Inferring long-term foraging trends of individual juvenile loggerhead sea turtles using stable isotopes

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ABSTRACT: Individual variation in diet composition has important evolutionary, ecological, and conservation implications. However, few studies of marine turtles have examined long-term foraging behavior of individuals. Using stable carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope values from blood plasma, we examined long-term variation in resource use of 27 juvenile loggerhead turtles *Caretta caretta* captured multiple times in North Carolina between 2001 and 2010. Seven turtles displayed a marked increase in δ^{15}N values consistent with a shift from oceanic to neritic habitat. These turtles, which we designated as 'recruits', had initial straightline carapace lengths (SCL) and δ^{15}N values at first sampling that were significantly lower (p = 0.007 and p < 0.0001, respectively) than the remaining 20 'resident' turtles. For the resident group, the influence of SCL on δ^{13}C (p = 0.02) and δ^{15}N (p = 0.05) values was significant. Individual effects on δ^{13}C values were also significant (p < 0.001), indicating that foraging patterns vary among individuals; however, individual effects were not significant for δ^{15}N (p = 0.07). Stable isotope niche width calculations suggested that residents were consistent in resource selection over time, and individuals were specialized in resource use relative to the population. Also, the resident population was more specialized than generalized in resource use, and stable isotope mixing (MixSIAR) model results suggest their diet is largely comprised of horseshoe crabs *Limulus polyphemus*. These findings improve understanding of the foraging ecology of juvenile loggerhead turtles, and highlight the importance of examining the long-term diet composition of individuals.

KEY WORDS: *Caretta caretta* · Individual specialization · Niche width · Resource use · Stable isotopes

INTRODUCTION

Diet composition and the nutritional contribution of consumed food can influence an individual's growth rate, life stage durations, and age at maturation; thus, the effective management of threatened and endangered species benefits from a clear understanding of foraging behavior (Bjorndal 1997, Bolnick et al. 2003). However, obtaining such information can often be challenging, especially for species such as sea turtles, which have long life spans, late maturity, slow growth rates, and complex life histories involving multiple life stages and habitat shifts (Chaloupka & Musick 1997, Bolten 2003).

Stable isotope analysis has become an increasingly widespread and powerful tool in ecological research for detection of dietary shifts in organisms, tracing major food sources, and assessing habitat use and migratory movements (Rubenstein & Hobson 2004). Such dietary inferences are possible because the stable isotope composition of a consumer's tissues are derived from its habitat and prey (DeNiro & Epstein

1978, 1981). In marine environments, a consumer's stable isotopic ratio of ^{13}C:^{12}C (δ^{13}C) reflects foraging habitat (oceanic vs. neritic, or pelagic vs. benthic), and the ratio of ^{15}N:^{14}N (δ^{15}N) indicates trophic position (DeNiro & Epstein 1978, 1981, Hobson et al. 1994, Post 2002). Additionally, δ^{13}C and δ^{15}N values can provide information on foraging location as a result of the effect of biogeochemical processes on baseline δ^{13}C and δ^{15}N (McKinney et al. 2010, Pajuelo et al. 2010, 2012b, Ceriani et al. 2012, Seminoff et al. 2012, Vander Zanden et al. 2013a, 2015). The time it takes for a consumer's tissue to reflect the isotopic composition of its prey (known as isotopic turnover) varies among tissues (Hesslein et al. 1993). For instance, in ectotherms such as sea turtles, plasma reflects recent resource use history (approximately 2 to 5 wk for juveniles), skin reflects intermediate resource use history (4 to 6 mo) and bone represents resource use over a much longer period (many years) (Seminoff et al. 2006, 2007, Reich et al. 2008, Snover et al. 2010, Avens et al. 2013, Thomas & Crowther 2015).

When examining the foraging trends of a population, it is important to consider not only population-wide trends, but also the foraging trends of individuals within the population, as such individual characteristics can greatly affect a population's evolutionary, ecological, and conservation dynamics (Roughgarden 1972, 1974, Bolnick et al. 2003). For example, many animal populations have generalized diets, but individuals within a population may favor a specific subset of habitat and dietary resources used by the population, possibly resulting in differential survival and reproductive consequences (Bolnick et al. 2003, Vander Zanden et al. 2013b). One quantitative measure of a population's dietary resource use is the total niche width (TNW), which is defined as the variance of resources that a population consumes (Roughgarden 1972, Bearhop et al. 2004). TNW consists of the sum of 2 variables: the within-individual component (WIC), which reflects the average variance of resources found within individuals' diets, and the between-individual component (BIC), which is the variation in resource use among individuals. The ratio of WIC/TNW is used to measure the degree of individual specialization, with values close to 0 indicating that individuals utilize a narrow range of resources (specialist), and values near 1 suggesting that individuals use the range of the population's niche (generalist) (Roughgarden 1974, Bolnick et al. 2003). Therefore, most of the variation in TNW in a specialist population results from variation among individuals (i.e. BIC), while the majority of variation in a generalist population can be attributed to variation within individuals (i.e. WIC).

In addition to considering the degree of individual specialization within a population, it is also beneficial to examine the consistency of an individual's resource use over time (temporal consistency, sensu Vander Zanden et al. 2013b) (Bolnick et al. 2003, Araújo et al. 2007, Vander Zanden et al. 2013b). For instance, a single sampling of the stomach contents of an individual may serve more as a reflection of prey availability during one particular foraging event instead of an individual's long-term preference in prey. This may especially be true if prey abundance varies over time (i.e. seasonally or annually), or is unequally distributed, and can inaccurately lead one to conclude that individuals are more specialized in their foraging behavior than they actually are (Bolnick et al. 2002). Prey selection may also vary depending on an individual's life-stage or body size (Scharf et al. 2000, Pajuelo et al. 2010). In wild populations, sampling an individual's temporal consistency can be accomplished through repeat captures of the individual, or longitudinal sampling using stable isotope analysis of tissues that remain inert after synthesis (e.g. bone, scute, otoliths) (Bolnick et al. 2003, Vander Zanden et al. 2010, 2013b, Avens et al. 2013).

