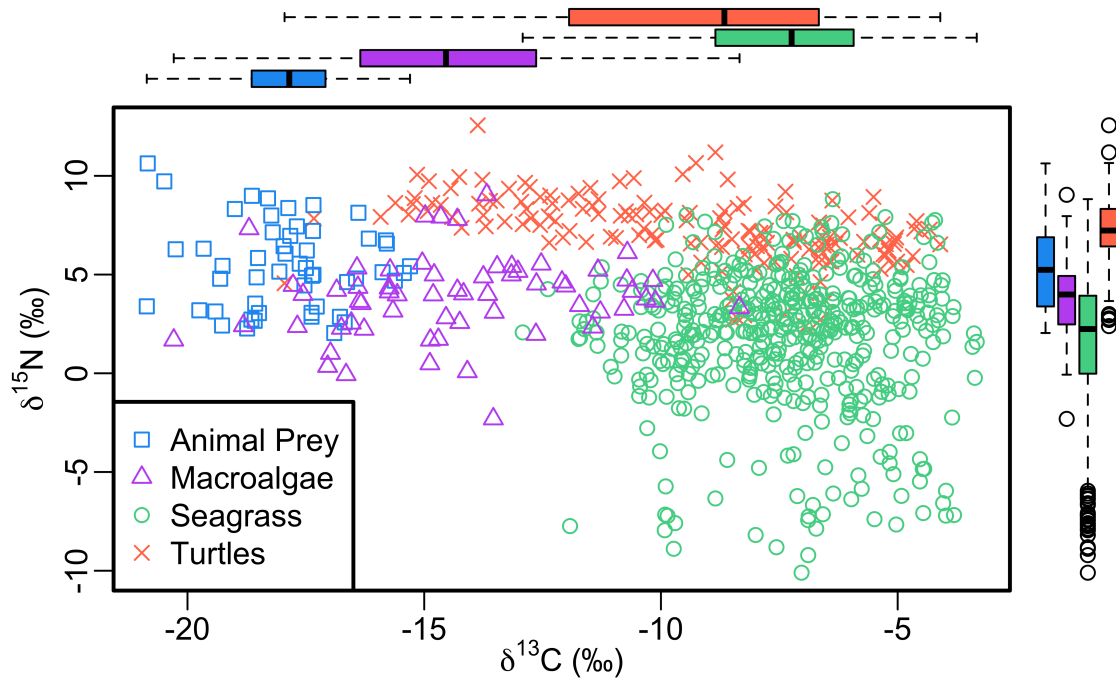
Figure 2. Isotope Ratios for All Groups. Nitrogen and carbon stable isotope ratios (in standard δ notation in ‰) for all green turtles (*Chelonia mydas*) and potential food groups (macroalgae, animals, and seagrass) on the Bermuda Platform. Descriptive box and whisker plots in the margins show the distribution of the values for each group, with median at the central line, first to third quartile in the boxes, and the 95% confidence interval in the whiskers.

B. SIZE DISTRIBUTION AND STABLE ISOTOPE RATIOS OF CAPTURED

TURTLES

The 157 turtles measured in 2012 ranged in size from 25.1 to 68.9 cm SCL. The size

distribution was skewed towards smaller turtles (Fig. 3); the mean SCL was 38.4 ± 10.5

cm. Skin samples from the captured turtles had an average $\delta^{15}N$ of 7.3 ± 1.6 ‰ and

average $\delta^{13}C$ of -9.3 ± 3.1 ‰ (Table 1), but there was considerable variation in both

isotope ratios (Figure 2). Plotted as a function of the size of individual turtles, a clear

trend in increasing $\delta^{13}C$ with size was evident, no similar clear trend was evident in $\delta^{15}N$

with length, but the scatter in $\delta^{15}N$ was larger for smaller turtles (Figure 4). When analyzed using 10 cm size classes as groups (Figure 5), there were significant differences among size classes in $\delta^{13}C$ (F=35.6, p<0.001), but no significant differences in $\delta^{15}N$ (F=1.6, p=0.173).

