Mar Biol (2012) 159:1255–1267
DOI 10.1007/s00227-012-1906-9

ORIGINAL PAPER

# Distribution of foraging habitats of male loggerhead turtles (*Caretta caretta*) as revealed by stable isotopes and satellite telemetry

**Mariela Pajuelo · Karen A. Bjorndal · Kimberly J. Reich · Michael D. Arendt · Alan B. Bolten**

Received: 13 October 2011 / Accepted: 20 February 2012 / Published online: 7 March 2012


**Abstract** Most studies on the foraging ecology of loggerhead turtles (*Caretta caretta*) have focused on adult females and juveniles. Little is known about the foraging patterns of adult male loggerheads. We analyzed tissues for carbon and nitrogen stable isotopes ($\delta^{13}$C and $\delta^{15}$N) from 29 adult male loggerheads tracked with satellite transmitters from one breeding area in Florida, USA, to evaluate their foraging habitats in the Northwest Atlantic (NWA). Our study revealed large variations in $\delta^{13}$C and $\delta^{15}$N and a correlation between both $\delta^{13}$C and $\delta^{15}$N and the latitude to which the loggerheads traveled after the mating season, thus reflecting a geographic pattern in the isotopic signatures. Variation in $\delta^{13}$C and $\delta^{15}$N can be explained by differences in food web baseline isotopic signatures rather than differences in loggerhead trophic levels. Stable isotope analysis may help elucidate residency and migration patterns and identify foraging sea turtle subpopulations in the NWA due to the isotopically distinct habitats used by these highly migratory organisms.

Communicated by R. Lewison.

**Electronic supplementary material** The online version of this article (doi:10.1007/s00227-012-1906-9) contains supplementary material, which is available to authorized users.

M. Pajuelo (✉) · K. A. Bjorndal · K. J. Reich · A. B. Bolten
Archie Carr Center for Sea Turtle Research
and Department of Biology, University of Florida,
Gainesville, FL 32611, USA
e-mail: mpajuelo@ufl.edu

M. D. Arendt
Marine Resources Division, South Carolina Department
of Natural Resources, Charleston, SC 29412, USA

## Introduction

Knowledge of foraging ground distribution of highly migratory animals is critical for understanding their foraging behavior and habitat use. Identification of key habitats helps not only to characterize life history features of populations (Block et al. 2001), but also to assess the impact of threats that populations may face (Hays et al. 2003). Most efforts to identify key habitats and movement patterns have used flipper tags (Limpus et al. 1992), genetic markers (Bolker et al. 2007), chemical analysis (Thorrold et al. 2001), and electronic tagging (Block et al. 2005; Hawkes et al. 2011). Electronic tagging is an excellent tool for assessing the movement and foraging behavior of marine animals, but this tool is constrained to small sample sizes due to expense and to organisms large enough to be tagged (but see Block et al. 2005). Additional information on migration patterns and foraging habitat use of highly migratory and elusive marine animals can be obtained using stable isotopes (SI) (Reich et al. 2007; Rooker et al. 2008; Newsome et al. 2009).

In marine ecosystems, $\delta^{15}$N values vary predictably with trophic level (Minagawa and Wada 1984), while $\delta^{13}$C values vary with source of primary production (Michener and Kaufman 2007) and habitat type: pelagic versus benthic or oceanic versus neritic (Hobson et al. 1994). Additionally, both $\delta^{15}$N and $\delta^{13}$C may vary with geographic location as a result of the effect of oceanic processes on baseline $\delta^{15}$N and $\delta^{13}$C (Goericke and Fry 1994; Montoya 2007), which in turn are reflected in higher trophic level organisms (Cherel and Hobson 2007; Pajuelo et al. 2010). Marine phytoplankton and particulate organic matter $\delta^{13}$C values decrease from the equatorial zones toward the polar regions (Goericke and Fry 1994) as a result of differential plankton growth

rates, dissolved $CO_2$ concentration in seawater, and seawater temperature, among other factors (Goericke and Fry 1994; Graham et al. 2010). Characteristic nitrogen cycle regimes—nitrogen fixation and denitrification—lower and increase, respectively, the $\delta^{15}N$ of primary producers (Montoya 2007). These baseline isotopic differences create isotopically distinct regions, which can then be used to assess movements of individuals migrating among them (Graham et al. 2010). Therefore, it is important to know the community baseline $\delta^{13}C$ and $\delta^{15}N$ when identifying foraging habitats in highly migratory organisms.

Loggerhead sea turtles (*Caretta caretta*) are listed as Endangered on the IUCN Red List (IUCN 2011). Understanding the foraging ecology and movement patterns of loggerheads improves their conservation outlook. While several studies have addressed various aspects of the foraging ecology of adult female and juvenile loggerheads in the North Atlantic (Hawkes et al. 2007, 2011; Wallace et al. 2009; Frick et al. 2009; McClellan et al. 2010; Vander Zanden et al. 2010), little is known about the foraging strategies of adult male loggerhead turtles (but see Arendt et al. 2012a, b).

Recent work by Reich et al. (2010) revealed a large range in the $\delta^{13}C$ and $\delta^{15}N$ signatures of skin samples in nesting loggerheads in Florida, USA. Two clusters were identified based on $\delta^{13}C$ signatures that were consistent with differences in habitat use (oceanic versus neritic waters; Fig. 1a). However, the authors could not rule out the possibility of other factors affecting carbon signatures, such as geographic location or differential source of primary production. Furthermore, even though the range from 2 to 15‰ in $\delta^{15}N$ of females was not assessed, this could represent differences in trophic levels (Post 2002) or baseline isotopic values (Pajuelo et al. 2010). Recent observations of migration patterns of adult male loggerheads in Florida through satellite telemetry have revealed the use of different geographic foraging areas after the mating season (Fig. 2; Arendt et al. 2012a, b). Do adult male loggerheads in Florida exhibit a pattern in SI values similar to that in nesting loggerheads? If so, how do patterns in $\delta^{13}C$ and $\delta^{15}N$ of male loggerheads compare with their satellite tracking data? To answer these questions, we collected tissues from 29 satellite-tracked adult male loggerheads at one breeding area in Florida and analyzed them for $\delta^{13}C$ and $\delta^{15}N$. Tissues from additional male turtles not fitted with satellite transmitters were used to compare SI patterns between adult males and females and to assess SI values of different tissues within individual males. By integrating SI with satellite telemetry, we seek to reveal the foraging strategy of adult male loggerheads in the Northwest Atlantic.

