


Foraging area, not trophic position, is linked to head size variation in adult female loggerhead turtles

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Keywords

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Abstract

Variation in trophic morphology among individuals within a population may suggest intrapopulation variation in diet and resource use. In such situations, individuals may occupy more specialized roles within a generalist population. Among loggerhead turtles (*Caretta caretta*), adults exhibit variation in head size, a likely predictor of bite-force generation and therefore feeding performance. We investigated several factors that may affect variation in head size for female loggerheads nesting on Wassaw Island, Georgia, USA. We first quantified the amount of variation in head size (width, length and depth) that was explained by differences in body size. We then investigated whether variation in absolute head size and variation in head size not explained by body size (relative head size) were related to foraging area, trophic position or both using stable isotope analysis of carbon and nitrogen. We found that greater than 50% of the variation in head size was not explained by body size and that foraging area contributed at least partially to differences in head size, while trophic position was not correlated with differences in head size. These results suggest that there may be some trophic specialization within foraging areas, such that turtles foraging in distinct areas maintain different relative head sizes as a result of differences in diet and resource availability. However, the variation in head size that does exist within a foraging area does not appear to be related to specialization at different trophic positions. Understanding factors that affect variation in trophic morphology can provide valuable insight into the trophic interactions of a species and reveal mechanisms that reduce intraspecific competition.

Introduction

Animal populations that occupy a large generalist niche can exhibit more phenotypic variation than specialized populations (Van Valen, 1965; Bolnick *et al.*, 2003, 2011). Variation in trophic morphology among individuals within a population may suggest that individuals occupy specialized roles within the wider foraging niche of the species. Specialized roles may be related to intrapopulation variation in foraging habitat, dietary selection or both (Vander Zanden *et al.*, 2010). Understanding how these factors are related to variation in phenotypic traits is important because these factors may affect the degree of intraspecific competition among individuals, a selective pressure that can affect both the ecology and conservation of a species.

Animals with varied resource use often exhibit corresponding differences in trophic morphology, such as head size (Wainwright *et al.*, 1991; Verwajen, Van Damme & Herrel, 2002). Increasing head size generally correlates with an

increase in bite-force generation, which allows individuals to consume dietary resources that require greater mechanical force to process (Pfaller *et al.*, 2010; Pfaller, Gignac & Erickson, 2011; Marshall *et al.*, 2012). Intraspecific variation in head size and bite force in connection with dietary variation has been observed in several vertebrate groups, including fishes (Mittelbach, Osenberg & Wainwright, 1999), lizards (Herrel *et al.*, 1999; Huyghe *et al.*, 2007), snakes (Forsman, 1991; Forsman & Shine, 1997) and birds (Clabaut *et al.*, 2009). For generalist species, variation in bite-force generation and feeding performance among individuals may allow populations to use a greater diversity of dietary resources across a wider geographic range.

Loggerhead sea turtles (*Caretta caretta*) are generalist marine carnivores that feed on a wide range of benthic invertebrates, but also on sea jellies and other pelagic organisms (Dodd, 1988; Hatase *et al.*, 2002; Seney & Musick, 2007). Especially as adults, loggerheads possess relatively large heads and high bite-force generation compared to other marine turtle

species, allowing loggerheads to increase their dietary breadth as they grow larger and consume prey items that may be inaccessible to other turtle species (Dodd, 1988; Seney & Musick, 2007; Marshall *et al.*, 2012). Variation in resource use extends beyond ontogenetic shifts in dietary selection, however, as some loggerhead populations also display fidelity to geographically distinct foraging areas (e.g. Hatase, Omuta & Tsukamoto, 2010; Zbinden *et al.*, 2011; Pajuelo *et al.*, 2012a; Tucker, MacDonald & Seminoff, 2014).

Loggerheads nesting in Georgia, USA, use three well-characterized foraging areas within the Northwest Atlantic Ocean (Wilkinson *et al.*, 2009; Vander Zanden *et al.*, 2014): (1) Mid-Atlantic Bight (MAB), (2) South Atlantic Bight (SAB) and (3) Subtropical Northwest Atlantic (SNWA). Using satellite telemetry of adult loggerheads and stable isotope analysis of epidermal tissue, Pajuelo *et al.* (2012b) demonstrated that individuals could be assigned to these foraging areas with high accuracy. Subsequently, Vander Zanden *et al.* (2014) found that body size differs among females using different regions, which was attributed to differences in oceanographic characteristics in each region (e.g. productivity and temperature) and not to genetic differences among females (Shamblin *et al.*, 2011). However, head size variation has not been characterized within and among females using different regions, and it remains unknown how this morphological feature is related to foraging area, trophic position or both. The goal of this study was to examine several factors that may be related to variation in head size among females in this population. Because head size is often highly correlated with body size, we first quantified the proportion of head size variation that was explained by differences in body size. We then used carbon and nitrogen stable isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) values to test two non-mutually exclusive hypotheses that might explain additional variation in head size: (1) head size variation is related to the foraging area of an individual and (2) head size variation is related to the trophic position of an individual.

Materials and methods

Morphometrics and skin sample collection

Female loggerheads were measured and sampled on Wassaw Island, Georgia, USA (31.89°N 80.97°W) (Fig. 1) during the nesting seasons of 2013 and 2014 (May to August). Metal calipers were used to take straight measurements (± 1 mm) of head width ($N = 108$), head length ($N = 101$) and head depth ($N = 92$) (Fig. 2). All three head dimensions could not be obtained from every individual, due to the position of the turtle or the stage of the nesting process when each turtle was encountered. Curved carapace length (CCL; notch-to-notch) was also measured (± 1 mm) using a flexible measuring tape and measurements that were skewed by excessive epibiota were noted and excluded. Head and body size measurements were collected at every encounter and the median value from repeated measurements of the same turtle was used for statistical analyses. Relative head length, width and depth were calculated using the residuals from the linear regression of the Log_{10} head dimensions on Log_{10} CCL for each individual.