Range 25.1-68.9
Mean = 38.4
Median = 35.0
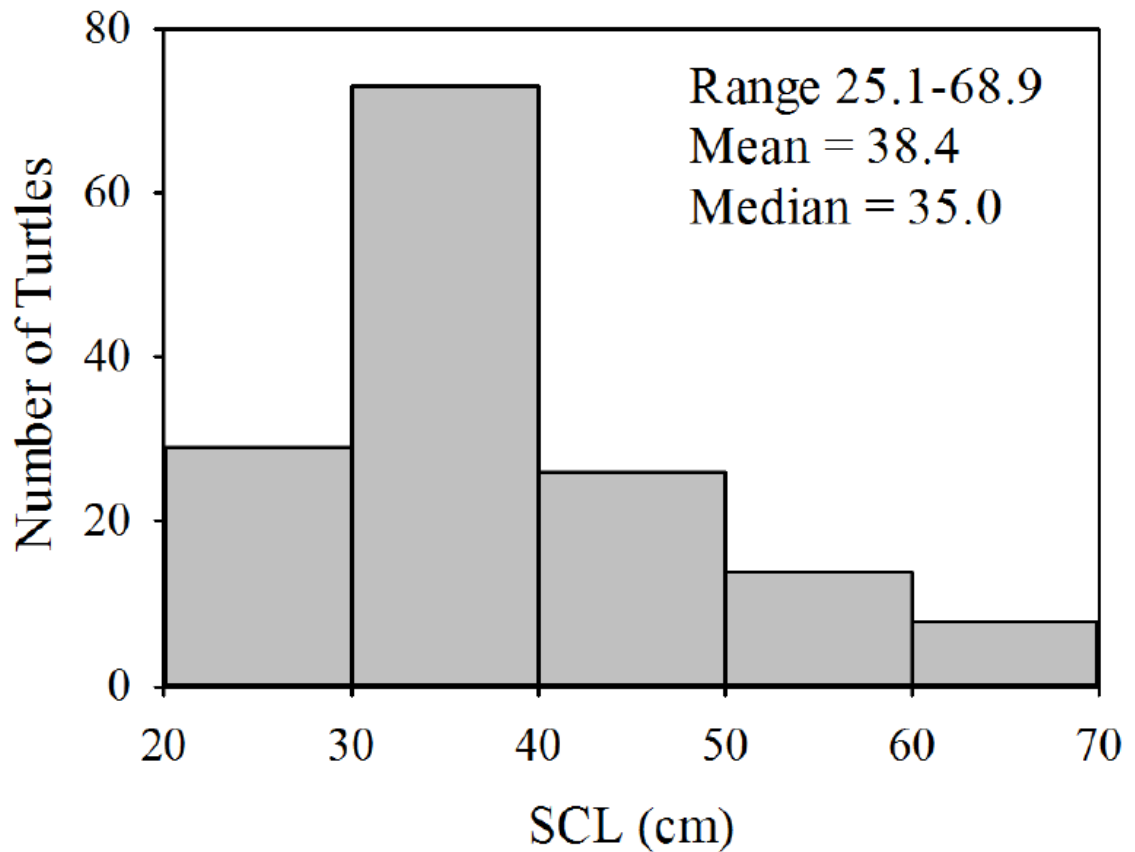
Figure 3. Size Distributions of Green Turtles (*Chelonia mydas*) Captured in 2012. Size distribution of the green sea turtles (*Chelonia mydas*), given in the frequency of observations within 10 cm categories of Straight Carapace length (SCL).
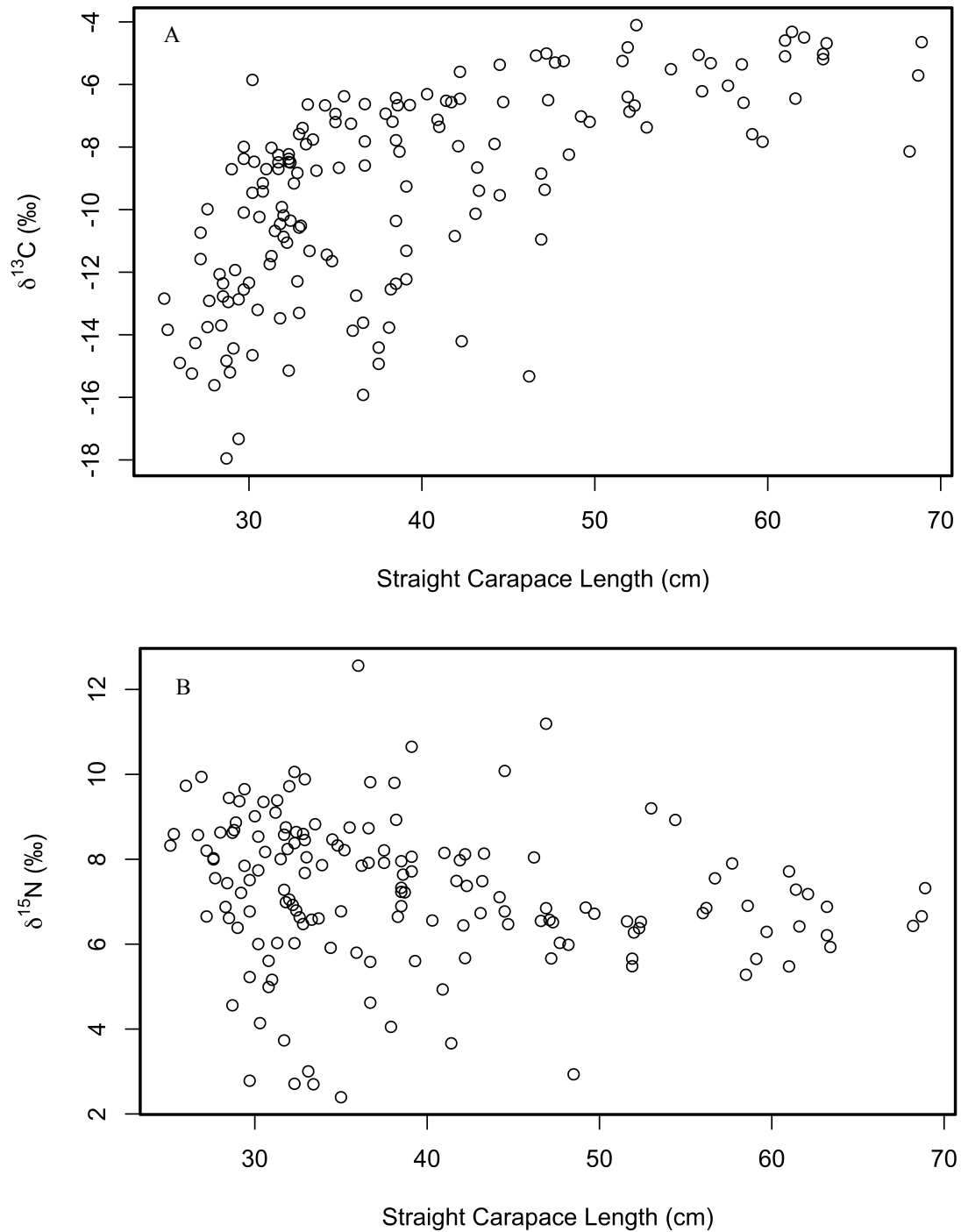
Figure 4. Green Turtle (*Chelonia mydas*) Stable Isotope Ratios in Relation to Turtle Size. Stable isotopic ratios (A: $\delta^{13}C$, B: $\delta^{15}N$, both in ‰) for skin samples from green sea turtles (*Chelonia mydas*) in relation to turtle size (Straight Carapace Length, SCL) on the Bermuda Platform. Samples shown in these graphs are non-recaptures collected in August 2012 or August 2013.
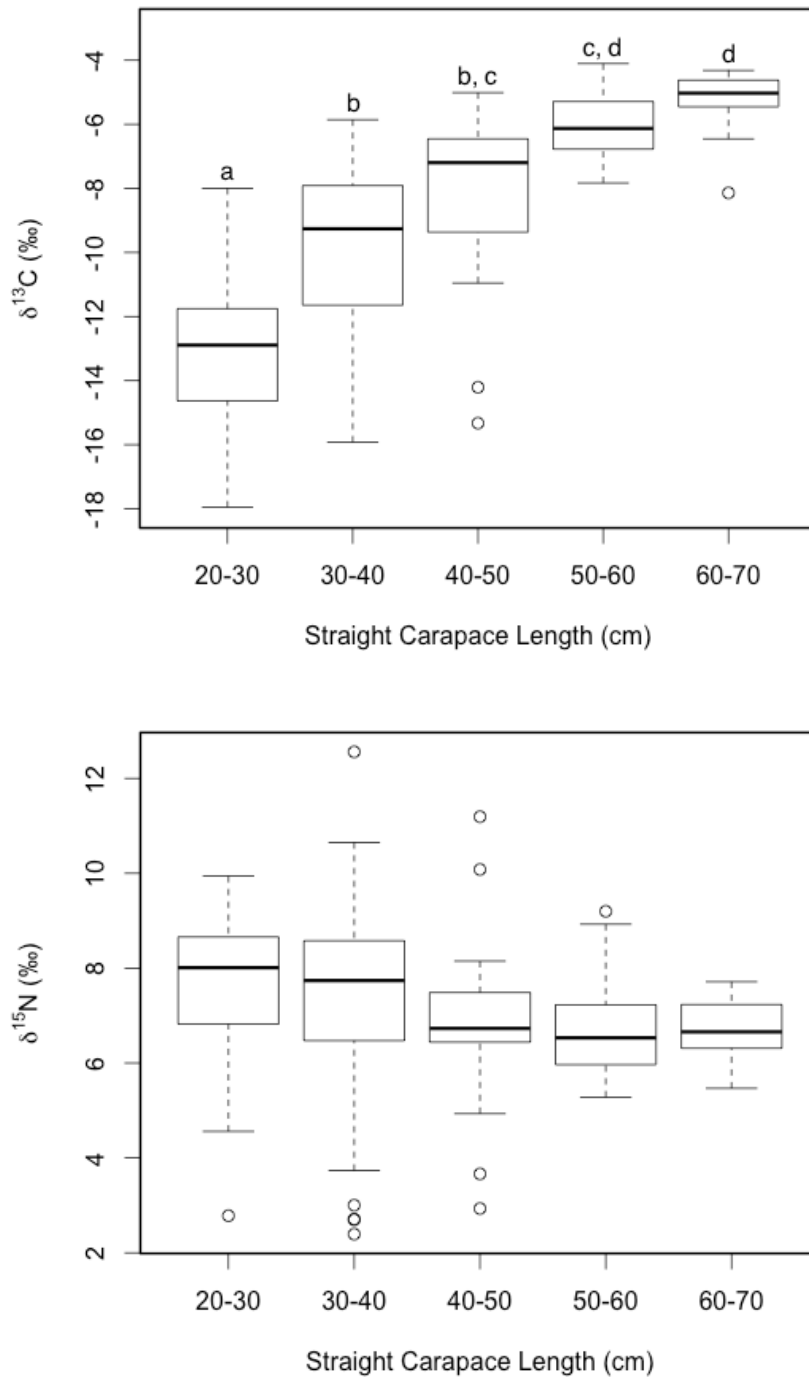
Figure 5. Variation in Green Turtle (*Chelonia mydas*) Stable Isotope Ratios as a Function of Size Class. Variation in stable isotope ratios (δ^{13}C and δ^{15}N, in ‰) of skin samples as a function of size class for captured green turtles (*Chelonia mydas*). There were significant differences among size classes in δ^{13}C (F=35.6, p<0.001), but no significant differences in δ^{15}N (F=1.6, p=0.173). Letters denote homogenous subsets of the data (Tukey post-hoc test).

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A.

B.
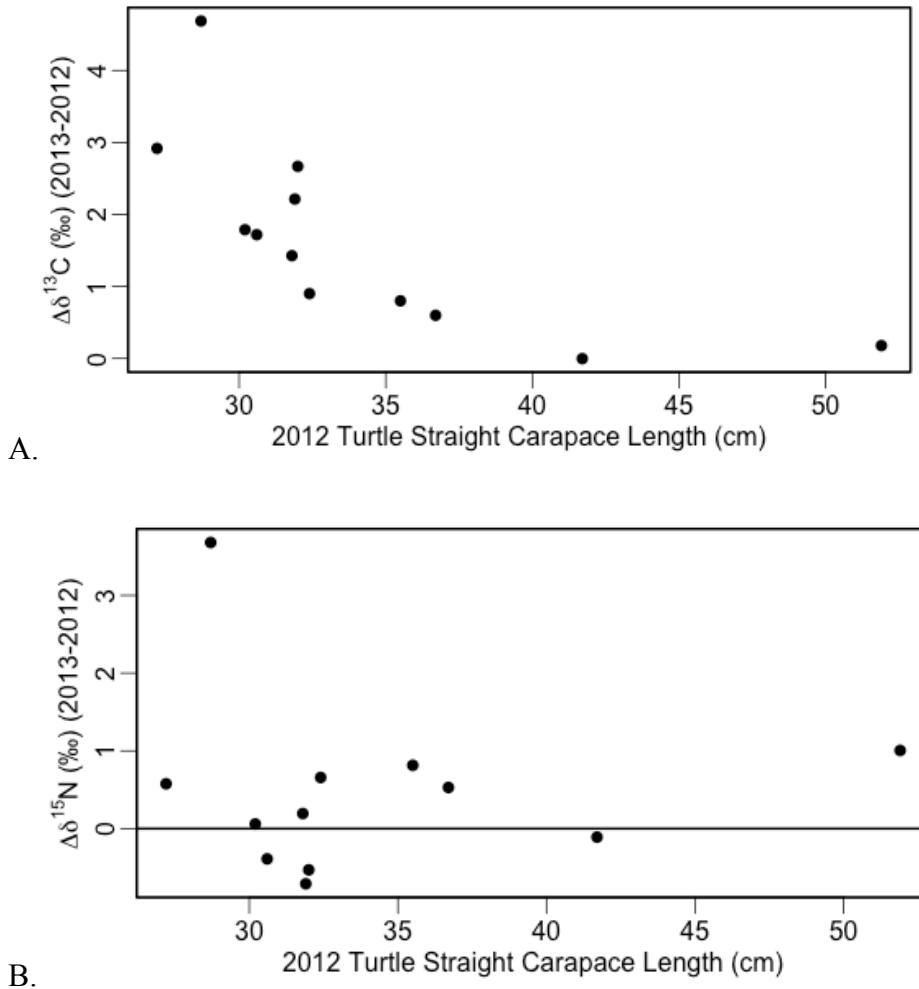
Figure 6. Isotope Ratios in Relation to Size for Recaptured Green Turtles (*Chelonia mydas*). A. Straight carapace length in relation to change in $\delta^{15}N$ for all recaptured green turtles (*Chelonia mydas*) from Bermuda. B. Straight carapace length in relation to change in carbon isotope values for all recaptured turtles from Bermuda. Y-axis indicates difference in stable isotope ratios between years or each individual.

