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# Foraging ecology and diet selection of juvenile green turtles in the Bahamas: insights from stable isotope analysis and prey mapping

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ABSTRACT: Species' foraging choices influence their somatic growth rates, age at maturity, and time spent in vulnerable early life stages. Thus, differences in population demographics are often attributed to variability either in diet type, quality, and/or quantity ingested. Knowledge of diet selection, though currently limited, can enhance our understanding of the roles of marine turtles in marine ecosystems and, at a finer scale, elucidate how nutrition and diet influence their growth and productivity. To investigate this relationship, we coupled stable isotope analysis with a diet preference index to provide insights into the selection and plasticity of juvenile green turtle *Chelonia mydas* diet. The study was conducted at 2 sites (Bonefish Hole and South Bimini) in Bimini, Bahamas, in 2016. Habitat surveys were conducted to gather habitat data and determine resource availability. A dichotomy in diet was found between the sites: at Bonefish Hole, turtles exhibited a more generalist omnivorous diet, selecting for sessile filter feeders and green algae, whereas turtles in South Bimini had a more specialist herbivorous diet, primarily consuming seagrasses and selecting for red algae, when available. The foraging dichotomy found in this study expands our understanding of the spatial differences in green turtle biology in the Bahamas and provides novel information for turtle foraging in Bimini. Knowledge about differences in intra-specific diet, with a focus on diet selection and potential drivers, can shed light on the factors that influence critical life history traits and ultimately inform species management.

KEY WORDS: Trophic ecology · MixSIAR · Bayesian ellipses · Carbon · Nitrogen · *Chelonia mydas* · Habitat use



## INTRODUCTION

Species' foraging choices and consequently their nutrient acquisition influence their somatic growth rates, which, in places of high nutrient availability, can expedite the attainment of sexual maturity and reduce the time spent in vulnerable early life stages (Stearns 1992, Guiñez & Castilla 2001, Harrison et al. 2011). Diet variability, whether in type, quality, and/or quantity, can often contribute to observed differences in species' growth rates (Pyke 1984, Bjorndal 1985, Kubis et al. 2009). Species' diets are often reported as a species-specific trait; however, individual- and/or population-level species variations in diet have been attributed to geographic location, age/size class, and food availability (Tinker et al. 2008, Arnould et al. 2011, Vélez-Rubio et al. 2016). An understanding of differences in intra-species diet, with a focus on diet selection and potential drivers, can elucidate the factors that influence critical life traits and ultimately inform species management (Fuentes et al. 2006, Kim et al. 2012, Kiszka et al. 2015).

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Several approaches have been used to infer marine turtle resource use and foraging ecology, including gut content analysis of stranded and deceased individuals (Meylan 1988, Seney & Musick 2007), fecal analysis (Bjorndal 1980), esophageal lavage (Fuentes et al. 2006), biotelemetry (Taquet et al. 2006), and video observation (Burkholder et al. 2012). Stable isotope analysis has also been used to infer the foraging ecology of marine turtles (Godley et al. 1998, Wallace et al. 2009, Vander Zanden et al. 2013). Stable isotope ratios of predator tissues, particularly for stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$), reflect that of the forage items consumed by individuals (Hobson & Clark 1992). When consumer and prey tissues are sampled, mixing models can be used to infer the contribution of sampled items to a population's diet (Parnell et al. 2013). Subject to variation between ecosystem types and the ecological processes present, carbon isotope ratios are reflective of the baseline resource values within the food web (Craig 1953, DeNiro & Epstein 1978), whereas nitrogen isotope ratios experience stepwise enrichment between trophic levels, reflecting the trophic position of consumers (DeNiro & Epstein 1981, Minagawa & Wada 1984, Post 2002).

Comparisons of environmental factors and trophic dynamics between prey and consumers have aided in answering vital ecological and trophic niche questions. Carbon and nitrogen reflect baseline environmental resources and trophic interactions between consumer and prey, respectively, and thus provide the fundamental axes to construct isotopic niche spaces (Newsome et al. 2007, Jackson et al. 2011). Not to be confused with a trophic niche, a species' isotopic niche provides fundamental ecological information, and has been considered a viable proxy for a species' ecological niche (Jackson et al. 2011). Further, measures of isotopic niche width can be obtained from variability in population isotopic space, a reflection of potential inter-population diet variability and foraging strategy (Bearhop et al. 2004). Populations with a large isotopic niche width may reflect a generalist diet where there is individual specialization and group clustering around specific forage items in the isospace (Bearhop et al. 2004, Bolnick et al. 2007), while populations with a small isotopic niche width may be employing a more specialist or generalist diet. Abundant utilization of a select few items by all individuals would result in a specialist population (Bearhop et al. 2004, DiBeneditto et al. 2017). Conversely, individuals may consistently forage on a wide variety of prey items, resulting in a generalist population (Vander Zanden et al. 2010). Implementation of these strategies may occur in response to a variety of factors, including, but not limited to, variability in forage item richness and/or competition (Bolnick et al. 2003).

Green turtles *Chelonia mydas* are considered the only herbivorous species of marine turtles, specializing on seagrasses and macroalgae in many areas, particularly in the western Atlantic and Caribbean Sea (Bjorndal 1997, DiBeneditto et al. 2017, Holloway-Adkins & Hanisak 2017). Recent studies, however, have suggested that there is more plasticity in green turtle diet, with demonstrated omnivory across several age classes in various geographic locations (Hatase et al. 2006, Amorocho & Reina 2007, Lemons et al. 2011). This variability in intra-species foraging ecology seems to be influenced by local and environmental factors (Cardona et al. 2009, González Carman et al. 2012, Santos et al. 2015).

Although recent studies have increased our understanding of the variability in green turtle diet, knowledge of diet selection is still limited. Information on diet selection, the comparison of prey use/consumption with availability of items to consumers (Johnson 1980), can enhance our understanding of the roles of marine turtles in marine ecosystems and, at a finer scale, inform how nutrition and diet influence growth and productivity of marine turtles (Bjorndal 1997, Kubis et al. 2009, Sampson et al. 2017). As a result, inferences into the selection of ideal nutrients and maximized somatic growth by green turtles can be made. However, only a few studies have explored the diet selection of green turtles, warranting further research into this topic (Fuentes et al. 2006, López-Mendilaharsu et al. 2008, Sampson et al. 2017).

Here, we coupled stable isotope analysis with a diet preference index (Johnson 1980) to provide further insights into the diet selection and foraging plasticity of juvenile green turtles. Our goal was to explore whether turtles at 2 foraging sites within Bimini present similar foraging ecology and diet selection across both sites. This research provides a foundation for further studies in the Bahamas and provides baseline data to explore how foraging ecology influences key life traits at each site.