North Carolina's estuarine waters serve as an important developmental and foraging habitat for several subpopulations of juvenile, neritic-stage loggerhead sea turtles *Caretta caretta* (Bass et al. 2004), as well as the location of a long-term in-water research site for this species (Epperly et al. 2007). Turtles enter the estuary in spring as waters warm and emigrate in late fall/early winter when water temperature declines (Epperly et al. 2007). Some turtles show residency to the estuarine waters and are encountered over multiple years (Avens et al. 2003, Epperly et al. 2007). In the current study, we describe the long-term foraging behavior of individual loggerhead turtles resident to these waters by examining trends in δ^{13}C and δ^{15}N values of plasma samples from individuals that were captured during multiple years between 2001 and 2010. Since we were interested in focusing our analyses on turtles that were resident to our study site, we examined the δ^{15}N values of individual turtles over time to see if we could distinguish among individuals whose capture history indicated recruitment into the estuary from oceanic waters over the course of their capture history (classified as 'recruits'), and those who had already made the transition from oceanic to neritic habitat at the time of first sampling (classified as 'residents'). For resident turtles, we also quantified the temporal consistency in resource use of individuals (i.e. WIC) and the degree of specialization in resource use by individu-

als relative to the population (i.e. WIC/TNW). Finally, we determined estimates of the proportions of potential prey items that contributed to the diet of resident turtles using a stable isotope mixing model (Mix-SIAR). Results of this study provide insight into the ecological roles of individual resident loggerhead turtles within a foraging population.

MATERIALS AND METHODS

Study area

The study site included eastern Pamlico, Core, and Back Sounds, which are part of the Pamlico-Albemarle Estuarine Complex (PAEC) (Fig. 1) in North Carolina. This system consists of shallow, productive, lagoonal-type ecosystems (Copeland & Gray 1991) that are bounded on the east side by barrier islands, commonly known as the Outer Banks.

Sample collection and preparation

Turtles were incidentally captured in commercial pound nets (see Epperly et al. 2007 for a detailed description of this fishery). Upon capture, body size was measured as straightline carapace length (SCL), new captures received Inconel tags and a passive integrated transponder (PIT) tag, and blood samples were obtained from the dorsal cervical sinus. Blood samples were separated into plasma and red blood cell components by centrifuge and stored in −80°C freezers. To examine trends in δ^{13}C and δ^{15}N values associated with individual turtles over time, we selected plasma samples from loggerhead turtles that had been captured during foraging seasons (April through December) of multiple years from 2001 to 2010 between May and November (n = 66 samples from 27 turtles: 19 turtles with 2 samples, 6 turtles with 3 samples, 1 turtle with 4 samples, and 1 turtle with 6 samples). Of these samples, 30 were processed prior to this study by Wallace et al. (2009) using the same methodology as in the current study. Plasma was selected for our analysis because of its short isotopic turnover (i.e. 2 to 5 wk) (Seminoff et al. 2007, Reich et al.

2008), which increased the likelihood that isotopic values would reflect the diet of turtles while foraging at our study site. After the plasma samples had dried for 48 to 72 h at 60°C, we crushed them and weighed 0.3 to 1.8 mg of each sample into sterilized tin capsules (Wallace et al. 2009) for mass spectrometry analysis at the Duke University Environmental Stable Isotope Laboratory (DEVIL), in Durham, North Carolina (see Wallace et al. 2009 for analytical details). A lipid correction factor (δ^{13}C$_{normalized}$ = δ^{13}C$_{untreated}$ − 3.32 + 0.99 × C:N), following the methodology of Post et al. (2007) was applied to our carbon isotope ratios as we did not extract lipids from the plasma samples. C:N values ranged 2.62 to 4.04.

Data analysis

Individuals classified as recruits exhibited an increase in δ^{15}N values over time, consistent with a dietary shift during their transition from oceanic to neritic foraging habitat (Snover et al. 2010, Avens et al. 2013). These turtles also had lower δ^{15}N values (<12.00‰) at initial capture, and their δ^{15}N values increased by at least 2.00‰ over the course of their capture history. All other turtles were classified as residents, and were considered to have already made the transition from oceanic to neritic habitat at the time of first sampling. Initial SCL and δ^{13}C and δ^{15}N
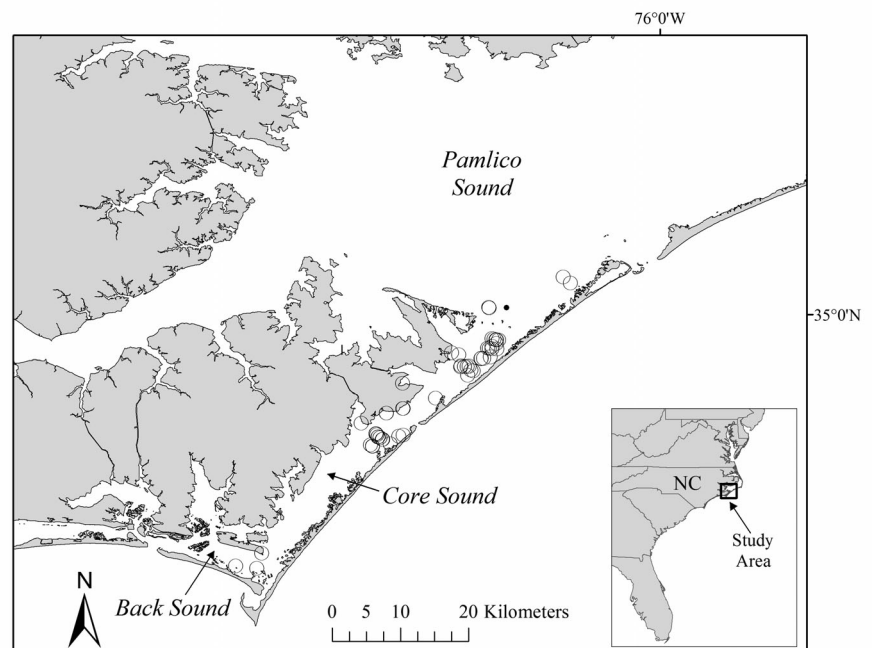

Fig. 1. Capture locations (open circles) of 27 juvenile loggerhead turtles *Caretta caretta* from which samples were collected in this study between 2001 and 2010 in the Pamlico-Albemarle Estuarine Complex, North Carolina, USA

values at first sampling were compared among recruits and residents using a Student's *t*-test (significance level α = 0.05).