We recaptured 12 of the turtles sampled in 2012 again in 2013. Eleven out of 12 of our recaptures were captured at the same site as the previous year's capture, while the other turtle was caught at a site 1 km away. All recaptured turtles had longer SCL in 2013, compared to 2012, but the fractional increment in growth was not a linear function

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of initial SCL (linear regression, $r^2 = 0.28$, $p = 0.41$). On average, recaptured turtles had

6.4 ± 2.6 % greater SCL in 2013 than in 2012, with individual growth increments ranging

between 1.6 % y^{-1} and 9.2 % y^{-1} for turtles that ranged between 27.2 cm and 51.9 cm

SCL. Smaller turtles had large changes in $\delta^{13}C$ from 2012 to 2013, while turtles above

40 cm in SCL showed no change over the year, while year-on-year changes in $\delta^{15}N$ were

small in magnitude, variable, and not a function of the size of the turtles in 2012 (Figure

6).

C. DIET MIXING MODELS

Averaged across all size classes and using Platform-wide averages of the isotopic

composition 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 the population as a whole, 53% 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, as the diets of the largest sampled turtles were dominated by seagrass and the diets

of the smallest sampled turtles were dominated by animal prey (Figure 7). 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 compared to using the

Platform average seagrass data. The range in seagrass proportions in turtle diets

calculated for individual turtles using site specific data, was 5% to 80% with an average

of 47% while the range in seagrass proportions in turtle diets calculated using Platform

average data was 6% to 83% with an average of 51%.
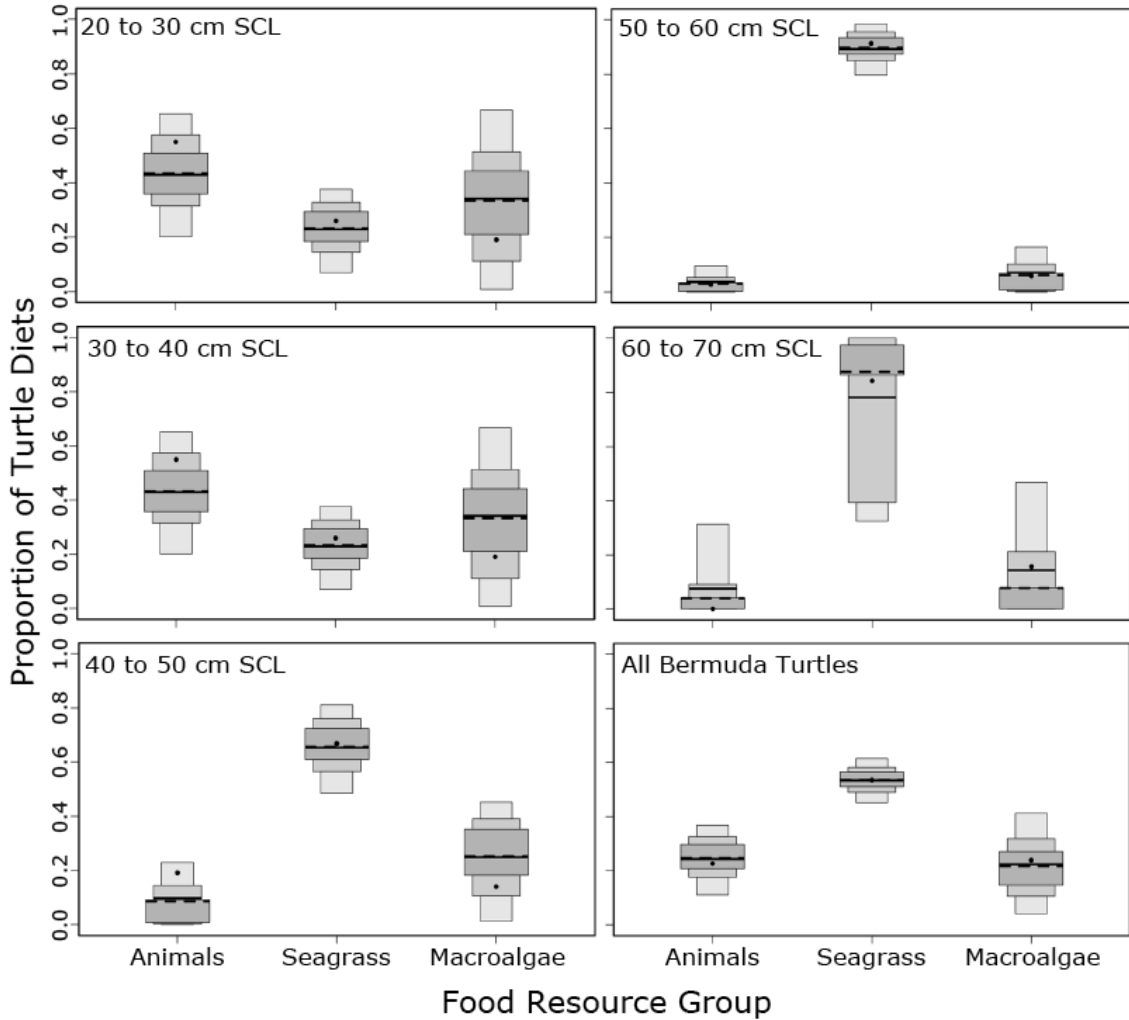
Figure 7. Diet Composition Across Green Turtle (*Chelonia mydas*) Size Classes. The gray stacked boxes represent 50%, 75%, and 95% credibility intervals for the mixing model outputs of the turtle diet proportions. The thick black line represents the mean, the dotted line represents the median, and the dot represents the mode of the mixing model iterations for each group.

When plotted as a function of SCL, the predicted fraction of seagrasses in the

diets of turtles increased with size, asymptotically approaching a maximum value (Figure

8). We determined the rational function with the formula $S_i = 1 + S_{Max} - (SCL_i/(SCL_i-V))$

best described our data (see Table S3 and Figure S2 in Supplementary Information for

details of candidate models), where S_i was the proportion of seagrass consumed for

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 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 x-intercept represents the size of turtles when entering the Bermuda Platform. We found S_{Max}= 0.90 and V=10.71, which solves for an x-intercept of 22.6 cm SCL. The S_{max} of 0.90 shows that the percentage of seagrass in the diet of even our largest sampled turtles was likely to still be increasing, albeit slowly. Our largest sampled turtle (68.9 cm SCL) was expected to consume 71% seagrass based on this relationship and was observed at 76% seagrass. The average-sized turtle in our sample (39.0 cm SCL) is 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%) is reached at 30.5 cm SCL, reflecting the decrease in the rate of diet change over the time an individual turtle is on the Platform.