## MATERIALS AND METHODS

### Study site

This study was conducted in Bimini, Bahamas (Fig. 1). Bimini (25° 44′ 11.36″ N, 79° 16′ 53.98″ W) is the western-most island in the Bahamas chain and is

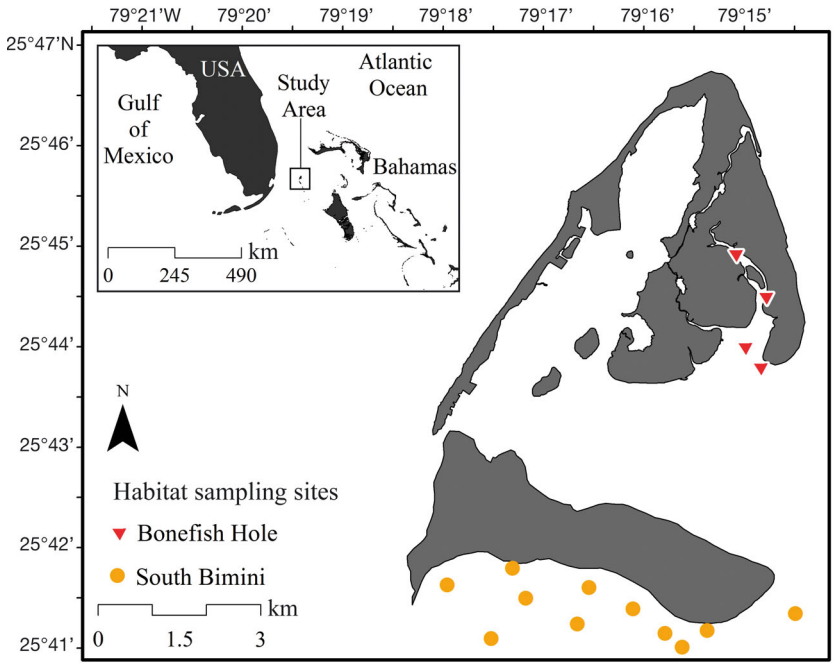


Fig. 1. Bimini, Bahamas, showing the habitat sampling sites surveyed at Bonefish Hole and South Bimini in July 2016

located on the Great Bahama Bank, approximately 86 km east of Miami, Florida, USA. The western edge of the 2-island chain is directly adjacent to the eastern edge of the Gulf Stream. Bimini is comprised of a northern and a southern island, separated by a 0.15 km wide channel on the western side of the chain. All sides of the islands are mangrove-fringed, except for the western sides which are white sand beaches (Jennings et al. 2012, Gledhill et al. 2015). Surveys and captures of marine turtles were conducted at 2 locations: South Bimini, an open coastal seagrass bed, approximately 0.5 km south of the island; and Bonefish Hole, a mangrove tidal estuary located on the north island, approximately 0.22 km$^2$ and on average 1.5 m in depth (Fig. 1). Dense seagrass beds, dominated by *Thalassia testudinum* and *Halodule wrightii*, with sparse patches of sand/silt bottoms can be found at each site, providing foraging grounds for green turtles.

### Turtle capture and sampling

Vessel transects and marine turtle captures were conducted during 2 sampling trips in 2016: June (Bonefish Hole, 2 d; South Bimini, 3 d) and July (Bonefish hole, 4 d; South Bimini, 5 d). Transects and turtle captures were conducted on either a 17 ft (~5.2 m) Sundance skiff with a 50 HP outboard motor or on a 20 ft (~6.1 m) Sundance center-console vessel with a 115 HP outboard motor. Turtles were captured using the 'rodeo' technique (Limpus & Walter 1980, Fuentes et al. 2006, Hazel et al. 2013). Upon capture, each turtle was brought to the boat and body measurements were taken, including straight and curved carapace lengths (±0.1 cm; SCL and CCL, respectively), following protocols described by Balazs (1999). Body weight (W, ±0.1 kg) was obtained using a hanging balance (Pesola, PHS100). Body condition index (BCI = W/SCL$^3$) was calculated to evaluate the size versus weight relationship of each turtle (Bjorndal et al. 2000). Each individual turtle was tagged with 2 Inconel flipper tags, one on the trailing edge of each front flipper (National Band and Tag Company, Style 681), and a passive integrated transponder was inserted sub-dermally in the front left flipper (PIT tag, Biomark, GPT12; Balazs 1999). Captured turtles were also checked for the presence of fibropapillomatosis (FP), which is a herpes virus characterized by the growth of external and internal tumors (Smith & Coates 1938, Landsberg et al. 1999). We assigned a total tumor count and Balazs tumor score (1: light, 2: moderate, 3: heavy) for all turtles on which tumors were observed (Work & Balazs 1999). Epidermis (i.e. skin) samples were collected from the dorsal surface of the neck using a sterile razor blade (Lemons et al. 2011). This technique allowed for collection of epidermis only and no underlying connective tissue (Lemons et al. 2011). Epidermis samples were then placed in a vial with dry salt for preservation and stored at room temperature. Salt has no effect on isotopic values of tissues and was most feasible, logistically, for international transportation (Arrington & Winemiller 2002). Differences in SCL, CCL, weight, and BCI between the study sites were explored using a Welch's *t*-test. A Mann-Whitney *U*-test was then conducted to determine if there was a significant difference between CCL size class distributions at each site.

### Habitat characterization

Habitat surveys and forage item collection were conducted at both Bonefish Hole and South Bimini using the plot-based (quadrat) method. Fifteen sites (4 at Bonefish Hole and 11 at South Bimini; Fig. 1)

were selected from sites originally used by Hussey (2003) to characterize Bimini's habitat, ensuring spatial variability in habitat type was represented adequately in the current sampling. Upon reaching a site, 2 standard quadrats (1 $m^2$) were cast in opposite directions, for a total of 4 quadrats $site^{-1}$ (Fuentes et al. 2006). For each quadrat, forage percent coverage and epiphyte percent coverage were visually estimated while snorkeling. Potential green turtle forage items were collected at each sampling location and preserved in dry salt for transport. Forage item samples were labeled by sample number and site of collection and were later identified to species.

