

# Long-term resource use and foraging specialization in male loggerhead turtles

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Received: 27 July 2016 / Accepted: 7 October 2016  
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**Abstract** Intra-population variation in resource use has been increasingly reported for different taxa. In particular, foraging specialization of individuals has been quantified for various generalist populations. Because individual differences in resource use can have a great effect on a population's ecological and evolutionary dynamics, it is essential to accurately assess how individuals exploit resources. Recent studies have shown that female sea turtles exhibit long-term individual specialization in resource use. In this study, we used stable isotope analysis ( $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ) of serially sampled sea turtle scutes from two foraging areas in the Northwest Atlantic to evaluate whether male loggerhead sea turtles (*Caretta caretta*) exhibit patterns in resource use over time similar to those reported for female turtles. We found that some male loggerheads show individual specialization and a long-term consistency

in resource use over several years—which adds support to previous findings that male loggerheads exhibit site fidelity to their foraging areas—while others are less consistent or only exhibit consistency for shorter periods of time. This variation in patterns of resource use among male loggerheads appears to be linked to foraging area locations, which were characterized by distinct resource diversity. Thus, these results suggest that resource diversity (habitat and prey items) present at the foraging areas may affect the degree of temporal consistency in resource use and potentially individual foraging specialization in loggerheads. Understanding the drivers of intra-population variation in resource use in loggerheads will allow us to predict how they will respond to changing environmental conditions.

## Introduction

Many generalist populations are composed of individuals of similar age and sex that use a narrow subset of the population's niche. This individual specialization in resource use is now known to be widespread within natural populations in a wide range of vertebrate and invertebrate taxa (Bolnick et al. 2003). However, only recently have studies quantified the degree of this individual specialization within natural populations (Araújo et al. 2011; Vander Zanden et al. 2013a; Newsome et al. 2015; Kernaléguen et al. 2015; Rosenblatt et al. 2015). Knowledge of the degree of individual specialization is fundamental to understanding the effects of ecological interactions on an individual's resource use, which in turn can affect population and community ecological and evolutionary dynamics (Araújo et al. 2011).

Two distinct metrics have been used to address two aspects of individual resource use in populations: temporal

Responsible Editor: L. Avens.

Reviewed by Undisclosed experts.

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consistency and individual specialization. Based on the framework proposed by Roughgarden (1972), the total niche width of a population (TNW) is composed of a within (WIC)- and between (BIC)-individual component. Temporal consistency in resource use in populations is examined using the metric WIC, as it measures the variation in resource use within individuals through time (Vander Zanden et al. 2013a). The degree of individual specialization is examined using the ratio WIC/TNW, as it measures how the individuals' niche width compares to that of the population as a whole. A high degree of individual specialization is not a function of a low WIC but a low WIC in relation to TNW (Bolnick et al. 2003). Thus, examining temporal consistency in resource use, in addition to the degree of individual specialization, allows us to understand whether patterns of individual resource use are temporary or long term, which is important because it will impact how individuals in the population will respond to environmental changes. Therefore, these two metrics, WIC and WIC/TNW, allow for a more comprehensive examination of resource use in populations.

Among the ecological interactions that can affect the degree of individual specialization are intra-specific competition (Svanbäck and Bolnick 2007; Tinker et al. 2008), inter-specific competition (Bolnick et al. 2010), predation (Peacor and Pfister 2006) and ecological opportunity (e.g., diversity of available resources; Araújo et al. 2011). Few studies have assessed how diversity of available resources affects the magnitude of specialization among individuals (Herrera et al. 2008; Darimont et al. 2009; Rosenblatt et al. 2015). Information on how a higher trophic predator, such as the loggerhead, *Caretta caretta*, uses resources among foraging areas with varying resource availability will increase our understanding of the role these predators play across different ecosystems.

In recent years, the use of the isotopic niche as a proxy for the ecological niche (Bearhop et al. 2004; Newsome et al. 2007) has allowed stable isotope analysis to become one of the primary tools to study individual specialization in resource use (Araújo et al. 2011). This is because stable isotopes can reflect the integrated foraging history (diet and foraging habitat) of organisms over long periods of time, which allows investigating not only how individuals within populations vary in their foraging choices but also whether these dietary choices are maintained consistently through time. The dietary history revealed using stable isotopes will depend on the tissue analyzed. A longer foraging history has been reported from stable isotope analyses of continually growing inert tissues such as otoliths in fish (Rooker et al. 2008), baleen in whales (Schell et al. 1989), whiskers in otariids (Cherel et al. 2009) and the gladius in squids (Lorrain et al. 2011). Sea turtle scutes—the keratinized inert tissue covering the carapace—also provide a

sequential, long-term record, because biomarkers in foraging areas are incorporated and retained in this inert tissue (Vander Zanden et al. 2010).

Nitrogen and carbon stable isotope values,  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ , respectively, have been analyzed in serially sampled scutes of Northwest Atlantic (NWA) female loggerhead sea turtles, *C. caretta*, and revealed that, although generalists at the population level, nesting turtles exhibit individual specialization in resource use that is maintained for up to a decade (Vander Zanden et al. 2010). However, it is not known whether male sea turtles exhibit a similar pattern, mainly because, unlike female sea turtles, males do not come ashore and thus are more difficult to sample.