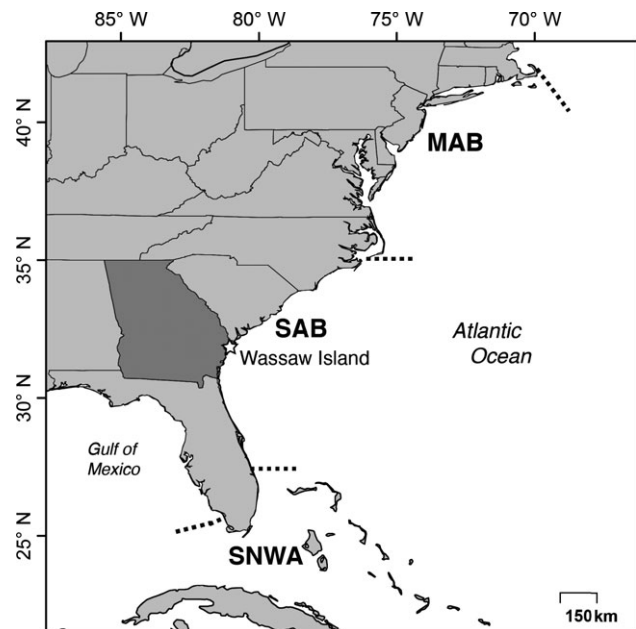


Figure 1 Loggerhead foraging areas in the Northwest Atlantic Ocean and nesting beach location (Wassaw Island, Georgia). Dashed lines divide the three foraging areas. MAB, Mid-Atlantic Bight; SAB, South Atlantic Bight; SNWA, Subtropical Northwest Atlantic.

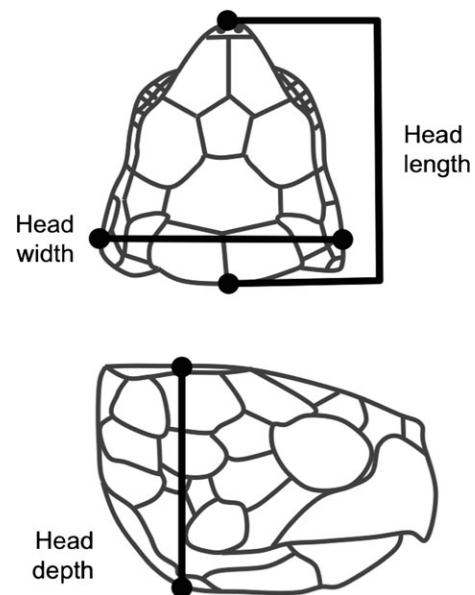


Figure 2 Schematics illustrating head size measurements of female loggerhead turtles.

Skin samples from the 108 individuals with at least one head size measurement ($N = 65$ and 43 in 2013 and 2014, respectively) were collected for stable isotope analysis. Samples were taken from the “shoulder” area using a 6-mm biopsy punch and were stored in 70% ethanol prior to isotopic

analysis, as used in previous protocols (Pajuelo *et al.*, 2012a; Vander Zanden *et al.*, 2014). Epibionts, sand and other debris were removed with deionized water and isopropyl alcohol swabs. The epidermis was separated from the underlying tissues with a scalpel and then cut into fine pieces prior to drying at 60°C for a minimum of 24 h. Because lipid extraction does not significantly affect the $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values (Vander Zanden *et al.*, 2014), no lipid removal procedures were used, and we are confident that the samples are comparable to past studies in which lipids were removed.

Stable isotope analysis

Skin samples weighing 0.5–0.6 mg were analyzed for carbon and nitrogen stable isotope composition at the Department for Geological Sciences, University of Florida, Gainesville, Florida, using a Costech ECS 4010 elemental analyzer interfaced via a ConFlo III to a DeltaPlus XL isotope ratio mass spectrometer (ThermoFisher Scientific, Waltham, MA, USA). Isotope abundance is expressed as a ratio relative to a standard using δ notation in parts per thousand (‰):

$$\delta = [(R_{\text{sample}}/R_{\text{standard}}) - 1]$$

where R_{sample} and R_{standard} correspond to the ratios of heavy-to-light isotopes ($^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$) in the sample and international standard, respectively. Standardized reference materials (USGS40, USGS41 and a homogenized loggerhead scute) were used to evaluate the accuracy and precision of our results. Two reference materials USGS40 (L-glutamic acid with isotopic compositions of $\delta^{13}\text{C} = -26.29$ and $\delta^{15}\text{N} = -4.52$ ‰) and USGS41 (L-glutamic acid enriched in ^{13}C and ^{15}N with isotopic compositions of $\delta^{13}\text{C} = 37.63$ ‰ and 47.57 ‰) were used to calibrate results. The standard deviation of USGS40 was 0.14 ‰ for $\delta^{13}\text{C}$ and 0.11 ‰ for $\delta^{15}\text{N}$ values ($N = 24$), and the standard deviation of USGS41 was 0.23 ‰ for $\delta^{13}\text{C}$ values and 0.40 ‰ for $\delta^{15}\text{N}$ values ($N = 6$). Repeated measurements of a laboratory reference material, homogenized loggerhead scute, were used to examine consistency in a sample with similar isotopic composition to samples in this study. The standard deviation of the laboratory reference material was 0.12 ‰ for $\delta^{13}\text{C}$ values and 0.36 ‰ for $\delta^{15}\text{N}$ values ($N = 8$).