## Stable isotopes

### Sample preparation

All marine turtle epidermis and putative prey samples were prepared by first removing residual dry salt using a soft-bristled toothbrush. Each sample was then placed in a drying oven for 1 h at 60°C to ensure that all moisture was completely removed (Lemons et al. 2011, Levin & Currin 2012). Epidermis samples were then cut into smaller pieces and homogenized using a sterile scalpel blade. Forage items were homogenized using a mortar and pestle. All epidermis and forage samples were lipid-extracted, using an accelerated solvent extractor (Model 200, Dionex) with petroleum ether (3 cycles of 5 min of heating followed by 5 min of static purging) at the Paleoclimatology, Paleoceanography and Biogeochemistry Laboratory at the University of South Florida College of Marine Science (Reich & Seminoff 2010, Vander Zanden et al. 2013).

### Stable isotope analysis

Samples for stable isotope analysis were measured using a Mettler Toledo micro balance and placed into Costech 3.5 × 5 mm tin cups. Roughly 0.5–0.7 mg of epidermis and 1.5 mg of forage items were placed into tin cups. Samples were then converted to $N_2$ and $CO_2$ via a Carlo-Erba NA2500 Series 2 Elemental Analyzer (Thermoquest Italia) and analyzed in a continuous flow isotope ratio mass spectrometer (Delta PlusXP, Thermofinnigan) at the University of South Florida. Sample ratios were expressed in conventional notation as parts per thousand (‰). The equation used to determine isotopic ratios is:

$$\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000 \quad (1)$$

where $X$ is $^{15}N$ or $^{13}C$, and $R$ is the ratio $^{15}N$:$^{14}N$ or $^{13}C$:$^{12}C$. Standards for $^{15}N$ and $^{13}C$ were atmospheric nitrogen and Vienna Pee Dee Belemnite, respectively. Working standards (NIST 1577B bovine liver for animal tissues and NIST 1579a spinach leaves for plant material) were inserted into the analytical process roughly every 6 samples. Analytical precision, expressed in standard deviation, was obtained from replicate measurements of the working standards. Animal tissue precision (n = 19) was ±0.17‰ and ±0.14‰ for $\delta^{15}N$ and $\delta^{13}C$, respectively. Plant material precision (n = 25) was ±0.21‰ and ±0.07‰ for $^{15}N$ and $^{13}C$, respectively.

## Statistical analysis

The $\delta^{13}C$ and $\delta^{15}N$ values of marine turtle epidermis were compared between sampling locations with a Welch's *t*-test, due to unequal sample sizes between sites. Additionally, a nested ANOVA with a Satterthwaite approximation was used to determine whether there was a significant difference in forage item values between Bonefish Hole and South Bimini. The relationship and correlation between turtle CCL, $\delta^{13}C$, and $\delta^{15}N$ was determined using Pearson's correlation test. Additionally, the relationship of FP tumor counts to $\delta^{15}N$ values was also analyzed using Pearson's correlation test. To further identify potential differences at each location, MixSIAR, a Bayesian mixing model package for R (Stock & Semmens 2016), was used to model the diet composition of marine turtles at each foraging site. Before the MixSIAR analysis was conducted, forage items were grouped by similar life history traits. All 3 species of seagrasses (*Thalassia testudinum, Halodule wrightii, Syringodium filiforme*) were grouped together, as were all species of red algae (*Laurencia intricata*, *Hypnea* sp., and *Amphiroa* sp.) and green algae (*Batophora oerstedii*, *Halimeda lacrimosa*, *H. incrassata*, *H. tuna*, *H. monile*, *Rhipocephalus phoenix*, *Penicillus capitatus*, *P. dumetosus*, *Caulerpa prolifera*, *C. cupressoides*, *Udotea flabellum*, *U. cyathiformis*, *Udotea* sp., *Acetabularia crenulata*, *Anadyomene* sp., *Chaetomorpha linum*, *Avrainvillea longicaulis*, and coralline green algae). Non-plant species were grouped into sessile filter feeders (Demospongiae sp. and tunicates). Once analyzed with MixSIAR, forage item contribution distributions, via posterior density plots, were determined for Bonefish Hole and South Bimini individually. Because of differing isotope incorporation rates by tissues, trophic enrichment factors previously established for green turtle epidermis (+0.17

for $\delta^{13}C$, +2.80 for $\delta^{15}N$; Seminoff et al. 2006) were used to account for discrimination during digestion of forage items by turtles in this study. Isotopic niche width, at each site, was then determined by calculating the convex hull total area (TA) and standard ellipse area (SEA) of epidermis isotope values using the Stable Isotope Bayesian Ellipses in R (SIBER; Jackson et al. 2011). TA and SEA were selected as valid measures of isotopic niche width, as they provide areal measures of the isospace occupied by consumers (Layman et al. 2007, Jackson et al. 2011).

### Diet selection

Dietary contribution at an individual level was determined with the MixSIAR package, as previously described. The relationship between use and availability of food items for Bonefish Hole and South Bimini was quantified using Johnson's (1980) selection index in the Prefer package (Pankratz 1995), ranking preferential selection of each group from most to least. This allowed for the exploration of whether specific forage groups were selected for (as per MixSIAR outputs) in proportion to the group's availability. Average difference in use and availability for individuals (Tbar) was calculated for each food group. Tbar values <0 indicate a forage item that was selected for, Tbar values between 0 and 1 mean forage items were selected equally to their availability, and values ≥1 are assigned to items that were not selected for. Statistical significance was established with the provided $F$ statistic (testing of $H_0$: all items were equally selected) and a critical value ($W$) for a Waller-Duncan multiple comparison procedure with $K$ = 100, which has been determined to be closely comparable to a significance level of p = 0.05 (Waller & Duncan 1969, Johnson 1980).

## RESULTS

### Turtle captures

Fifty-eight juvenile green turtles were captured (14 at Bonefish Hole and 44 at South Bimini) during 2 trips in 2016. Turtle sizes ranged from 28.6 to 63.9 cm SCL (Bonefish Hole: mean ± SD = 42.1 ± 6.3 cm; South Bimini: 46.0 ± 9.3 cm) and from 30.5 to 69.9 cm CCL (Bonefish Hole: 45.6 ± 6.5 cm; South Bimini: 49.7 ± 10.1 cm; Fig. 2). Mean SCL of Bimini turtles was compared to the mean SCL of known mature green turtle individuals within the Northwestern Atlantic population (96.7 ± 5.1 cm; Goshe et al. 2010), which indicated that all turtles captured during this study were juveniles. Weights ranged from 2.9 to 35.1 kg (Bonefish Hole: 10.3 ± 5.3 kg; South Bimini: 13.0 ± 7.6 kg). BCI ranged from 0.82 to 1.7 (Bonefish Hole: 1.25 ± 0.21; South Bimini: 1.28 ± 0.153). There was no significant difference between SCL and CCL, weight, and BCI between the 2 study sites (SCL: df = 32.74, $t$ = −1.8204, p = 0.0779; CCL: df = 34.506, $t$ = −1.7478, p = 0.08939; weight: df = 32.22, $t$ = −1.4257, p = 0.1636; BCI: df = 18.089, $t$ = −0.5876, p = 0.5641). The Mann-Whitney $U$-test showed no significant difference in CCL size class distribution between Bonefish Hole and South Bimini ($W$ = 247, p = 0.2716). Ten out of 14 turtles at Bonefish Hole were recorded with FP tumors (mean ± SD tumor count = 21.6 ± 19.8), whereas only 4 out of 44 in South Bimini exhibited FP (4.4 ± 5.0).