Mixing model outputs for diet compositions showed large variations in diets within the turtle populations at most sites and indicated that there were differences in foraging preferences based on site (See Figure S3 in Supplemental Materials). However, there were differences in the distribution of size classes among sites, and the size classes had different diet compositions (Figure 7). Plotting the average seagrass percentage in the diet by the average size of the turtles captured at a site generally followed the relationship between individual turtle diets and size (Figure 9). The most significant site-wise deviation from this relationship was seen at Chub Heads, our turtle capture site at which seagrasses were known to be overgrazed (Fourqurean *et al.* 2010).
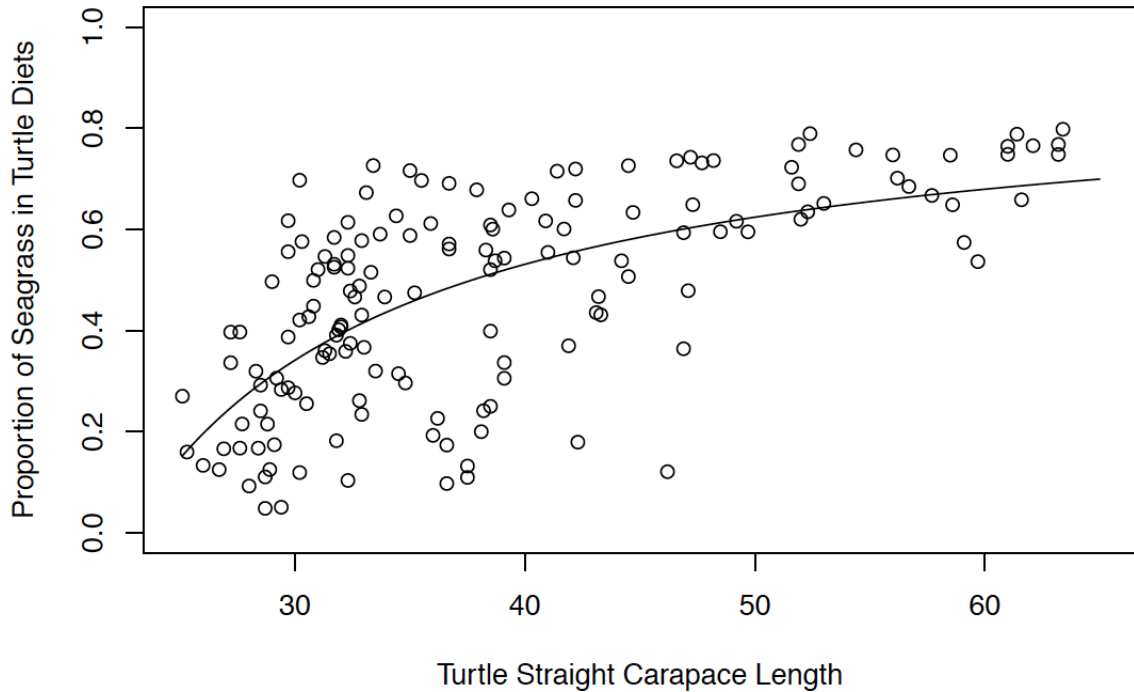
Figure 8. Relationship Between Green Turtle (*Chelonia mydas*) Size and Seagrass Consumption for All Individuals. The line was determined using non-linear regression in SPSS using the relationship $S_i = 1 + S_{Max} - (SCL_i/(SCL_i-V))$ where S_i is the proportion of seagrass consumed for individual 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 $S_i = 1 + 0.897 - (SCL_i/(SCL_i-10.709))$, $R^2_{adj} = 0.40$.
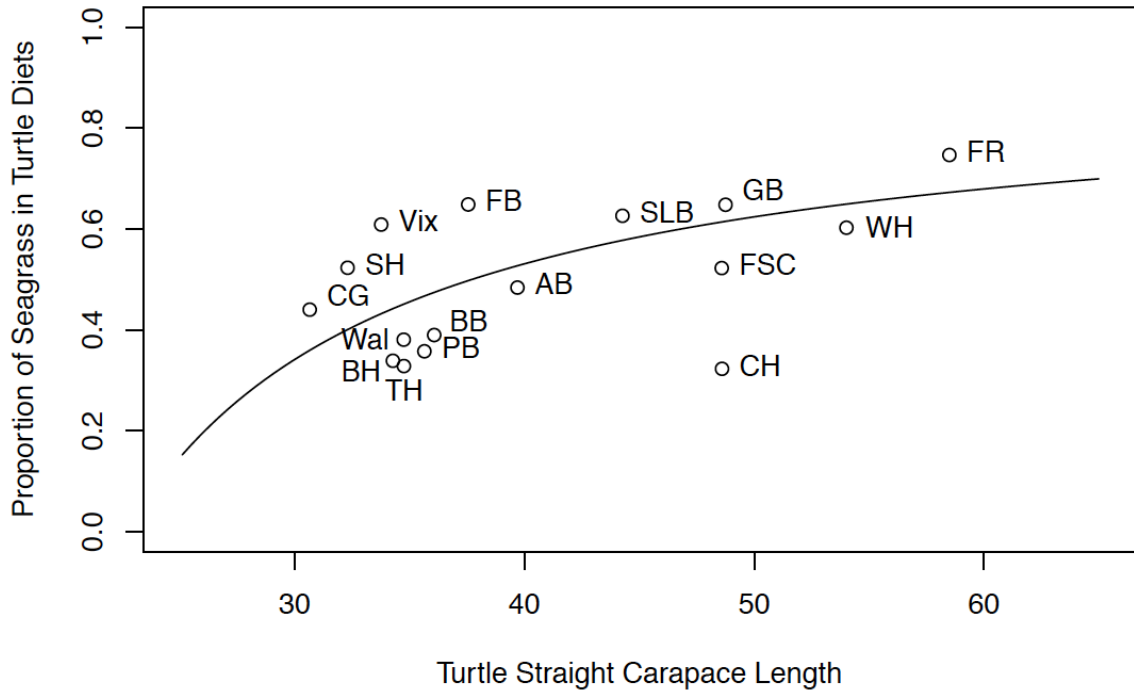
Figure 9. Relationship Between Green Turtle (*Chelonia mydas*) Size and Seagrass Consumption by Site. The line plotted represents the relationship between straight carapace length and proportion of turtle diet comprised of seagrass determined using individual values. The means of the turtle size and 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.

IV. DISCUSSION

The isotopically-distinct nature of food sources available to green sea turtles on the Bermuda Platform and the broad ranges in the δ^{15}N and δ^{13}C of turtle skin tissues indicate that individual turtles had a wide range of diets. However, the variation in diets was driven by diet differences among size class rather than within the size classes of larger turtles, indicating that there is a clear ontogenetic shift in the diets of green sea turtles during their residency on the Bermuda Platform. With the possible exception of turtles collected from one location, the apparent lack of dietary specialization of larger turtles indicates that older turtles are not diversifying their diets in response to the recent, drastic reductions in the seagrass communities in Bermuda.

Theory predicts that a population of organisms that have evolved an ontogenetic diet shift that accompanies a habitat shift from an early juvenile, low resource availability habitat to a later life stage, high resource availability habitat should not deplete resources in the later life stage habitat (Mittelbach, Osenberg & Liebold 1988; Polis *et al.* 1996). However, given the decline in seagrass communities being driven by sea turtle overgrazing on the Bermuda Platform (Murdoch *et al.* 2007; Fourqurean *et al.* 2010), older turtles that have undergone an ontogenetic shift to a seagrass-based diet are indeed overexploiting the seagrass beds. This apparent contradiction of a theoretical prediction is likely driven by the large disparity in the area of the early life stage, low-resource, pelagic habitat of the early life stage turtles compared to the very small, neritic, high-resource availability later life stage habitat. The area of the western North Atlantic is vast compared to the small size of the Bermuda Platform (502 km^2 shallower than 30m) and the even smaller area of seagrass meadows on that platform (no more than 24% of the

area of the shallow Platform, (Manuel *et al.* 2013)). Hence, there is a large discrepancy between per-capita resource availability and the total stock of resources between the early- and later-stage habitats.

In other locations where seagrass resources are scarce, sub-adult and adult turtles have been shown to incorporate higher proportions of macroalgal and animal food in their diets (e.g. (Hatase *et al.* 2006; Cardona, Aguilar & Pazos 2009; Shimada *et al.* 2014; Santos *et al.* 2015; Howell *et al.* 2016), and surveys of the benthic habitats of the Bermuda Platform indicate that macroalgae and benthic animals known to be consumed by turtles are plentiful (Coates *et al.* 2013; Manuel *et al.* 2013). We may have detected an early indicator that Bermuda turtles have the capacity to switch from a seagrass diet in later life stages: the turtles captured at Chub Heads, a site with known overexploitation and recent collapse of the seagrass beds (Fourqurean *et al.* 2010), consume less seagrass as a percentage of their total diet than would be predicted based on their size classes. Future sampling will be needed to detect whether the population of turtles on the Bermuda Platform respond to decreasing seagrass abundance by shifting their food preferences and specializing on macroalgae or animal foods.

Of course, it seems possible that turtles whose seagrass meadows decline could find unexploited ones elsewhere instead of shifting diets, but this does not seem very likely in this case. Bermuda is at least 1000 km from any other seagrass habitats in the western North Atlantic, making foraging trips off of the Bermuda Platform to other neritic habitats impossible for Bermuda-resident turtles. Further, green turtles establish strong site fidelity following migration to a neritic foraging ground (Reich, Bjorndal & Bolten 2007; Arthur, Boyle & Limpus 2008; Howell *et al.* 2016) and evidence suggests that

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green turtles on the Bermuda Platform have very small home ranges. Bermuda green turtles have high site fidelity as 88% of recaptured turtles in the long-term BTP are recaptured over the same small (less than 1 Ha) seagrass beds as their initial capture (Meylan, Meylan & Gray 2011). Our recapture data further corroborate that green sea turtles in Bermuda have small home ranges and high site fidelity, only 1 in 12 of our recaptured turtles was caught at a different location in the second year, and that one turtle was recaptured only 1 km from the site of original capture. As such, it appears that Bermuda sea turtles forage over very restricted home ranges.

