

Assignment of nesting loggerhead turtles to their foraging areas in the Northwest Atlantic using stable isotopes

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Abstract. Differential foraging area use can affect population demographics of highly migratory fauna because of differential environmental changes and anthropogenic threats among those areas. Thus, identification of foraging areas is vital for the development of effective management strategies for endangered migratory species. In this study, we assigned 375 loggerhead turtles (*Caretta caretta*) nesting at six locations along the east coast of the United States to their foraging areas in the Northwest Atlantic (NWA) using carbon and nitrogen stable isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$). We first evaluated the epidermis $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from 60 adult loggerheads with known foraging grounds. Twenty-two females from 6 nesting beaches and 23 males from one breeding area were tracked with satellite transmitters to identify their foraging locations following breeding, and 15 adult turtles were sampled at one foraging ground. Significant trends were observed between both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of satellite-tracked loggerheads and the latitude of the foraging grounds to which the turtles migrated, reflecting a geographic pattern in the stable isotope values. Both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values characterized three geographic areas—with distinct abiotic and biotic features—used by adult loggerheads in the NWA. Discriminant analysis assigned all 375 female loggerheads to one of the three foraging areas; 91% were assigned with probabilities of $\geq 80\%$. The proportion of nesting turtles using each foraging ground varied geographically; most turtles nesting in northern beaches (72–80%) tend to forage at higher latitudes while most turtles nesting in southern beaches (46–81%) tend to forage at lower latitudes. Stable isotopes can reveal the foraging location of loggerhead turtles in the NWA, which will allow robust analyses of foraging ground effects on demography and improve the design of management strategies for the conservation of loggerhead populations. The conclusions and methods developed in this study are also relevant for other populations of sea turtles and for other highly migratory species.

Key words: *Caretta caretta*; $\delta^{15}\text{N}$; $\delta^{13}\text{C}$; foraging area; loggerhead turtles, Mid-Atlantic Bight; Northwest Atlantic; satellite telemetry; South Atlantic Bight; stable isotopes.

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INTRODUCTION

For endangered migratory fauna, knowledge of demographic parameters is key to accurately

assess the status and trends of populations (Esler 2000, National Research Council 2010, Wallace et al. 2010). Because values of demographic parameters can vary with environmental conditions at

the foraging habitats (Cooch et al. 2001, Chaloupka et al. 2008, Saba et al. 2008), information on movement patterns and foraging locations of populations are of crucial importance.

Populations of the loggerhead sea turtle (*Caretta caretta*) nesting in the Northwest Atlantic (NWA) represent one of the major nesting aggregations for the species in the world (Ehrhart et al. 2003). NWA loggerhead nesting aggregations are composed of genetically and demographically distinct populations (Encalada et al. 1998; Shamblin et al., *in press*). Loggerheads swim hundreds of kilometers from a wide range of foraging grounds to their nesting beaches. Concern was raised when nesting activity in one of these NWA populations declined markedly from 1998 to 2007 (Witherington et al. 2009); however, an increase in nesting numbers has been reported in recent years (Van Houtan and Halley 2011). Anthropogenic threats (Jackson et al. 2001, Witherington et al. 2009, Finkbeiner et al. 2011) and changing oceanographic conditions (Chaloupka et al. 2008, Saba et al. 2008, Van Houtan and Halley 2011) have been proposed as the main drivers of fluctuations in sea turtle abundance. Because these factors may change depending on geographic location (Kot et al. 2010 and references therein), efforts to identify foraging grounds of sea turtles are vital to understand spatial and temporal fluctuations in nesting numbers.

To better understand how environmental changes and human threats at different foraging grounds affect the various nesting populations in the NWA, it is important to evaluate not only the demographic parameters of each breeding population but also the proportions of females in each breeding population located in different foraging areas. Initial efforts have been undertaken to understand how differential foraging locations and oceanographic conditions affect demographic parameters such as clutch size, number of clutches per nesting season, clutch sex ratio, and female body size in loggerhead populations (Hatase et al. 2002, Hawkes et al. 2007a, b, Zbinden et al. 2011, Bailey et al. 2012).

Satellite telemetry studies have revealed that NWA adult female loggerheads have at least two different migration patterns (seasonal shuttling migration and year-round residency) when they leave the nesting beaches and return to their

foraging areas. Females may travel up to hundreds of kilometers and forage in coastal areas along the U.S. Atlantic coast, Gulf of Mexico, Cuba, and the Bahamas (Plotkin and Spotila 2002, Dodd and Byles 2003, Foley et al. 2008, Hawkes et al. 2007a, 2011). They also show site fidelity to their foraging areas, characterized by different environmental features (Hawkes et al. 2007a, 2011), thus revealing patterns of migratory connectivity between nesting sites, foraging areas, and wintering areas.

Stable isotope analysis, a technique that uses ratios of stable isotopes of naturally occurring elements (e.g., carbon, nitrogen), can complement information from satellite telemetry on population connectivity (Webster et al. 2002). Because stable isotopes in the environment are incorporated into primary producers and then transferred up the food chain (DeNiro and Epstein 1978, Minagawa and Wada 1984), the isotopic values of tissues of higher trophic level organisms reflect differences in the stable isotope values of primary producers of the environment in which these organisms foraged (Schell et al. 1989, Minami and Ogi 1997, Burton and Koch 1999, Kurle and Worthy 2002, Cherel and Hobson 2007, Pajuelo et al. 2010). These spatial isotopic differences in primary producers create isotopically distinct regions that can be used to infer residency and movement patterns of organisms migrating among them (Rubenstein and Hobson 2004, Graham et al. 2010). Within an organism, different tissues incorporate and turnover stable isotopes at different rates. In sea turtles, epidermis, keratin, and red blood cells reflect a longer-term foraging history (Reich et al. 2008). Therefore, such tissues collected for turtles at breeding areas reflect their dietary history at foraging grounds prior to migration to the breeding area (Wallace et al. 2006, Caut et al. 2008, Reich et al. 2010, Vander Zanden et al. 2010, Zbinden et al. 2011, Pajuelo et al. 2012, Seminoff et al. 2012).

