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

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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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Michael R. Heithaus

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James W. Fourquarean, Major Professor

Date of Defense: March 27, 2017

The thesis of Claire Margaret Burgett is approved.

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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

We thank AB Meylan, PA Meylan, Jennifer Grey, and the rest of the Bermuda Turtle Project, for allowing us to join them in their turtle capturing trips and sharing data with us. Rachel Decker and other members of FIU’s Seagrass Ecosystems Research Laboratory for assistance processing samples in the laboratory. The Department of Conservation Services (now the Department of Environment and Natural Resources) of the Government of Bermuda provided logistics and financial support for this work. 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.
ABSTRACT OF THE THESIS

GREEN SEA TURTLES (CHELONIA MYDAS) IN BERMUDA EXHIBIT AN ONTOGENETIC DIET SHIFT DESPITE OVEREXPLOITATION OF RESOURCES IN THEIR DEVELOPMENTAL HABITAT

by

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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.
# TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>CHAPTER</th>
</tr>
</thead>
<tbody>
<tr>
<td>I.</td>
</tr>
<tr>
<td>INTRODUCTION .................................................................</td>
</tr>
</tbody>
</table>

| II. MATERIALS AND METHODS ........................................................ | 4 |
|---------------------------------------------|-----------------
| A. FOOD WEB SAMPLE COLLECTION ....................... | 4 |
| B. TURTLE TISSUE COLLECTION .......................... | 5 |
| C. STABLE ISOTOPE ANALYSIS ......................... | 6 |
| D. STATISTICAL ANALYSIS ....................................... | 7 |
| E. DIET MIXING MODELS ........................................... | 7 |

| III. RESULTS .............................................................. | 8 |
|---------------------------------------------|-----------------
| A. POTENTIAL TURTLE FOOD SOURCES ............... | 8 |
| B. SIZE DISTRIBUTION AND STABLE ISOTOPE RATIOS OF CAPTURED TURTLES | 10 |
| C. DIET MIXING MODELS ........................................... | 15 |

| IV. DISCUSSION ........................................................... | 20 |

| V. DATA ACCESSIBILITY .................................................. | 26 |

| REFERENCES ............................................................. | 27 |

| SUPPLEMENTAL FIGURES .................................................. | 32 |

| SUPPLEMENTAL TABLES .................................................... | 35 |
# LIST OF FIGURES

<table>
<thead>
<tr>
<th>FIGURE</th>
<th>PAGE</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Capture Locations of Green Turtles on the Bermuda Platform</td>
<td>5</td>
</tr>
<tr>
<td>2. Isotope Ratios for All Groups</td>
<td>10</td>
</tr>
<tr>
<td>3. Size Distributions of Green Turtles Captured in 2012</td>
<td>11</td>
</tr>
<tr>
<td>4. Turtle Stable Isotope Ratios in Relation to Turtle Size</td>
<td>12</td>
</tr>
<tr>
<td>5. Variation in Turtle Stable Isotope Ratios as a Function of Size Class</td>
<td>13</td>
</tr>
<tr>
<td>6. Isotope Ratios in Relation to Size for Recaptured Turtles</td>
<td>14</td>
</tr>
<tr>
<td>7. Diet Composition Across Green Turtle Size Classes</td>
<td>16</td>
</tr>
<tr>
<td>8. Relationship Between Green Turtle Size and Seagrass Consumption</td>
<td>18</td>
</tr>
<tr>
<td>9. Relationship Between Green Turtle Size and Seagrass Consumption by Site</td>
<td>19</td>
</tr>
<tr>
<td>S1. Diet Composition of Green Turtles (<em>Chelonia mydas</em>) for Each Capture Location</td>
<td>32</td>
</tr>
<tr>
<td>S2. Relationship Between Green Turtle Size and Seagrass Consumption with Multiple Candidate Models</td>
<td>33</td>
</tr>
<tr>
<td>S3. Comparison of Model Outputs Using Site-Specific Seagrass Values and Platform-Average Seagrass Values</td>
<td>34</td>
</tr>
</tbody>
</table>
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).
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; Fourquarean 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 (Fourquarean 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 (Fourquarean 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 (Fourquarean 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 (Fourquean *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 δ13C.
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); δ¹⁵N = 2.80 ± 0.11‰, δ¹³C = 0.17 ± 0.03‰ and (Vander Zanden et al. 2013); δ¹⁵N = 3.77 ± 0.40‰, δ¹³C = 1.87 ± 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...
*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 δ¹⁵N, from -10.1 ‰ to 8.8 ‰. However, the δ¹⁵N of seagrasses from turtle capture sites had a much narrower range (\(\bar{X} = 2.9 \pm 1.6 \) ‰, with a range of 0.1 – 6.3 ‰) since the capture sites were generally close to shore where δ¹⁵N of seagrasses varied less than they do across the whole Platform. There were no significant relationships between seagrass δ¹⁵N and the δ¹⁵N 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).