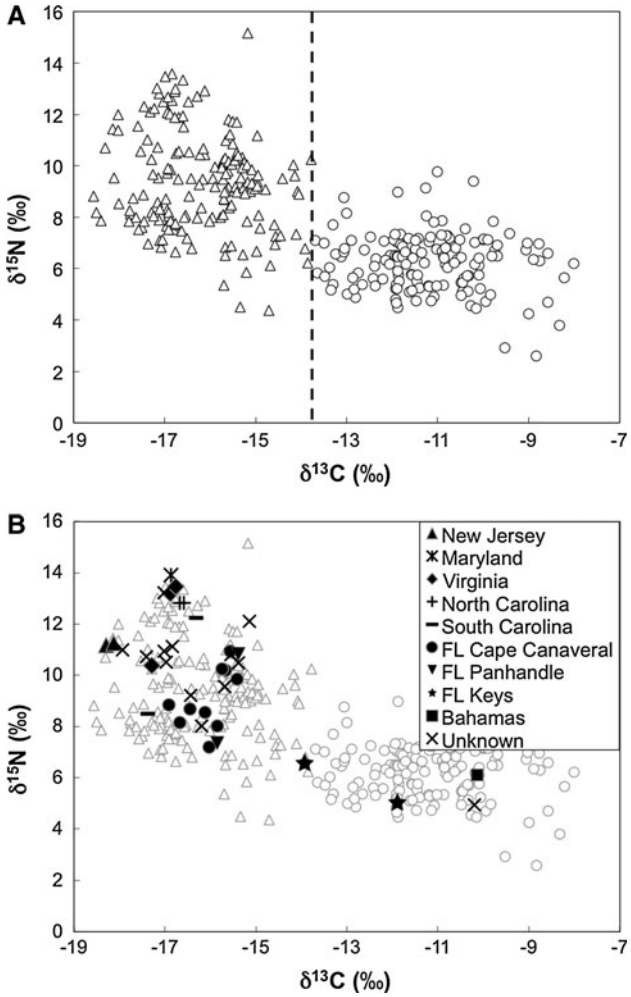


**Fig. 1** Stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) of adult female ($N = 310$) and male ($N = 37$) loggerheads in Florida. **a** Adult female loggerhead signatures show the 2 clusters identified using $\delta^{13}C$ (denoted by *open triangles* and *open circles*) by Reich et al. (2010). **b** Comparison of $\delta^{13}C$ and $\delta^{15}N$ values of adult female (*open symbols*) and male (*filled symbols*) loggerheads in Florida. Male loggerhead samples were collected during mating seasons at Cape Canaveral, FL, in 2006 and 2007. Female samples from Florida were collected during nesting seasons in 2003 and 2004. *Labels* indicate the foraging locations to which satellite-tracked male loggerheads ($N = 25$) migrated after the mating season. FL Panhandle refers to the northeast Gulf of Mexico area in Florida and FL Keys refers to the Florida Keys. Unknown turtles are males without transmitters and satellite-tracked males for which foraging location could not be determined. Samples are red blood cells (RBC) for males and epidermis samples converted to RBC values for females (see "Results" for regression equation). Other male samples (epidermis and plasma) show the same pattern as RBC (see supplementary Fig. S1)

## Materials and methods

### Data and sample collection

Thirty-seven adult male loggerhead turtles (straight carapace length, SCL > 86 cm) were captured by trawling from

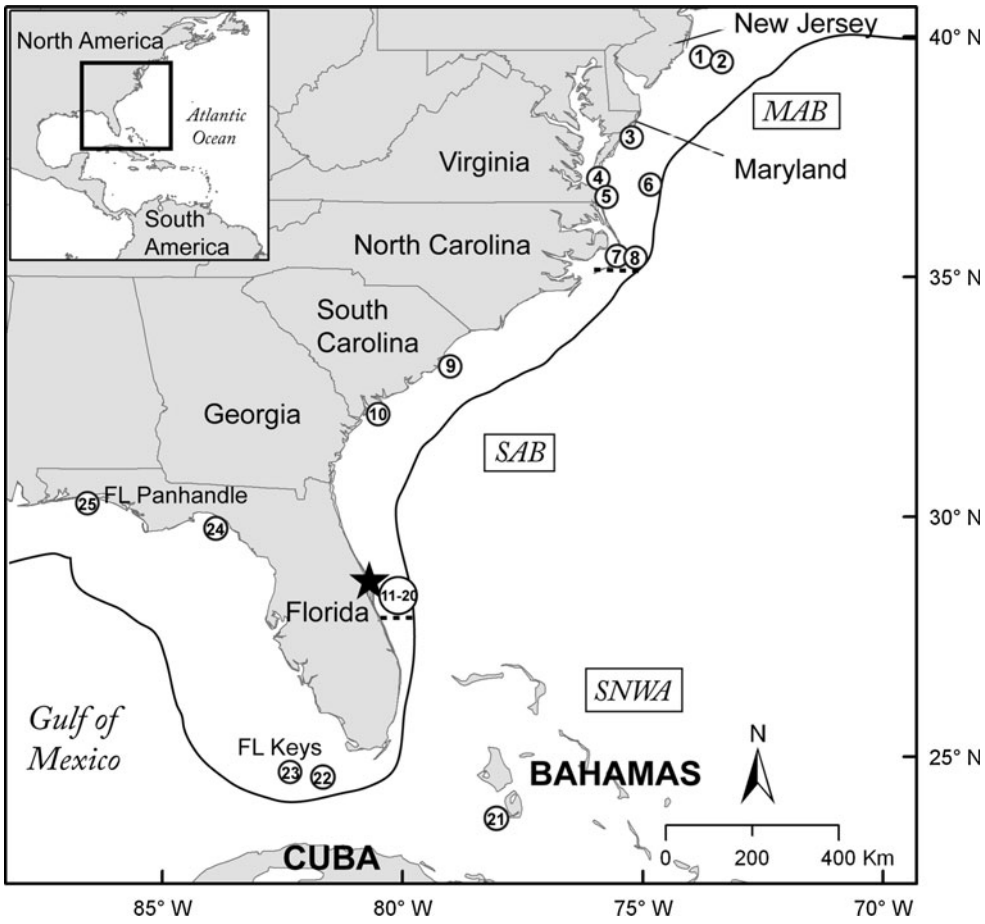


**Fig. 2** Spatial distribution of satellite-tracked male loggerheads from Cape Canaveral, Florida (*filled star*), after mating season in April 2006 and 2007. Turtles stayed in waters near Cape Canaveral (11–20; *numbered circle*) or migrated and remained in various continental shelf locations (1 through 10 and 21 through 25; *numbered circles*). FL Panhandle refers to the northeast Gulf of Mexico area in Florida and FL Keys refers to the Florida Keys. *Dark line* denotes the 200 m bathymetry. *Dotted lines* separate coastal regions: Mid-Atlantic Bight (MAB) and South Atlantic Bight (SAB). The Subtropical Northwest Atlantic (SNWA) is also shown. Adapted from Arendt et al. (2012b)