To investigate how head size variation is related to foraging area and trophic position, we first grouped individuals geographically using both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values, and then examined remaining isotopic variance in $\delta^{15}\text{N}$ values as an indicator of dietary differences. Because isotopes are assimilated through the diet, the isotopic composition of an animal's tissue can reflect both trophic patterns and foraging location when baseline isotopic values vary spatially (Wunder, 2012). In the Northwest Atlantic Ocean, different biogeochemical processes create a predictable latitudinal gradient in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values among primary producers at the base of the food web (Goericke & Fry, 1994; Montoya, 2007), which in turn is reflected in higher trophic level organisms including loggerhead turtles (Pajuelo *et al.*, 2010, 2012b; Ceriani *et al.*, 2014). Following the approach described in Pajuelo *et al.* (2012b), we used $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values to assign each turtle to a foraging

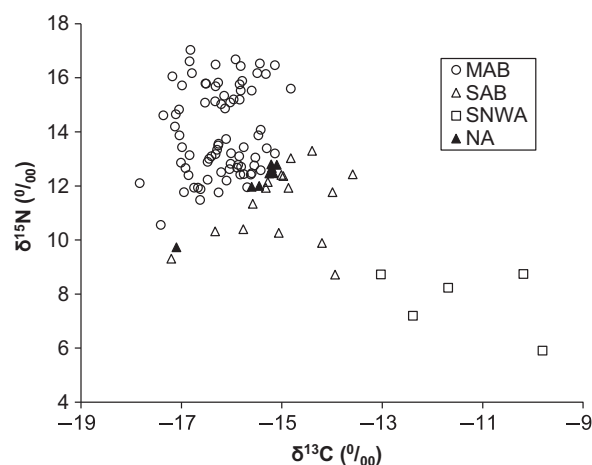


Figure 3 Stable carbon and nitrogen isotope values of female loggerhead turtles nesting on Wassaw Island, Georgia, in 2013 and 2014. The turtles were assigned to three different foraging areas within the Northwest Atlantic through discriminant analysis with posterior probability of group membership ≥ 0.6 . MAB, Mid-Atlantic Bight; SAB, South Atlantic Bight; SNWA, Subtropical Northwest Atlantic, NA, Not assigned.

area within the Northwest Atlantic Ocean: (1) Mid-Atlantic Bight (MAB), (2) South Atlantic Bight (SAB) and (3) Subtropical Northwest Atlantic (SNWA) (Figs 1 and 3). Each female in this study was assigned to one of the three foraging areas with discriminant function analysis and selecting posterior probabilities of ≥ 0.8 and ≥ 0.6 , which represent an eightfold and threefold improvement over random odds, respectively (Wunder, 2012). Additional details for this method can be found in Pajuelo *et al.* (2012b).

Stable isotope signatures also vary predictably with trophic position within a foraging area (Minagawa & Wada, 1984). Specifically, $\delta^{15}\text{N}$ values tend to increase the higher up the food web an organism or an individual is positioned (Post, 2002). Therefore, we used $\delta^{15}\text{N}$ values as a proxy for relative trophic position among individuals within each foraging area to investigate relationships between relative trophic position and trophic morphology. Although isotopic turnover rates have not been measured for adult loggerheads, we estimate that the isotopic composition of skin samples collected from nesting turtles reflect the diet assimilated in foraging areas several months prior to nesting (Reich, Bjorndal & Martinez del Rio, 2008; Prior, Booth & Limpus, 2015).

Statistical analyses

Log-transformed linear regressions were used to analyze relationships between absolute head size metrics and body size, as well as between absolute and relative head size metrics and trophic position. Differences in body size and both absolute and relative head size among turtles using different foraging areas were first evaluated using ANOVA, however, data were not always normally distributed or homoscedastic (requirements of ANOVA). Thus, we tested relationships between head size

and foraging area using the non-parametric Kruskal–Wallis one-way analysis of variance and the Bonferroni-corrected Dunn’s post hoc test to account for unequal sample sizes. We used Levene’s test and found homoscedasticity among all datasets except relative head length, and therefore confirmed the comparisons among these data using Welch’s *t*-test (data not shown). All analyses were performed using the program R version 3.0 (R Core Team, 2015) and an alpha level of 0.05.

Results

Each head size metric was positively correlated with body size (Fig. 4). Body size (CCL) explained 43% of variation in head width (Fig. 4a), 22% of variation in head length (Fig. 4b) and 18% of variation in head depth (Fig. 4c).