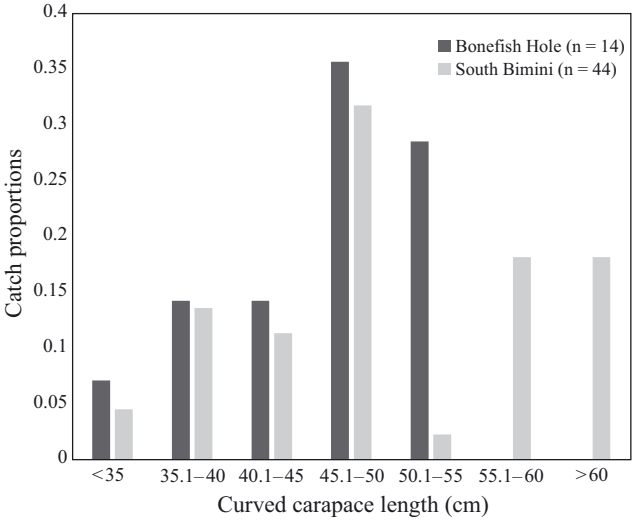


Fig. 2. Proportion of green turtles in different size classes captured at each foraging site during the June and July 2016 trips in Bimini, Bahamas

### Habitat characterization

The habitat at Bonefish Hole (Table A1 in the Appendix) was dominated by seagrass, particularly *Thalassia testudinum* (mean ± SD = 35.0 ± 23.5%) and *Halodule wrightii* (2.3 ± 5.7%). Red algae comprised the next highest occurring taxonomic group in Bonefish Hole, with *Laurencia intricata* being the most dominant species (14.5 ± 22.7%). Green algae had the third highest percent coverage in Bonefish Hole, where the predominant green algae species were *Batophora oerstedii* (6.0 ± 6.8%), *Penicillus* sp. (1.8 ± 1.9%), and coralline green algae (1.0 ± 2.1%).

Table 1. Niche width metrics and epidermis stable isotope values for juvenile green turtles at foraging grounds in the northwestern Atlantic. Turtles captured in Bimini in this study are highlighted in **bold**, and the remaining values were obtained from Vander Zanden et al. (2013). n: number of individuals, CCL: curved carapace length, TA: convex hull total area, SEA: Bayesian standard ellipse area

| Site | Country | n | CCL range (cm) | Year(s) sampled | TA | SEA | Mean ± SD (min, max) $\delta^{13}C$ (‰) | Mean ± SD (min, max) $\delta^{15}N$ (‰) |
|---|---|---|---|---|---|---|---|---|
| Inagua | Bahamas | 62 | 38.9–65.5 | 2008, 2009 | 18.5 | 4.0 | −6.4 ± 0.1 (−8.0, −4.5) | 1.7 ± 0.4 (−1.9, 5.2) |
| Long Island | Bahamas | 9 | 30.8–44.8 | 2010 | 7.5 | 6.1 | −9.4 ± 0.7 (−12.2, −6.4) | 5.2 ± 0.4 (3.5, 7.1) |
| **Bonefish Hole, Bimini** | **Bahamas** | **14** | **33.6–54.1** | **2016** | **22.1** | **10.3** | **−11.7 ± 3.2 (−16.3, −5.9)** | **4.1 ± 1.4 (1.4, 6.7)** |
| **South Bimini, Bimini** | **Bahamas** | **44** | **30.5–69.9** | **2016** | **15.8** | **3.5** | **−6.8 ± 1.5 (−13.2, −4.7)** | **2.1 ± 1.2 (0.3, 4.5)** |
| St. Joe Bay, Florida | USA | 20 | 31.7–60.5 | 2010 | 13.7 | 5.3 | −12.3 ± 0.5 (−15.7, −9.0) | 8.1 ± 0.4 (4.9, 11.1) |

Sessile filter feeders had the smallest percent coverage (0.3 ± 1.1%). In South Bimini, the most dominant group was seagrass, with *T. testudinum* being most prevalent (33.4 ± 29.2%) followed by *H. wrightii* (1.1 ± 2.1%). The second most prevalent group was green algae, which consisted of *Halimeda* sp. (4.6 ± 2.1%), *B. oerstedii* (3.8 ± 2.2%), *Penicillus* sp. (3.2 ± 2.3%), and *Udotea* sp. (1.5 ± 1.9%). Red algae, consisting predominantly of *L. intricata* (1.7 ± 4.2%), and sessile filter feeders (1.7 ± 3.0%) were the third most dominant groups in South Bimini (Table A1).

### Stable isotopes

Overall turtle epidermis values ranged from −16.3 to −4.7 (mean ± SD = −8.1 ± 2.9‰) for $\delta^{13}C$ and from 0.28 to 6.7 (2.6 ± 1.5‰) for $\delta^{15}N$. Bonefish Hole (Table 1, Fig. 3a) epidermis values were more depleted in $^{13}C$ ($\delta^{13}C$ = −11.7 ± 3.2‰) and more enriched in $^{15}N$ ($\delta^{15}N$ = 4.1 ± 1.4‰) when compared to South Bimini ($\delta^{13}C$ = −6.8 ± 1.5‰; $\delta^{15}N$ = 2.1 ± 1.2‰; Table 1, Fig. 3b). Welch's *t*-test run for $\delta^{13}C$ and $\delta^{15}N$ revealed a significant difference between South Bimini and Bonefish Hole epidermis values in carbon and nitrogen isotopes ($\delta^{13}C$: $t$ = −5.5854, df = 14.903, p = 0.00005; $\delta^{15}N$: $t$ = 5.0442, df = 19.642, p = 0.00006). Pearson's correlation revealed a significant correlation between green turtle CCL with $\delta^{13}C$ (r = 0.3697 and p = 0.0043, Fig. 4a) and $\delta^{15}N$ (r = −0.3582 and p = 0.0058, Fig. 4b) values. Further, a significant correlation (r = 0.4219 and p = 0.0009) between $\delta^{15}N$ values and FP tumor score was determined using Pearson's correlation.