the Port Canaveral shipping channel, Florida, USA (28.38°N, 80.53°W) during mating season in April 2006 and 2007. Sexual maturity of each turtle was confirmed by laparoscopy (Blanvillain et al. 2008). All turtles were used to evaluate SI values within and among adult male loggerhead tissues, while 29 turtles were used to assess turtle movements by combining satellite telemetry and SI data.

Satellite transmitters (ST-20, Model A2020; Telonics, Inc., Mesa, Arizona, USA) were attached to 29 males (see Arendt et al. 2012a), and their movements were tracked during and after the mating season. Arendt et al. (2012a, b) characterized the distinct movement patterns of these males that we classify here into five groups: (1) residency in waters near the breeding area in Cape Canaveral, FL, (2) northern migration and residency in waters off South Carolina in the South Atlantic Bight, (3) northern migration to foraging grounds along the continental shelf from North Carolina to New Jersey in the Mid-Atlantic Bight (MAB), (4) southern migration to shallow waters of the Florida Keys and the Bahamas in the subtropical NWA, and (5) southern migration and ultimate residency in coastal waters of the northeast Gulf of Mexico (Fig. 2). We grouped turtles based on their migration patterns and foraging locations with similar oceanographic conditions.

Body size (SCL) was recorded using tree calipers marked with 0.1 cm units, and blood samples were collected for each adult male loggerhead. Epidermis (EPI) samples were also collected for 26 turtles, 20 of them corresponding to satellite-tracked turtles. Only one turtle was recaptured in consecutive years, and blood samples were collected in both years.

Epidermis samples ($N = 26$) were collected from the dorsal surface of the neck using a 6-mm biopsy punch. Blood samples were collected from the dorsal cervical sinus (Owens and Ruiz 1980) using a vacutainer tube with sodium heparin, fitted with a 21-gauge needle. Sodium heparin does not affect isotopic values (Lemons et al. in press). Blood was centrifuged for 5 min within 1 h of collection and separated into red blood cells (RBC, $N = 38$) and plasma (PLA, $N = 38$), which were stored in cryovials. All samples were stored frozen until dried at 60°C prior to sample preparation and analysis. EPI and RBC reflect the turtle's dietary history over a longer period of time (at least 4.2 months) than PLA (at least 2 months) based on studies conducted with growing juvenile loggerheads (Reich et al. 2008). Isotope turnover (i.e., the time the isotopic composition in the consumer tissue reaches equilibrium after a shift in resource use) for adult loggerheads may be longer because rates of isotopic incorporation slow with reduced growth rates (Reich et al. 2008),

**Table 1** Foraging area, sample size (*N*), and body size (SCL) of the five groups determined according to the migration that satellite-tracked male loggerheads followed after the mating season

| Group | Foraging area | *N* | SCL (cm) | |
|---|---|---|---|---|
| | | | Mean ± SD | Min–max |
| 1 | Off Cape Canaveral | 10 | 89.0 ± 2.1 | 86.6–96.2 |
| 2 | South Atlantic Bight* | 2 | 88.5 ± 1.5 | 87.4–89.5 |
| 3 | Mid-Atlantic Bight | 8 | 97.8 ± 5.3 | 89.0–102.8 |
| 4 | Subtropical Northwest Atlantic | 3 | 94.1 ± 7.6 | 86.9–102 |
| 5 | Northeast Gulf of Mexico | 2 | 98.3 ± 12.4 | 89.5–107.0 |

*SCL* Straight carapace length

* Refers to foraging areas in the South Atlantic Bight not including waters off Cape Canaveral

and because these rates are allometrically dependent on body mass (Carleton and Martínez del Rio 2005).

To evaluate turtle movements, turtles from Group 1 (resident males) were only included if they stayed near Cape Canaveral for at least 60 days, well after all migrants left the breeding area. Turtles from Groups 2 through 5 (migratory males) were included if transmissions lasted a minimum of 30 days at the foraging ground. Following these criteria, movements of 4 turtles could not be determined because transmissions failed before the 30- or 60-day cutoffs, and a total of 25 turtles (Table 1) was used to relate SI with satellite telemetry data. We used the median latitude where turtles occurred at the foraging grounds to evaluate the relationship between SI and geographic location. Location data were extensively filtered (see Arendt et al. 2012a, b for details). Additionally, we compiled isotopic data from the literature on lower trophic-level organisms from the geographic areas where male loggerheads traveled after the mating season.

### Sample preparation and analysis

Turtle EPI samples were washed with deionized water and alcohol swabs 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. Blood samples (RBC and PLA) were dried for 24 h at 60°C and then ground to a fine powder using a mortar and pestle. Lipids were extracted from EPI samples with petroleum ether using an accelerated solvent extractor. Lipids were not extracted from RBC and PLA samples because, for these tissues, C:N $\leq$ 3.5. According to Post et al. (2007), no extraction of lipids is necessary when tissue C:N < 3.5. Lipids were extracted from EPI samples to allow for comparison with previously published EPI isotopic data.