<table>
<thead>
<tr>
<th></th>
<th>δ¹⁵N</th>
<th></th>
<th></th>
<th></th>
<th>δ¹³C</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>Min</td>
<td>Max</td>
<td>SD</td>
<td>Mean</td>
<td>Min</td>
<td>Max</td>
<td>SD</td>
</tr>
<tr>
<td>Turtles</td>
<td>7.2</td>
<td>2.4</td>
<td>12.6</td>
<td>1.7</td>
<td>-9.5</td>
<td>-17.9</td>
<td>-4.1</td>
<td>3.2</td>
</tr>
<tr>
<td>Animals</td>
<td>5.5</td>
<td>2.0</td>
<td>10.6</td>
<td>2.1</td>
<td>-17.9</td>
<td>-20.9</td>
<td>-15.3</td>
<td>1.4</td>
</tr>
<tr>
<td>Seagrass</td>
<td>1.7</td>
<td>-10.1</td>
<td>8.8</td>
<td>3.5</td>
<td>-7.4</td>
<td>-12.9</td>
<td>-3.3</td>
<td>1.9</td>
</tr>
<tr>
<td>Macroalgae</td>
<td>3.8</td>
<td>-2.3</td>
<td>9.0</td>
<td>2.1</td>
<td>-14.3</td>
<td>-20.3</td>
<td>-8.3</td>
<td>2.5</td>
</tr>
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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 δ¹⁵N of 7.3 ± 1.6 ‰ and average δ¹³C 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 δ¹³C with size was evident, no similar clear trend was evident in δ¹⁵N.
with length, but the scatter in $\delta^{15}\text{N}$ 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 $\delta^{13}\text{C}$ ($F=35.6, p<0.001$), but no significant differences in $\delta^{15}\text{N}$ ($F=1.6, p=0.173$).

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).
A. Straight carapace length in relation to change in δ^{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.
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 (Fourquarean 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 $S_i = 1 + S_{\text{Max}} - \left(SCL_i/(SCL_i-V)\right)$ where $S_i$ is the proportion of seagrass consumed for individual $i$, $S_{\text{Max}}$ 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 $S_i = 1 + 0.897 - \left(SCL_i/(SCL_i-10.709)\right)$, $R^2_{adj} = 0.40$. 
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 \( \delta^{15}N \) and \( \delta^{13}C \) 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; Fourquarean 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 (Fourquean 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
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 δ^{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 δ^{15}N fractionation of ca. 3 ‰ per trophic level (Wada 1980), and the measured δ^{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 δ^{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 δ^{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 (Fourquarean et al. 2005) and the Mediterranean Sea (Fourquarean et al. 2007) so they should be considered when designing stable isotope food web investigations.

Interestingly, we saw a clear pattern in the $\delta^{13}C$ 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 $\delta^{15}N$ 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 $\delta^{15}N$ with age is driven by more variability in $\delta^{15}N$ in the diets of early life stage omnivores than in the later life-stage, predominantly seagrass grazing, subadults. Our $\delta^{13}C$ -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 $\delta^{13}C$-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.
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 & Fourquarean 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/)
REFERENCES


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 *Turtle Straight Carapace Length*, 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.

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- Bailey's Bay | 68.7 | 6.66 | -5.71 |
- Bailey's Bay | 46.2 | 8.04 | -15.33 |
- Baileys Bay  | 54.4 | 8.93 | -5.51 |
- Grotto Bay   | 61.0 | 7.71 | -4.60 |
- Grotto Bay   | 44.7 | 6.47 | -6.56 |
- Long Bay     | 64.6 |      |       |
- Annie's Bay  | 52.3 | 6.38 | -6.67 |
- Annie's Bay  | 49.7 | 6.72 | -7.20 |
- 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.

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<th>Function</th>
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<th>AIC value</th>
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<td>Linear</td>
<td>$S_i = mx + b$</td>
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<td>$S_i = 0.012256*SCL_i + 0.007319$</td>
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<td>$S_i = S_0 + S_{max}*(SCL_i/(SCL_i + SCL_K))$</td>
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<td>$S_i = 0.1840 + 0.7982*(SCL_i/SCL_K + 20.0190)$</td>
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<td>$S_i = S_{max}*(SCL_i/(SCL_i + SCL_K))$</td>
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<td>$S_i = 0.788 *(SCL_i/(SCL_i + 6.655))$</td>
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<td>$S_i = 1 + S_{Max} - (SCL_i/(SCL_i - V))$</td>
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<td>$S_i = 1 + 0.897 - (SCL_i/(SCL_i - 10.709))$</td>
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<td>$S_i = 1 + S_{Max} - (SCL_i/(SCL_i - V))$</td>
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<td>without overgrazed site</td>
<td>$S_i = 1 + 0.9048 - (SCL_i/(SCL_i - 10.7904))$</td>
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