Stable isotope values of animals can be used to identify their foraging areas if (1) different foraging areas are isotopically distinct and (2) sampled tissues reflect the isotopic signatures of the foraging grounds (Rubenstein and Hobson 2004). These requirements are met for adult loggerheads in the NWA and have been demonstrated for adult males (Pajuelo et al. 2012). Male loggerheads show differences in their stable

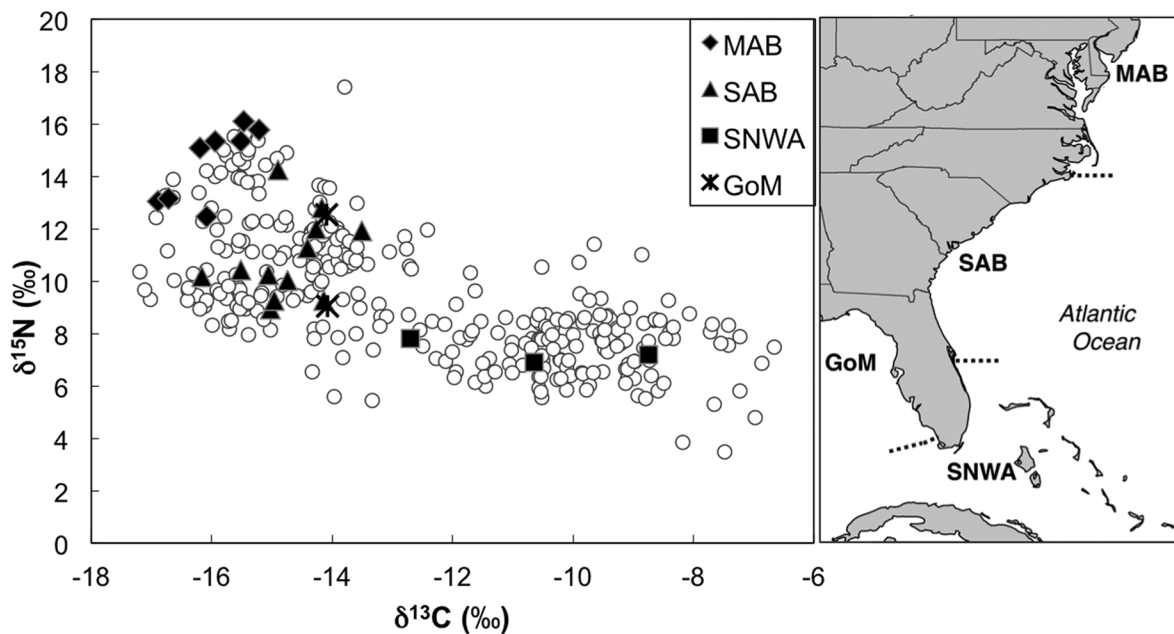


Fig. 1. Distribution of stable isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of adult male ($n = 25$) and female ($n = 310$) loggerheads in the Northwest Atlantic (NWA). Male loggerheads (black symbols) are coded by the foraging area used based on satellite telemetry: Mid-Atlantic Bight (MAB), South Atlantic Bight (SAB), Subtropical Northwest Atlantic (SNWA). Two male turtles that used coastal waters of the Gulf of Mexico (GoM) are also shown. Female data (open circles) are from Reich et al. (2010) and were sampled at various nesting beaches in Florida; male data are from Pajuelo et al. (2012). The right panel depicts the main geographic areas used by adult male loggerheads in the NWA and the Gulf of Mexico.

isotope values reflecting the use of three geographic areas: the Mid-Atlantic Bight (MAB), the South Atlantic Bight (SAB), and the subtropical NWA (SNWA) (Pajuelo et al. 2012; Fig. 1), which represent well-established biogeographic regions with distinctive biotic and abiotic features (Hutchins 1947, Wilkinson et al. 2009). Moreover, based on satellite telemetry, adult males appear to use foraging grounds similar to those of adult females in the NWA (Arendt et al. 2012). The large variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from nesting loggerheads in Florida, USA (Reich et al. 2010) is similar to that observed in the satellite-tracked male loggerheads (Fig. 1), and probably represents a gradient of north to south foraging locations used by adult female loggerheads in the NWA.

The main objective of our study was to assign loggerhead sea turtles nesting along the U.S. Atlantic coast to their foraging locations in the NWA using stable isotope analysis. First, we evaluated whether satellite-tracked adult female

loggerheads have the same relationship between geographic areas and stable isotope values as adult males. Second, we characterized the geographic areas used by adult loggerheads with isotopic values of satellite-tracked adult loggerheads and additional turtles with known foraging locations. Then, we compared the isotopic values of nesting turtles not fitted with satellite transmitters with those of adult loggerheads with known foraging location to determine their foraging areas based on assignments from discriminant analysis. Finally, we estimated the proportion of each nesting population foraging in each geographic area. By combining stable isotope analysis and satellite telemetry to identify foraging locations of breeding populations, we can then rely on stable isotope analysis alone to assign large numbers of female loggerheads to their foraging grounds rapidly and at low cost. This knowledge will allow us to assess with robust sample sizes how different environmental factors and threats at the different foraging

Table 1. Location (state, breeding/foraging area, and latitude), year of collection, and sample size of epidermis samples from adult loggerhead turtles with known and unknown foraging grounds used in this study.

Area	Latitude (°N)	Year	<i>n</i>	Foraging area		Isotope data source
				Known†	Unknown	
Breeding area						
North Carolina						
Bald Head Island	33.9	2004	10	4	6	This study
Georgia		2005	12		12	This study
Wassaw Island	31.8	2005	47		47	This study
Blackbeard Island	31.6	2005	4	4		This study
Sapelo Island	31.4	2004	2	2		This study
		2005	8	8		This study
Jekyll Island	31.1	2004	3	3		This study
Cumberland Island	30.9	2004	1	1		This study
Florida						
Canaveral National Seashore	28.8	2003	44		44	Reich et al. 2010
		2004	31		31	Reich et al. 2010
Melbourne Beach	28.1	2003	60		60	Reich et al. 2010
		2004	46		46	Reich et al. 2010
Juno Beach	26.9	2003	41		41	Reich et al. 2010
		2004	41		41	Reich et al. 2010
Broward County	26.2	2003	47		47	Reich et al. 2010
Port Canaveral	28.4	2006–07	23	23		Pajuelo et al. 2012
Foraging area						
Florida						
Florida Bay	25.0	2011	15	15		This study
Total			435	60	375	

†Turtles fitted with satellite transmitters except for turtles sampled at Florida Bay.

grounds affect the demography of adult loggerheads in the NWA and focus management and conservation efforts appropriately.

MATERIAL AND METHODS

Data and sample collection

Epidermis samples were collected from 87 adult female loggerhead turtles during the 2004 and 2005 nesting seasons (May–Jul) at six nesting areas (Table 1; Fig. 2): Bald Head Island in North Carolina (BHI; 33.86° N, 77.99° W), and Wassaw (WAS; 31.84° N, 80.98° W), Blackbeard (BLA; 31.61° N, 81.14° W), Sapelo (SAP; 31.40° N, 81.28° W), Jekyll (JEK; 31.07° N, 81.42° W), and Cumberland (CUM; 30.85° N, 81.45° W) Islands in Georgia. Additionally, 15 adult-size turtles (curved carapace length, CCL ≥ 84 cm) were sampled at one foraging area in Florida Bay, Florida (24.08° N, 81.03° W) in March and June 2011 (Table 1; Fig. 2). Previously published isotopic data from epidermis samples of adult female loggerheads collected at four nesting areas in Florida (*n* = 310; Reich et al. 2010) and adult male loggerheads collected at one breeding area in Florida (*n* = 23; Pajuelo et al. 2012) were also included in this study (Table 1; Fig. 2).