Current knowledge on the foraging behavior of male loggerhead sea turtles comes from two sources: satellite telemetry, which provides information on foraging location, and stable isotope analysis of soft tissues, which provides short-term diet and habitat information. These studies have revealed that male loggerheads appear to use resources similar to those of female loggerheads over a short temporal scale of several months (but see Schofield et al. 2010). For instance, male loggerhead turtles in the North Pacific (Hatase et al. 2002a; Saito et al. 2015) exhibit the same foraging dichotomy as reported for adult females (Hatase et al. 2002b). In the NWA, recent studies based on satellite telemetry showed that male loggerheads use foraging areas similar to those of female loggerheads (Arendt et al. 2012a, b). Also, a recent study in the NWA using stable isotope values suggested that male and female loggerheads use similar habitats and prey items over short periods of time based on isotopic values of soft tissues (blood and epidermis) that integrate the foraging history of loggerheads in the order of months, not years (Pajuelo et al. 2012a). Additionally, the foraging site fidelity that was widely reported for females in sea turtle populations was first confirmed for an aggregation of male loggerheads in the Mediterranean (Schofield et al. 2010) and was suggested for NWA males based on isotopic values and satellite telemetry data (Pajuelo et al. 2012a). Thus, the extent of foraging site fidelity among male loggerhead aggregations is not known.

Accurate parameter estimates are needed for models of population dynamics to predict how sea turtles will respond not only to climatic changes, but also to conservation and management strategies. Most data on sea turtle biology and ecology have focused on results at the population level, but studies on a wide range of organisms reveal that individual differences in resource use can strongly influence a population's ecological and evolutionary dynamics (see reviews by Bolnick et al. 2003 and Araújo et al. 2011). In addition, incorporating male-specific parameters in population models will increase understanding of sea turtle population demographics.

**Table 1** Mean and range of carapace lengths for individual loggerhead turtles and mean and total range of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values of loggerhead turtle scute tissue sampled at two foraging areas: South Carolina/Georgia (SC/GA) and Florida Bay (FLB)

Foraging area	<i>N</i>	Layers	SCL mean, min–max (cm)	$\delta^{15}\text{N}$ individual, total (‰)	$\delta^{13}\text{C}$ individual, total (‰)
SC/GA	13	6–21	83.5, 78.7–90.5	1.66, 4.44	1.35, 3.76
FLB	3	12–22	84.9, 83.8–86.2	4.75, 6.85	2.32, 4.69

For isotope values, individual is the mean range of isotopic values within-individual turtles and total is the range of isotopic values across all individuals. *N* is number of individuals, layers indicate the range of scute layers analyzed per turtle, and SCL is straight carapace length, and min–max are the minimum and maximum SCL

We had two main objectives in this study. We serially sampled scutes of adult male loggerheads at two foraging areas, South Carolina/Georgia (SC/GA) and Florida Bay (FLB), FL, USA, to: (1) investigate the long-term consistency in resource use (diet and habitat) within-individual male loggerhead turtles and (2) evaluate the degree of individual foraging specialization among male loggerhead turtles. Additionally, because male loggerhead samples were collected at two separate foraging areas with distinct biotic and abiotic factors, we provide initial insights from these samples with respect to the effect of resource availability on the degree of resource use consistency and individual specialization between two loggerhead aggregations that use distinct foraging areas.

## Methods

### Data collection

Scute samples were collected from 16 male loggerheads (straight carapace length, SCL > 78 cm) at two foraging areas in SC/GA and FLB (Table 1). Sex was determined via testosterone assay (SC/GA) or laparoscopy (FLB). Based on their SCL, male loggerheads were already matured (SC/GA and FLB) or maturing (SC/GA) (Avens et al. 2015). SCL was measured from the anterior nuchal scute to the posterior notch (Bolten 1999). Samples were taken from the posterior medial region of the third lateral scute, using a 6-mm biopsy punch. Sampling took place during boreal summers of 2011 through 2013 off SC/GA in the South Atlantic Bight (SAB) and during March and June 2011 in FLB in the Subtropical Northwest Atlantic (SNWA) (Fig. 1). The SAB and SNWA are well-established biogeographic areas with distinct oceanographic and biological characteristics (Wilkinson et al. 2009).

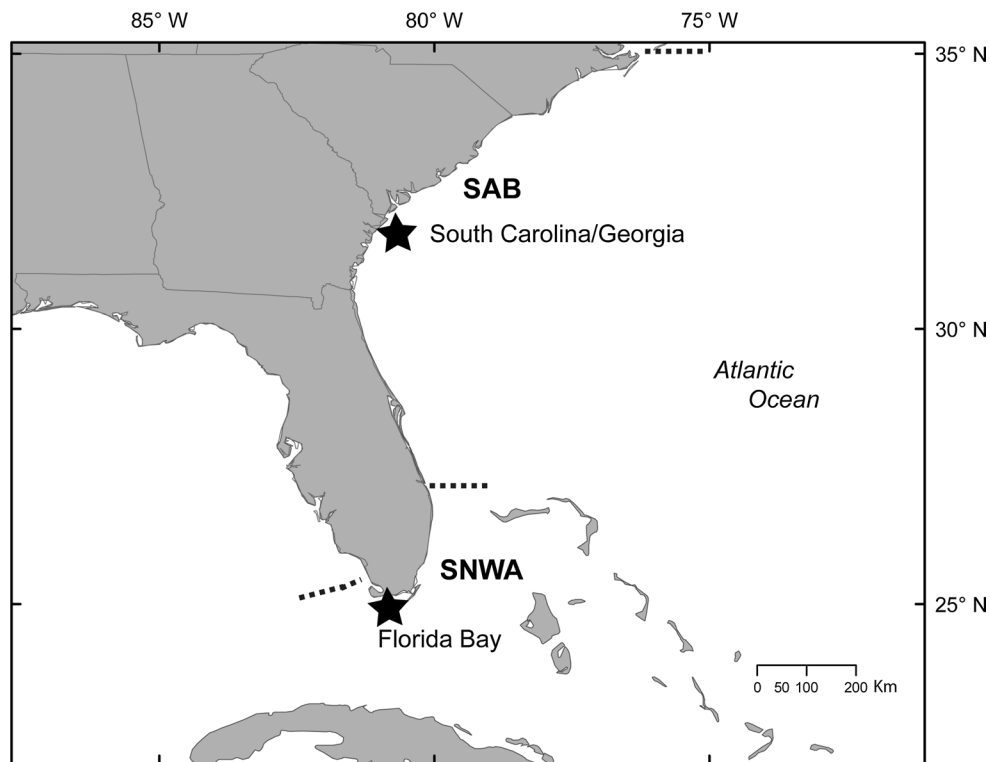
Three males at SC/GA sampled in 2013 and the only three males sampled at FLB in 2011 were fitted with satellite transmitters (Telonics TAM-4525-3 for SC/GA turtles and Wildlife Computers SPLASH10 for the FLB turtles), and their movements were tracked after release from 77 to 258 days in SC/GA (M. Arendt unpubl. data) and 136 to