Stable carbon and nitrogen analysis of forage items determined the range across Bonefish Hole and South Bimini to be −32.09 to −1.9 (mean ± SD = −9.7 ± 5.8‰) for $\delta^{13}C$ and −6.8 to 5.0 (0.5 ± 2.5‰) for $\delta^{15}N$, respectively. Bonefish Hole (Table 2, Fig. 3a) was determined to be more depleted in $\delta^{13}C$ (−12.3 ± 7.1‰) compared to South Bimini (−8.4 ± 4.5‰; Table 2, Fig. 3b). However, there was a relatively small difference in $\delta^{15}N$ between Bonefish Hole and South Bimini (0.4 ± 2.1‰ and 0.5 ± 2.7‰, respectively). Red algae were determined to be the most $^{13}C$-depleted forage item at both sites (Bonefish Hole: −21.1 ± 11.2‰ and South Bimini: −11.1 ± 5.9‰). Further, sessile filter feeders were the most $^{15}N$-enriched forage item group at Bonefish Hole (1.2 ± 1.2 ‰) and South Bimini (3.4 ± 2.3‰). A significant difference in $\delta^{13}C$ of forage items between Bonefish Hole and South

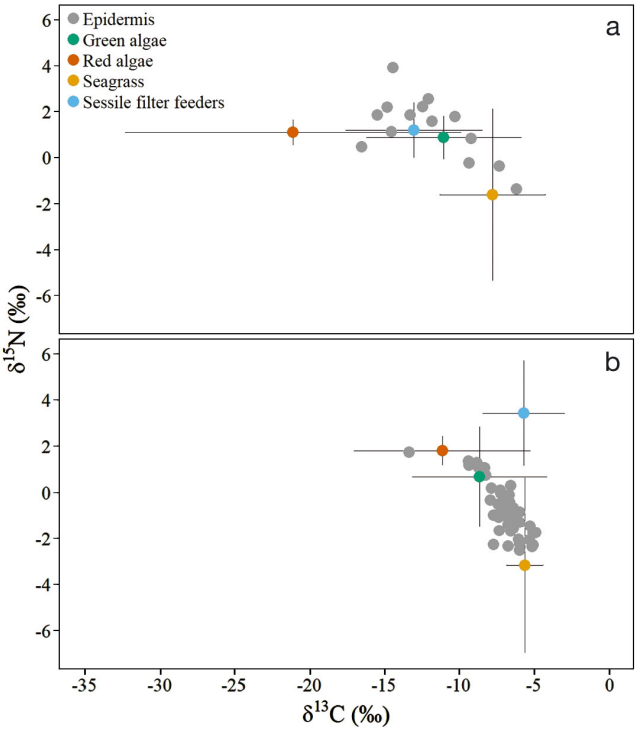


Fig. 3. Isospace plots indicating green turtle epidermis isotope values, adjusted for diet–epidermis discrimination values (grey circles), and the mean and standard deviation (as indicated by whiskers) of $\delta^{13}C$ and $\delta^{15}N$ for groups in (a) Bonefish Hole and (b) South Bimini

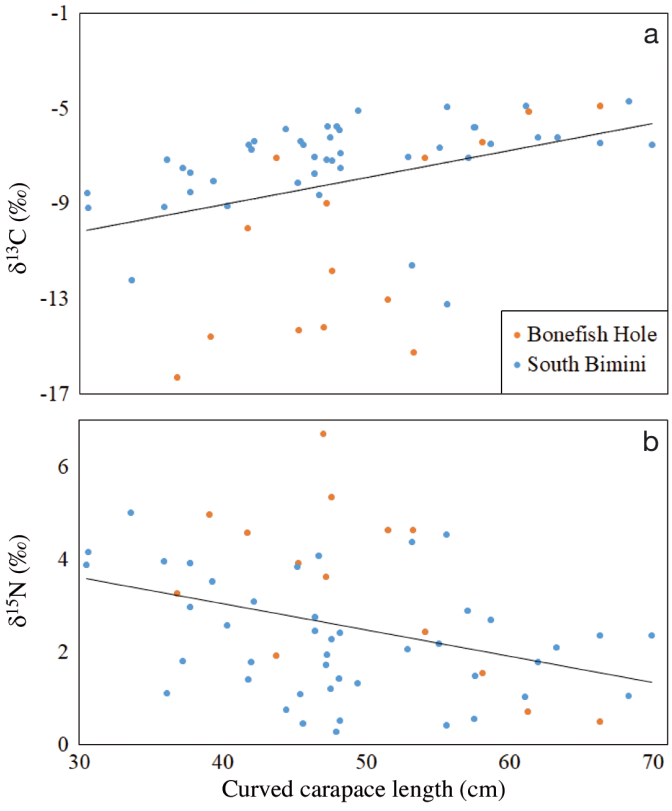


Fig. 4. Epidermis isotope values for (a) $\delta^{13}C$ and (b) $\delta^{15}N$ as a function of carapace length for green turtles in Bimini, Bahamas, suggesting recent recruitment to the neritic seagrass beds for smaller individuals. Regression lines reflect the relationship for all turtles sampled in this study

Bimini was observed (nested ANOVA, with the Satterthwaite approximation, $F_{1,47.97}$ = 6.78, p = 0.012). However, no significant difference was observed in $\delta^{15}N$ for forage items between each site ($F_{1,47.61}$ = 0.0022, p = 0.963).

## Green turtle diet

In Bonefish Hole, sessile filter feeders (mean ± SD = 29.9 ± 20.7%, 95% credible interval [CI] = 1.4–77.3%) contributed the largest proportion to the diet of turtles, followed closely by green algae (24.9 ± 19.1%, CI = 0.8–69.5%), red algae (24.3 ± 19.0%, CI = 0.7–68.9%), and seagrass (21.0 ± 17.6%, CI = 0.7–64.2%; Fig. 5a). Conversely, in South Bimini, seagrass contributed the most to the diet of turtles (54.4 ± 12.8%, CI = 25.2–77.2%). Red algae (20.5 ± 9.7%, CI = 3.0–40.4%), green algae (14.9 ± 9.7%, CI = 1.3–37.8%), and sessile filter feeders (10.1 ± 9.2%, CI = 0.5–35.2%) contributed noticeably less to the diet composition of turtles in South Bimini (Fig. 5b).