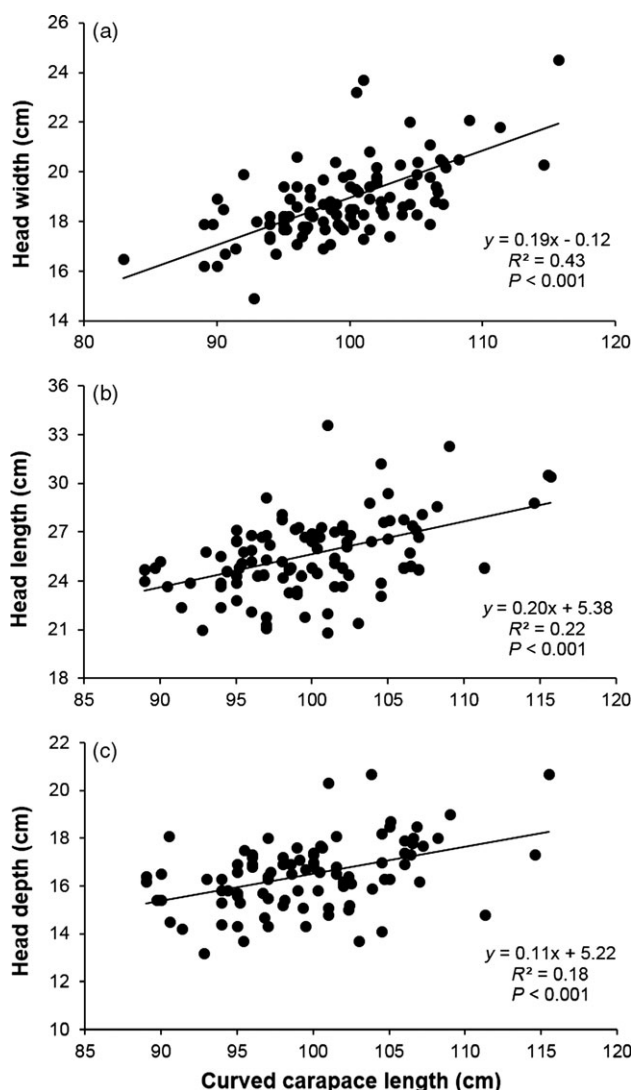


Figure 4 Relationship between body size (curved carapace length) and (a) head width, (b) head length and (c) head depth in female loggerhead turtles. All relationships were significant and positive.

The number of turtles assigned to each foraging area is shown in Table 1. The number of individuals assigned to a foraging area increased from 80% (86 of 108) to 92% (99 of 108) as the posterior probability threshold was decreased from 0.8 to 0.6, respectively. Because we found no qualitative differences in the results at different thresholds, we have presented the results from the more inclusive dataset only using the 0.6 posterior probability threshold. Body size for turtles foraging in the MAB was significantly greater than turtles foraging in the SAB ($Z = 3.563$, $P = 0.001$) (Fig. 5c). Only absolute head depth was significantly larger for turtles foraging in the SNWA than in the MAB ($Z = -2.502$, $P = 0.037$), whereas both absolute head width and depth were significantly larger for turtles in the SNWA than in the SAB (HW, $Z = -2.656$, $P = 0.024$; HD, $Z = -2.752$, $P = 0.018$) (Fig. 5b–d). All other comparisons of absolute head size metrics among turtles using different foraging areas were not significantly different. A complete summary of head size data is shown in Table 2.

Turtles foraging in the SNWA had significantly larger relative head width ($Z = -3.185$, $P = 0.004$), relative head length ($Z = -2.789$, $P = 0.016$) and relative head depth ($Z = -3.048$, $P = 0.005$) than in the MAB (Fig. 6). In addition, turtles foraging in the SNWA had significantly larger relative head depth ($Z = -2.217$, $P = 0.021$) than those in the SAB. No other significant differences were found for any metric of relative head size (Fig. 6). Turtles foraging in the MAB also had more variation in head size; the ranges in relative head size metrics were up to three-fold greater than turtles foraging in the SNWA and SAB (Fig. 6).

Among turtles foraging within each area, there was no correlation between $\delta^{15}\text{N}$ values (proxy for trophic position) and body size: MAB ($R^2 = <0.001$; $P = 0.25$), SAB ($R^2 = 0.025$; $P = 0.26$) and SNWA ($R^2 = <0.001$; $P = 0.59$). In addition, among turtles foraging within each area, there were no correlations between $\delta^{15}\text{N}$ values and any absolute head size metric (MAB, R^2 range = <0.001 – 0.01 ; P range = 0.33 – 0.37 ; SAB, R^2 range = <0.001 – 0.08 ; P range = 0.15 – 0.75 ; SNWA, R^2 range = <0.001 ; P range = 0.43 – 0.96) or any relative head size metric (MAB, R^2 range = <0.001 ; P range = 0.70 – 0.86 ; SAB, R^2 range = <0.001 – 0.02 ; P range = 0.28 – 0.95 ; SNWA, R^2 range = <0.001 – 0.16 ; P range = 0.16 – 0.77). All body size, head size, and stable isotope data used in this study is presented in Table S1.

Discussion

In this study, body size and foraging location, but not trophic position, may be related to variation in head size within a nesting population of loggerhead turtles, a generalist marine predator. These results provide insights into how variation in trophic morphology of a generalist species may be related to factors that cause individuals to use a more specialized range of available resources and reduce intraspecific competition.

Differences in overall body size among individuals have an important effect on population-wide variation in head size. Although loggerheads display negative allometry in head size relative to body size across ontogeny (Kamezaki & Matsui, 1997; Marshall *et al.*, 2012), we found that adults with larger bodies also tend to have larger heads. Consequently, any

Table 1 Number of female loggerhead turtles ($N = 108$) assigned to each foraging area using two posterior probability thresholds (0.8 and 0.6)

Foraging area	Number of turtles assigned					
	2013		2014		Total	
	≥ 0.8	≥ 0.6	≥ 0.8	≥ 0.6	≥ 0.8	≥ 0.6
Mid-Atlantic Bight (MAB)	51	54	22	24	73	78
South Atlantic Bight (SAB)	3	6	5	10	8	16
Subtropical Northwest Atlantic (SNWA)	2	2	3	3	5	5
Total assigned (% assigned)	56 (86%)	62 (95%)	30 (70%)	37 (86%)	86 (80%)	99 (92%)
Total unassigned	9	3	13	6	22	9