For stable isotope analysis, approximately 500–600 μg of each sample was weighed and sealed in a tin capsule. Samples were analyzed for $\delta^{13}C$ and $\delta^{15}N$ by combustion in a COSTECH ECS 4010 elemental analyzer interfaced via a Finnigan-MAT ConFlow III device to a Finnigan-MAT DeltaPlus XL 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: $\delta X = [(R_{sample}/R_{standard}) - 1] \times 1{,}000$, where $\delta X$ 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 ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) in the sample and international standard, respectively. The standard used for $^{13}C$ was Vienna Pee Dee Belemnite and for $^{15}N$ was atmospheric $N_2$. Working standards, L-glutamic acid USGS40 ($\delta^{13}C = -26.39‰$ and $\delta^{15}N = -4.52‰$), were calibrated monthly against international standards and were inserted in all runs at regular intervals to calibrate the system. In addition, a loggerhead scute standard ($\delta^{13}C = -18.36‰$ and $\delta^{15}N = 7.68‰$) was used in all runs. The analytical accuracy of our measurements—calculated as the SD of replicates of standards—was 0.11 and 0.12‰ for $\delta^{13}C$ and $\delta^{15}N$ of working standards ($N = 29$), respectively, and 0.12 and 0.16‰ for $\delta^{13}C$ and $\delta^{15}N$ of scute standards ($N = 10$), respectively.

### Statistical analysis

Levene's test was used to assess homogeneity of variances of $\delta^{13}C$ and $\delta^{15}N$ among the three tissues sampled. The relationships between the isotopic signatures of the two tissues with similar temporal isotopic assimilation, EPI and RBC, were evaluated with linear regressions. To explore the effect of geographic location on $\delta^{13}C$ and $\delta^{15}N$, the correlation between isotopic signatures and the latitude of the foraging grounds of the turtles was evaluated using Spearman rank test. Additionally, Wilcoxon rank sum test was used to assess body size differences between two main migration patterns, northern (Group 3) versus southern (Group 4). Body size differences among remaining Groups (1, 2, and 5) were not assessed because samples sizes were too small ($N < 3$) or because turtles did not migrate to a different geographic area after the mating season. Finally, the relationship between body size and isotopic signatures of males within a foraging area was evaluated using linear regression whenever sample size allowed. All data were analyzed using program R (R Development Core Team 2009) with an $\alpha$ level of 0.05.

## Results

The ranges (the difference between maximum and minimum values) of isotopic signatures for each tissue from all adult

male loggerhead samples varied between 7.53 and 8.19‰ for $\delta^{13}$C, while $\delta^{15}$N ranges varied from 8.96 to 9.68‰ (Table 2). The variance of isotopic values was similar among tissues for both $\delta^{13}$C (Levene's test, $F = 0.19$, $P = 0.827$) and $\delta^{15}$N (Levene's test, $F = 0.58$, $P = 0.562$) (Table 2). Also, visual inspection of Fig. 1b reveals a pattern in the SI values of male turtles similar to that of female loggerheads.

When EPI and RBC—tissues reflecting the turtle's longer-term foraging history—were compared, we found that RBC had lower values for both $\delta^{13}$C and $\delta^{15}$N among all turtles with both tissues sampled. Furthermore, there was a significant positive relationship between RBC and EPI samples for both $\delta^{13}$C (linear regression, $r^2 = 0.96$, $F_{1,24} = 623.8$, $P < 0.001$; Fig. 3a) and $\delta^{15}$N ($r^2 = 0.98$, $F_{1,24} = 1{,}208$, $P < 0.001$; Fig. 3b). However, we should be cautious when using the $\delta^{13}$C correction factor to obtain specific carbon isotopic values, as the data distribution is unequal (Fig. 3a).

We analyzed three different tissues collected from satellite-tracked loggerheads, but our conclusions about turtle movements will be based on RBC because this was the only tissue available for all turtles sampled that reflect the longer-term foraging history of the turtle prior to capture. Male turtles that migrated south to the Bahamas and the Florida Keys had the highest $\delta^{13}$C and lowest $\delta^{15}$N values (Fig. 1b). In contrast, the lowest values of $\delta^{13}$C were found in males that migrated northward to New Jersey, while the highest $\delta^{15}$N value was found in a turtle that established residency in Maryland (Fig. 1b). A strong negative correlation was found between the latitude of the residential foraging location and the $\delta^{13}$C RBC values (Spearman rank correlation, $r_s = -0.73$, $N = 25$, $P < 0.001$; Fig. 4Aa). Similarly, a strong but positive correlation was found between the latitude and the $\delta^{15}$N RBC values ($r_s = 0.78$, $N = 25$, $P < 0.001$; Fig. 4Ba). Moreover, EPI and PLA had similar correlation patterns as that of RBC. EPI and PLA $\delta^{13}$C values were correlated negatively with latitude (EPI: $r_s = -0.77$, $N = 17$, $P < 0.001$; PLA: $r_s = -0.82$, $N = 25$, $P < 0.001$; Fig. 4Ab, Ac), and $\delta^{15}$N was positively correlated with latitude (EPI: $r_s = 0.86$, $N = 17$, $P < 0.001$; PLA: $r_s = 0.75$, $N = 25$, $P < 0.001$; Fig. 4Bb, Bc). Only one male turtle (from Group 1) was recaptured in Port Canaveral in consecutive years and had similar RBC $\delta^{13}$C (−15.57 and −15.55‰) and $\delta^{15}$N (10.95 and 10.80‰) values in both years.

Body size had a significant negative relationship with $\delta^{15}$N (linear regression: $r^2 = 0.62$, $F_{1,8} = 15.7$, $P = 0.004$; Fig. 5), but not with $\delta^{13}$C (linear regression: $r^2 = 0.047$, $F_{1,8} = 1.445$, $P = 0.264$) in the turtles that remained near Cape Canaveral (Group 1). Sample size in other foraging areas was too small to analyze a relationship between body size and isotopic signatures. Additionally, body sizes were not significantly different between turtles with northernmost foraging grounds (Group 3: using waters in

**Table 2** Adult male loggerhead population range (maximum–minimum) and variance (Var) of $\delta^{13}$C and $\delta^{15}$N values in red blood cells (RBC), epidermis (EPI), and plasma (PLA) samples

| | RBC ($N = 37$) | | EPI ($N = 26$) | | PLA ($N = 37$) | |
|---|---|---|---|---|---|---|
| | Range (‰) | Var | Range (‰) | Var | Range (‰) | Var |
| $\delta^{13}$C | 8.15 | 3.22 | 7.53 | 3.93 | 8.19 | 3.54 |
| $\delta^{15}$N | 8.97 | 5.33 | 9.68 | 7.15 | 8.96 | 5.39 |