Table 2. Stable isotope values for forage item groups collected from quadrats at Bonefish Hole and South Bimini, Bahamas, in 2016. Values are mean ± SD (min, max; n)

| Forage item group | Bonefish Hole | | South Bimini | |
|---|---|---|---|---|
| | $\delta^{13}C$ (‰) | $\delta^{15}N$ (‰) | $\delta^{13}C$ (‰) | $\delta^{15}N$ (‰) |
| Seagrass | −7.68 ± 3.53 (−12.3, −4.12; 4) | −1.62 ± 3.73 (−5.99, 2.08; 4) | −5.59 ± 1.22 (−6.29, −3.76; 4) | −3.17 ± 3.8 (−6.25, 2.35; 4) |
| Red algae | −21.08 ± 11.24 (−32.09, −9.63; 3) | 1.09 ± 0.56 (0.71, 1.73; 3) | −11.13 ± 5.88 (−18.39, − 4.34; 3) | 1.79 ± 0.63 (1.23, 2.41, 4) |
| Green algae | −10.97 ± 5.19 (−19.99, −3.09; 8) | 0.86 ± 0.95 (−0.65, 1.91; 8) | −8.63 ± 4.53 (−19.28, −1.90; 24) | 0.67 ± 2.16 (−6.75, 3.54; 24) |
| Sessile filter feeders | −12.97 ± 4.58 (−16.94, −7.96; 3) | 1.18 ± 1.20 (0.30, 2.54; 3) | −5.68 ± 2.74 (−3.74, −7.61; 2) | 3.42 ± 2.28 (1.81, 5.03; 2) |

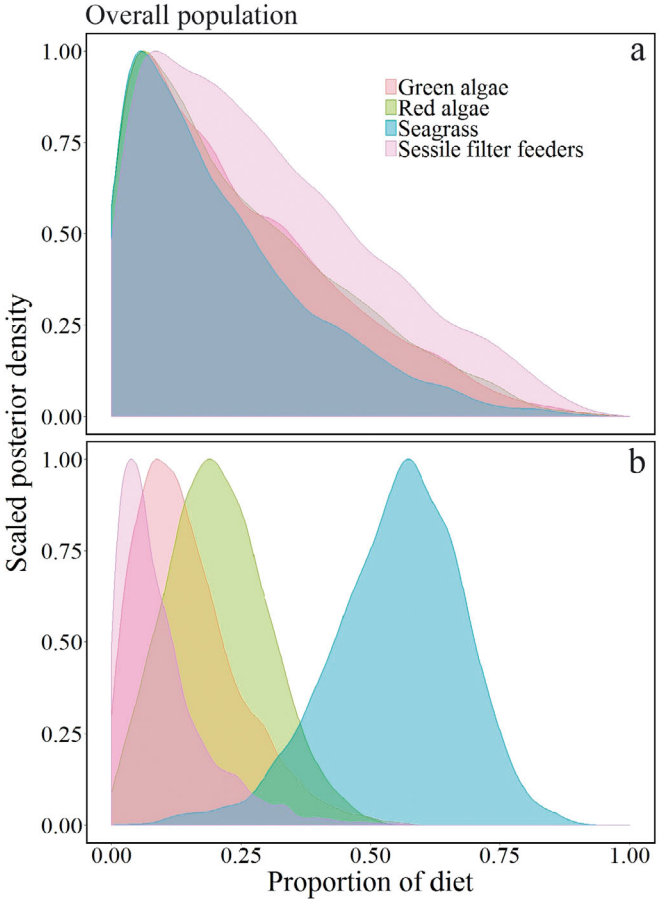


Fig. 5. MixSIAR density distribution, revealing the percent contribution of forage item groups to the diets of green turtles captured in (a) Bonefish Hole and (b) South Bimini

### Isotopic niche width

Both TA and Bayesian SEA were larger in Bonefish Hole than in South Bimini (TA: Bonefish Hole = 22.13 and South Bimini = 15.8; SEA: Bonefish Hole = 10.3 and South Bimini = 3.5). Ellipse overlap analysis indicated that there was 22% overlap between Bonefish Hole and South Bimini (Fig. A1 in the Appendix).

### Diet selection

The Johnson selection index showed that green turtles in Bonefish Hole consumed sessile filter feeders and green algae in larger proportions relative to their availability, while red algae were consumed in proportion to their availability and seagrasses were avoided (Table 3). Conversely, green turtles in South Bimini preferentially consumed red algae. Lastly, consumption of seagrasses, green algae, and sessile filter feeders matched their availability in South Bimini (Bonefish Hole: $F_{3,11}$ = 38.62, $W$ = 2.01 [alpha approximating 0.05]; South Bimini: $F_{3,41}$ = 455.48, $W$ = 1.79 [alpha approximating 0.05]; Table 3). All forage groups were considered significantly different from each other in their selection.

## DISCUSSION

Stable isotope analysis and the Johnson selection index provided insights into the foraging ecology of juvenile green turtles at Bimini, an understudied site on the Great Bahama Bank of the Northwestern Atlantic. $\delta^{13}C$ ranges for turtles at Bonefish Hole and South Bimini overlapped with the global ranges reported for juvenile green turtles that have recruited to neritic foraging areas (Burkholder et al. 2011, Howell et al. 2016, Sampson et al. 2017). Conversely, $\delta^{15}N$ values were considerably depleted, reflecting a regional neritic signature (Reich et al. 2007) attributed to $N_2$ fixation within oligotrophic areas, such as the Bahamas (France et al. 1998, Montoya et al. 2002). Bjorndal & Bolten (2010) reported a mean (±SD) epidermis $\delta^{15}N$ = 1.7 ± 1.2‰ for green turtles captured in Great Inagua, Bahamas, between 2002 and 2003. Additionally, for green turtles captured in 2008 and 2009, Vander Zanden et al. (2013) reported a similar epidermis value, with $\delta^{15}N$ = 1.7 ± 0.4‰ for Great Inagua. The results presented in this study provide the first

Table 3. Selection ranking of forage item groups for green turtles in Bonefish Hole and South Bimini. Average difference in use and availability for individuals (Tbar) was calculated for each forage item group. Tbar values <0 (values ≥1) indicate forage items that were (were not) selected for, Tbar values between 0 and 1 mean that forage items were consumed equally to their availability

| Forage item group | Bonefish Hole | | South Bimini | |
|---|---|---|---|---|
| | Tbar | | Tbar | |
| Seagrass | 2.214 | Not selected | 0.204 | Consumed in proportion to availability |
| Red algae | 0.571 | Consumed in proportion to availability | –1.625 | Selected |
| Green algae | –0.714 | Selected | 0.943 | Consumed in proportion to availability |
| Sessile filter feeders | –2.071 | Selected | 0.477 | Consumed in proportion to availability |

insights into the isotopic values for juvenile green turtles in Bimini, Bahamas.