For the resident group, generalized additive mixed models (GAMMs) (Wood 2006, R Core Team 2015) that accounted for random, individual effects that may have been introduced by longitudinal sampling were initially used to evaluate the effects of potential covariates on $\delta^{13}C$ and $\delta^{15}N$ values (significance level α = 0.05). Potential covariates included SCL, Julian date (to assess seasonal effects) and calendar year. Further analysis was conducted on covariates with significant effects on $\delta^{13}C$ or $\delta^{15}N$ values using a linear mixed effects modeling approach, which also accounted for random, individual effects. These analyses were not conducted for turtles classified as recruits since our intent was to examine the foraging behavior of resident turtles whose isotopic history was most likely to reflect foraging within our study site.

In addition, for the resident group we used the variance in $\delta^{13}C$ and $\delta^{15}N$ values to examine the temporal consistency in resource use of individual turtles and the degree of individual specialization in resource use relative to the population. We used methods similar to Vander Zanden et al. (2013b); WIC was used as a measure of temporal consistency. The mean sum of squares within individuals was used to calculate WIC:

$$\text{WIC} = \Sigma_i \Sigma_j \, (x_{ij} - \overline{x}_i)^2 \, / \, (N - k) \qquad (1)$$

BIC, was calculated using the mean sum of squares between individuals:

$$\text{BIC} = \Sigma_i \, (\overline{x}_i - \overline{x})^2 \, / \, (k - 1) \qquad (2)$$

where *i* represents an individual, *j* represents a single $\delta^{13}C$ or $\delta^{15}N$ value of a sample, *N* is the total number of observations and *k* is the number of individuals. TNW = WIC + BIC, and the degree of specialization in resource use by individual turtles relative to the population was calculated as WIC/TNW.

We used the Bayesian stable isotope mixing model, MixSIAR GUI (Moore & Semmens 2008, Semmens et al. 2009, Stock & Semmens 2013), in the R computing environment (R Core Team 2015) to determine estimates of the proportions of potential prey items that contributed to the diet of resident turtles. MixSIAR estimates the probability distributions (5th, 25th, 50th, 75th, and 95th percentiles) of each source (potential prey item) to a consumer's stable isotope values while accounting for variability among consumer and source isotopic values and uncertainty associated with tissue–diet discrimination factors (Phillips et al.

2014). We ran the model once including all resident turtles to examine the proportions of potential prey items for the population, and once for each individual to examine these proportions on an individual level. In the model run for the resident population, $\delta^{13}C$ and $\delta^{15}N$ values associated with each individual were assigned a separate group number (e.g. $\delta^{13}C$ and $\delta^{15}N$ values for turtle 1 were assigned to group 1, and so on), and group was included as a random effect since multiple samples were collected for each turtle. Including group as a random effect also allowed us to examine if the variation in the diet of residents was explained more by variation in the diet of individuals or variation in diet between individuals. The $\delta^{13}C$ and $\delta^{15}N$ values of potential prey items were derived from samples collected (in 2007) and analyzed by Wallace et al. (2009). Prey samples were collected when turtles were present in the estuary (April through December). Similar to our turtle plasma samples and following the methodology of Post et al. (2007), a lipid correction factor was also applied to our carbon isotope ratios as we did not extract lipids from the prey samples. Potential prey items with statistically similar isotopic values were grouped to simplify the analysis and interpretation of the results (Phillips et al. 2005, Wallace et al. 2009). Prey items included blue crab *Callinectes sapidus* + whelk *Busycon* spp., horseshoe crab *Limulus polyphemus*, spider crab *Libinia emarginata*, cannonball jellies *Stomolophus meleagris*, and fish (spot *Leiostomus xanthurus* + southern flounder *Paralichthys lethostigma*) (Table 1). We used prey item values that were adjusted for the tissue–diet discrimination factor using plasma values ($\Delta_{dt} \delta^{13}C$: −0.12‰, $\Delta_{dt} \delta^{15}N$: 2.92‰) for juvenile green turtles *Chelonia mydas* derived by Seminoff et al. (2006). A tissue–diet discrimination factor was not available for juvenile loggerhead turtles of a similar size class to those in our study, so we chose to use the discrimination factor of Seminoff et al. (2006) because the green turtles were similar in size to our turtles and our results could be more easily compared to previous stable isotope studies of loggerhead prey (Wallace et al. 2009, McClellan et al. 2010) that also used the discrimination factor of Seminoff et al. (2006).

RESULTS

Of the 27 turtles, 7 exhibited a pronounced increase in $\delta^{15}N$ values consistent with recruitment from oceanic to neritic foraging habitat (mean shift = 3.2‰, mean pre-shift = 10.24 ± 1.31‰, mean post-shift = 13.45 ± 1.18‰) (Fig. 2). Initial SCL and $\delta^{15}N$ values at first sampling for this group ('recruits') was signifi-

Table 1. Stable isotope mixing (MixSIAR) model results with predicted diet proportions (5th to 95th percentile) of each potential prey item compared to $\delta^{13}C$ and $\delta^{15}N$ mixture values for juvenile loggerhead turtles classified as residents. Mean values are in parentheses. Turtle numbers refer to individuals identified in Fig. 5. Only the 12 turtles whose $\delta^{13}C$ and $\delta^{15}N$ values were within the convex hull polygon formed by the potential prey items were included in the model run. Values in **bold** are the highest prey item contribution. 'All turtles' refers to the predicted diet proportions of the 12 resident turtles that fit within the convex hull polygon