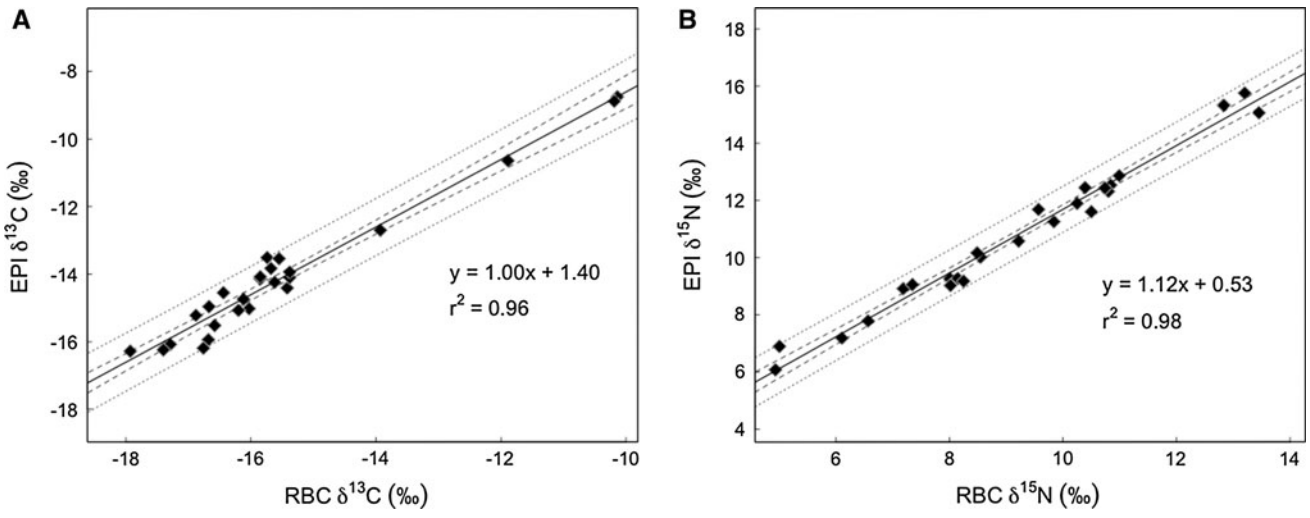


**Fig. 3** Linear relationships between epidermis (EPI, $N = 26$) and red blood cells (RBC, $N = 26$) for **a** $\delta^{13}$C and **b** $\delta^{15}$N of adult male loggerheads. The relationship between these tissues that reflect similar temporal resource assimilation is significant for both $\delta^{13}$C and $\delta^{15}$N (see "Results"). The *solid line* is the best-fit line, the *dashed lines* denote the 95% confidence interval for the linear regression, and the *dotted lines* denote the 95% prediction interval (the range in which future observations will fall)

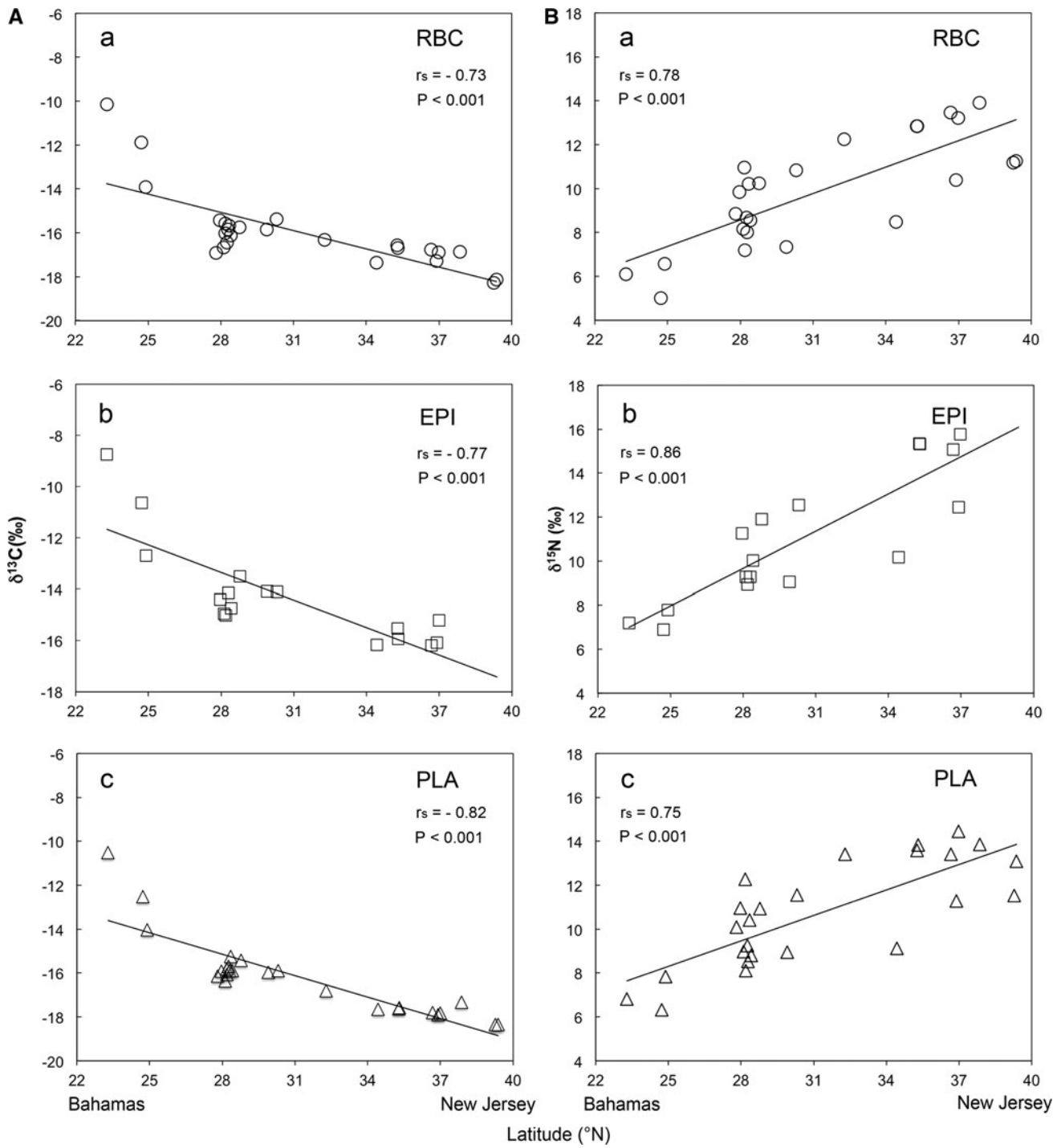


**Fig. 4** Stable isotope ratios of carbon ($\delta^{13}$C; column *A*) and nitrogen ($\delta^{15}$N; column *B*) of red blood cells (RBC; $N = 25$; *open circle*), epidermis (EPI; $N = 17$; *open square*), and plasma (PLA; $N = 25$; *open triangle*) from adult male loggerheads collected at Cape Canaveral, FL, versus the latitude to which turtles migrated after the mating season