The small home ranges of Bermuda green turtles make understanding spatial variation in potential food sources incorporated into diet mixing models very important. Very steep spatial gradients in seagrass $\delta^{15}N$ are present on the Bermuda Platform, ranging -10.1 ‰ to 8.8 ‰ over a linear distance of only 8 km (Fourqurean $et\ al.$ 2015). Given the average food-web $\delta^{15}N$ fractionation of ca. 3 ‰ per trophic level (Wada 1980), and the measured $\delta^{15}N$ fractionation during assimilation by green turtles of 2.8 – 3.8 ‰ (Seminoff $et\ al.$ 2006; Vander Zanden $et\ al.$ 2013) we used in our mixing models, using values of seagrass $\delta^{15}N$ from the wrong end of a spatial gradient from a turtle's small home range could lead to an apparent change of 3 trophic levels for the green turtle diets and the severe under- or overestimation of the importance of animal foods in their diet. While we did find that mixing models gave different predictions of the amount of seagrasses consumed by turtles when Bermuda average seagrass isotope values or site-specific isotope values were used in the models, the differences were small in our case because all of our turtles were collected from locations where the $\delta^{15}N$ of the seagrasses (0.1 – 6.3 ‰) fell in the middle of the total range for Bermuda. Spatial patterns in stable

isotopic composition of primary producers are common around the world (e.g. south

Florida (Fourqurean *et al.* 2005) and the Mediterranean Sea (Fourqurean *et al.* 2007) so

they should be considered when designing stable isotope food web investigations.

Interestingly, we saw a clear pattern in the δ^{13}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 in decreasing δ^{15}N as they became more

seagrass-based. Mixing models consistently predicted a high probability that animal

foods play a role in green turtle diets both in our study and elsewhere (e.g. (Hatase *et al.*

2006; Cardona, Aguilar & Pazos 2009; Shimada *et al.* 2014; Santos *et al.* 2015; Howell *et

al.* 2016). Perhaps the lack of a trend in δ^{15}N with age is driven by more variability in

δ^{15}N in the diets of early life stage omnivores than in the later life-stage, predominantly

seagrass grazing, subadults. Our δ^{13}C -SCL relationship for Bermuda green turtles is

remarkably similar in shape to the relationship found along the southern Texas coastline

of the western Gulf of Mexico (Howell *et al.* 2016) where seagrass meadows were

abundant; however, from the northern part of their study area (*op. cit.*), green turtles in

the 30-60 cm SCL size classes had isotopic signatures indicative of a variety of diet

specializations, from macroalgal- to seagrass-based, which the authors hypothesized to be

caused by decreased seagrass abundance and faunal diversity in that part of their

sampling range.

The derived parameters of our rational function model of the δ^{13}C-SCL suggests that

for most of their residency on the Bermuda Platform, most of the diet of green turtles is

composed of seagrasses. Solving the model equation for the size at which green turtles

first arrive on the platform estimated an SCL of 22.6 cm for new recruits. This estimate is

similar to the minimum SCL of sea turtles captured in the BTP (22.3 cm, (Meylan,

Meylan & Gray 2011), and the smallest recorded neritic green turtle reported globally

(20.8 cm SCL, (Bressette, Gorham & Peery 1998). Both the relationship between $\delta^{13}C$

and SCL for the population and the change in $\delta^{13}C$ with size in recaptured turtles suggest

that the ontogenetic diet change occurs between the time the turtles appear on the

Platform at ca. 22.6 cm SCL, and 40 cm SCL. Using our average growth rates of our

recaptured turtles of 6.4% y^{-1}, turtles converge on a consistent, seagrass-derived diet $\delta^{13}C$

signature by 9 years after they arrived on the platform. Using the reported average growth

rate of Bermuda turtles of 2.5 cm SCL y^{-1} (Meylan, Meylan & Gray 2011), produces an

estimated time of diet stabilization of 7 years following recruitment. These estimates are

similar to the timing of the ontogenetic diet change in other green turtle populations.

Green turtles from Australia exhibit changes in $\delta^{13}C$ for 4 years post-recruitment to

neritic seagrass beds, while their $\delta^{15}N$ stabilizes at an herbivorous signal after 6 years

(Arthur, Boyle & Limpus 2008). Our calculations suggest that turtle diets are dominated

by seagrasses for the majority of their residency on the Bermuda Platform (longest

recorded residency from recapture data is 14 years and estimated to be as long as 20

years; (Meylan, Meylan & Gray 2011). While it is possible that the rapid increase in

carbon isotope values at small turtle sizes seen in our study is reflective of slow turnover

within turtle tissues of pelagic recruits, a study of green turtles fed a controlled diet

showed that turtle tissue isotopes stabilized and reflected their new diet within 371 days

(Seminoff *et al.* 2006). This indicates that turtles would undergo a full turnover of their

epidermal tissues many times during their residency on the Bermuda Platform.

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Resource supply and predation risk interact to determine if ontogenetic shifts will maximize a population's fitness, because food availability is not the sole factor driving the diet of animals (Werner & Gilliam 1984). The non-lethal effects of predators create landscapes of risk that can have marked influences over the feeding behavior and food selection of foraging animals, resulting in alterations to the structure and function of plant communities (Estes *et al.* 2011). It has been shown that green 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 tiger shark populations near Bermuda have apparently declined drastically since the 1980's (Baum *et al.* 2005). The continued reliance of Bermuda's turtles on a declining seagrass resource base instead of switching to non-seagrass foods may be partially caused by lack of predation risk, leading to low cost of vigilance and a resulting low giving up density (GUD, sensu (Brown 1988). As green turtles abandon feeding patches when biomass falls below GUD (Lacey, Collado-Vides & Fourqurean 2014), it is possible that low cost of vigilance reduces GUD so low as to lead to seagrass loss. Lack of top-down pressure on rebounding sea turtle populations may be contributing to ecosystem crash in some of the world's seagrass meadows (Heithaus *et al.* 2014).

Given our documentation of the large dependence of Bermuda's green sea turtles on seagrass diets and the recent decline in Bermuda's seagrasses, the sustainability of Bermuda as a developmental habitat for green sea turtles needs to be quantitatively assessed. As the Bermuda green turtle population is believed to be an important

developmental habitat for green turtles from a mixed stock of nesting beaches throughout

the North Atlantic and Caribbean (Meylan, Meylan & Gray 2011), further collapse of this

habitat could have wide ranging effects on green turtles in the NW Atlantic.

V. DATA ACCESSIBILITY

Data available at the Florida Coastal Everglades LTER Data Resources website

(http://fcelter.fiu.edu/data/)