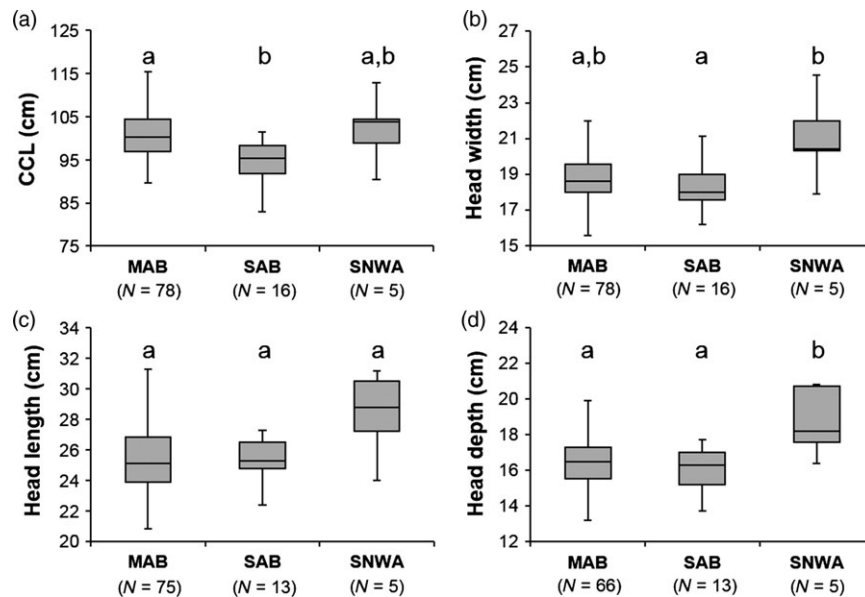


Figure 5 Box plots showing absolute (a) curved carapace length (CCL), (b) head width, (c) head length and (d) head depth of female loggerhead turtles assigned to three different foraging areas. MAB, Mid-Atlantic Bight; SAB, South Atlantic Bight; SNWA, Subtropical Northwest Atlantic. Letters above boxes indicate significant differences between turtles using different foraging areas.

Table 2 Summary statistics and analyses comparing body and head size among turtles using different foraging areas

Measurement	MAB			SAB			SNWA		
	Mean	SD	Sig.	Mean	SD	Sig.	Mean	SD	Sig.
Absolute (cm)									
CCL	100.60	5.20	a	94.84	4.86	b	102.34	9.62	a,b
HW	18.87	1.46	a,b	18.42	1.77	a	21.36	3.08	b
HL	25.43	2.50	a	25.42	1.34	a	28.34	2.88	a
HD	16.46	1.38	a	15.99	1.27	a	18.72	1.92	b
Relative (to CCL)									
HW	0.19	0.01	a	0.19	0.01	a,b	0.21	0.01	b
HL	0.25	0.02	a	0.27	0.01	a,b	0.28	0.01	b
HD	0.16	0.01	a	0.17	0.01	a	0.18	0.01	b

MAB, Mid-Atlantic Bight; SAB, South Atlantic Bight; SNWA, Subtropical Northwest Atlantic; CCL, curved carapace length; HW, head width; HL, head length; HD, head depth. Letters indicate significant differences (as identified by Bonferroni-corrected Dunn's test) between turtles using different foraging areas.

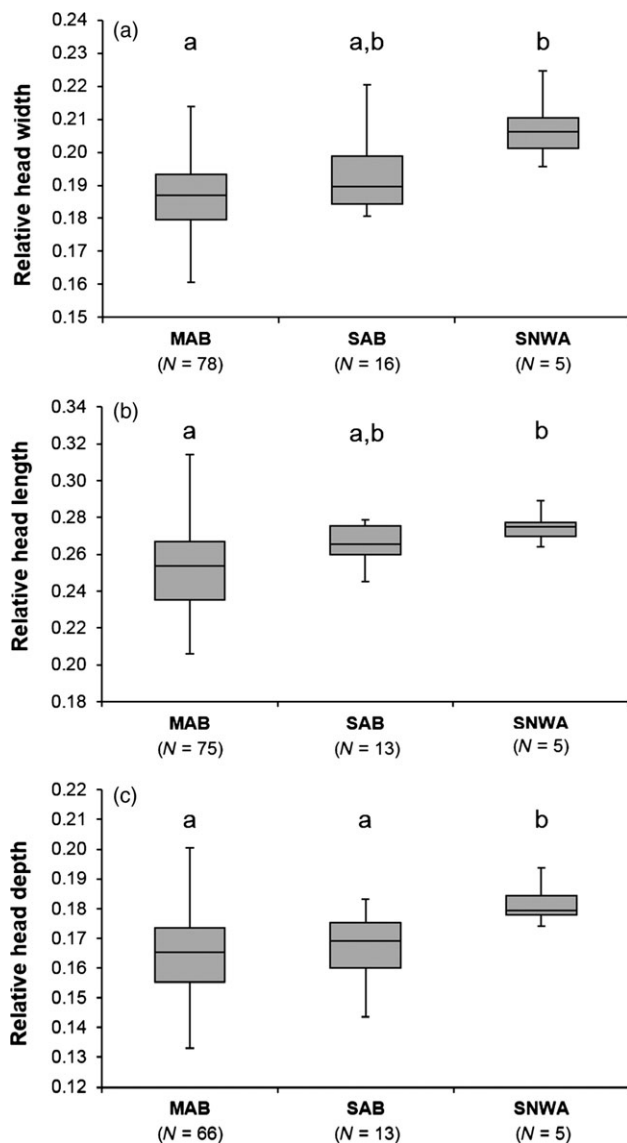


Figure 6 Box plots showing relative (a) head width, (b) head length and (c) head depth of female loggerhead turtles assigned to three different foraging areas. MAB, Mid-Atlantic Bight; SAB, South Atlantic Bight; SNWA, Subtropical Northwest Atlantic. Letters above boxes indicate significant differences between turtles using different foraging areas.

resource partitioning or specialization related to variation in trophic morphology might also be linked to factors that influence variation in body size among individuals in this population (e.g. migration distance, density-dependent growth and predation pressure). Larger individuals with concomitantly larger heads and higher bite forces (Marshall *et al.*, 2012) likely utilize a different range of dietary resources than smaller individuals. Indeed, dietary data indicate that larger loggerheads tend to consume more robust prey, including gastropod mollusks and hermit crabs (Seney & Musick, 2007). Resource partitioning by body size among adults is frequently evoked as a

mechanism to reduce intraspecific competition in animal populations (Forsman & Shine, 1997; Herrel *et al.*, 1999; Lindeman, 2000).