Our analyses indicated a dichotomy in foraging ecology, diet selection, and isotopic niche in the region. The green turtle population within Bonefish Hole exhibited a more generalist omnivorous diet, with similar diet composition from each forage group and selected for sessile filter feeders and green algae, despite seagrass being the most abundant group at this site. Conversely, the South Bimini population exhibited a more specialist herbivorous diet, with high consumption of seagrass, and the preferential selection for red algae when available. The selection of green algae in Bonefish Hole and the red algae in South Bimini may be due to richer nutrients (Sampson et al. 2017) and energetic advantages (Bjorndal 1985). Though not considered to be a staple in the diet of green turtles, spongivory has been previously observed in Bahamian (Bjorndal 1980, 1990) and Nicaraguan Caribbean green turtles (Mortimer 1981). Further, an overlap was observed in stable isotope ranges reported here ($\delta^{13}C$: −16.3 to −5.9; $\delta^{15}N$: 1.4 to 6.7) with those of Bahamian hawksbill turtles *Eretmochelys imbricata* ($\delta^{13}C$: −11.5 to −8.8; $\delta^{15}N$: 3.7 to 7.4), a known spongivorous species, suggesting that green turtles in Bonefish Hole also consume sponges (Bjorndal & Bolten 2010).

The disparity in foraging ecology and diet selection among the 2 sites in Bimini is further demonstrated by the isotopic niche width at each site (Newsome et al. 2007, Jackson et al. 2011). The large SEA and omnivorous diet observed for green turtles in Bonefish Hole indicate that the local population has a broader trophic niche and selects for a more generalist diet, with individuals specializing on certain forage items (e.g. Demospongiae, *Penicillus* sp., *Halimeda* sp.). Conversely, the reduced SEA at South Bimini, with a stable diet of seagrass, may be suggestive of a population specializing on herbivory (Bolnick et al. 2007, Vander Zanden et al. 2010, DiBeneditto et al. 2017). Further, the 22% overlap in ellipse area found between the 2 study sites in Bimini suggests that some individuals in Bonefish Hole, where the population diet is more variable, may still select for a more herbivorous diet. Broad isotopic niche width, as evidenced in Bonefish Hole, may result from a generalist population with specialized individuals to ease competition with conspecifics (Bolnick et al. 2003, 2007, Vander Zanden et al. 2010). However, with no quantifiable knowledge of carrying capacity in Bimini, the degree of competition that may drive the observed foraging dichotomy in the region cannot be determined.

Differences in foraging strategies between sites may also be driven by variability in habitat complexity between sites. The close proximity of mangrove roots to the foraging area at Bonefish Hole provides structure for sessile filter feeders and algae. Thus, future studies should expand the habitat characterization employed here to measure those prey items. Additionally, the size classes of each turtle at each site may potentially drive this foraging dichotomy. Although no significant difference in size class distributions was found between the 2 sites, a higher proportion of small turtles (<35 and 35.1–40 cm size classes) was observed at Bonefish Hole and a greater proportion of larger turtles (55.1–60 and >60 cm) in South Bimini. Additionally, $\delta^{13}C$ and $\delta^{15}N$ were more depleted and enriched, respectively, in smaller individuals, suggesting that these turtles may have recently recruited to the neritic environments of Bimini (Reich et al. 2007, Howell et al. 2016). Further, if individuals recruited to Bimini, particularly Bonefish Hole, then the previously mentioned variability in available prey items may delay their ontogenetic shift to a herbivorous diet (Cardona et al. 2009), reflecting a more pelagic omnivorous diet and a broader isotopic niche at Bonefish Hole. The presence of sharks and predation on other marine megafauna species has been observed in Bimini (Jennings et al. 2012, Melillo-Sweeting et al. 2014), thus reduced predation risk may drive the recruitment of smaller individuals to Bonefish Hole. However, anecdotal evidence suggests that predation on marine turtles in Bimini is infrequent and may not notably affect juvenile turtle distribution in the region. The lack of significant differences in sizes between each site and the potential reflection of a pelagic diet may be an artifact of the small and unequal sample sizes of turtles captured at each site as well as limitations of the capture method used. Limited maneuverability in the narrow mangrove channels in Bonefish Hole reduced our ability to capture smaller, faster turtles. Conversely, the use of deeper areas by large size classes (>60 cm) in South Bimini limited our ability to follow and capture larger turtles in this region. Thus, increasing the overall sample size at Bonefish Hole and a greater effort in sampling the most abundant and the underrepresented size classes at each site would allow for further investigation into the potential effects of individual size on foraging strategies.

FP may potentially drive the inferred foraging strategies, as FP has been reported to impede ingestion and limit the range of motion of marine turtles (Herbst 1994, Aguirre & Lutz 2004, Jones et al. 2016). FP was recorded at both sites; however, a higher

prevalence (71% of turtles captured in Bonefish Hole, averaging 21 tumors turtle$^{-1}$) was observed at Bonefish Hole, compared to 14% of South Bimini turtles, averaging 4 tumors ind.$^{-1}$. Although FP has been reported to inhibit certain fundamental physical abilities, it was reported to have no effect on foraging dive time and somatic growth rates in Hawaiian green turtles (Brill et al. 1995, Chaloupka & Balazs 2005). However, deficiencies in vital macronutrients (i.e. proteins, carbohydrates, lipids) associated with FP (Aguirre & Balazs 2000) may drive green turtles to consume and select items, such as sponges, that are richer in these macronutrients (Bjorndal 1990, Chanas & Pawlik 1995), to maximize nutrient intake and assimilation (Simpson et al. 2004, Kohl et al. 2015, Remonti et al. 2016). Thus, nutrient deficiencies may drive turtles in Bonefish Hole to select a broader range of nutrient-rich forage items that were more enriched in $^{15}$N, as observed in the algae and sessile filter feeder forage groups in Bimini. However, there is a need to compare turtle blood parameters with macronutrient content of prey items between marine turtles with and without FP to elucidate potential supplementation of nutrients through the consumption of varying forage items.