790 days in FLB (A. Foley, B. Schroeder, B. Witherington unpubl. data). One of the FLB turtles had its satellite transmitter replaced in 2013 and was tracked for a total of 851 days. The three satellite-tracked FLB turtles remained within the western FLB waters throughout the duration of tracking and only one made a short excursion to waters outside of the FLB, on the ocean side of the Florida Keys (A. Foley, B. Schroeder, B. Witherington unpubl. data). Two of the SC/GA turtles with shorter tracks remained closer to the SC/GA area, and the one turtle with the longest tracking duration overwintered off of northern Florida and later returned to coastal waters of GA (M. Arendt unpubl. data).

### Scute preparation and analysis

Prior to microsampling, all scutes were rinsed with deionized water and dried at 60 °C for 24 h. Each scute sample was glued to a glass slide with the ventral side down and the dorsal surface (oldest tissue) exposed and was then microsampled in 50- $\mu\text{m}$  increments using a carbide end mill. Scute tissue grows continually, such that new tissue grows underneath old tissue layers, placing the oldest tissue in the most exterior part of the sample and the most recent tissue in the most interior part. A previous study determined that each 50- $\mu\text{m}$  scute layer, the minimum amount necessary for stable isotope analysis, represents ~0.6 years of resource use in adult loggerhead turtles (Vander Zanden et al. 2010). In cases for which single layers did not provide enough material for stable isotope analysis, consecutive 50- $\mu\text{m}$  scute layers were combined.

Samples were analyzed for  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  by combustion in a Carlo Erba NA 1500 CNS elemental analyzer interfaced via a ConFlo II device to a DeltaV Advantage isotope ratio mass spectrometer in the Stable Isotope Geochemistry Lab at the University of Florida, Gainesville, USA. Results are presented as stable isotope ratios of a sample relative to an international standard and reported in the conventional  $\delta$  notation:  $\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$ , where  $\delta X$  is the relative abundance of  $^{13}\text{C}$  or  $^{15}\text{N}$  in the sample expressed in parts per thousand (‰);  $R_{\text{sample}}$  and  $R_{\text{standard}}$  are the ratios of heavy to light isotope ( $^{13}\text{C}/^{12}\text{C}$  and  $^{15}\text{N}/^{14}\text{N}$ ) in the sample and



**Fig. 1** Foraging locations (stars), South Carolina/Georgia and Florida Bay, where male loggerhead turtles were sampled for scute tissue. Foraging areas are found within distinct biogeographic areas (delim-

ited with dashed lines): South Atlantic Bight (SAB) and Subtropical Northwest Atlantic (SNWA)

international standard, respectively. The standard used for  $^{13}\text{C}$  was Vienna Pee Dee Belemnite and for  $^{15}\text{N}$  was atmospheric  $\text{N}_2$ . Working standards, L-glutamic acid USGS40 ( $\delta^{13}\text{C} = -26.39\text{‰}$  and  $\delta^{15}\text{N} = -4.52\text{‰}$ ) and L-glutamic acid USGS41 ( $\delta^{13}\text{C} = 37.63\text{‰}$  and  $\delta^{15}\text{N} = 47.57\text{‰}$ ), were used to calibrate results. In addition, a reference laboratory standard, homogenized loggerhead scute ( $\delta^{13}\text{C} = -18.36\text{‰}$  and  $\delta^{15}\text{N} = 7.68\text{‰}$ ), was used to examine consistency in isotopic values in a sample similar to the samples used in this study. The analytical precision of measurements—calculated as the SD of replicates of standards—was 0.10 and 0.17 ‰ for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of L-glutamic acid USGS40 ( $N = 53$ ) and 0.28 for  $\delta^{13}\text{C}$  and 0.23 for  $\delta^{15}\text{N}$  of L-glutamic acid USGS41 ( $N = 10$ ), respectively, and 0.17 and 0.29 ‰ for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of scute standards ( $N = 27$ ), respectively.