Variation in overall body size, and therefore head size, is at least partially explained by differences among turtles using different foraging areas. Similar to Vander Zanden *et al.* (2014), we found that turtles foraging in the SAB tend to be smaller than turtles foraging in the MAB and SNWA, although the small sample size of the latter may reduce the resolution of that result. These differences in overall body size and therefore head size may be attributed to higher productivity in the MAB and more consistent productivity in the SNWA relative to the SAB (Vander Zanden *et al.*, 2014). In part, this phenomenon may explain the larger head sizes (particularly absolute head depth) of turtles within the SNWA, although the head sizes of turtles in the MAB and SAB did not differ significantly. However, we found that after correcting for body size, turtles foraging in the MAB tend to have relatively smaller heads compared to turtles foraging in the SNWA. Turtles foraging in the SAB generally have similar head sizes (relative to body size) compared to turtles foraging in both the MAB and SNWA, except in the case of relative head depth, which was significantly smaller in the SAB than in the SNWA. As there are no genetic distinctions between turtles using different foraging areas (Shamblin *et al.*, 2011), such differences are likely related to trophic ecology. Differences in relative head size between turtles foraging in the MAB versus the SNWA may be related to geographic differences in selection and/or availability of dietary resources (primarily benthic invertebrates), whereas dietary resources available to turtles foraging in the SAB (geographically between MAB and SNWA) may overlap with those of the MAB and SNWA, leading to similar relative head sizes. Because benthic invertebrate size and diversity tend to decrease with increasing latitude (Macpherson, 2002; Berke *et al.*, 2013), turtles foraging in the SNWA may benefit from having relatively larger heads and greater bite-force capacity than turtles foraging in areas farther to the North. While dietary tendencies for loggerheads in the MAB are fairly well characterized and indicate that larger individuals do indeed tend to consume larger and more robust prey (Seney & Musick, 2007), comparable dietary information for loggerheads in the SNWA is unavailable. In addition, our sample size of turtles foraging in the SNWA was low and more head size data are needed to generate robust conclusions.

The MAB represents the most important foraging area for turtles in this nesting population: 78 of 99 (79%) assigned turtles in this study and 144 of 183 (79%) assigned turtles in Vander Zanden *et al.* (2014). We found that turtles foraging in the MAB tend to have smaller head dimensions for a given body size, as well as considerably more variation in head size, than turtles foraging in other areas. A wider range in head size among turtles foraging in the MAB is at least partially the result of a larger sample size, but may also be related to trophic ecology. Turtles foraging in the MAB have relatively small home ranges but make seasonal migrations to the south (below $\sim 35^{\circ}\text{N}$) in the winter, and a small portion of individuals shift to feeding in oceanic waters (Hawkes *et al.*, 2011). Migratory animal populations are known to exhibit relatively

wide morphological variation, as environmental conditions and resource availability can differ between locations (Durell, 2000). For turtles foraging in the MAB, the greater range of habitats and dietary resources used during seasonal migrations may contribute to wider variation in head size and perhaps greater individual specialization. Moreover, the consumption of soft-bodied, oceanic prey (e.g. sea jellies and other pelagic animals) may convey a selective advantage for turtles with relatively smaller heads that allow for greater feeding agility, but a lower bite-force capacity. These morphological and behavioral factors likely act synergistically to reduce intraspecific competition for turtles using this important foraging area.

We hypothesized that variation in head size may be related to differences in trophic position (i.e. $\delta^{15}\text{N}$ values) among individuals in this population. In principle, if turtles with larger bodies and/or heads gain access to prey at higher trophic positions, as in other aquatic and marine vertebrate systems (Akin & Winemiller, 2008; Romanuk, Hayward & Hutchings, 2011), then we would expect a positive relationship. Conversely, if turtles with larger bodies and/or heads are better suited for dietary resources at lower trophic positions, such as large filter-feeding mollusks that require higher bite forces to consume (Marshall *et al.*, 2012), then we would expect a negative relationship. Indeed, Pajuelo *et al.* (2012a) presents a negative relationship between body size and $\delta^{15}\text{N}$ values among male loggerheads foraging near Cape Canaveral, Florida. However, we found no relationship – neither positive nor negative – between body size or head size (absolute and relative) and trophic position among turtles within each foraging area (analyzed separately because $\delta^{15}\text{N}$ values vary with trophic position as well as geographic location). These results indicate that the relationship between morphology and trophic position is more complex. Although the sample sizes of turtles foraging in the SAB and SNWA may be too small to detect correlations, the absence of correlations among turtles using each foraging area may suggest that (1) individual turtles tend to forage at multiple trophic levels (i.e. no specialization in trophic position) or (2) individual turtles may forage at specific trophic levels, but specialization is simply not related to differences in body or head size. Moreover, dietary shifts associated with seasonal migrations may also disrupt any persistent correlations or reduce the usefulness of trophic specialization for turtles foraging in the MAB, especially for turtles that shift to oceanic resources (Hawkes *et al.*, 2011). Resource partitioning associated with variation in trophic morphology is apparently not related to trophic position, but more work (e.g. prey item sampling, as in Hatase *et al.*, [2002]) is needed to understand whether dietary specialization of any kind remains an important mechanism to reduce intraspecific competition among individuals using the same foraging area (Pajuelo *et al.*, 2016).