While our results are extremely interesting and provide further insight into the diet plasticity exhibited by some foraging populations, we suggest caution while interpreting these results. Given the large amount of variability (e.g. red algae) and isotopic overlap between foraging groups, we recognize that this may have directly influenced the results of MixSIAR analysis. Additionally, the broad isotopic niche may be an artifact of this same variability leading to a wide spread of individual values in Bonefish Hole. Further suggested improvements to our study include: (1) improved habitat sampling, (2) adjustment of the spatial scale of resources assumed to be available to turtles at each site, and (3) increased sampling of prey items for stable isotope analysis. The use of quadrats inherently excludes mangrove roots and the forage items that anchor there (i.e. green algae, sessile filter feeders), potentially leading to an underestimation of anchored forage items and an overestimation in selection of these forage groups. Additionally, sampling of prey items was conducted solely on neritic, benthic prey items and excluded pelagic prey items. Future studies should include pelagic prey items to reveal the potential for recent recruitment to the neritic environment by juvenile turtles. Further, we assumed that turtles used the entire foraging site and therefore that food availability was consistent throughout the entire site; however, green turtles often have concentrated home ranges (Seminoff et al. 2002, Makowski et al. 2006), and likely use only a subset of the foods and habitat types available to them. Thus, future studies exploring diet selection should consider turtle home ranges and calculate food availability within these areas. Lastly, we found wide isotopic variability with the prey groups and considerable isotopic overlap among prey groups (especially at Bonefish Hole), which was likely a result of the small sample size of prey items collected. The observed high variability in red algae may serve as the underlying cause for the wide isotopic niche and variation among individuals in Bonefish Hole. Future studies should increase the sample size of prey items at each habitat site.

Diet selection studies can increase our knowledge of the influences that prey items and their availability in a given habitat have on species development, foraging, and the ecological niches that species inhabit (Bjorndal 1997, Fuentes et al. 2006, López-Mendilaharsu et al. 2008). Further, determining intra-species diet plasticity expands our understanding of variations in fine-scale habitat use exhibited between and within foraging habitats. Within the Bahamas, amendments made to the Fisheries Resource Act of 2010 fully protect marine turtles across all life stages (Bjorndal & Bolten 2009); however, coastal development still poses a threat to adjacent habitat and species (Jennings et al. 2008, Crain et al. 2009, Stump 2013). Our results, coupled with spatially explicit data on habitat available, can inform management and conservation measures, expanding beyond the traditional species-specific population-oriented targets to one inclusive of critical habitats for threatened and endangered species.

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## APPENDIX

Table A1. Habitat characterization, expressed in mean ± SD percent coverage for forage item groups and individual species found in Bonefish Hole and South Bimini, Bahamas

| Forage item group | Bonefish Hole (%) | South Bimini (%) | Forage species | Bonefish Hole (%) | South Bimini (%) |
|---|---|---|---|---|---|
| Seagrass | 37.3 ± 23.8 | 34.8 ± 32.4 | *Syringodium filiforme* | 0.0 | 0.2 ± 1.1 |
| | | | *Halodule wrightii* | 2.3 ± 5.7 | 1.1 ± 2.1 |
| | | | *Thalassia testudinum* | 35.0 ± 23.5 | 33.4 ± 29.2 |
| Red algae | 14.5 ± 22.6 | 1.7 ± 4.2 | *Hypnea* sp. | 0.0 | 0.0 |
| | | | *Amphiroa* sp. | 0.0 | 0.0 |
| | | | *Laurencia intricata* | 14.5 ± 22.7 | 1.7 ± 4.2 |
| Green algae | 9.0 ± 7.0 | 16.0 ± 14.7 | *Rhipocephalus phoenix* | 0.0 | 0.5 ± 0.6 |
| | | | *Caulerpa* spp. | 0.0 | 0.3 ± 0.8 |
| | | | *Udotea* spp. | 0.0 | 1.5 ± 1.9 |
| | | | Filamentous green algae | 0.0 | 0.2 ± 0.5 |
| | | | *Acetabularia crenulata* | 0.0 | 1.0 ± 1.1 |
| | | | *Chaetomorpha linum* | 0.0 | 0.3 ± 1.1 |
| | | | *Dictyosphaeria cavernosa* | 0.0 | 0.2 ± 0.8 |
| | | | *Acanthophora spicifera* | 0.0 | 0.2 ± 0.8 |
| | | | *Halimeda* spp. | 0.3 ± 0.6 | 4.6 ± 2.1 |
| | | | Coraline green algae | 1.0 ± 2.1 | 0.0 |
| | | | *Penicillus* spp. | 1.8 ± 1.9 | 3.2 ± 2.3 |
| | | | *Batophora oerstedii* | 6.0 ± 6.8 | 3.8 ± 2.2 |
| Sessile filter feeders | 0.3 ± 1.1 | 1.7 ± 3.0 | Demospongiae spp. | 0.3 ± 1.1 | 1.7 ± 3.0 |
| | | | Tunicata spp. | 0.0 | 0.0 |

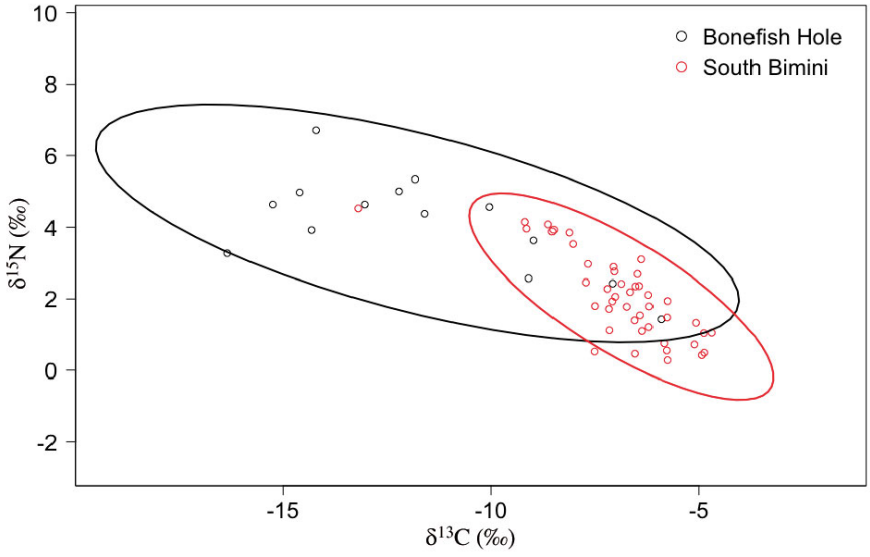


Fig. A1. Green turtle epidermis isotopic values (open circles) with the Bayesian ellipses depicting potential isotopic niche at Bonefish Hole (black; isotopic niche width = 10.3) and South Bimini (red; isotopic niche width = 3.5)

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