### Data analysis

The total niche width (TNW) of a population is determined by the sum of the within-individual component (WIC), which is the mean variability in resource use within individuals, and the between-individual component (BIC), which is the variability of resource use among individuals, such that  $\text{TNW} = \text{WIC} + \text{BIC}$ , and the ratio  $\text{WIC}/\text{TNW}$  is used as a measure of the degree of individual specialization (Bolnick

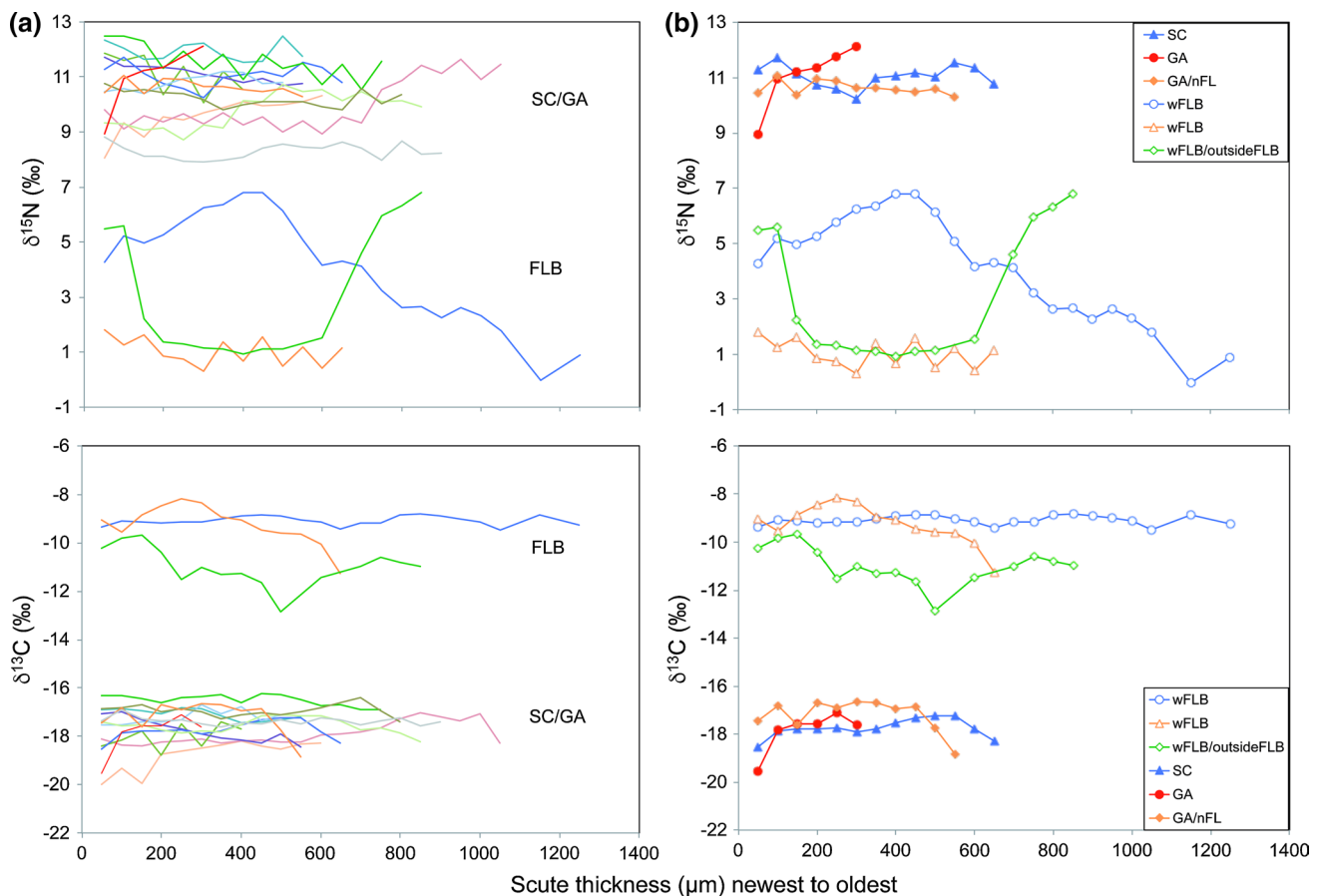
et al. 2003). Values close to 0 indicate that individuals are specialists or use a narrow range of resources, and values close to 1 indicate that individuals are generalists or use a wider range of resources (Bolnick et al. 2002). WIC has been used as a proxy for temporal consistency, as it measures how variable an individual's resource use is over time (Matich et al. 2011; Vander Zanden et al. 2013a). Thus, following the methods of Matich et al. (2011) and Vander Zanden et al. (2013a), we used the variance in  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ , estimated using the ANOVA framework, to calculate the temporal consistency in resource use and the degree of individual specialization among male loggerheads. The mean sum of squares within individuals (MSW) was used as a proxy for WIC:

$$\text{MSW} = \frac{\sum_i \sum_j (x_{ij} - \bar{x}_i)^2}{(N - k)}$$

The mean sum of squares between individuals (MSB) was used as a proxy for BIC:

$$\text{MSB} = \frac{\sum_i \sum_j (\bar{x}_i - \bar{x})^2}{(k - 1)}$$

where  $i$  represents an individual,  $j$  represents a single scute layer,  $N$  is the total number of observations, and  $k$  is the



**Fig. 2** **a** Resource use of individual male loggerhead turtles ( $N = 16$ ) at two foraging areas as indicated by  $\delta^{15}\text{N}$  (top panel) and  $\delta^{13}\text{C}$  (bottom panel) values of successive scute layers. Foraging areas are South Carolina/Georgia (SC/GA) and Florida Bay (FLB). **b** A subset of male loggerheads in SC/GA ( $N = 3$ ) and all FLB males ( $N = 3$ ) were satellite tracked, and the areas they used after release are noted. SC, turtle remained in SC waters; GA, turtle remained in GA waters;

GA/nFL, turtle spent the summer in GA and overwintered in northern Florida; wFLB, turtle remained in the west side of the FLB; and wFLB/outsideFLB, turtle remained the majority of the time in the west side of the FLB but also embarked on a short excursion outside the FLB. Every 200  $\mu\text{m}$  represents approximately 2.4 years of foraging history

number of individuals. The sum of MSW and MSB was used as a proxy for TNW, and the degree of specialization was calculated as WIC/TNW.