the MAB) and turtles using southernmost foraging areas (Group 4: using waters in the subtropical NWA) (Wilcoxon rank sum test, $W = 7$, $N_1 = 3$, $N_2 = 8$, $P = 0.376$). However, sample sizes between north and south were unequal with only 3 turtles migrating to southernmost foraging areas (Fig. 2).

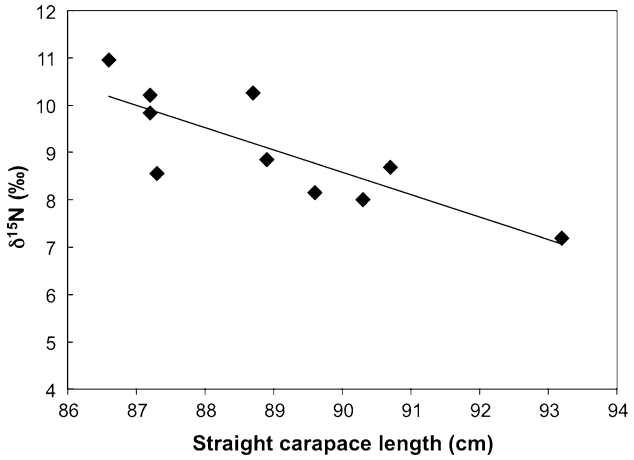


**Fig. 5** Red blood cell $\delta^{15}$N versus straight carapace length in male loggerhead turtles that remained off Cape Canaveral ($r^2 = 0.64$, $F_{1,8} = 15.7$, $P = 0.004$)

## Discussion

### Isotopic signatures among different tissues of adult male loggerheads

We found that the isotopic values of male tissues reflecting different temporal integration of diet and habitat use (RBC, EPI, and PLA) were similar in range and variance. RBC and EPI isotopic values were expected to be similar in range and variation because these tissues provide the turtle's longer-term dietary information. On the other hand, PLA reflects a relatively more recent foraging history of a turtle (up to at least 2 months). Therefore, if males had been feeding in waters off Cape Canaveral when captured, then PLA signatures would have been similar among turtles. The fact that PLA samples presented a similar pattern as RBC and EPI samples indicates that either (1) turtles had not spent enough time to allow the Cape Canaveral isotopic signature to be incorporated or (2) turtles had not been feeding in the breeding area.

The significant positive relationship between $\delta^{13}$C and $\delta^{15}$N of RBC and EPI (Fig. 3) allows us to predict EPI signatures for a given RBC sample and vice versa. EPI samples are more easily collected than RBC samples. Correction factors of this nature can be useful when trying to compare isotopic values among individuals, and the same tissues are not available. In this study, these correction factors allowed for general comparison between male and female turtles. However, a systematic experiment in captivity in which turtles are consistently fed a diet with known isotopic signatures would be the ideal way to evaluate isotopic discrimination among different tissues, especially when specific tissue isotopic values are required to estimate diet composition. Few such experiments have been conducted in sea turtles (Seminoff et al. 2006, 2009; Reich et al. 2008; Vander Zanden et al. unpubl. data), and no such experiments have been conducted in adult loggerheads.

### Variation in $\delta^{13}$C and $\delta^{15}$N among satellite-tracked male loggerheads

In this study, we found a significant relationship between both the $\delta^{13}$C and $\delta^{15}$N of male loggerheads and the latitude of their foraging grounds. The ranges of isotopic values were 8.2‰ and 8.9‰ for RBC $\delta^{13}$C and $\delta^{15}$N, respectively, over a range of 16° latitude (Fig. 4Aa, Ba). Large differences in the isotopic signatures of turtles in the NWA could be attributed to differences in (1) trophic level (based on $\delta^{15}$N), (2) habitat type (i.e., pelagic versus benthic or oceanic versus neritic, based on $\delta^{13}$C) and/or (3) geographic location (based on both $\delta^{13}$C and $\delta^{15}$N).

Turtle–diet isotopic discrimination factors for $^{15}$N are not available for adult loggerheads. However, given the discrimination factor of 2.5‰ for RBC in adult green turtles, *Chelonia mydas* (H. B. Vander Zanden et al., unpubl. data), the observed range in $\delta^{15}$N values in male loggerheads would imply a variation of approximately 3.6 trophic levels in male loggerheads, if nitrogen baseline signatures were equal across all foraging areas. Such trophic-level differences are unlikely to occur in NWA loggerhead turtles because they are known to prey mainly on benthic invertebrates in coastal waters (see references cited in Hopkins-Murphy et al. 2003). A historic shift in diet from horseshoe crabs to crustaceans and then to mostly fish has been recently reported in loggerheads in Chesapeake Bay, Virginia, USA, through analysis of stomach contents; however, no turtle with SCL > 90 cm showed this diet change (Seney and Musick 2007). Male loggerhead RBC $\delta^{15}$N signature (mean ± SD = 12.3 ± 1.70‰) is higher than $\delta^{15}$N of horseshoe crabs and blue crabs (10.3 and mean ± SD = 11.5 ± 2.40‰, respectively; Knoff et al. 2001) and lower than those of fish (range: 13.9–18.0‰; Buchheister and Latour 2011), which suggests that adult male loggerheads in this region may be relying more on benthic invertebrates than on fish.