Turtle	Blue crab + whelk	Cannonball jellyfish	Fish	Horseshoe crab	Spider crab
1	0.011–0.408 (0.151)	0.006–0.231 (0.086)	0.027–0.487 (0.230)	**0.035–0.683 (0.339)**	0.013–0.490 (0.195)
2	0.013–0.409 (0.160)	0.007–0.254 (0.098)	0.023–0.442 (0.200)	**0.034–0.654 (0.327)**	0.015–0.531 (0.215)
3	0.010–0.450 (0.162)	0.006–0.279 (0.099)	0.029–0.558 (0.268)	**0.027–0.647 (0.285)**	0.013–0.480 (0.185)
4	0.010–0.411 (0.153)	0.005–0.249 (0.090)	0.028–0.497 (0.244)	**0.032–0.689 (0.320)**	0.014–0.502 (0.194)
5	0.009–0.469 (0.160)	0.005–0.261 (0.090)	0.025–0.599 (0.287)	**0.023–0.648 (0.289)**	0.010–0.449 (0.174)
6	0.014–0.415 (0.174)	0.005–0.214 (0.079)	0.021–0.490 (0.231)	**0.034–0.699 (0.348)**	0.011–0.464 (0.168)
7	0.009–0.396 (0.155)	0.005–0.225 (0.084)	0.035–0.562 (0.289)	**0.022–0.688 (0.298)**	0.010–0.465 (0.174)
8	0.012–0.364 (0.148)	0.013–0.340 (0.143)	0.022–0.442 (0.202)	0.021–0.565 (0.245)	**0.025–0.615 (0.262)**
9	0.007–0.355 (0.130)	0.011–0.353 (0.145)	0.015–0.604 (0.244)	0.014–0.544 (0.204)	**0.032–0.540 (0.276)**
10	**0.027–0.639 (0.306)**	0.018–0.404 (0.183)	0.010–0.366 (0.138)	0.014–0.458 (0.182)	0.013–0.508 (0.191)
11	0.027–0.506 (0.238)	0.120–0.322 (0.142)	0.011–0.316 (0.131)	0.016–0.534 (0.220)	**0.028–0.560 (0.269)**
12	0.007–0.371 (0.135)	0.004–0.211 (0.075)	0.051–0.568 (0.298)	**0.027–0.707 (0.325)**	0.010–0.452 (0.169)
All turtles	0.010–0.275 (0.108)	0.002–0.143 (0.048)	0.006–0.293 (0.105)	**0.226–0.786 (0.522)**	0.029–0.486 (0.218)

cantly lower (Student's t-test, SCL: $t = 3.862$, df = 32, $p = 0.007$ and $\delta^{15}N$: $t = 8.937$, df = 25, $p < 0.0001$) than that observed for the remaining 20 turtles ('residents') (Table 2). In contrast, no significant difference in $\delta^{13}C$ values at first sampling was observed between recruits and residents ($t = 1.538$, df = 24, $p > 0.05$).

For the resident group, the GAMM indicated no significant effects of calendar year or Julian date on $\delta^{13}C$ or $\delta^{15}N$ values ($p > 0.05$ in both cases), but significant linear relationships were found between SCL and both $\delta^{13}C$ values ($p = 0.02$) and $\delta^{15}N$ ($p = 0.04$) (Table 3). Further analysis using a linear mixed ef-

fects modeling approach indicated a significant influence of SCL on $\delta^{13}C$ ($p = 0.02$, and SCL accounted for 76% of the variance in $\delta^{13}C$ values) and $\delta^{15}N$ values ($p = 0.05$, and SCL accounted for 37% of the variance in $\delta^{15}N$ values) (Fig. 3, Table 4). Individual effects were highly significant for $\delta^{13}C$ values ($p < 0.001$), indicating that foraging patterns vary among loggerheads inhabiting this area. Individual effects were not significant for $\delta^{15}N$ values ($p = 0.07$).

Median $\delta^{13}C$ (0.28) and $\delta^{15}N$ (0.23) WIC values for residents were low, indicating that individual turtles within our study site are consistent in their resource
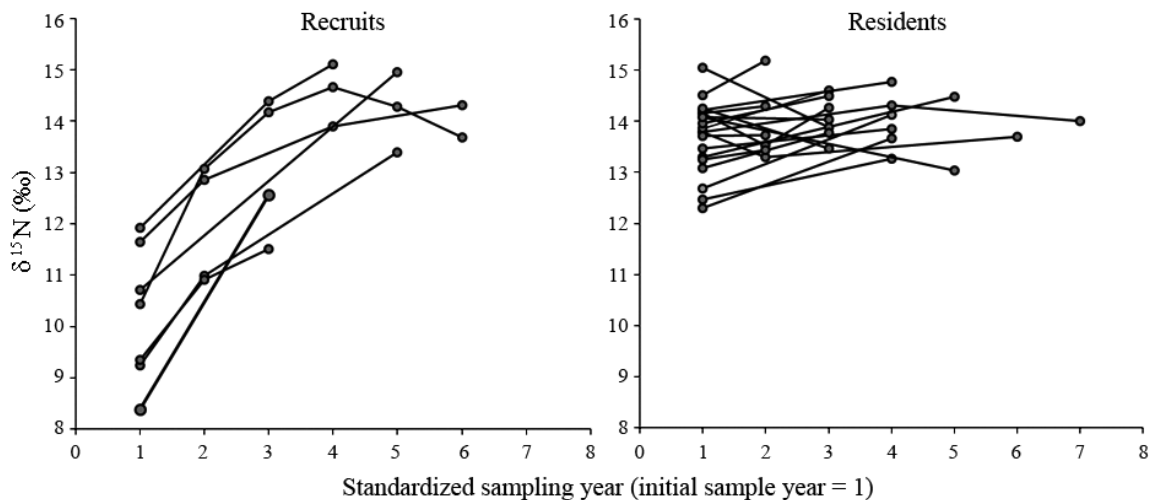

Fig. 2. Temporal trends in $\delta^{15}N$ values of juvenile loggerhead turtles classified as recruits (n = 7, straightline carapace length [SCL] range: 54.5 to 66.8 cm) and residents (n = 20, SCL range: 55.3 to 81.8 cm) in the estuarine waters of North Carolina. Each circle represents a capture event, and circles connected by solid lines represent individuals. For each individual, the absence of a circle during a sampling year indicates the number of years that passed between capture events

Table 2. Initial straightline carapace length (SCL), δ^{13}C and δ^{15}N values at first sampling event for juvenile loggerhead turtles designated as recruits and residents in the estuarine waters of North Carolina

| | Initial SCL (cm) | | | Initial δ^{13}C | | | Initial δ^{15}N | | |
	Min.	Max.	Mean ± SD	Min.	Max.	Mean ± SD	Min.	Max.	Mean ± SD
Recruits (n = 7)	54.5	66.8	60.2 ± 4.3	−15.05	−18.17	−17.16 ± 1.07	8.38	11.92	10.24 ± 1.3
Residents (n = 20)	55.3	81.8	66.2 ± 5.9	−14.36	−19.2	−16.38 ± 1.14	12.29	15.04	13.70 ± 0.69