Body size difference between foraging areas was assessed using a two-tailed  $t$  test, and a Pearson correlation test was used to evaluate the correlation between thickness of scute and turtle body size. Because our sample size was small for FLB, we could not test for significant differences of WIC and WIC/TNW between foraging areas. All statistics were conducted in R (R Development Core Team 2014) with an  $\alpha$  level of 0.05.

## Results

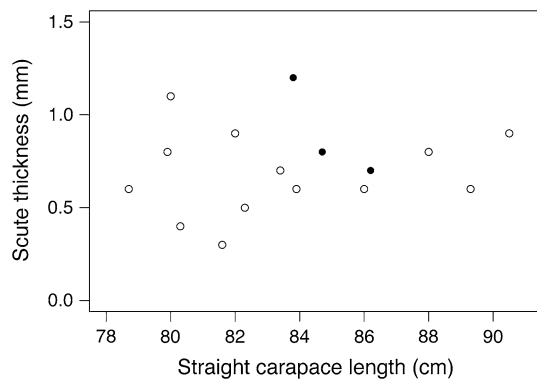
Thickness of scutes ranged from 300 to 1250  $\mu\text{m}$ , representing approximately 3.6–15 years of foraging history (Fig. 2a). The longest record was obtained from the scute

of a turtle using FLB waters. Body size did not differ between turtles sampled in SC/GA and FLB ( $t = -1.0783$ ,  $df = 11.553$ ,  $P = 0.3029$ ), and scute thickness and body size were not correlated among all turtles combined (Pearson's  $r = 0.1243$ ,  $N = 16$ ,  $P = 0.646$ ) or within foraging areas (SC/GA,  $r_s = 0.136$ ,  $N = 13$ ,  $P = 0.659$ , and FLB,  $r_s = -0.888$ ,  $N = 3$ ,  $P = 0.304$ ; Fig. 3).

Temporal consistency within individuals was high in SC/GA male loggerheads as mean within-individual variance (WIC) was small for both  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  (Table 2). In contrast, WIC  $\delta^{15}\text{N}$  values were high for FLB male turtles (Table 2). FLB males appear to be less consistent in resource use through time for  $\delta^{15}\text{N}$  but not for  $\delta^{13}\text{C}$ , which had considerably lower WIC values (Table 2).

WIC/TNW, representing the degree of individual specialization, had values close to 0 (WIC/TNW < 0.1; Table 2), indicating that male loggerheads at both foraging areas exhibit a high degree of individual specialization.





**Fig. 3** Thickness of scute in relation to straight carapace length in loggerhead turtles from South Carolina/Georgia (open circles) and Florida Bay (filled circles)

## Discussion

In this study, we examined the long-term individual patterns in resource use of male loggerhead turtles by using two metrics of resource use. Male loggerheads analyzed were sampled at two distinct foraging locations, SC/GA and FLB. We found that individual resource use in male loggerheads varied with foraging location. However, because our sample size was small for FLB, our results for FLB male loggerheads should be interpreted with caution.

### Temporal consistency in resource use

Male loggerhead turtles were highly consistent in the use of resources through time in SC/GA, but not in FLB, particularly for  $\delta^{15}\text{N}$ , except for one turtle (Fig. 2). The pattern of long-term consistency in SC/GA males is similar to that observed in adult female loggerheads from a nesting beach in Florida, USA (Vander Zanden et al. 2010), and adult female green turtles, *Chelonia mydas*, from a nesting beach in Costa Rica (Vander Zanden et al. 2013a). Only one of these nesting aggregations had WIC estimates available (WIC < 0.4, Vander Zanden et al. 2013a), and they are similar to those of SC/GA males. FLB males were not very consistent in resource use; the  $\delta^{15}\text{N}$  WIC (>1.0) in these

turtles was higher than that of adult green turtles and even oceanic juvenile green turtles (Vander Zanden et al. 2013a), which most likely feed opportunistically in oceanic waters (Bolten 2003) and thus were expected to show lower temporal consistency than adult green turtles (Vander Zanden et al. 2013a). However, comparisons among turtle populations, without knowledge of how isotopic values vary among available resources at the foraging area (e.g., isotopic variation in prey items), should be made with caution (Cummings et al. 2012), because turtles feeding on prey with high isotopic variation will exhibit lower consistency in resource use than turtles feeding on similar prey items with less isotopic variation.