All epidermis samples were collected using a 6 mm biopsy punch and stored in 70% ethanol at room temperature until dried at 60°C prior to sample preparation and analysis. Epidermis samples reflect the turtle's dietary history over a long period of time (i.e., up to 4 months) based on studies conducted on juvenile loggerheads (Reich et al. 2008). An even longer foraging history is probable in adult loggerheads because rates of isotopic incorporation slow with reduced growth rates (Reich et al. 2008) and increasing body mass (Carleton and Martínez del Río 2005).

Twenty-two female turtles were fitted with satellite transmitters after clutch deposition in Georgia (*n* = 18) and North Carolina (*n* = 4) beaches (Table 1). Hawkes et al. (2007a, 2011) characterized the distinct movement patterns of these adult female loggerheads and classified them into two groups, (1) turtles with seasonal migration between summer and winter coastal areas and (2) turtles with migration to year-round foraging areas. We grouped turtles into three groups according to the coastal region to where they migrated: the first group is the MAB turtles, with seasonal migration between summer foraging areas in the MAB and wintering areas in the SAB; the second and third groups are the SAB

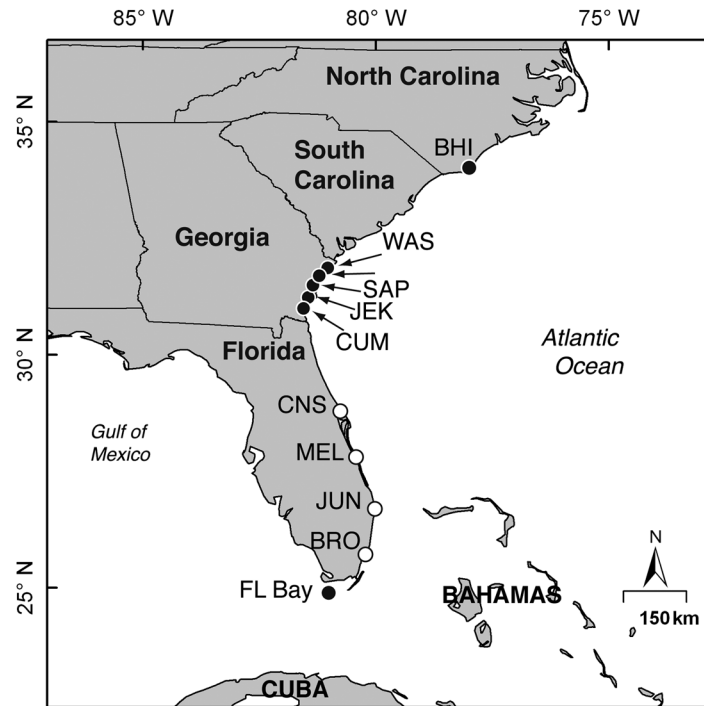


Fig. 2. Map showing the locations of the six nesting areas and single foraging ground (filled symbols) sampled in this study: Bald Head Island (BHI), Wassaw Island (WAS), Sapelo Island (SAP), Blackbeard Island (BLA), Jekyll Island (JEK), Cumberland Island (CUM), and Florida Bay (FL Bay). Nesting areas sampled in the Reich et al. (2010) study (open symbols) are also shown: Canaveral National Seashore (CNS), Melbourne Beach (MEL), Juno Beach (JUN), and Broward County (BRO).

and SNWA turtles, with migration to year-round foraging areas in waters of the SAB and SNWA, respectively. Turtles were tracked for 344.2 ± 148.4 days (mean \pm SD) (individuals 5–8, 40–43, 49–52, and 54–63; Hawkes et al. 2011: Table S1). Most of the turtles ($n = 19$) were tracked for the entire foraging period for turtles using MAB waters, and for 6 months or more at the foraging ground for turtles using SAB and SNWA waters. The remaining turtles were tracked for a period of 80 days or more after reaching the foraging ground. Telemetry data were filtered following Hawkes et al. (2011) to retain location classes 3, 2, 1 and A, and turning angles greater than 25° , and the latitude of the centroid of the foraging ground (arithmetic mean of all the filtered location points from the foraging ground) was used to evaluate the relationship between stable isotope values and geographic location.

Stable isotope values of epidermis samples from satellite-tracked female turtles ($n = 22$) were

used to characterize the three geographic areas used by adult loggerheads, assuming that isotopic values from foraging areas used prior to nesting reflected those used post-nesting (identified by satellite telemetry), as adult female loggerheads are known to exhibit site fidelity to foraging areas (Hawkes et al. 2007a, 2011, Vander Zanden et al. 2010). Also, because the isotopic values of satellite-tracked male loggerheads have shown a geographic pattern consistent with the use of the three geographic areas mentioned above (Pajuelo et al. 2012), male data ($n = 23$) were incorporated in the isotopic characterization of the three geographic areas used by adult loggerheads. Few satellite tracked turtles migrated to the SNWA, so we included additional epidermis samples from adult-size loggerheads collected at one foraging ground in the SNWA (Florida Bay; $n = 15$).

Finally, we used the isotopic values from epidermis samples of nesting turtles not fitted

with satellite transmitters from BHI in North Carolina ($n = 18$) and WAS in Georgia ($n = 47$), in combination with published isotopic data from nesting turtles at four nesting areas in Florida ($n = 310$; Reich et al. 2010) (Table 1), to compare to those of turtles with known foraging ground to assign them to one of the three geographic areas used by adult loggerheads in the NWA.

Sample preparation and analysis

Epidermis samples were washed with deionized water and wiped with isopropyl alcohol to remove epibionts and extraneous particles. The outermost layer of the turtle epidermis was separated from the underlying tissue, finely diced with a scalpel blade, and dried at 60°C for 24 h. Lipids were extracted from samples with petroleum ether using an ASE300 accelerated solvent extractor (Dionex).