Table 3. Summary of statistical output from the generalized additive mixed models (GAMM) applied to analyze the influence of potential covariates on δ^{13}C and δ^{15}N for resident juvenile loggerhead turtles (n = 20) in the estuarine waters of North Carolina. Edf: estimated degrees of freedom; SCL: straightline carapace length; AIC: Akaike's information criterion. Significant linear relationships (in **bold**) were found between SCL and both δ^{13}C and δ^{15}N values

| Model | Adjusted r^2 | AIC | Smooth terms | | | | Parametric coefficients | | | | |
			Variable	Edf	F	Prob(F)	Variable	Estimate	SE	t	Pr > |t|
GAMM$_{\delta^{15}N\_SCL+Year+Julian\ date}$ (n = 43)	0.06	87.9	SCL (cm)	1	3.465	0.07	Year	0.06	0.046	1.286	0.206
			Julian date	1	0.158	0.69					
GAMM$_{\delta^{15}N\_SCL}$ (n = 43)	0.06	84	SCL (cm)	1	4.447	**0.04**					
GAMM$_{\delta^{13}C\_SCL+Year+Julian\ date}$ (n = 43)	0.13	126.4	SCL (cm)	1	6.913	0.01	Year	−0.08	0.073	−1.084	0.285
			Julian date	1	0.075	0.78					
GAMM$_{\delta^{13}C\_SCL}$ (n = 43)	0.16	121.58	SCL (cm)	1	6.153	**0.02**					
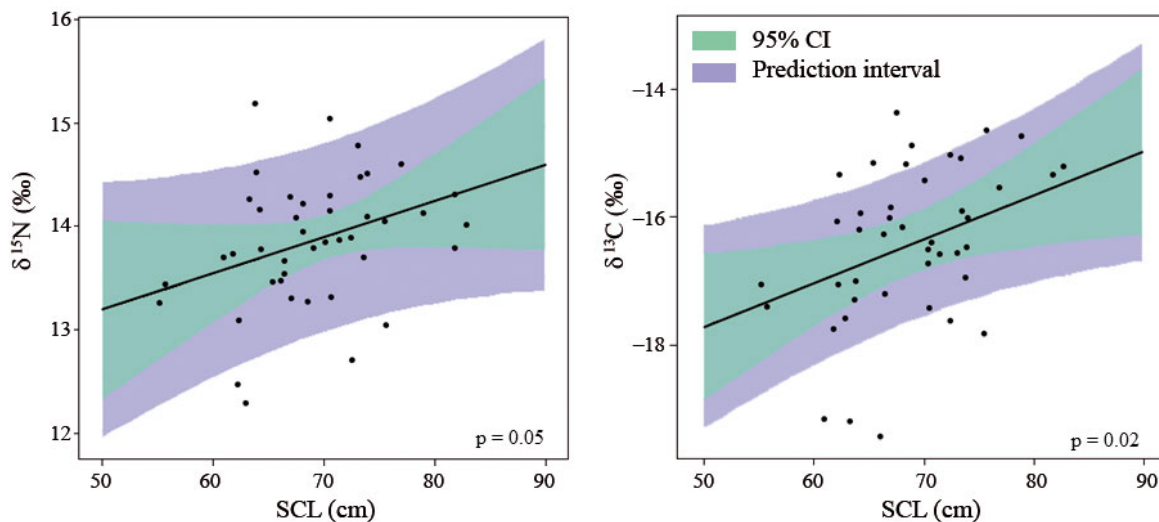
Fig. 3. Linear mixed effects models indicating that the relationship between straightline carapace length (SCL) and δ^{13}C and δ^{15}N values of resident loggerhead turtles was significant in both cases. Black dots depict all capture events for each turtle

selection over time (Fig. 4a). In addition, the low median δ^{13}C (0.16) and δ^{15}N (0.32) WIC/TNW values suggest that individuals are specialized in resource use relative to the population (Fig. 4b). This is further supported by high BIC values (BIC was 82% of TNW for δ^{13}C and 62% for δ^{15}N), and the smaller mean range in δ^{13}C and δ^{15}N values for individuals compared to that of the population (Table 5). Lastly, δ^{13}C

(1.77‰) and δ^{15}N (0.72‰) TNW values were small, indicating that the population is more specialized than generalized.

Our intention was to include all 20 resident turtles in the MixSIAR model runs, but for 8 individuals, either a portion (5 ind.) or all (3 ind.) of their δ^{13}C and δ^{15}N plasma sample values fell outside of the convex hull polygon formed by the potential prey items (see

Table 4. Summary of statistical output from the linear mixed effects model applied to analyze the influence of straightline carapace length (SCL) on $\delta^{13}C$ and $\delta^{15}N$ for resident juvenile loggerhead turtles (n = 20) in the estuarine waters of North Carolina. Significant values in **bold**

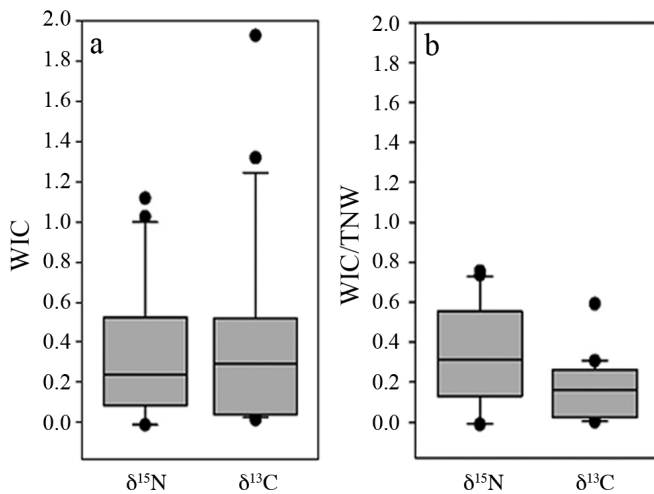| Model	Variable	Value	SE	df	t	Pr > |t|
$\delta^{13}C\_SCL$	Intercept	−21.170	1.952	41.000	−10.845	<0.001
(n = 43)	SCL	0.069	0.028	40.980	2.436	**0.019**
$\delta^{15}N\_SCL$	Intercept	11.440	1.151	24.930	9.937	<0.001
(n = 43)	SCL	0.035	0.017	24.801	2.097	**0.046**