Loggerhead turtles using waters of the NWA exhibit geographic variation in  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  (Pajuelo et al. 2012b; Ceriani et al. 2014) that can be traced to isotopic differences at the base of the food web (Pajuelo et al. 2012a). Thus, large shifts in both  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  in loggerhead turtles indicate that individuals migrated to an isotopically distinct foraging area. SC/GA male loggerheads exhibited long-term consistency in  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ , with values in agreement with those found within this foraging area (from 7.5 to 13.5 ‰ for  $\delta^{15}\text{N}$  and −18.6 to −14.7 ‰ for  $\delta^{13}\text{C}$ ; Pajuelo et al. 2012b). Even though FLB males exhibited a high degree of isotopic variation within individuals, the overall isotopic values found within (and among) individuals correspond to isotopic values expected in turtles using this foraging area (from −0.4 to 6.6 ‰ for  $\delta^{15}\text{N}$  and to −13.8 to −6.7 ‰ for  $\delta^{13}\text{C}$ ; Pajuelo et al. 2012b; Ceriani et al. 2014; Vander Zanden et al. 2015). Satellite telemetry data revealed that SC/GA male loggerheads remained in continental shelf waters of SC/GA or within the SAB throughout the duration of the transmission. Similarly, FLB male loggerheads, in general, remained in continental shelf waters of the west side of the FLB. Thus, the concordant stable isotope values and the satellite tracks of male loggerheads indicate that they exhibit high foraging site fidelity.

Foraging site fidelity was first revealed in an aggregation of male loggerheads in the Mediterranean (Schofield et al. 2010) and was suggested for male loggerheads in the NWA (Pajuelo et al. 2012a). In this study, by looking at long-term isotopic data in male loggerhead scute records at SC/GA

**Table 2** Within-individual variation (WIC), between-individual variation (BIC) and total niche width (TNW) for nitrogen ( $\delta^{15}\text{N}$ ) and carbon ( $\delta^{13}\text{C}$ ) stable isotope values of successive scute layers of male loggerhead turtles at two foraging areas: South Carolina/Georgia (SC/GA) and Florida Bay (FLB)

Foraging area	N	$\delta^{15}\text{N}$				$\delta^{13}\text{C}$			
		WIC	BIC	TNW	WIC/TNW	WIC	BIC	TNW	WIC/TNW
SC/GA	13	0.29	19.51	19.8	0.02	0.16	4.32	4.48	0.04
FLB	3	3.37	38.64	42.01	0.08	0.37	17.70	18.07	0.02

WIC is a measure of the temporal consistency in resource use, and the WIC/TNW ratio provides a measure of the degree of individual specialization in male loggerheads turtles. WIC/TNW values can range from 0 to 1, indicating a population is composed of specialist or generalist individuals, respectively

and FLB, we expand our knowledge on male loggerhead foraging behavior over long periods of time in these foraging areas. Thus, high foraging site fidelity may be characteristic of male loggerhead turtles in general. Consistent use of a known foraging ground that provides sufficient resources is considered a more beneficial strategy than wandering through unexplored new areas (Schofield et al. 2010). However, this behavior can prove detrimental if foraging areas become heavily impacted by anthropogenic activities. A recent study showed that loggerhead turtles in the Gulf of Mexico maintained their dietary patterns and continued to forage near the site of the Deepwater Horizon oil spill in the Northeastern Gulf of Mexico in 2010, thereby risking exposure to the effects of oil and chemical dispersants (Vander Zanden et al. 2016). Isotopic changes within the range of isotopic values expected in turtles using a particular foraging area indicate changes in diet and/or habitat use. Thus, initial results for FLB male loggerheads in this study, revealing large variation in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values, combined with satellite telemetry data (A. Foley, B. Schroeder, B. Witherington unpubl. data) suggest that FLB loggerheads might shift their habitats and/or diet.

The low isotopic variation within SC/GA male loggerheads indicates that turtles may be consistently feeding on similar prey items or on prey items with similar isotopic composition. Stomach content analysis in loggerheads at this foraging area has revealed that turtles rely on prey items with similar trophic levels, such as crabs, and that some turtles were selectively consuming particular prey items over a few days (Youngkin 2001). Two SC/GA male loggerheads showed a large change in both  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values (up to 3.3 ‰ for  $\delta^{15}\text{N}$  and 2.2 for  $\delta^{13}\text{C}$ , Fig. 2a). These values, however, were within the isotopic values expected for turtles within this foraging area. Such changes in both  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values suggest that the turtles moved to another area within its foraging region where both isotope values were different at the base of the food web. It could also indicate that when the turtles moved to a new habitat, as reflected by the  $\delta^{13}\text{C}$  values, it utilized prey items of different trophic position, which would have changed the  $\delta^{15}\text{N}$  values.

Recent studies indicate that SAB loggerheads spend the winter in waters further offshore than their near-shore summer habitats (Hawkes et al. 2011; Griffin et al. 2013). However, the scute records of SC/GA male loggerheads did not show cyclical changes in  $\delta^{13}\text{C}$  reflecting this seasonal variation in habitat use. Indeed, the single SC/GA (labeled GA/nFL in Fig. 2b) that was tracked to outer continental shelf waters off of northern Florida during winter exhibited low variation in  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ , except in its oldest records where a decrease of ~2 ‰ in  $\delta^{13}\text{C}$  (Fig. 2b) may be evidence of the use of oceanic habitats prior to settlement in continental shelf waters. The period of time represented in each scute

sample (0.6 years) may not allow documentation of these seasonal variations in habitat use (Vander Zanden et al. 2015). Additionally, it is possible that time for isotopic turnover in the adult loggerhead scute and thus, time represented in the scute record, may have been underestimated as differences in temperature—which can affect biological turnover rates—were not taken into account when estimating the age of adult loggerhead scute (Vander Zanden et al. 2010). These potential factors need to be taken into consideration when using sea turtle isotopic scute records and suggest that these records may not reflect short-term or seasonal animal movement. Experimental work is needed to determine empirically the growth rate and isotopic turnover time in scute of adult loggerhead turtles to accurately estimate the length of time reflected in each scute sample and improve the interpretation of isotopic changes in turtle scute records.