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SUPPLEMENTAL FIGURES
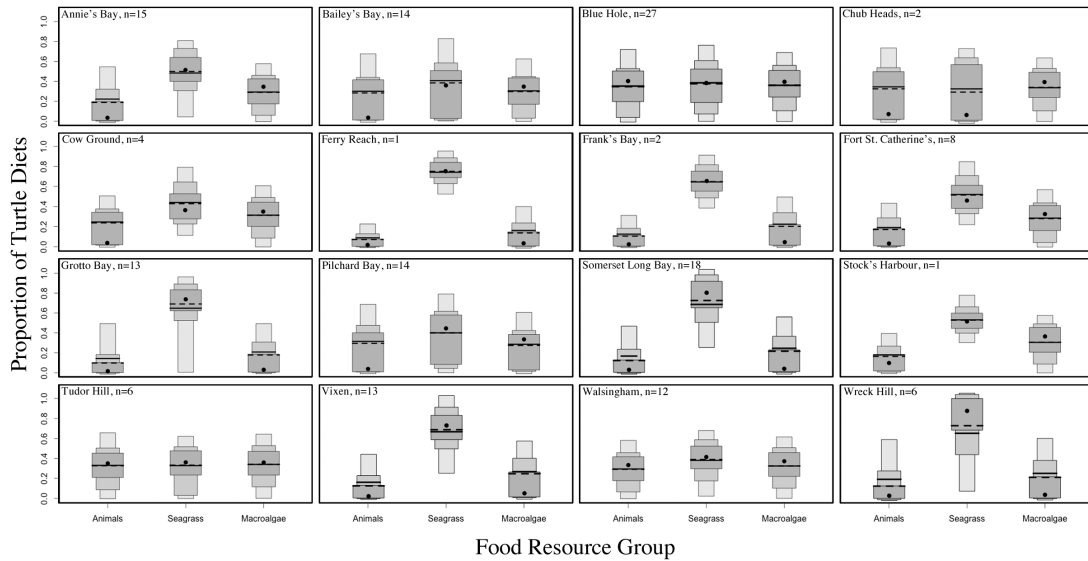
Figure S1. Diet Composition of Green Turtles (*Chelonia mydas*) for Each Capture Location. The gray stacked boxes represent 50%, 75%, and 95% credibility intervals for the mixing model outputs of the turtle diet proportions. The thick black line represents the mean, the dotted line represents the median, and the dot represents the mode of the mixing model iterations for all individuals at each site.
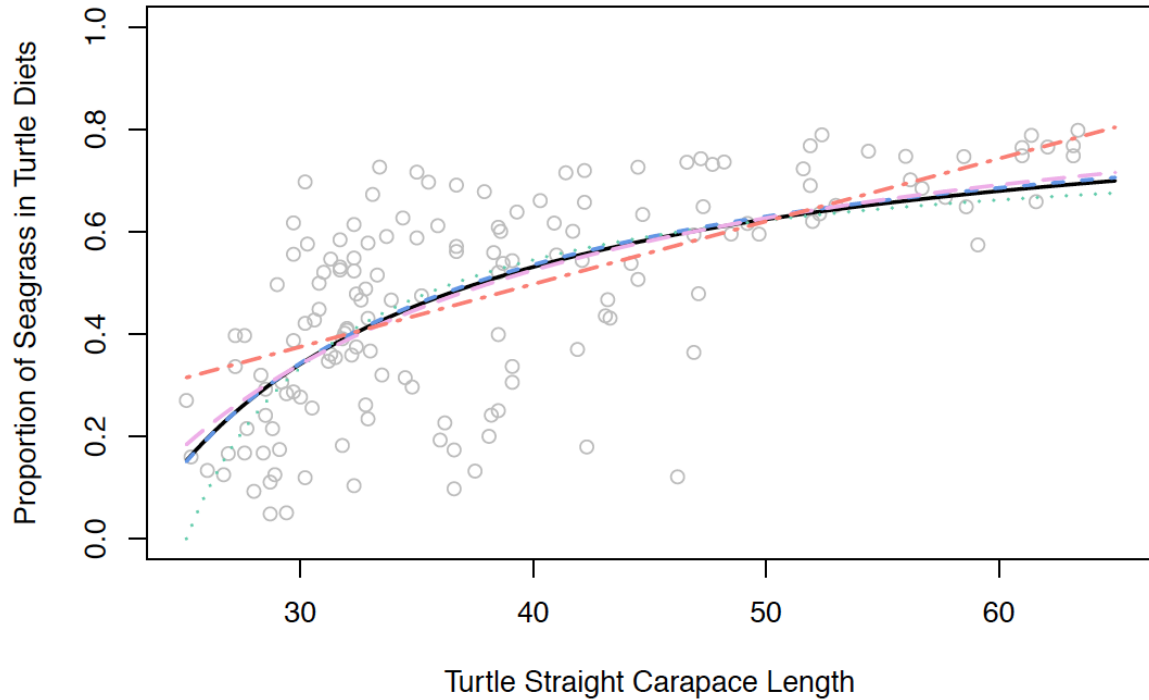
Figure S2. Relationship Between Green Turtle (*Chelonia mydas*) Size and Seagrass Consumption with Multiple Candidate Models. Proportion of seagrass in the diets of individual turtles, as predicted by the isotope mixing models, as a function of turtle size in Straight CarapaceLength, with the best-fit lines of the 6 candidate models described in Supplementary Materials Table S3. Black solid line is the chosen rational model, Blue small-dashed = our rational model excluding Chub Heads data, Green dotted= Michaelis-Menton model, Purple long dashed= Michaelis-Menton model with a non-zero y intercept, and Red two-dashed= linear relationship.
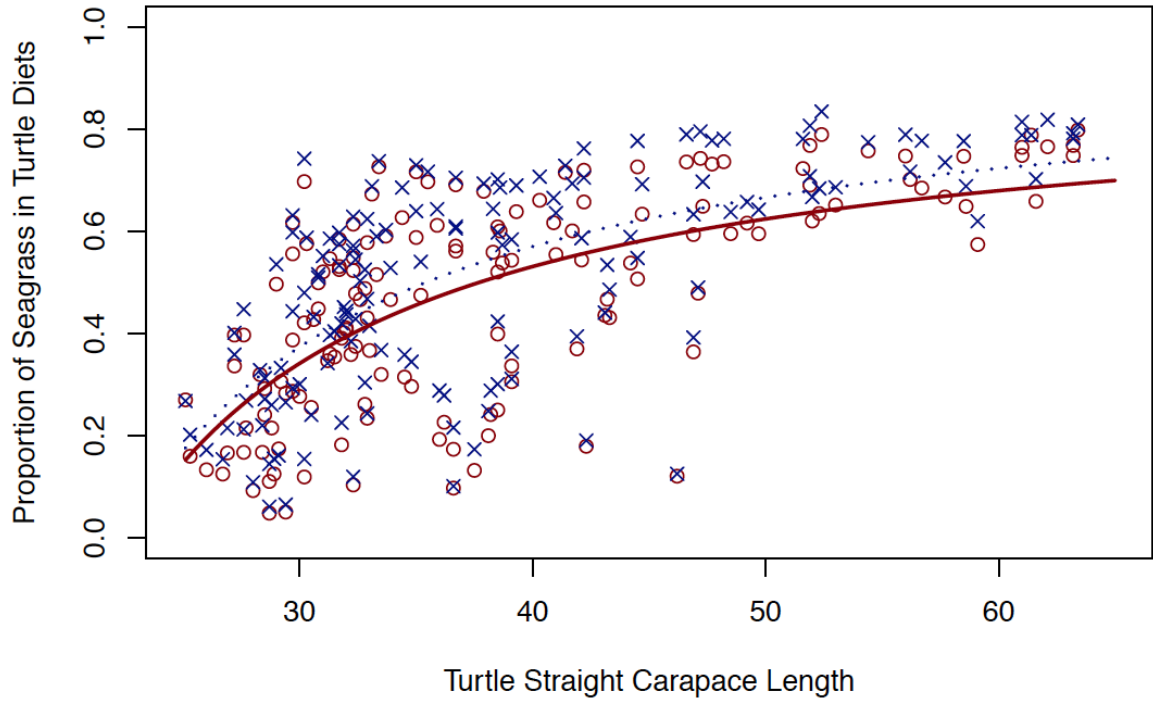
Figure S3. Comparison of Model Outputs for Site-Specific Seagrass Values and Platform-Average Seagrass Values. Outputs based on site-specific seagrass values are shown in red circles with the corresponding non-linear regression shown as a solid red line. Outputs based on Platform-average seagrass values are shown as blue X's with the corresponding non-linear regression shown as a dashed blue line.

SUPPLEMENTAL TABLES

Table S1. $\delta^{15}N$ and $\delta^{13}C$ of potential green turtle food organisms from the Bermuda Platform, summarized by subgroup and the Food Groups used in the diet mixing models. SD = Standard Deviation.

Food Group	Sub group	Lowest Identified Taxon	n	$\delta^{15}N$ (‰)				$\delta^{13}C$ (‰)			
				Min	Max	Mean	SD	Min	Max	Mean	SD
Seagrass	Seagrass		455	-10.1	8.8	1.7	3.5	-12.9	-3.3	-7.4	1.9
		Halodule	96	-8.9	6.1	1.5	3.3	-12.4	-6.7	-9.7	1.1
		Halophila	75	-1.2	7.5	2.1	2.0	-12.9	-5.7	-8.4	1.4
		Syringodium	169	-7.7	8.8	1.2	4.0	-10.0	-3.3	-5.6	1.2
		Thalassia	115	-10.1	8.0	2.3	3.7	-9.9	-5.5	-7.4	0.9
Macroalgae			60	-2.3	9.0	3.7	2.1	-20.3	-8.3	-14.4	2.5
	Calcareous Green Algae		27	-2.3	5.6	3.6	2.0	-17.0	-10.2	-13.7	2.0
		Halimeda	13	0.1	5.3	3.0	1.9	-17.0	-14.1	-15.2	0.9
		Penicillus	5	-2.3	5.6	3.8	3.4	-15.0	-12.5	-13.5	0.9
		Udotea	9	3.1	5.2	4.3	0.8	-13.7	-10.2	-11.5	1.2
	Non-Calcareous Green Algae		17	1.7	9.0	5.1	2.2	-20.3	-8.3	-14.2	3.0
		Avrainvillea	1			1.7				-20.3	
		Caulerpa	11	3.3	9.0	4.8	1.5	-16.9	-8.3	-13.0	2.7
		Chaetomorpha	2	7.3	7.9	7.6	0.4	-18.7	-14.6	-16.7	2.9
		Cladophora	2	7.8	8.0	7.9	0.1	-15.0	-14.3	-14.6	0.5
		Dictyosphaeria	1			1.7				-14.9	
	Brown Algae		8	-0.1	3.5	1.9	1.3	-17.0	-11.4	-14.9	2.5
		Dictyota	3	1.0	3.5	2.4	1.3	-17.0	-16.3	-16.6	0.3
		Padina	3	2.0	3.4	2.6	0.8	-12.6	-11.4	-11.9	0.6
		Sargassum	2	-0.1	0.3	0.1	0.3	-17.0	-16.6	-16.8	0.3
	Red Algae		8	2.2	4.4	3.2	1.0	-18.8	-14.2	-16.7	1.6