Fig. 4. Resource use in resident loggerhead turtles, showing a comparison of (a) the within-individual component (WIC) of total niche width (TNW), which represents temporal consistency in resource use, and (b) the ratio of WIC/TNW, which represents the degree of individual specialization in resource use relative to the population. WIC/TNW values close to 0 indicate that individuals utilize a narrow range of resources (i.e. specialist), and values near 1 suggest that individuals use the range of the population's niche (i.e. generalist). The horizontal line within the boxes represents the median value, the upper quartile represents the 75% value, the lower quartile represents the 25% value. Top whisker: the greatest value excluding outliers; bottom whisker: the lowest value excluding outliers; black circles: outliers

Table 5. Minimum, maximum and mean ranges of $\delta^{13}C$ and $\delta^{15}N$ for individual juvenile loggerhead turtles identified as residents (n = 20). The population range is the difference between the minimum and maximum values for all individuals

	Min. range	Max. range	Mean range (±SD)	Population range
$\delta^{13}C$	0.22	1.89	0.73 (±0.48)	5.06
$\delta^{15}N$	0.03	1.44	0.68 (±0.41)	2.89

turtles 13 to 20 in Fig. 5). Therefore, these 8 individuals were not included in the model runs since their positioning violates the assumptions of the mixing model. For the remaining 12 individuals (turtles 1 to 12 in Fig. 5), the mixing model indicated that horseshoe crabs (5th to 95th percentile = 0.226 to 0.786) made up the largest contribution to the diet of the population (Fig. 5, Table 1). On an individual level, horseshoe crabs contributed the most to the diet of 8 turtles, spider crabs to the diet of 3 turtles, and blue crabs + whelks to the diet of 1 turtle (see Table 1 for mixture values). The variation in the diet of residents was explained more by variation in diet between individuals (mean = 1.62, SD = 1.57, 5th to 95th percentile = 0.22 to 4.05) than by variation in the diet of individuals (mean = 0.74, SD = 0.47, 5th to 95th percentile = 0.11 to 1.63).
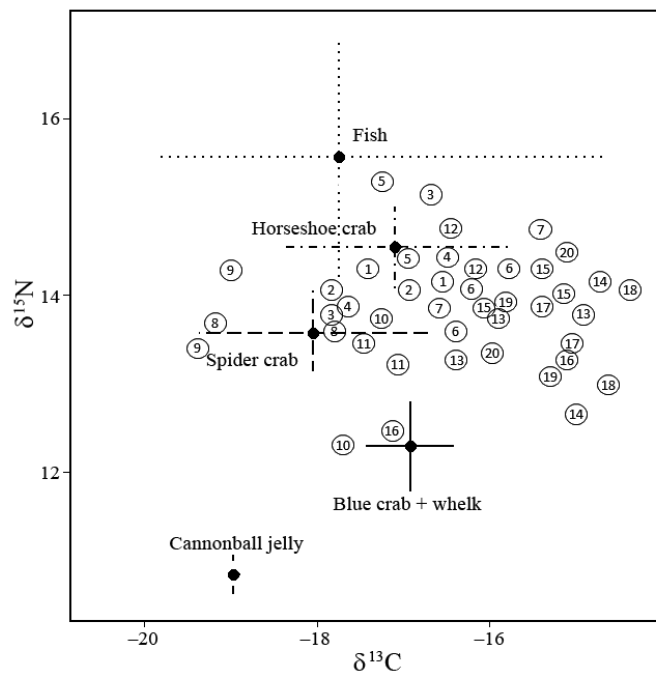

Fig. 5. Isospace plot of potential prey items that contributed to the diet of juvenile loggerhead turtles classified as residents (n = 20). Each numbered circle represents a single $\delta^{13}C$ and $\delta^{15}N$ sample value associated with an individual turtle; the number within the circle identifies individuals. Stable isotope values for the prey items are from Wallace et al. (2009). Prey item values of $\delta^{13}C$ and $\delta^{15}N$ were adjusted for isotopic discrimination between diet and tissue. All 20 resident turtles were included in this figure to allow for a visual comparison of their $\delta^{13}C$ and $\delta^{15}N$ values with those of potential prey items, but only turtles whose $\delta^{13}C$ and $\delta^{15}N$ values were within the convex hull polygon formed by prey items (turtles 1 to 12) were included in the stable isotope mixing (MixSIAR) model runs

DISCUSSION

By examining long-term trends in $\delta^{13}C$ and $\delta^{15}N$ plasma sample values collected from juvenile loggerhead turtles within our study site, we were able to distinguish individuals that had transitioned from the oceanic environment into neritic foraging grounds since sampling first began (recruits), from those that had already shifted into neritic habitat upon first sampling (residents). This allowed us to focus our analyses on resident turtles whose sampling histories were most likely to reflect foraging behavior within our study site. Results of mixed modeling approaches incorporating only resident data indicated that SCL was significantly correlated with both $\delta^{13}C$ and $\delta^{15}N$ values, and that foraging patterns varied significantly among individuals. Examination of the TNW of the resident population indicated that individuals were consistent in resource selection over time, and were specialized in resource use relative to the population. In addition, the resident population as a whole was more specialized in resource use than generalized. In particular, the MixSIAR results suggested that while a range of prey items were available to turtles, horseshoe crabs comprised the majority of the diet of the resident population. In the following paragraphs, we discuss the implications of these findings as they relate to the long-term foraging behavior of loggerhead sea turtles at a single foraging site.

Detection of ontogenetic habitat shift

The ontogenetic habitat shift that juvenile sea turtles undertake from the oceanic environment to neritic foraging grounds is accompanied by a change in diet that is also reflected in the stable isotope values associated with an individual's tissues (Reich et al. 2007, Snover et al. 2010, Avens et al. 2013). In the Northwest Atlantic, baseline $\delta^{15}N$ values have been found to be lower in offshore areas compared to nearshore (McKinney et al. 2010), and this isotopic variation may also be reflected in the isotopic values of a consumer's tissues (Pajuelo et al. 2010, 2012b). The ontogenetic shift in habitat use from offshore to nearshore waters was apparent in individuals that we classified as recruits, as they exhibited a distinct increase in $\delta^{15}N$ values (mean shift = 3.2‰, mean pre-shift = 10.24‰, mean post-shift = 13.45‰) between initial and subsequent sampling events. This increase in $\delta^{15}N$ values is similar to that reported by Avens et al. (2013) (mean shift = 2.5‰, mean pre-

shift = 9.65‰, mean post-shift = 12.12‰) and Snover et al. (2010) (mean shift = 3.1‰, mean pre-shift = 11.0‰, mean post-shift = 14.1‰) for juvenile loggerhead turtles in the Northwest Atlantic, determined using a combination of skeletochronology and stable isotope analysis.