The second possible explanation relates the large variation in $\delta^{13}$C to differential habitat use. Because all male loggerheads dispersed to coastal locations (Fig. 2), the variation in $\delta^{13}$C may be reflecting a pelagic versus benthic habitat use in neritic waters, which would result in low versus high $\delta^{13}$C values, respectively. Indeed, lowest values of $\delta^{13}$C were found in turtles that migrated to high latitude areas (New Jersey; Fig. 1b), where turtles used deeper waters (mean water depth = 28 m; M. Arendt, unpubl. data) contrasted with high $\delta^{13}$C turtles that migrated to lower latitude foraging areas (Bahamas and Florida Keys; Fig. 1b) and used shallow waters (mean water depth = 8 m; M.

Arendt, unpubl. data). Diving data for two northern turtles revealed use of both bottom and surface waters, suggesting that these feed throughout the water column (M. Arendt, unpubl. data). However, low $\delta^{13}C$ signatures were also present in turtles using shallow waters in North and South Carolina (mean water depth = 5 and 7 m, respectively; M. Arendt, unpubl. data) (Fig. 1b). Reich et al. (2010) found similar results in some nesting loggerheads in Florida, which presented low $\delta^{13}C$ values as well as neritic/benthic epibionts suggesting use of shallow waters. Thus, although we cannot rule out the pelagic versus benthic foraging strategy in male loggerheads, we propose that $\delta^{13}C$ signatures are being affected primarily by other factors.

The third possible explanation for the large variation of $\delta^{13}C$ and $\delta^{15}N$ is geographic location. The differences in $\delta^{15}N$ and $\delta^{13}C$ at the base of the food web are conserved through higher trophic levels (Cherel and Hobson 2007; Pajuelo et al. 2010). Thus, if baseline signatures change with geographic area, then the isotopic differences observed in males would reflect the location of the foraging area rather than differences in diet or habitat use.

Indeed, different oceanographic processes and nutrient sources influence the baseline signatures of the foraging areas used by male loggerheads. In the NWA, nitrogen fixation, which lowers the $\delta^{15}N$ signature of primary producers, is highest in the tropical and subtropical NWA (Montoya et al. 2002). On the other hand, highly productive coastal waters near estuaries in the Mid-Atlantic Bight are characterized by high $\delta^{15}N$ values in primary producers apparently due to the high $\delta^{15}N$ contribution from human sources to these waters (McKinney et al. 2010). Also, denitrification, a process that increases values of $\delta^{15}N$ (Montoya 2007), has been reported in the MAB (Fennel et al. 2006). To what extent denitrification affects the $\delta^{15}N$ of coastal biota of the MAB has not yet been assessed (McKinney et al. 2010).

Therefore, we would expect male loggerheads foraging from Virginia to New Jersey to have the highest $\delta^{15}N$ signatures, while turtles foraging in areas with high rates of $N_2$ fixation (e.g., the Bahamas) will present the lowest $\delta^{15}N$ signatures. This clearly corresponds with the increase in male $\delta^{15}N$ with latitude (Fig. 4B), but does not necessarily support a latitudinal effect on coastal waters from equator to polar regions because $\delta^{15}N$ of primary producers slowly decreases at latitudes north of the Delaware estuary (McKinney et al. 2010). The probable human influence revealed in the $\delta^{15}N$ signatures of males in northern waters corresponds with the elevated concentrations of persistent organic pollutants recently found in the same male loggerheads (Ragland et al. 2011).

Carbon isotope signatures can also reflect geographic location. High latitude primary producers have much lower $\delta^{13}C$ than primary producers at lower latitudes (Goericke and Fry 1994). Water temperature has recently been proposed as a proxy for baseline $\delta^{13}C$ values because it affects plankton growth rates and dissolved $CO_2$ concentrations in seawater—which in return have an effect on baseline $\delta^{13}C$ values—(Mackenzie et al. 2011) and could explain the $\delta^{13}C$ latitudinal gradient. This latitudinal gradient in $\delta^{13}C$ agrees with the lowest male $\delta^{13}C$ value found in cooler waters off New Jersey (39.4°N) and highest male $\delta^{13}C$ value found in warmer waters of the Bahamas (23.3°N) (Fig. 4A). This gradient could also explain why turtles foraging in shallow waters off North and South Carolina (35.3 and 33.3°N, respectively) that were expected to have high $\delta^{13}C$—reflecting benthic feeding—had low $\delta^{13}C$ values.

Ultimately, variations in the isotopic signatures by geographic location should also be reflected in other food web organisms. Isotopic data available in the literature for lower trophic-level organisms in those geographic locations where male loggerheads migrated reveal that they follow a similar pattern to that of male loggerheads (Fig. 6). For instance, known trophic-level organisms such as omnivorous shrimps and lobsters in the Florida Keys (~25°N) show lower $\delta^{15}N$ than those of omnivorous crabs and horseshoe crabs off North Carolina (~35°N), and even similar or lower to those of filter feeding bivalves in Virginia and Delaware (~37° and 39°N, respectively). Food web baseline signatures along the latitudinal gradient used by loggerheads are scarce; however, nitrogen isotopic signatures of particulate organic matter (proxy for primary producer) are available for the Florida Keys (~25°N) and coastal waters of Virginia and Delaware (~37° and 39°N, respectively). Nitrogen values range from −0.9 (Macko et al. 1984) to 3.6‰ in waters of the Florida Keys (Behringer and Butler 2006; Evans et al. 2006; Lamb and Swart 2008) and 7.2–7.7‰ in near-shore waters off Virginia and Delaware (McKinney et al. 2010). Hence, although we did not assess the isotopic signatures of loggerhead prey items in all the geographic locations visited by the turtles, the results indicate that the variation in the $\delta^{13}C$ and $\delta^{15}N$ of male loggerheads is due to geographic location. Additionally, because the range of values in males is similar to that of female loggerheads (Fig. 1b), we believe that the 2-cluster females probably represent a gradient of North to South geographic locations used by adult female loggerheads in the NWA. The relationship between female isotopic signatures and geographic areas used are being addressed in another study. Our results highlight the need for knowledge of baseline isotopic signatures when identifying foraging habitats of highly migratory organisms.

Even though there appears to be a separation of geographic location for at least northernmost versus southernmost foraging areas (i.e., foraging grounds in the MAB versus subtropical NWA, respectively) using combined $\delta^{13}C$ and $\delta^{15}N$ values, isotopic signatures from the northeast Gulf of Mexico overlap with those of Cape Canaveral (Fig. 1b).

The use of other markers (such as trace elements) could help reveal unique characteristics of the distinct geographic locations in the NWA for which carbon and nitrogen are not informative.