For stable isotope analysis, 0.5–0.6 mg of each sample was weighed and sealed in a tin capsule. Samples were analyzed for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios by combustion in a COSTECH ECS 4010 elemental analyzer interfaced via a ConFlo III device to a DeltaPlus XL isotope ratio mass spectrometer (ThermoFisher Scientific) in the Stable Isotope Geochemistry Lab at the University of Florida, Gainesville. Results are presented as stable isotope ratios of a sample relative to an international standard and reported in the conventional δ notation: $\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$, where δX is the relative abundance of ^{13}C or ^{15}N in the sample expressed in parts per thousand (‰); R_{sample} and R_{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 international standard, respectively. The standard used for ^{13}C was Vienna Pee Dee Belemnite and for ^{15}N was atmospheric N_2 . The reference material USGS40 (L-glutamic acid) ($n = 22$) was used to normalize all results, $\text{SD} = 0.05\text{‰}$ and 0.13‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively.

Statistical analyses

The effect of geographic location on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values was evaluated with a Spearman rank correlation test between isotope values and the latitudes of the foraging grounds of the adult female turtles.

To determine the similarity of the isotopic values of samples from turtles of unknown foraging ground (hereafter referred to as un-

known turtles) to those of samples from turtles of known foraging location (hereafter referred to as known turtles), we classified the isotopic values of known turtles into three groups: MAB, SAB, and SNWA. Multivariate analysis of variance (MANOVA) was used to test for variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values among groups to test if they were quantitatively discrete. Then, these three isotopically defined groups were combined with the unknown turtles in a quadratic discriminant analysis, due to unequal variance among groups. The discriminant analysis assigned each unknown turtle to the geographic area for which it had the highest probability of membership. To test the accuracy of assignment, we applied the leave-one-out cross validation method to the reference groups, where a single turtle is removed from the total and classified to a foraging region by the functions derived from all turtles other than the excluded turtle, with the process being repeated for each remaining turtle.

Following the determination of geographic area for unknown turtles, we evaluated the population structure of all breeding populations using only turtles assigned to one of the three groups with $\geq 80\%$ probability of group membership (Rocque et al. 2006, Seminoff et al. 2012) (340 out of 375 turtles). Finally, a chi-square test was performed to test for inter-annual variation in the proportion of turtles using different foraging grounds for nesting beaches that were sampled in two consecutive years, whenever sample size allowed (i.e., CNS, MEL, and JUN beaches; Table 1). All data were analyzed using program R (R Development Core Team 2011) with an α level of 0.05.

RESULTS

Epidermis isotopic values of adult females in the NWA ranged from 3.5 to 18.7‰ and -6.9 to -17.6‰ for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, respectively (Fig. 3).

The epidermal isotope values from satellite-tracked female loggerheads (tracked long enough to identify their foraging areas) revealed a geographic pattern: females that migrated north to seasonal foraging grounds in the MAB (e.g., New Jersey, Virginia, and Delaware) after the nesting season had high $\delta^{15}\text{N}$ values and low $\delta^{13}\text{C}$ values (Fig. 3). The lowest $\delta^{15}\text{N}$ value and highest $\delta^{13}\text{C}$ value were found in a female that

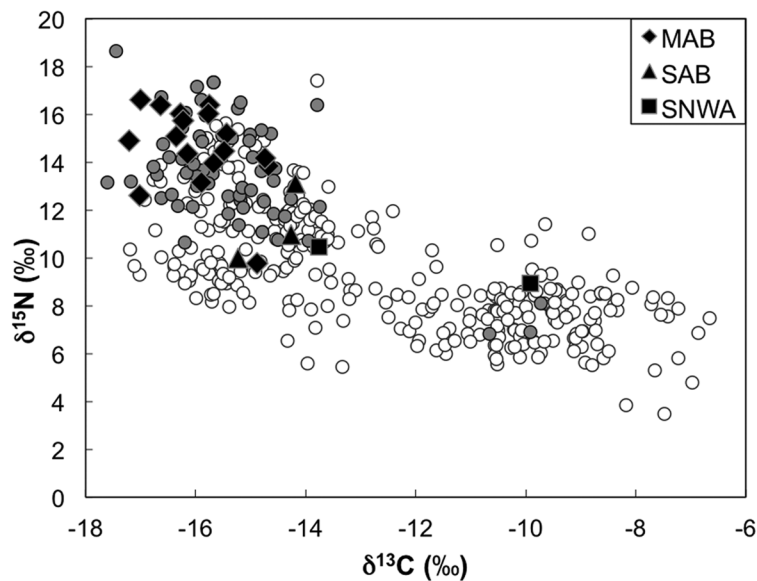


Fig. 3. Stable isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of adult female loggerheads in the Northwest Atlantic. Females tracked with satellite telemetry ($n = 22$; black filled symbols) were sampled during nesting seasons in 2004 and 2005 at Bald Head Island, Sapelo Island, Blackbeard Island, Jekyll Island, and Cumberland Island, and are grouped based on the geographic area to which they migrated after the nesting season: Mid-Atlantic Bight (MAB), South Atlantic Bight (SAB), or Subtropical Northwest Atlantic (SNWA). Additional females sampled (grey filled circles) in this study and females sampled in the Reich et al. (2010) study (open circles) of unknown foraging location are also shown.

migrated south to a year-round foraging ground in the SNWA (The Bahamas) (Fig. 3). Intermediate $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values were found in turtles migrating to coastal waters of the SAB (e.g., Georgia and northern Florida) (Fig. 3). A significant negative correlation was found between $\delta^{13}\text{C}$ values and the latitude to which females migrated after the nesting season (Spearman's rank correlation $r_s = -0.64$, $n = 22$, $P = 0.001$; Fig. 4A), while a significant positive correlation was found between $\delta^{15}\text{N}$ values and latitude (Spearman's rank correlation $r_s = 0.46$, $n = 22$, $P = 0.029$; Fig. 4B).

Stable isotope values of epidermis from adult loggerhead males and females using the same geographic areas were similar. Even though three satellite-tracked turtles had isotopic values that were not consistent with the geographic area to which they migrated (turtles 1, 2, and 3; Fig. 5A), we found significant differences in combined $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values among geographic areas used by adult loggerheads in the NWA (MANOVA, $F = 29.32$, $P < 0.001$). The isotopic

signatures of these three groups were used as a reference from which to compare the isotopic values of unknown turtles. Discriminant analysis assigned all unknown turtles to one of the three geographic areas with 91% (340 out of 375) of those turtles assigned to a unique geographic area with a probability $\geq 80\%$ of group membership (Table 2; Fig. 5B). The percentages of turtles assigned at higher probabilities were lower but remained substantial: 85 and 79% with a probability ≥ 90 and 95%, respectively. Leave-one-out cross validation revealed a 6% ($n = 4$) misclassification rate, which corresponded to the misclassification of turtles 1, 2, 3, and an additional turtle. Unknown turtles assigned with $\geq 80\%$ probability to a geographic area were used to evaluate the foraging structure of breeding populations. A latitudinal trend in the foraging area use by nesting loggerheads was revealed; the proportion of turtles using the MAB increased from south to north and the proportion using the SNWA increased from north to south (Fig. 6). The majority of turtles (72–80%) nesting at higher