In inert tissues such as bone, the distinct increase in $\delta^{15}N$ values evidencing a shift from oceanic to neritic habitat is apparent from the year prior to and directly following the shift; however, this marked change was not always evident from the initial capture event to the subsequent recapture of recruits in our study, but rather sometimes occurred more gradually over the course of several capture events. This is likely (at least in part) the result of differences in sampling methodology, as well as the examination of different tissues (i.e. blood plasma vs. bone). For instance, unlike bone in which distinct growth marks are deposited annually and therefore provide a consistent, sequential record of stable isotope values over time, our sampling effort was confined to chance encounters with the same individual each year. Thus, for some individuals, a period of years passed between their initial capture and subsequent recapture (see Fig. 2). Additionally, the gradual increase in $\delta^{15}N$ values may be related to the amount of time individuals were foraging within our study site before they were captured, or the gradual change in prey selection as recruits adjust to new prey and foraging techniques.

Despite the short turnover rate of plasma, we were able to detect lower $\delta^{15}N$ values typically associated with foraging in oceanic habitat for the recruits captured in the estuary. Similarly, McClellan et al. (2010) found that the plasma samples of juvenile loggerhead turtles from the same population as our study, whose satellite tracks indicated migration into open-ocean habitats after leaving the estuary, also reflected lower $\delta^{15}N$ values than those of loggerheads whose satellite tracks indicated that they remained in neritic waters. This occurrence may be related to a number of factors, including: (1) recruits may have been sampled shortly after transitioning into the neritic habitat; (2) isotopic turnover may have been slower than has previously been assumed; (3) recruits may grow faster than larger juveniles and therefore may have a lower nitrogen discrimination value (the difference in isotopic ratios between consumer tissue and diet) (Martínez del Rio & Wolf 2005, Reich et al. 2008, Pajuelo et al. 2010); or (4) they may be foraging on prey with lower $\delta^{15}N$ values in the estuary out of familiarity or due to a smaller gape size (Pajuelo et al. 2010).

Although $\delta^{13}C$ values have been shown to vary among loggerhead sea turtles foraging in oceanic versus neritic habitats (Hatase et al. 2002, Snover et al. 2010), as well as latitudinally different areas (Pajuelo et al. 2012a,b), we found no significant difference in $\delta^{13}C$ plasma values at first sampling between recruits and residents. Snover et al. (2010) found that $\delta^{13}C$ varied significantly among oceanic and neritic juvenile loggerhead turtles in the Northwest Atlantic; however, this was based on sampling using cross-sections of humeri that reflects diet over a much longer period of time, and it is possible that the isotopic turnover rate for $\delta^{13}C$ in our plasma samples may have occurred too quickly to reflect foraging in the oceanic habitat. Values of $\delta^{13}C$ may also vary more with latitude than in oceanic versus neritic habitats, and turtles in our study may not have been using geographic areas that differed significantly enough in latitude to result in differing $\delta^{13}C$ values. Similarly, McClellan et al. (2010) found that $\delta^{13}C$ values (for both red blood cells and plasma) did not vary significantly between neritic and oceanic loggerhead turtles from the same population as in the current study, leading them to hypothesize that (1) isotopic turnover rates may not be the same for $\delta^{13}C$ and $\delta^{15}N$ values in turtle blood, or (2) turtles in oceanic waters of the Northwest Atlantic may have access to prey from the continental shelf that becomes entrained in Gulf Stream waters, and similarly, Gulf Stream waters meandering over the continental shelf may provide oceanic prey to neritic turtles.

Individual and population-wide foraging trends of resident turtles

The significant influence of SCL on $\delta^{15}N$ values for resident turtles may indicate that turtles are foraging at a higher trophic level in the estuary as they increase in size. This scenario could occur if turtles continued foraging upon prey that was more familiar to them in the oceanic environment (such as jellyfish) upon first entering the neritic environment, and gradually switched over to a more neritic diet as they adapt to a new environment and feeding strategy. Alternatively, the increased gape size of larger turtles may allow them to eat larger prey (Pajuelo et al. 2010) such as horseshoe crabs, as opposed to smaller turtles which may prey upon smaller invertebrates like spider crabs that also have lower $\delta^{15}N$ values (Table 1). Lastly, smaller and larger juveniles may be foraging on similar prey items, but larger juveniles with slower growth rates may have higher nitrogen

discrimination values resulting in higher $\delta^{15}N$ values (Martínez del Rio & Wolf 2005, Reich et al. 2008, Pajuelo et al. 2010).

The significant influence of SCL on $\delta^{13}C$ values for resident turtles was unexpected since they were foraging consistently in the estuarine waters where it might be less likely that $\delta^{13}C$ values would vary enough for such a trend to occur. However, individual turtles had a greater range in values of $\delta^{13}C$ compared to $\delta^{15}N$ (Table 5), and their main source of prey (horseshoe crabs) also had a higher variation in values of $\delta^{13}C$ compared to $\delta^{15}N$ (Table 1, Fig. 5). This larger amount of variation in $\delta^{13}C$ values may also explain why individual effects (indicating varying foraging patterns among individuals) were highly significant for values of $\delta^{13}C$, but not $\delta^{15}N$. Similar to the significant influence of SCL on $\delta^{15}N$ values, the positive correlation between SCL and $\delta^{13}C$ values could occur if turtles were eating prey with lower $\delta^{13}C$ values (e.g. jellyfish) upon first entering the estuary, and then gradually switching to benthic prey sources with higher $\delta^{13}C$ values (e.g. crabs) as they acclimate to their new environment and attain a larger size.