FLB is located in the SNWA, where warm waters are characterized by great biotic and habitat diversity (Wilkinson et al. 2009). Benthic invertebrate diversity along the US east coast increases with decreasing latitude and is high in the SNWA (Roy et al. 1998), as are the available habitats such as seagrass beds, mangroves and coral reefs (Wilkinson et al. 2009). Loggerheads in the NWA mostly feed on benthic invertebrates (Hopkins-Murphy et al. 2003). Thus, the larger isotopic variation observed within male loggerheads using FLB waters suggests that these turtles exploit a variety of resources with isotopic values that are different from those of turtles using SC/GA waters. Carbon sources (e.g., seagrass, macroalgae and phytoplankton) in the FLB have wide-ranging  $\delta^{13}\text{C}$  values, from −18 to −6 ‰ (Behringer and Butler 2006). The  $\delta^{13}\text{C}$  values observed in FLB loggerheads range from −12 to −7.4 ‰ (Pajuelo et al. 2012b, and this study), which suggest that FLB loggerheads may potentially consume prey items that use different carbon sources. Preliminary data from FLB loggerhead gut contents and feces reveal that FLB turtles often rely on sponges (B. Stacy pers. comm. and B. Witherington unpubl. data).

Stable nitrogen isotopic values of sponges and other benthic invertebrates, such as mollusks and arthropods in the FLB, have values ranging from −1.6 to 7.4 ‰ (Behringer and Butler 2006), similar to the wide range in  $\delta^{15}\text{N}$  values found in FLB loggerheads (Pajuelo et al. 2012b, and this study). Future research using compound-specific stable isotope data will allow examination of the degree to which FLB loggerhead isotopic variation is driven by dietary variation among loggerheads. Additionally, visual inspection of Fig. 2a reveals shorter intervals with less isotopic variation (i.e., flat or uniform sections) within FLB turtles, which are assumed to reflect habitat residency (for  $\delta^{13}\text{C}$ ) or consumption of similar prey items over time (for  $\delta^{15}\text{N}$ ). Thus, FLB turtles may be consistent in the use of resources for shorter periods of time.

Overall, SC/GA and, possibly, FLB male loggerhead turtles show  $\delta^{13}\text{C}$  values over time that are strikingly more consistent than their  $\delta^{15}\text{N}$  values. This indicates that male loggerheads are consistently using the same foraging habitat(s) or ultimate carbon sources (reflected by  $\delta^{13}\text{C}$ ), while the amount of dietary variation (reflected by  $\delta^{15}\text{N}$ ) may depend on the availability of resources within a particular foraging area.

### Individual specialization

Exhibiting temporal consistency in resource use alone does not necessarily indicate the degree of individual foraging specialization in a population, as the latter will depend upon how individuals partition the range of available resources (Bolnick et al. 2003). However, it is essential to obtain information on individual resource use through time to understand whether the pattern of resource use (i.e., individualization or generalization) is maintained over time.

In this study, SC/GA male loggerheads exhibited both consistency in resource use through time and a high degree of individual specialization, similar to those observed in nesting loggerheads (Vander Zanden et al. 2010) and quantified in nesting green turtles (Vander Zanden et al. 2013a) and juvenile loggerheads (Goodman Hall et al. 2015). The isotopic range within SC/GA and some FLB male turtles is smaller than the total isotopic range found across all individuals at each foraging area, revealing that male loggerheads are part of a generalist population with specialized individuals. However, Vander Zanden et al. (2010, 2013a) reported on individual specialization in nesting populations, which are composed of individuals that migrate from different foraging areas. Because geographic area can account for the large isotopic variation found among nesting sea turtles (Ceriani et al. 2012; Pajuelo et al. 2012b; Vander Zanden et al. 2013a), the degree of individual specialization (WIC/TNW) in nesting turtles cannot be compared with that of turtles from one foraging ground. TNW is affected by both WIC and BIC values. If WIC values are similar between two populations, a greater isotopic variability among individuals (BIC) within one population will increase its TNW value, which in return will indicate a greater degree of individual specialization (WIC/TNW) for that population. By sampling turtles at their foraging grounds, we assume that the variations in  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values within (WIC) and between (BIC) turtles represent resource use variations within the foraging area.

The first observations of dietary specialization in long-assumed opportunistic loggerhead turtles were reported by Ruckdeschel and Shoop (1988). They analyzed stomach contents of hundreds of loggerhead turtles and showed that some individuals selectively consumed the same prey types. However, the dietary information obtained from stomach

contents reveals what an organism consumed within the past few days, not whether the organism's dietary preferences are maintained through time. Even though we do not have information on the specific prey items or groups of prey items the SC/GA male loggerheads consume in this foraging area, the isotopic evidence reveals that males forage consistently on the same prey items or groups of prey items with similar isotopic values over a long period of time. This also suggests that availability of resources in SC/GA waters remained consistent or that environmental variability that affects resource abundance was low, so that turtles could maintain individualized foraging behaviors for long periods of time.