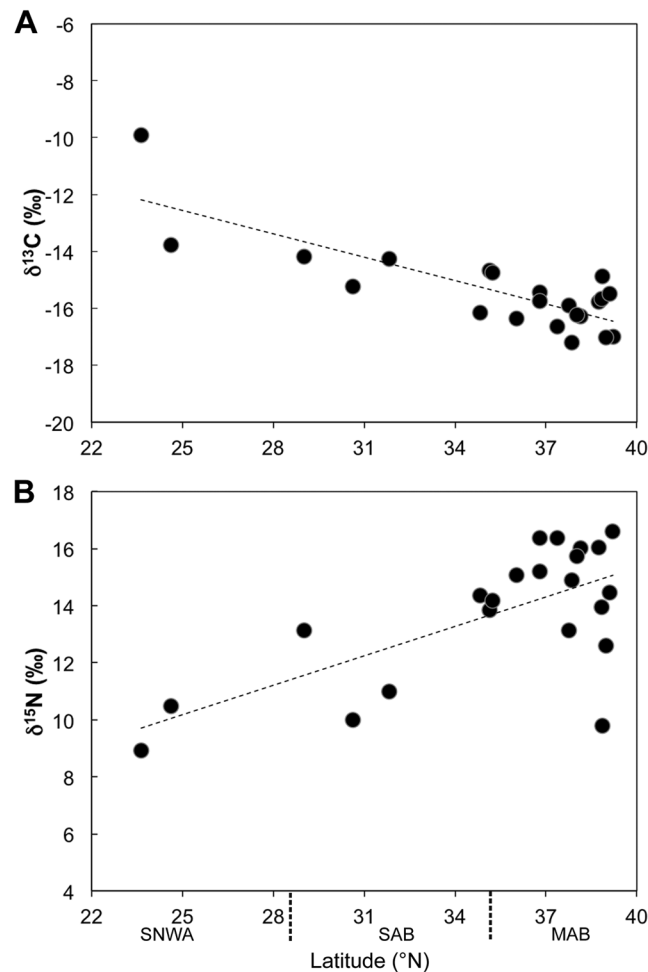


Fig. 4. Relationship between (A) carbon ($\delta^{13}\text{C}$) and (B) nitrogen ($\delta^{15}\text{N}$) stable isotope values of adult female loggerheads ($n = 22$) and the latitude ($^{\circ}\text{N}$) to which they migrated after the nesting season. Spearman rank correlation is significant for both $\delta^{13}\text{C}$ ($r_s = -0.64$, $P = 0.002$) and $\delta^{15}\text{N}$ values ($r_s = 0.46$, $P = 0.029$). Geographic regions in the Northwest Atlantic: Mid-Atlantic Bight (MAB), South Atlantic Bight (SAB), and Subtropical Northwest Atlantic (SNWA) are shown under the x-axis separated by dotted lines. Dashed lines denote trend lines.

latitudes (i.e., BHI and WI) used foraging areas in the MAB and few turtles (6%) used the SNWA (Fig. 6). Most turtles (46–81%) nesting at lower latitudes (i.e., Juno Beach and Broward County) used the SNWA and few (2–21%) used the MAB (Fig. 6). A large number (36–59%) of nesting turtles from CNS used the SAB. The use of the SAB declined north and south of CNS (Fig. 6).

The proportion of turtles using the different foraging areas varied between years in CNS (Pearson's chi-square test, $df = 2$, $\chi^2 = 11.51$, $P = 0.003$), MEL (Pearson's chi-square test, $df = 2$, $\chi^2 =$

11.39, $P = 0.003$), and JUN (Pearson's chi-square test, $df = 2$, $\chi^2 = 22.70$, $P < 0.001$) beaches (Fig. 6). A marked pattern in the reduction in the proportion of turtles using MAB waters and the increase of turtles using SNWA waters was observed in MEL and JUN in 2004 (Fig. 6).

DISCUSSION

Isotopic characterization of the geographic areas used by adult loggerheads in the NWA

In this study, a combination of stable isotope

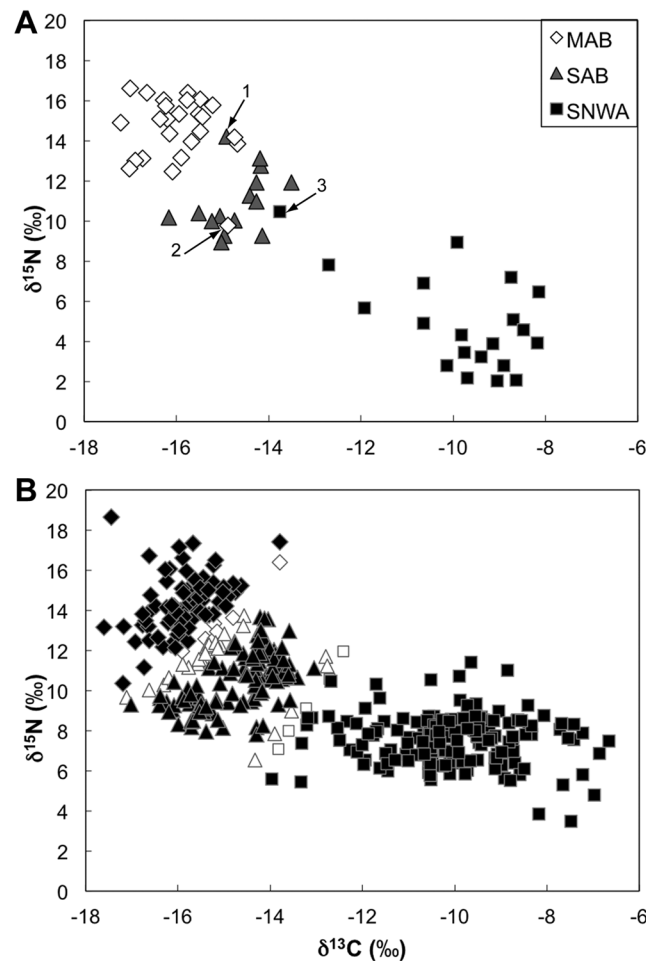


Fig. 5. (A) Stable isotope ratios of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) of adult loggerhead turtles with known foraging location ($n = 60$) showing three groups representing the three geographic areas used by adult loggerheads in the Northwest Atlantic: Mid-Atlantic Bight (MAB) South Atlantic Bight (SAB), and Subtropical Northwest Atlantic (SNWA). The isotopic values of turtles 1, 2, and 3 fell within a group that did not correspond to the foraging location as observed through satellite telemetry. Combined $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were significantly different among groups (MANOVA, $F = 29.62$, $P < 0.001$). (B) Stable isotope ratios of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) of 375 adult female loggerhead turtles of unknown foraging ground. Symbols (same as above) indicate the geographic area to which each individual unknown female turtle was assigned by the discriminant analysis. Turtles assigned with a probability $\geq 80\%$ of group membership are shown as filled symbols ($n = 340$). Open symbols represent additional turtles assigned with a probability $< 80\%$ of group membership ($n = 35$).

and satellite-telemetry data allowed us to characterize three main geographic regions used by adult loggerheads in the NWA (Fig. 5A). Recent studies have integrated telemetry data to validate marine geographic patterns in $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values of highly migratory animals such as seabirds (Jaeger et al. 2010) and sea turtles (Seminoff et al. 2012) over broad spatial scales

(e.g., within ocean basins). Here, we present the combined $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ spatial characterization for a highly migratory animal at a regional scale in the NWA.