Although loggerhead sea turtles are typically thought of as generalist foragers (Bjorndal 1997), our examination of TNW indicated that the resident individuals within our study site are consistent in resource selection over time, and that individuals are specialized in resource use relative to the population. Results of our linear mixed effects modeling also showed significant individual effects on $\delta^{13}C$, further supporting varying foraging patterns among individuals. The occurrence of individual specialists in populations of species that are traditionally thought of as generalist foragers is becoming more common as more studies examine the foraging behavior of individuals within populations (Bolnick et al. 2002, 2003, Sargeant 2007). A high degree of variation in resource use among individuals within a population may be associated with a reduction in intraspecific competition (Bolnick et al. 2003, Svanbäck & Bolnick 2007), and may also result in differential growth rates and reproductive fitness (Bolnick et al. 2003). An assessment of the growth rates of 160 juvenile loggerhead turtles within our study site indicated a high degree of variability in growth rates among individuals (Braun-McNeill et al. 2008), and it is possible that this occurrence could be related to our finding of individual specialization and consistency in resource use by individuals over time. If so, population dynamics such as age at sexual maturity may vary considerably for this population, and should be considered during the development of species recovery plans.

Not only were individuals found to be specialized in resource selection over time, but the small δ^{13}C (1.77‰) and δ^{15}N (0.72‰) TNW values indicated that the resident population in our study was more specialized than generalized. The high degree of specialization in resource use for individuals within our population, as well as the specialization of the population itself, may result from the limited geographic range that individuals use while inhabiting the foraging grounds within our study site and the absence of extreme isotopic values among the resources available to turtles while in the estuary. Many of the resident individuals in our study were encountered multiple times within each sampling year, indicating that they were foraging consistently within the estuarine waters. Loggerhead turtles within our study site have also shown a high degree of site fidelity (Avens et al. 2003), and satellite tracking efforts have shown limited movements for some individuals while present in estuarine waters (Braun-McNeill et al. 2010).

In comparison to our population of individuals from a single foraging ground with a narrow isotopic range, sea turtle populations that comprise individuals from multiple geographically distinct foraging grounds often display a broader range in stable isotope values (Vander Zanden et al. 2010, 2013a, Zbinden et al. 2011, Ceriani et al. 2012, Pajuelo et al. 2012a,b, Seminoff et al. 2012). For instance, the population range in stable isotope values in our study (5.06‰ for δ^{13}C and 2.89‰ for δ^{15}N) was much smaller than that of a nesting population of loggerheads at Cape Canaveral National Seashore, FL, USA, that was characterized as a generalist foraging population (10.45‰ for δ^{13}C and 9.03‰ for δ^{15}N) (Vander Zanden et al. 2010). Vander Zanden et al. (2010) suggested that the high isotopic variability of this nesting population was likely the reflection of individual differences in geographically separated foraging areas used by females prior to migration to the nesting site. Within our study site, even though the resident population had a narrow isotopic range, the majority of isotopic variation came from variation in resource use among individuals (i.e. BIC). These findings may indicate that isotopic variability in a single foraging population is more likely to be driven by dietary differences among individuals, whereas isotopic variability in a nesting population is influenced by females using isotopically distinct foraging grounds. Additional studies that examine these characteristics in foraging and nesting populations would be beneficial.

For the 12 individuals whose δ^{13}C and δ^{15}N values were within the convex hull polygon formed by the potential prey items, the MixSIAR model run for the population indicated that although resident loggerhead turtles had a fairly wide range of prey items with varying δ^{13}C and δ^{15}N values to choose from, horseshoe crabs made up the majority of their diet. The model runs on an individual level also indicated that horseshoe crabs were the primary prey of the majority of individuals, but some turtles were also found to feed primarily on spider crabs or blue crabs + whelk. Similar to our examination of TNW, the MixSIAR model also indicated that the variation in the diet of residents was explained more by variation in diet between individuals than by variation in the diet of individuals. Previous stable isotope diet studies of juvenile loggerhead turtles within our study site found the high contribution of benthic crabs and whelks to the diet of turtles, but not horseshoe crabs (Wallace et al. 2009, McClellan et al. 2010). While diet shifts (to finfish species) have been shown for loggerhead turtles in Chesapeake Bay as a result of overfishing of their target prey (horseshoe crab and blue crab) (Seney & Musick 2007), the absence of a significant influence of calendar year in our GAMM analysis would appear to indicate that prey preference or availability remained consistent among sampling years. Instead, the difference in loggerhead diets that we report is likely to be more related to the use of different stable isotope mixing models (Wallace et al. 2009 used IsoSource and McClellan et al. 2010 used SIAR) and variations in the subset of turtles that each study examined. For instance, unlike these previous stable isotope diet studies, our MixSIAR analysis focused on resident turtles (which had higher δ^{15}N values than recruits), and we also examined multiple samples from individuals.

There were 8 resident turtles whose δ^{15}N values were within the convex hull polygon formed by the potential prey items, but whose δ^{13}C values were less negative and fell outside of the polygon. One possible explanation for this occurrence is that these turtles may have been foraging primarily on prey items with less negative δ^{13}C values than those of the potential prey items that we included in the MixSIAR analysis. It is also possible that the tissue–diet discrimination factor that we used may be more accurate for δ^{15}N than δ^{13}C. Last, as reported by other stable isotope studies (Reich et al. 2007, Seminoff et al. 2007), δ^{13}C might be incorporated into tissues at a slower rate than δ^{15}N.

CONCLUSIONS

Our study found that individual juvenile logger-head sea turtles resident in the estuarine waters of North Carolina were consistent in their selection of resources over time and were specialized in resource use relative to the population. In addition, the population as a whole was found to utilize a narrow range of resources. This finding is likely related to high site fidelity within the estuary, and also suggests a strong dependence on primary prey items consumed, particularly horseshoe crabs. The consistency in resources used by individuals over time may underlie significant observed variability in individual growth rates, which in turn may influence individual age at maturation, and ultimately, population dynamics. Given that resource and habitat use is likely to vary among foraging grounds, additional studies examining the long-term foraging behavior of loggerheads in other geographic locations would be beneficial. Finally, our ability to detect the ontogenetic habitat shift from oceanic to neritic foraging grounds in some individuals using stable isotope values of plasma samples may indicate that this methodology could serve as another tool for examining this life stage in sea turtles.

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