		Amphiroa	2	4.0	4.4	4.2	0.3	-17.8	-17.8	-17.8	-17.8
		Laurencia	6	2.2	4.0	2.9	0.9	-18.8	-14.2	-16.4	1.7
Animals			52	2.0	10.6	5.4	2.1	-20.9	-15.3	-17.9	1.4
	Gelatinous Zooplankton		11	2.6	9.7	5.8	2.0	-20.5	-15.3	-18.0	1.8
		Aurelia	2	5.1	5.1	5.1	0.1	-18.1	-15.4	-16.7	1.9
		Cassiopea	5	2.6	9.7	5.6	3.0	-20.5	-15.3	-17.5	1.9
		Ctenophore	3	5.4	6.3	6.0	0.5	-20.2	-19.3	-19.7	0.5
		Unknown Jellyfish	1			7.1				-18.2	
	Gelatinous Benthic		3	3.2	4.9	4.3	1.0	-19.7	-17.4	-18.8	1.3
		Other Tunicates	2	3.2	4.9	4.1	1.2	-19.7	-17.4	-18.6	1.7
		Ascidians	1			4.8				-19.3	
	Sponges		20	2.0	10.6	6.9	1.9	-20.8	-15.8	-17.7	1.2
		Chondrilla	1			7.0				-17.8	
		Unknown Sponge	19	2.0	10.6	6.9	1.9	-20.8	-15.8	-17.7	1.2
	Gorgonians and Bryozoans		14	2.3	5.3	3.7	1.0	-20.9	-15.6	-17.8	1.5
		Gorgonian (Sea Whip)	12	2.3	5.3	3.6	1.0	-19.3	-15.6	-17.6	1.2
		Gorgonia (Sea Fan)	1			5.1				-15.9	
		Wiry Bryozoan	1			3.4				-20.9	
	Crustaceans		4	2.7	4.4	3.5	0.7	-18.7	-10.3	-13.1	3.8
		Lobster	1			4.4				-17.5	
		Sargassum Crab	1			8.0				-18.2	
		Sargassum Shrimp	1			2.9				-16.8	
		Unknown Crab	1			2.7				-18.7	

Table S2. Raw data from the collection of green turtles from the Bermuda Platform. Stable isotope values are from epidermal tissue.

				2012				2013			
Primary Tag	Left tag	Right tag	Pit tag	Location	SCL	δ15N	δ13C	Location	SCL	δ15N	δ13C
MB1050	MB1050	MM919	65629026	Chub Heads	59.7	6.29	-7.83				
M6080	M6080	M6081	65770841	Chub Heads	37.5	8.21	-14.93				
			65770858	Pilchard Bay	26.7	8.57	-15.24				
			65624372	Pilchard Bay	26.0	9.73	-14.90				
			65778268	Pilchard Bay	26.9	9.94	-14.26				
			65636785	Pilchard Bay	28.9	8.87	-15.20				
			65622033	Pilchard Bay	31.3	9.39	-11.49				
			65625566	Pilchard Bay	32.0	9.72	-10.87				
			65630769	Pilchard Bay	32.9	9.89	-10.58				
M6082	M6082	M6083	65773532	Pilchard Bay	36.7	9.82	-8.59				
M6084	M6084	M6085	65782123	Pilchard Bay	38.1	9.80	-13.77				
M6068	M6086	M6087	65781612	Pilchard Bay	36.0	12.56	-13.87				
M6088	M6088	M6089	65770033	Pilchard Bay	39.1	10.65	-9.26				
M6090	M6090	M6091	65622376	Pilchard Bay	44.5	10.08	-9.54				
MB1051	MB1051	M6092	65628022	Pilchard Bay	46.9	11.19	-8.85				
MB1052	MB1052	MM920	65630008	Pilchard Bay	53.0	9.20	-7.37				
			65775065	Frank's Bay	32.9	8.45	-7.58				
M6093	M6093	none	65781020	Frank's Bay	42.2	8.12	-5.60				
F7260	F7260	F7261	65781043	Stock's Harbour	32.3	6.02	-8.23				
	M6094	M6095	18269017	Bailey's Bay	35.5	8.75	-6.38	Bailey's Bay	37.7	9.56	-5.58

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	F7262	F7061	38855032	Bailey's Bay	27.2	8.20	-10.74	Bailey's Bay	29.7	8.78	-7.82
	F7263	F7264	65624778	Bailey's Bay	30.6	8.17	-10.24	Bailey's Bay	32.4	7.78	-8.52
	F7265	F7267	65628376	Bailey's Bay	30.5	9.35	-13.21				
F7357	F7052	F7057	38822276	Bailey's Bay	28.7	4.56	-17.95	Bailey's Bay	30.6	8.24	-13.27
	F7177	F7178	39075028	Bailey's Bay	32.3	8.38	-8.38				
	F7268	F7269	65638811	Bailey's Bay	25.1	8.32	-12.84				
	F7270	F7271	65628274	Bailey's Bay	29.1	9.37	-14.44				
	F7272	F7273	65777022	Bailey's Bay	31.2	9.10	-11.74				
	F7274	F7275	65638867	Bailey's Bay	29.4	9.65	-12.87				
	M6301	M6302	18267589	Walsingham	43.3	8.13	-9.39				
	M6096	M6097	18299804	Walsingham	38.6	7.64	-6.66				
	M6099	M6100	39093302	Walsingham	35.2	8.21	-8.66				
	M6098	M5451	97814101	Walsingham	41.0	8.15	-7.35				
	F7278	F7279	65778868	Walsingham	27.6	8.00	-13.75				
	F7280	F7281	65626873	Walsingham	27.6	8.02	-9.99				
	M6303	M6304	65772329	Walsingham	31.9	8.24	-9.92	Grotto Bay	34.9	7.53	-7.71
	M6305	M6306	65778342	Walsingham	34.5	8.47	-11.44				
	M6307	M6308	65778072	Walsingham	37.5	7.91	-14.41				
	M6309	M6310	65782567	Walsingham	32.8	8.60	-12.29				
	M6311	M6312	65772350	Walsingham	33.9	7.86	-8.75				
	M6313	M6314	65622373	Walsingham	33.0	8.05	-10.52				
	M6315	M5107	39101380	Blue Hole	56.7	7.55	-5.32				
	F7282	F7283	65780092	Blue Hole	30.2	8.53	-14.65	Blue Hole	31.2	8.59	-12.87
	F7284	F7285	65778575	Blue Hole	29.4	7.84	-17.33				
	M6316	M6317	65629048	Blue Hole	34.8	8.33	-11.65				
	M6318	M6319	65781000	Blue Hole	31.8	8.75	-13.47				

	M4836	M4837	98123588	Ft. St. Catherine's	38.7	7.22	-8.15				
	MM980	MM979	39102571	Ft. St. Catherine's	68.2	6.43	-8.14				
	F7286	F7287	65776792	Ft. St. Catherine's	32.0	7.05	-10.18	Ft St Catherine's	32.5	6.52	-7.52
M4834	M6320	M6321	99087517	Ft. St. Catherine's	49.2	6.86	-7.02				
	M6322	M6323	65777532	Ft. St. Catherine's	41.9	7.98	-10.85				
	M4957	M4958	18294291	Ft. St. Catherine's	58.6	6.90	-6.59				
	M5563	M5564	65782268	Ft. St. Catherine's	38.5	7.33	-10.36				
	F6841	F6842	18282048	Vixen	30.8	4.99	-9.42				
	F7258	F7259	65783279	Vixen	31.7	3.73	-8.49				
	F7290	F7291	65833883	Vixen	30.3	4.14	-8.47				
	F7292	F7293	65769629	Vixen	29.7	2.78	-8.38				
	M6324	M6325	65769105	Vixen	35.2						
	M6326	M6327	65778059	Vixen	33.1	3.00	-7.39				
	M6328	M6329	65623092	Vixen	32.9	7.68	-13.30				
	M6330	M6331	65623880	Vixen	33.4	2.70	-6.64				
	F7294	F7295	65782892	Tudor Hill	29.7	7.51	-12.55				
	F7296	F7297	65624276	Tudor Hill	31.7	7.28	-8.70				
	F7298	F7299	65777308	Tudor Hill	28.3	6.88	-12.07				
	M6332	M6333	65772066	Tudor Hill	43.1	6.73	-10.13				
	M6334	M6335	65623855	Tudor Hill	39.1	7.71	-12.23				
	M6336	M6337	65624376	Tudor Hill	36.6	7.92	-15.92				
	M3895	M6338	54879064	Wreck Hill	63.2	6.21	-5.19				
M6339	M6339	M6340	54876636	Wreck Hill	56.2	6.85	-6.22				
M6341	M6341	M6342	54879374	Wreck Hill	42.3	7.37	-14.21				
	M6343	M6344	54880820	Wreck Hill	51.9	5.66	-6.40	Wreck Hill	54.0	6.66	-6.22
	M6345	M6346	54872102	Wreck Hill	47.1	6.57	-9.37				