Isotopic turnover in epidermis samples of adult loggerhead turtles is estimated to be at least 4 months (see *Introduction*), longer than the expected migration period between the foraging

Table 2. Assignment of adult female loggerheads of unknown foraging location to a geographic area with $\geq 80\%$ probability of group membership. Values in parentheses are additional turtles assigned with a probability $< 80\%$ of group membership.

Nesting area	Latitude ($^{\circ}$ N)	<i>n</i>	Geographic area		
			MAB	SAB	SNWA
North Carolina					
Bald Head Island, BHI	33.9	18	10 (2)	3 (2)	1
Georgia					
Wassaw Island, WAS	31.8	47	31 (3)	6 (5)	2
Florida					
Canaveral National Seashore, CNS	28.8	75	10	34 (5)	25 (1)
Melbourne Beach, MEL	28.1	106	13 (2)	37 (2)	50 (2)
Juno Beach, JUN	26.9	82	9	16 (6)	50 (1)
Broward County, BRO	26.2	47	1	14 (3)	28 (1)
Total		375	74 (7)	110 (23)	156 (5)

Note: Abbreviations are: MAB: Mid-Atlantic Bight, SAB: South Atlantic Bight, SNWA: Subtropical Northwest Atlantic.

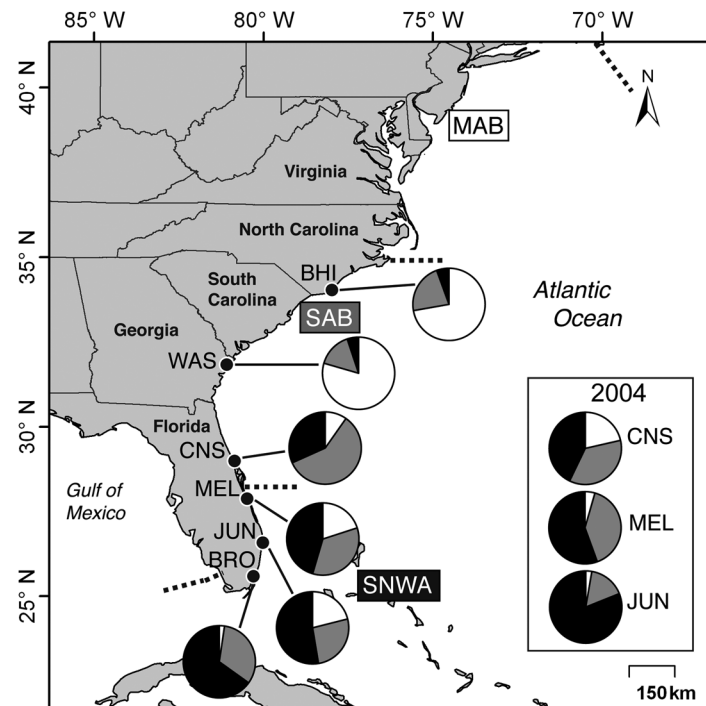


Fig. 6. Breeding population structure according to foraging area used by loggerheads nesting along the U.S. Atlantic coast as determined through discriminant analysis using carbon and nitrogen stable isotope values of adult loggerhead turtles with known foraging grounds as reference data. Foraging areas are Mid-Atlantic Bight (MAB; white fill), South Atlantic Bight (SAB; grey fill), and the Subtropical Northwest Atlantic (SNWA; black fill). Nesting turtles from Bald Head Island (BHI) and Wassaw Island (WAS) were sampled in 2004–2005 and 2005 nesting seasons, respectively. Florida nesting turtles were sampled in 2003 and 2004 nesting seasons; results from nesting season 2003 are shown in the main map. Inset shows results from 2004 for Canaveral National Seashore (CNS), Melbourne (MEL), and Juno (JUN) beaches. BRO is Broward County beaches. The proportion of turtles using the different geographic areas varied between years for CNS, MEL and JUN beaches (see text for statistics). The boundaries of the three geographic areas: MAB, SAB, and SNWA are depicted by dotted lines.

area and breeding ground for a satellite-tracked turtle used in this study (~1 month, based on mean travel duration between nesting area and foraging grounds and between foraging and wintering grounds; Hawkes et al. 2011; L. Hawkes, *unpublished data*). Thus, isotopic values of epidermis tissues from nesting loggerheads should reflect that of the foraging grounds used prior to migrating to the nesting beaches.

Satellite-tracked nesting loggerheads demonstrated a geographic pattern in the stable isotope values (Fig. 3) similar to the one previously observed in satellite-tracked male loggerhead turtles (Fig. 1; Pajuelo et al. 2012). Although the MAB turtles use waters of both the MAB (summer) and SAB (winter), they maintain distinct stable isotope values from those of turtles that use waters in the SAB year-round. The difference could result from very slow turnover rates in epidermis of adult turtles. Also, Hawkes et al. (2007a) suggested that seasonal turtles (i.e., MAB turtles) that migrate south into SAB areas during winter might undergo fasting during part of the winter. It has been proposed that $\delta^{15}\text{N}$ values might increase with fasting duration (Martínez del Río et al. 2009). Because the extent of the enrichment in $\delta^{15}\text{N}$ appears to be tissue-dependent, this hypothesis has received mixed support (Martínez del Río et al. 2009) and remains to be tested in sea turtles.

Nesting loggerhead turtles can be assigned to their coastal foraging areas in the NWA using stable isotope values because NWA adult female turtles show fidelity to their foraging grounds both within and between years (Hawkes et al. 2007a, 2011), as has been observed in other loggerhead populations (Broderick et al. 2007, Schofield et al. 2010, Thomson et al. 2012). However, some NWA turtles have been found to occasionally use oceanic waters (Hawkes et al. 2007a, 2011), which may result in unusual stable isotope values. The isotopic values of three turtles (1, 2, and 3; Fig. 5A) did not correspond to the geographic area to which they migrated after the breeding season. The most likely explanation is that these turtles did not return to the same geographic area from which they originally came. For example, if a turtle used waters of the SAB prior to its capture in the nesting beach and later migrated to waters in the MAB, its isotopic values would show lower $\delta^{15}\text{N}$

and higher $\delta^{13}\text{C}$ values than would be expected for a turtle using MAB waters (e.g., turtle 2; Fig. 5A). Although adult turtles are generally site-fixed to their foraging grounds, occasional shifts can be expected.