Understanding the factors related to variation in trophic morphology is important because these factors may affect the degree of intraspecific competition among individuals, a selective pressure that can affect both the ecology and conservation of a species. For generalist species, like loggerhead turtles, phenotypic variation in trophic morphology (i.e. head size) allows individuals to occupy more specialized roles within the

wider foraging niche of the species (Bolnick *et al.*, 2003, 2011; Vander Zanden *et al.*, 2010). In this study, we found that variation in trophic morphology within a generalist marine predator was related to differences in foraging location (an allopatric factor), but not to differences in trophic position (a sympatric factor). More research is needed to test whether other sympatric factors (e.g. dietary specialization or sex-specific differences) are related to variation in trophic morphology and therefore play a role in reducing intraspecific competition. Nevertheless, this study has applied an integrative approach to gain new insights into our understanding of the factors that affect phenotypic variation in animal populations.

Acknowledgments

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Raw body size, head size, and stable isotope data for female loggerhead sea turtles on Wassaw Island, GA, USA.

Table S1 Raw body size, head size, and stable isotope data for female loggerhead sea turtles on Wassaw Island, GA, USA.

Turtle Reference #	Year	CCL (cm)	Head Width (cm)	Head Length (cm)	Head Depth (cm)	d15N	d13C	0.6 Assign	0.8 Assign
1	2013	102.3	18.5	26.1	16.4	11.97	-15.6	NA	NA
2	2013	102.4	18.5	24.4	15.2	16.47	-15.14	MAB	MAB
3	2013	100.3	18.5	26	N/A	15.2	-15.96	MAB	MAB
4	2013	97	18.3	21.8	14.3	12.68	-15.89	MAB	MAB
5	2013	95	18.2	23.9	N/A	15.78	-16.51	MAB	MAB
6	2013	100	19.4	26.9	16.8	16.17	-16.79	MAB	MAB
7	2013	94	17.3	23.9	15.8	12.71	-15.81	MAB	MAB
8	2013	83	16.5	N/A	N/A	10.26	-15.06	SAB	SAB
9	2013	98.5	17.1	24.7	N/A	13.1	-15.85	MAB	MAB
10	2013	107	18.7	24.7	16.2	12.62	-16.04	MAB	MAB
11	2013	100.5	23.2	26.7	17.7	9.89	-14.2	SAB	SAB
12	2013	96	19.4	22.1	17.3	15.34	-16.15	MAB	MAB
13	2013	102	19.6	27.1	16.2	13.18	-16.32	MAB	MAB
14	2013	101.5	20.8	27	16.5	10.4	-15.77	SAB	SAB
15	2013	99.5	19.8	21.8	14.3	15.79	-16.52	MAB	MAB
16	2013	104.5	18.7	23.1	14.1	14.08	-15.42	MAB	MAB
17	2013	102	19.8	24.8	16	16.14	-15.32	MAB	MAB
18	2013	106.5	19.4	24.9	17.8	15.19	-15.84	MAB	MAB
19	2013	94	18.2	22.4	14.4	13.74	-16.11	MAB	MAB
20	2013	89.7	17.9	24.8	15.4	15.13	-16.33	MAB	MAB
21	2013	101	18.3	20.8	14.8	13.43	-16.99	MAB	MAB
22	2013	98.6	18.5	24.8	16.5	11.88	-16.62	MAB	MAB
23	2013	102.3	18.8	26.4	15	12.42	-15.62	MAB	NA
24	2013	91.4	16.9	22.4	14.2	11.93	-15.32	SAB	NA
25	2013	94	17.4	25.5	16.3	15.76	-15.84	MAB	MAB
26	2013	94	17.9	23.7	15.3	15.53	-15.6	MAB	MAB
27	2013	92.8	14.9	21	13.2	15.53	-15.82	MAB	MAB
28	2013	95	17.7	22.8	14.3	15.03	-16.21	MAB	MAB
29	2013	98	16.9	N/A	N/A	13.56	-16.26	MAB	MAB
30	2013	99.3	17.8	24.3	15.1	12.89	-16.48	MAB	MAB
31	2013	106.6	19.2	27.4	18	12.76	-15.55	MAB	MAB
32	2013	97	19	21.3	15.5	12.66	-16.92	MAB	MAB
33	2013	104.5	19.5	23.9	17	12.47	-15.6	MAB	NA
34	2013	96	17.1	25.2	16.8	16.44	-15.82	MAB	MAB