Initial results reveal that SC/GA and FLB male loggerheads have similar low WIC/TNW values suggesting no differences in individual specialization between turtles using these two different foraging areas. However, because our sample size was small in the FLB, these results should be interpreted with caution. The smaller isotopic mean range within individuals compared to that of the population (Table 1) may suggest that SC/GA male loggerheads could be more individually specialized than FLB males. Visual inspection of the scute records of two of the FLB male loggerheads reveals large within-individual isotopic variation for  $\delta^{15}\text{N}$  and/or  $\delta^{13}\text{C}$  (Fig. 2a), almost encompassing the range of isotopic values found in these turtles (Pajuelo et al. 2012b), suggesting that these two FLB males exhibit a variation in resource use, utilizing a wide range of available resources in their foraging area. However, because FLB males appear to be consistent in the use of resources for short periods of time (see *Temporal consistency in resource use* above), we hypothesize that they too can specialize their diet and habitat use, but this behavior is not consistent in the long term. This pattern in resource use may be related to environmental changes. FLB has experienced dramatic ecological changes since the late 1980s, including seagrass die-offs, and phytoplankton and cyanobacteria blooms, which have had repercussions on the diversity and abundance of food web organisms such as crustaceans, sponges and other prey species (Fourqurean and Robblee 1999; Matheson et al. 1999; Peterson et al. 2006). Further systematic research is needed to assess whether the pattern observed in FLB male loggerheads is consistent with a larger sample size and to explore whether environmental factors are driving the pattern observed in FLB turtles.

Previous studies in wolves (*Canis lupus*, Darimont et al. 2009) and American alligators (*Alligator mississippiensis*, Rosenblatt et al. 2015) have shown that an increase in resource diversity increased the degree of individual specialization in these generalist predators. Population niche width (TNW) expanded in both studies, similar to what we saw in FLB turtles, as a result of the increase in available resources, which affects individual specialization (WIC/



TNW) (Bolnick et al. 2003). Whether the degree of individual specialization in loggerhead turtles is also affected by variation in resource diversity remains to be determined.

Similar to other studies (Rodríguez and Herrera 2013; Vander Zanden et al. 2013b; Kernaléguen et al. 2015), we used isotopic data to represent the ecological niche and evaluate individual specialization in a generalist population. Another approach adjusts for prey isotopic values when assessing the degree of individual specialization in populations, as WIC and BIC, and ultimately TNW, are affected not only by the diversity of prey items but also by the isotopic variation in prey items (Newsome et al. 2007). Because we did not have access to all potential prey items for loggerheads at the two foraging areas sampled in this study, we could not compare WIC/TNW values using this approach. However, the higher diversity in benthic organisms and habitats encountered in SNWA waters compared to SAB waters, where the two foraging areas FLB and SC/GA are found, respectively, supports the finding of a wider isotopic niche (TNW) in FLB male loggerheads.

Intra- and inter-specific competition may also influence foraging decisions of individuals over time. Experimental and observational studies have found that high intra-specific competition leads to increased individual specialization (Araújo et al. 2011), whereas inter-specific competition weakens individual specialization (Bolnick et al. 2010). Data on loggerhead population density, prey abundance and possible competitors needed to assess intra-specific and inter-specific competition are not available. Sex has also been found to influence intra-specific variation in resource use (Elliot Smith et al. 2015), with the rationale that male and female individuals within a population face different evolutionary and energetic pressures, in particular related to reproduction. As an avenue for future research, we recommend assessments of sex-based differences in temporal resource use and individual specialization in loggerhead turtles within and among foraging areas. Information on how male and female loggerhead turtles use resources will allow us to better understand sea turtle population demographics and habitat needs.

## Conclusions

This study shows that SC/GA male loggerheads exhibit consistency in resource use over time and a high degree of specialization of resource use similar to that reported for female loggerhead and green turtles. The long-term consistency in resource use found among SC/GA male loggerheads revealed that, similar to female sea turtles, males exhibit fidelity to their foraging areas. This long-term consistency suggests that resource abundance may have been consistent in waters of the SC/GA, leading to a consistency

in male loggerhead foraging behavior. FLB males exhibited a different foraging behavior, and their use of resources was not consistent in the long term; however, our sample size was small. The initial results reported here on population-level variation in temporal consistency in resource use among loggerhead turtles that use distinct foraging areas, provide insights into how resource diversity and abundance may affect the foraging behavior of loggerheads. Future research should examine this pattern with larger sample sizes and in other populations to test the validity of our results. As higher trophic-level organisms, loggerhead sea turtles play an important role in their ecosystems. Understanding how sea turtles utilize resources will allow us to predict how they will respond and whether they will be able to adapt to changing climate and environmental conditions.

**Acknowledgments** We thank the captains and crew of the RV's *Georgia Bulldog* and *Lady Lisa* as well as J. Schwenter and J. Byrd for invaluable support during fieldwork. The US Fish and Wildlife Service, US National Marine Fisheries Service, National Oceanic and Atmospheric Administration and the National Fish and Wildlife Foundation provided funding support for this project. For comments on earlier versions of the manuscript, we thank L. C. Majure, M. Brenner, B. MacFadden and two anonymous reviewers. We also thank J. Curtis and the Stable Isotope Lab at the University of Florida for assistance with stable isotope analysis. Turtle samples were collected in compliance with the National Marine Fisheries Service (Section 10(A)(1)(a) Permit #15566 and Permit #14622), Georgia DNR Scientific Collection Permit (CN21303), Florida Fish and Wildlife Conservation Commission (Marine Turtle Permit #163), Everglades National Park (Permit # EVER-2012-SCI-0030) and the Institutional Animal Care and Use Committee of the University of Florida. The statements, findings, conclusions and recommendations are those of the authors and do not necessarily reflect the views of the National Oceanic and Atmospheric Administration, US Fish and Wildlife Service or any branch of the federal government.

## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

**Research involving human participants and/or animals** Turtle samples were collected and processed in compliance with various scientific collection permits listed in acknowledgment section.

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