The distinct biotic and abiotic characteristics of the three geographic areas used by loggerheads—MAB, SAB, and SNWA—likely influence isotopic values of turtles using those areas. High anthropogenic input appears to raise the $\delta^{15}\text{N}$ values of primary producers in the MAB (McKinney et al. 2010). Also, high rates of denitrification, which also raise baseline $\delta^{15}\text{N}$ values, have been reported in the MAB (Fennel et al. 2006) although its effect on the $\delta^{15}\text{N}$ coastal biota has not been assessed yet (McKinney et al. 2010). In addition, the rate of nitrogen fixation, which lowers the $\delta^{15}\text{N}$ values of primary producers, is highest in the SNWA (Montoya et al. 2002). Available $\delta^{15}\text{N}$ values of particulate organic matter (a proxy for primary producers) along the latitudinal gradient used by loggerheads reveal this pattern: nitrogen stable isotope ratios range from 7.2 to 7.7‰ in near-shore waters off of Virginia and Delaware in the MAB (McKinney et al. 2010), from 4.0 to 6.4‰ in near-shore waters off of South Carolina and Georgia in the SAB (M. Pajuelo and M. Arendt, *unpublished data*), and from -0.9 to 3.6‰ in Florida Bay in the SNWA (Macko et al. 1984, Behringer and Butler 2006, Lamb and Swart 2008).

Water temperature can also affect $\delta^{13}\text{C}$ values at the base of the food web by affecting cell growth rate and dissolved carbonate concentration, which have a direct effect on the $\delta^{13}\text{C}$ values of primary producers (MacKenzie et al. 2011). Sea surface temperatures in the MAB during summer—the season when adult loggerheads mainly use MAB waters—range from 15–27°C, while water temperatures in the SNWA range from 22.5–28°C year round (Wilkinson et al. 2009). Waters in the SNWA are also characterized by the presence of extensive seagrass communities (Wilkinson et al. 2009), whose contribution to benthic food webs may be evidenced by relatively low $\delta^{13}\text{C}$ values in food web organisms (Fry et al. 1982). Ultimately, variation in baseline isotopic values will be reflected in higher trophic level organisms such as NWA adult loggerheads, which prey mainly on benthic invertebrates in

coastal waters (Hopkins-Murphy et al. 2003). Stable isotope values of other food web organisms in the NWA exhibit a pattern similar to that of adult loggerhead turtles (Pajuelo et al. 2012) and indicate that baseline differences rather than trophic level differences are driving the large isotopic variation in adult loggerhead turtles.

While turtles using the MAB and SNWA have distinct stable isotope values (Fig. 5A), Pajuelo et al. (2012) found that isotopic values from male turtles using the SAB were similar to those of turtles using coastal waters in the Gulf of Mexico (which were not included in our analysis) (Fig. 1). Because we are interested in determining the foraging locations of loggerheads nesting along the U.S. Atlantic coast, we need to consider that adult female turtles use foraging areas in regions other than the NWA. Telemetry studies have revealed that adult female loggerheads nesting in Florida beaches use coastal waters in both the NWA and the Gulf of Mexico (Foley et al. 2008). Therefore, the isotopic values reflecting the use of waters in the SAB for turtles from southern nesting beaches may be confounded with those of turtles using waters in the Gulf of Mexico. Other markers, such as trace elements and lead stable isotopes, may help differentiate these two foraging areas with similar $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures (M. López-Castro, *personal communication*).

In this study, we chose to define the three loggerhead geographic foraging grounds in the NWA based on the knowledge that these represent well-established biogeographic regions, each of which shows distinct oceanographic conditions and faunal communities (Hutchins 1947, Wilkinson et al. 2009). Because stable isotopes may be influenced by factors (see above) that vary among the biogeographic areas, we were able to find significant differences in the stable isotope values of turtles among these three areas. However, within a particular foraging ground, stable isotope values of loggerheads can vary due to differences in habitat type and/or diet (Rubenstein and Hobson 2004). Thus, to identify feeding areas at a finer scale than the one presented here will likely require the use of additional biomarkers (e.g., trace elements).

Foraging locations of adult female loggerheads in the NWA

For many years, much of what was known about the foraging locations of adult female loggerheads in the NWA relied on information from flipper tag returns (Bell and Richardson 1978, Meylan et al. 1983, Williams and Frick 2008). While informative, tag return data can be biased because these data mainly rely on the capture of flipper tagged turtles by fisheries. In recent years, satellite transmitters have been deployed on nesting loggerheads, which have provided more accurate information on the post-nesting migratory routes, location of foraging grounds, and feeding behavior of adult female loggerheads in the NWA (Godley et al. 2008). However, the expense of satellite tags, which limits the number of individuals that can be tracked, has prevented more widespread use. Thus, stable isotope analysis, which is low cost and can yield results rapidly, can be useful in identifying foraging areas of a large number of individuals.

Carbon and nitrogen stable isotopes allowed us to assign most nesting loggerheads to a distinct geographic area in the NWA at a probability of $\geq 80\%$. The remaining turtles assigned to an area with a probability of $< 80\%$ do not suggest that they use unidentified foraging locations. Because we found a latitudinal trend in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ along the NWA (Fig. 4), we believe that those foraging locations are found within one of the three geographic areas in the NWA. We could not assign all turtles with a probability $\geq 80\%$ probably as a result of isotopic variation within each of the three geographic areas that was not captured by the satellite-tracked turtles, or because they travelled to the Gulf of Mexico.

We found that nesting loggerheads showed geographic segregation of foraging grounds; northern nesting turtles preferred higher latitude foraging areas while the opposite was seen in southern nesting turtles. Thus, our initial observations revealed that female loggerheads in the NWA generally use foraging areas in the vicinity of their natal nesting beaches. These results are consistent with satellite telemetry data from nesting loggerheads in the NWA. For turtles nesting in North Carolina, South Carolina, and Georgia, Hawkes et al. (2011) revealed that most

females ($n = 48$) migrated north to seasonal foraging grounds in the MAB, while few ($n = 18$) move to year-round waters of the SAB and SNWA after the nesting season. Similarly, based on smaller sample sizes, Dodd and Byles (2003) and Foley et al. (2008) revealed that nesting turtles from southern beaches in Florida migrated to waters in the SNWA and rarely migrated to northern waters in the MAB.