35	2013	102	19.6	23.7	16.1	16.68	-15.92	MAB	MAB
36	2013	115.5	26.2	30.5	20.7	5.91	-9.81	SNWA	SNWA
37	2013	105	18.3	26.6	16.3	12.51	-16.21	MAB	MAB
38	2013	95	19.4	26.4	16.6	9.73	-17.1	NA	NA
39	2013	115.7	24.5	30.4	N/A	15.82	-16.27	MAB	MAB
40	2013	103.8	20.3	28.8	20.7	8.23	-11.69	SNWA	SNWA
41	2013	96.4	17.4	24.3	N/A	13.2	-15.14	MAB	NA
42	2013	103	19	N/A	N/A	14.2	-17.13	MAB	MAB
43	2013	97	18.4	21.1	N/A	15.69	-16.32	MAB	MAB
44	2013	111.3	21.8	24.8	14.8	11.77	-16.95	MAB	MAB
45	2013	106.8	20.5	27.1	18.5	14.65	-17.11	MAB	MAB
46	2013	101.5	19.4	23.7	N/A	13	-16.45	MAB	MAB
47	2013	94.4	16.7	24.6	15.8	15.72	-16.99	MAB	MAB
48	2013	90.5	18.5	23.7	18.1	13.05	-15.53	MAB	MAB
49	2013	108.2	20.5	28.6	18	13.34	-16.29	MAB	MAB
50	2013	106	21.1	24.8	17.9	13.43	-15.76	MAB	MAB
51	2013	102	20.2	27.4	N/A	13.87	-17.04	MAB	MAB
52	2013	104	18.6	N/A	N/A	16.61	-16.84	MAB	MAB
53	2013	105.1	20.4	27.7	18.7	11.76	-16.26	MAB	MAB
54	2013	100	18.5	24.8	17	12.14	-15.28	SAB	NA
55	2013	97	19.3	25.3	16.4	12.37	-14.97	SAB	NA
56	2013	99.5	17.7	26.7	16.7	14.61	-17.36	MAB	MAB
57	2013	101.5	17.7	25.1	16.8	16.17	-15.49	MAB	MAB
58	2013	100	19.9	26.8	17.3	13.39	-15.3	MAB	MAB
59	2013	103	17.4	21.4	13.7	16.49	-16.32	MAB	MAB
60	2013	98.1	17.7	24.2	15.4	12.44	-15.76	MAB	MAB
61	2013	99	18.7	23.2	N/A	16.53	-15.44	MAB	MAB
62	2013	106.4	18.8	25.7	17.3	15.08	-16.53	MAB	MAB
63	2013	101.5	18.9	25.4	18.1	12.78	-15.87	MAB	MAB
64	2013	100.6	19.2	27.3	17.6	15.89	-15.79	MAB	MAB
65	2013	107	20.4	26.7	N/A	12.66	-15.2	NA	NA
66	2014	97.2	18.2	26.2	16.6	13.21	-16.01	MAB	MAB
67	2014	95	18.1	27.1	15.7	12.47	-15.18	NA	NA
68	2014	89	16.2	24.7	16.2	13.3	-14.4	SAB	SAB
69	2014	100.4	19.3	26.9	16.6	12.46	-15.25	NA	NA
70	2014	107.2	20.2	28.1	17.7	12.2	-16.1	MAB	MAB
71	2014	96.5	17.8	N/A	N/A	8.72	-13.94	SAB	SAB

72	2014	95	18.2	24.3	16.9	14.87	-16.13	MAB	MAB
73	2014	100.3	17.9	24.5	15.8	12.58	-15.42	MAB	NA
74	2014	96.8	17.8	24.4	14.7	12.78	-15.1	NA	NA
75	2014	95	17.9	26.5	15.6	11.34	-15.58	SAB	NA
76	2014	104.5	22	31.2	18.2	8.73	-13.03	SNWA	SNWA
77	2014	95.4	18.2	25.1	13.7	11.93	-14.87	SAB	SAB
78	2014	96	18.6	26.8	17.2	15.6	-14.82	MAB	MAB
79	2014	95.5	18.9	25.8	17.5	10.32	-16.33	SAB	NA
80	2014	104.7	19.5	27.6	16.3	13.14	-16.84	MAB	MAB
81	2014	92	19.9	23.9	N/A	12.43	-13.59	SAB	SAB
82	2014	101	17.3	22	15.1	11.95	-15.69	MAB	NA
83	2014	95.2	17.7	24.8	15.3	12.8	-15.21	NA	NA
84	2014	90	16.2	N/A	15.4	12	-15.45	NA	NA
85	2014	98.9	20.4	27.2	17.6	8.74	-10.19	SNWA	SNWA
86	2014	100	18.2	26.4	17.4	13.5	-16.27	MAB	MAB
87	2014	103.9	18.3	26.4	15.9	14.83	-17.05	MAB	MAB
88	2014	101	23.7	33.6	20.3	13.87	-15.47	MAB	MAB
89	2014	90	18.9	25.2	16.5	13.1	-16.4	MAB	MAB
90	2014	90.6	16.7	N/A	14.5	9.31	-17.2	SAB	NA
91	2014	96	20.6	25.9	16.9	10.56	-17.41	MAB	MAB
92	2014	97	18.4	29.1	18	12.82	-16.02	MAB	MAB
93	2014	99.1	17.9	27.3	17.1	11.77	-13.99	SAB	SAB
94	2014	93	18	25.8	16.3	13.03	-14.82	SAB	NA
95	2014	102.5	18.3	26.8	16.1	12.23	-16.48	MAB	MAB
96	2014	99	18.3	23.4	15.8	12.4	-16.86	MAB	MAB
97	2014	105	19.9	29.4	18.5	12.42	-15.83	MAB	MAB
98	2014	98	19.7	27.8	17.2	11.48	-16.63	MAB	MAB
99	2014	109	22.1	32.3	19	17.03	-16.82	MAB	MAB
100	2014	106	17.9	24.8	16.9	11.94	-16.67	MAB	MAB
101	2014	106	19.8	27.8	17.4	11.94	-16.75	MAB	MAB
102	2014	98.5	18.8	23.3	16.9	12.48	-15.17	NA	NA
103	2014	96.7	17.7	26.7	15.7	15.09	-16.03	MAB	MAB
104	2014	98	18.7	28.1	16.9	16.05	-17.18	MAB	MAB
105	2014	97	18.3	26.8	16.3	12.86	-17.01	MAB	MAB
106	2014	114.6	20.3	28.8	17.3	12.1	-17.83	MAB	MAB
107	2014	98	18	25.2	15.2	12.41	-15.01	SAB	NA
108	2014	89	17.9	24	16.4	7.2	-12.39	SNWA	SNWA