	MM938	MM939	54876012	Wreck Hill	63.4	5.47	-4.78				
	M6347	M6348	99077787	Annie's Bay	39.3	5.60	-6.66				
	M6350	M6351	107568281	Annie's Bay	36.7	5.58	-7.82	Annie's Bay	39.3	6.11	-7.22
	M6352	M6353	18311539	Annie's Bay	29.7	5.22	-7.99				
	F7133	F7134	39085531	Annie's Bay	32.6	6.63	-9.16				
	M6354	M6355	107319863	Annie's Bay	40.9	4.93	-7.13				
	F7225	F7224	65622329	Annie's Bay	28.5	9.44	-12.77				
	M5009	M5010	107338092	Annie's Bay	42.1	6.44	-7.97				
M5500	M6356	M6357	39096633	Annie's Bay	39.1	8.06	-11.32				
	MB1060	M6349	66823372	Annie's Bay	59.1	5.65	-7.59				
F7300	F7300	F7303	54875877	Annie's Bay	29.0	6.39	-8.71				
M6358	M6358	M6359	54879544	Annie's Bay	46.9	6.85	-10.95				
M6360	M6360	M6361	54873028	Annie's Bay	52.0	6.27	-6.87				
M6362	M6362	M6363	54875865	Annie's Bay	32.3	10.06	-15.15				
M6364	M6364	M6365	54868833	Annie's Bay	31.8	6.99	-10.46	Annie's Bay	34.6	7.18	-9.03
M6366	M6366	M6366	54882034	Annie's Bay	32.8	6.47	-8.83				
	F7304	F7305	54868513	Blue Hole	30.8	5.61	-9.15				
	F7307	F7308	65628518	Blue Hole		8.76	-11.95				
	M6368	M6369	65768093	Blue Hole	43.2	7.48	-8.66				
	M6370	M6371	65771637	Blue Hole	41.7	7.49	-6.57	Blue Hole	44.5	7.38	-6.57
	M6372	M6373	65769864	Blue Hole	38.5	6.90	-6.43				
	M6374	M6375	65776119	Blue Hole	38.5	7.95	-12.37				
	M6395	M6396	65777332	Blue Hole	33.3	6.58	-7.91				
	M6397	M6398	54870006	Blue Hole	36.6	8.73	-13.61				
	M6399	M6400	54879297	Blue Hole	33.5	8.82	-11.32				
	M6401	M6402	54880270	Blue Hole	32.4	8.64	-10.35				

M6403	M6404	54878030	Blue Hole	38.2	8.93	-12.55				
F7309	F7310	65771279	Blue Hole	28.8	8.69	-12.95				
F7311	F7312	65625062	Blue Hole	31.5	8.00	-10.68				
F7313	F7314	65622016	Blue Hole	28.4	7.44	-13.70				
F7815	F7316	65776303	Blue Hole	29.7	6.77	-10.09				
F7317	F7318	65624894	Blue Hole	28.7	8.63	-14.83				
F7319	F7320	65632831	Blue Hole	27.7	7.55	-12.92				
F7321	F7322	65780552	Blue Hole	25.3	8.59	-13.84				
F7323	F7324	65769817	Blue Hole	30.2	7.74	-9.46				
F7325	F7326	65623004	Blue Hole		7.18	-8.11				
M6405	M6406	65782060	Blue Hole	32.4	6.79	-8.50	Blue Hole	35.1	7.45	-7.60
M6407	M6408	65768830	Blue Hole	38.3	6.64	-7.19				
M6409	M6410	65624010	Blue Hole	38.5	7.23	-7.78				
M6411	M6412	65623299	Blue Hole	36.2	7.85	-12.75				
F7329	F7330	65633830	Cow ground	31.0	5.16	-8.71				
F7331	F7332	39098614	Cow ground	27.2	6.65	-11.58				
F7333	F7334	38855361	Cow ground	28.5	6.61	-12.36				
M6413	M6414	65629769	Cow ground	35.9	5.80	-7.25				
M6066	M6067	38841527	Somerset Long Bay	30.2	6.00	-5.85				
MB975	MB5053	18260288	Somerset Long Bay	48.5	2.93	-8.24				
F7335	F7336	39090296	Somerset Long Bay	30.0	9.01	-12.34				
F7337	F7338	39097865	Somerset Long Bay	31.3	6.03	-8.02				
F7339	F7340	39092293	Somerset Long Bay	29.2	7.21	-11.93				
M6415	M6416	39099627	Somerset Long Bay	51.9	5.48	-4.81				
M6417	M6418	38821547	Somerset Long Bay	42.2	5.67	-6.45				
M6419	M6420	39101096	Somerset Long Bay	48.2	5.98	-5.25				

M6421	M6422	39091794	Somerset Long Bay	47.3	6.52	-6.50
M6423	M6424	39102270	Somerset Long Bay	40.3	6.56	-6.31
M6425	M6426	39032525	Somerset Long Bay	44.5	6.77	-5.37
M6427	M6428	38837358	Somerset Long Bay	31.7	8.58	-8.25
M6429	M6430	39102017	Somerset Long Bay	32.2	6.92	-11.06
M6431	M6432	39099338	Somerset Long Bay	47.7	6.03	-5.30
M6433	M6434	39106310	Somerset Long Bay	56.0	6.73	-5.05
MM940	MM941	39091798	Somerset Long Bay	63.2	6.88	-5.03
MM942	MM943	38833372	Somerset Long Bay	61.0	5.47	-5.10
MM944	MM945	38852817	Somerset Long Bay	61.4	7.28	-4.32
M6435	M6436	39102338	Vixen	37.9	4.05	-6.93
M6437	M6438	39103529	Vixen	41.4	3.66	-6.52
M6439	M6440	39094889	Vixen	36.7	4.62	-6.63
M6441	M6442	39101835	Vixen	35.0	2.39	-6.94
M6443	M6444	39091098	Vixen	33.7	6.61	-7.76
M6445	M6446	16027536	Vixen	32.3	2.71	-8.48
M6447	M6448	15895772	Ferry Reach	58.5	5.28	-5.36
M4938	M4939	18313889	Grotto bay	44.2	7.11	-7.90
MB902	MB946	98611307	Grotto bay	57.7	7.90	-6.04
F7341	F7342	15891844	Grotto bay	28.0	8.63	-15.61
M6449	M6450	15881280	Grotto bay	52.4	6.53	-4.10
M6451	M6452	15894892	Grotto bay	47.2	5.66	-5.01
M6453	M6453	16011375	Grotto bay	51.6	6.54	-5.25
M6455	M6456	16007787	Grotto bay	46.6	6.55	-5.08
M6457	M6458	16032589	Grotto bay	34.4	5.91	-6.67
M6459	M6460	16033862	Grotto bay	35.0	6.77	-7.20

	MM947	MM948	15883039	Grotto bay	68.9	7.32	-4.65				
	MM949	MM950	15872078	Grotto bay	62.1	7.18	-4.50				
	M6378	M5597	65627864	Long Bay	55.4						
	M6376	M6377	54873364	Long Bay	47.0						
	M6379	M6380	54875848	Long Bay	44.4						
	M6381	M6382	54869820	Long Bay	32.2						
	M6383	M6384	54879337	Long Bay	46.7						
	M6385	M6386	54873262	Long Bay	34.0						
	M6387	M6388	54883001	Long Bay	42.7						
	M6389	M6390	65769522	Long Bay	39.0						
	M6391	M6392	54867597	Long Bay	43.1						
	M6393	M6394	54879266	Long Bay	47.1						
M3918	MM921	MM922	73595069					Bailey's Bay	68.7	6.66	-5.71
M6467	M6467	M6468	73771585					Bailey's bay	46.2	8.04	-15.33
M6491	M6491	M6492	73621046					Baileys Bay	54.4	8.93	-5.51
MM955	MM955	MM956	73774857					Grotto Bay	61.0	7.71	-4.60
M6499	M6499	M6500	73607793					Grotto Bay	44.7	6.47	-6.56
M3981	MM960	MM961	99097365					Long Bay	64.6		
M6556	M6556	M6557	73779635					Annie's Bay	52.3	6.38	-6.67
M6558	M6558	M6559	72606768					Annie's Bay	49.7	6.72	-7.20
R2670	MM966	MM967	24268341					Ft. St Catherine's	61.6	6.42	-6.45

Table S3. Details of 5 of the candidate models fit to the relationship between the fraction of seagrasses in the diet (S_i) and Straight Carapace Length (SCL_i) of green sea turtles (*Chelonia mydas*) on the Bermuda Platform. Akaike's information criterion (AIC) for the fit of each model to the data is provided.

Function	Equation	AIC value
Linear	$S_i = mx + b$ $S_i = 0.012256*SCL_i + 0.007319$	-125.3634
Michaelis-Menten with y intercept	$S_i = S_0 + S_{max}*(SCL_\Delta/(SCL_\Delta + SCL_K))$ $S_i = 0.1840 + 0.7982*(SCL_\Delta/ SCL_\Delta + 20.0190)$	-126.1088
Michaelis-Menten	$S_i = S_{max} * (SCL_\Delta/(SCL_\Delta + SCL_K))$ $S_i = 0.788 *(SCL_\Delta/(SCL_\Delta + 6.655)$	-127.2286
Rational Function	$S_i = 1 + S_{Max} – (SCL_i/(SCL_i-V))$ $S_i = 1 + 0.897 – (SCL_i/(SCL_i-10.709))$	-132.7758
Rational Function without overgrazed site	$S_i = 1 + S_{Max} – (SCL_i/(SCL_i-V))$ $S_i = 1 + 0.9048 – (SCL_i/(SCL_i-10.7904))$	-136.3316