The use of foraging grounds adjacent to natal nesting areas has been suggested previously for large juvenile loggerheads in the NWA by mixed stock analysis of mitochondrial DNA haplotypes for aggregations of juveniles along the U. S. east coast (Bowen et al. 2004). The stable isotope approach used in our study allowed us to sample adult female loggerheads at various nesting areas—where they are more easily accessible—without having to sample turtles at the different foraging areas to reveal a similar pattern of foraging ground segregation. Mixed stock analysis of mitochondrial DNA haplotypes has been widely used to assess the contribution of various nesting areas to feeding grounds (Bolker et al. 2007). Because this technique relies on differential haplotype frequencies at the various nesting areas, each nesting individual cannot be assigned to its foraging ground. The existence of habitat-specific stable isotope signatures allows stable isotope analysis to assign each individual to its foraging area (Rubenstein and Hobson 2004). Thus, geographic assignment models in sea turtles may be improved by incorporating traditional tools such as genetic analyses, mark-recapture data, and satellite telemetry along with stable isotope analyses to understand the connection between nesting areas and foraging grounds.

The temporal variation in the proportion of turtles using different geographic areas within three Florida nesting beaches, CNS, MEL and JUN, suggests differential remigration intervals may exist (i.e., the period of time between reproductive seasons) among foraging subpopulations. Given the greater distance that turtles foraging in MAB waters travel to reach southern beaches, there may be differential remigration intervals for these turtles within a southern nesting population. Adult female turtles that forage in highly productive waters of the MAB during summer are known to migrate to the SAB

during winter months (Hawkes et al. 2007a). Another possibility is that turtles using MAB waters seasonally may spend more energy undergoing seasonal migration (Hawkes et al. 2007a), which may be reflected in longer remigration intervals. Hawkes et al. (2007a), based on a small sample size of females from a northern nesting beach in North Carolina, did not find differences in remigration intervals (and other fecundity measures) between females using seasonal foraging areas in the MAB ($n = 9$) versus year round areas in the SAB and SNWA ($n = 3$), suggesting that neither differential foraging/migratory strategies within this northern breeding population was more advantageous (Hawkes et al. 2007a). However, females using MAB waters in the Hawkes et al. (2007a) study were closer to their northern nesting beach. Recently, variations in reproductive output and demography due to inter-basin differences in feeding and movement behavior have been reported in leatherback turtles (Bailey et al. 2012). Further research is needed to assess whether the pattern observed in northern nesting loggerheads is consistent with a larger sample size and in different nesting populations.

Our study incorporated previously published stable isotope values of epidermis from adult female loggerheads nesting in Florida beaches from Reich et al. (2010). Additionally, Vander Zanden et al. (2010) collected scute (carapace keratin) from a subsample of these loggerheads to investigate the long-term consistency in resource use through stable isotope analysis of scute layers. Both studies suggested that large differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ observed could be accounted for by foraging location (Reich et al. 2010, Vander Zanden et al. 2010). In this study, we confirmed that stable isotope values of female loggerheads in the NWA reflect their foraging locations by ground-truthing stable isotope values with information obtained through satellite telemetry. The much greater number of females that can be assigned to foraging grounds based on stable isotope analysis than on satellite telemetry will allow robust analyses of foraging ground effects on demographic parameters such as number of eggs per clutch, number of clutches deposited during a nesting season, and remigration intervals, which are critical to understand trends in sea turtle nesting populations (National

Research Council 2010).

Conservation implications

In order to effectively manage populations of highly migratory endangered species, an understanding of spatio-temporal distribution is essential. In the particular case of adult loggerhead populations in the NWA that use waters over a wide geographic range, knowing which feeding areas a major nesting population primarily uses is important, because it allows managers to focus conservation efforts where appropriate.

Adult female loggerhead populations segregate among foraging grounds, which is promising for refining management strategies. We can identify, at a large scale, what areas are more or less important for a particular nesting population in the NWA. For example, in this study we identified that foraging areas in the SNWA are highly important for turtles nesting in Florida beaches, followed by areas in the SAB; while areas in the MAB are used to a lesser degree. Fisheries bycatch is one of the major threats for loggerhead turtles in the NWA (Bolten et al. 2010). Research on sea turtle bycatch has revealed spatial and temporal variations in loggerhead bycatch in U.S. fisheries (Kot et al. 2010, Finkbeiner et al. 2011), with shrimp trawl fisheries in the SAB, SNWA and Gulf of Mexico accounting for the most interactions with loggerhead turtles in the U.S. (Finkbeiner et al. 2011). Thus, efforts can be focused in the SAB and SNWA to assess how fisheries interaction, as well as other environmental factors such as changing oceanographic conditions and prey distribution, impact fecundity measures of Florida nesting populations. Additionally, we can further our understanding of how these threats and factors drive the temporal fluctuations in the proportion of individuals within each nesting population that use the different foraging areas. However, more northerly and lesser used foraging areas may currently be important, regarding conservation efforts, because they are used by smaller or more at-risk nesting populations. These foraging areas may become even more important in the future, if southern turtle populations were to shift northward, as suggested under future climate scenarios (i.e., if southern beaches become too hot; Hawkes et al. 2007b).

Organic pollutants are another anthropogenic

threat to which turtles are exposed in the NWA (Alava et al. 2011 and references therein). Recent research revealed that adult loggerheads using northern foraging grounds in the MAB have higher concentrations of organic pollutants than turtles that use waters off central Florida, and our results support the hypothesis that this may be due to spatial structuring of foraging grounds by population (Ragland et al. 2011). Similarly, a recent study found that loggerhead eggs laid in a northern nesting beach in North Carolina had higher organic concentration of pollutants than eggs laid in southern nesting beaches in Florida (Alava et al. 2011). These differential threats can also affect demographic parameters and health of the foraging subpopulations and should also be considered in management plans.

Conclusions

Our study demonstrates that stable isotope analysis can be used parsimoniously to identify foraging areas of adult loggerheads in the NWA at a regional scale. Future research is needed to assess if stable isotope analyses, perhaps integrated with other biomarkers such as trace elements, could identify foraging areas at a finer scale. Additionally, we found that adult female loggerheads nesting along the U.S. Atlantic coast tend to use foraging areas closer to their natal nesting beaches; a smaller proportion of individuals undertake migrations to distant foraging grounds. These results are useful for the design of management strategies for the conservation of loggerhead turtle populations in the NWA. Assignment of large numbers of nesting females to foraging grounds with stable isotope analysis will allow future research to explore the effects of foraging ground location on demographic parameters. The conclusions and methods developed in this study are also relevant for other populations of sea turtles and for other highly migratory species.

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