Because isotopic signatures of male loggerhead tissues reflect integrated diet and habitat use of the turtles before their capture, the agreement between isotopic signatures and migration patterns–which reflects the foraging history after the mating season–suggests site fidelity to foraging areas. Hatase et al. (2002; 2006), McClellan et al. (2010), and Zbinden et al. (2011) have reported similar agreements between isotopic signatures and migration patterns in female and juvenile sea turtles. Foraging fidelity in NWA adult female loggerheads has also been observed through satellite telemetry data (Hawkes et al. 2007, 2011) and has been indicated by the long-term consistency in SI signatures of scute layers (Vander Zanden et al. 2010).

## Relation between body size and $\delta^{15}$N signatures

A surprising decrease in RBC $\delta^{15}$N with body size was revealed in adult male turtles that stayed in waters off Cape Canaveral (Fig. 5). Although the RBC $\delta^{13}$C varied from −15.42 to −16.91‰, the lack of a relationship between body size and $\delta^{13}$C suggests that males were feeding on prey utilizing similar carbon sources. Values of $\delta^{15}$N commonly increase with body size due to diet shift to higher trophic level (Reñones et al. 2002). Among individuals feeding on the same diet, low values of $\delta^{15}$N can provide evidence of a lower nitrogen discrimination value in smaller juveniles with fast growth rates (Martínez del Rio and Wolf 2005; Reich et al. 2008). Unlike juveniles, adult turtles grow very slowly after reaching sexual maturity (Bjorndal et al. 1983), thus no growth effect on $\delta^{15}$N may be evident in adult individuals (Martínez del Rio and Wolf 2005). In our study, smaller adult males may preferentially venture into inshore waters of the east central Florida where anthropogenic influence has been evidenced in primary producers, which show elevated $\delta^{15}$N values (Barile 2004). If this pattern is consistent when a larger sample size is analyzed, the cause for the pattern should be explored.

## Implications of the geographic variation of isotopic signatures

The geographic variation in the isotopic signatures of male loggerheads can potentially help us understand patterns of migratory connectivity between loggerhead foraging grounds and breeding areas. In particular, by identifying and differentiating foraging subpopulations within breeding areas in the NWA, we can assess how breeding populations are structured. This has important implications in the long term. Changes through time in the relative composition of individuals from a particular foraging ground observed in a breeding area may provide evidence of threats to which turtles are exposed (Hatase et al. 2002; Zbinden et al. 2011). For example, in the NWA, turtles using northern foraging grounds are at a higher risk of sublethal toxic effects from high concentrations of organic pollutants than are southern foragers (Ragland et al. 2011).

Environmental forces acting on resource availability have been reported to drive the life history of conspecifics, including leatherback (*Dermochelys coriacea*) and green (*Chelonia mydas*) sea turtles in marine regions (Suryan

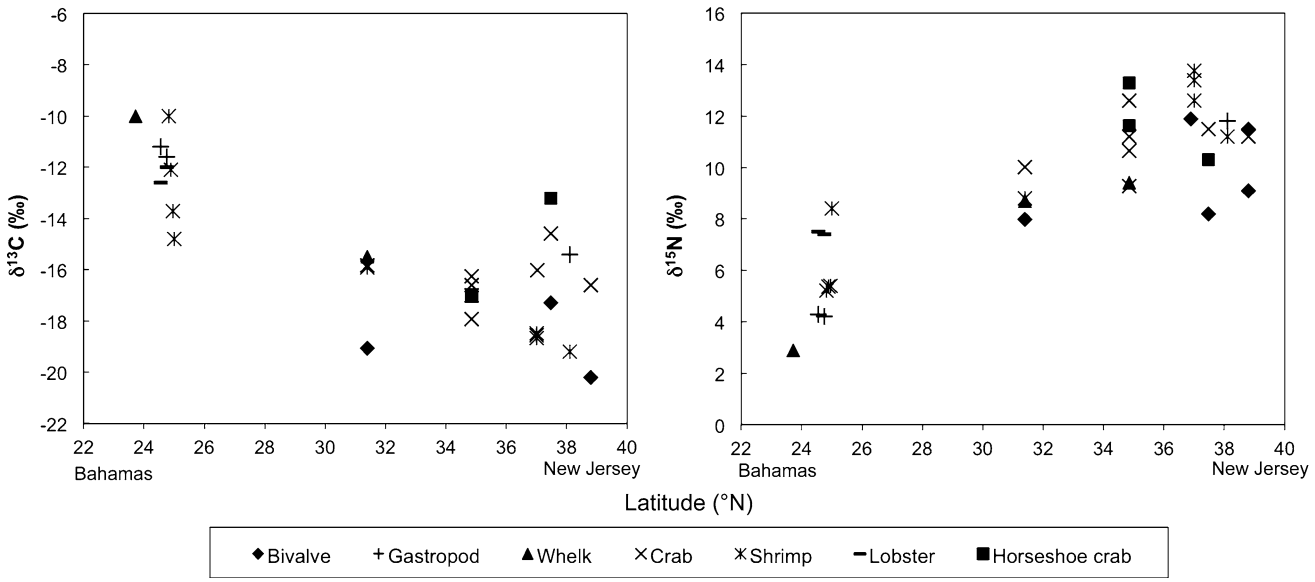


**Fig. 6** Comparison of stable isotope ratios of $\delta^{13}$C (*left*) and $\delta^{15}$N (*right*) of food web organisms at the different foraging locations visited by male loggerheads after the mating season (represented by latitude). Mean values are given. For scientific names, sample sizes, and references see Table 3

**Table 3** Stable isotope ratios of food web organisms at different geographic locations (represented by latitude) in the Northwest Atlantic visited by our satellite-tracked male loggerheads

| Species | Lat (°N) | *N* | $\delta^{13}$C (‰) | $\delta^{15}$N (‰) | Source |
|---|---|---|---|---|---|
| Bivalves | | | | | |
| Ribbed mussel *Geukensia demissa* | 38.8 | NA | NA | 11.5 | McKinney et al. (2010) |
| | 37.5 | 6 | −17.3 ± 0.24 | 8.2 ± 0.73 | Knoff et al. (2001) |
| | 36.9 | NA | NA | 11.9 | McKinney et al. (2010) |
| Blue mussel *Mytilus edulis* | 38.8 | 5 | −20.2 ± 0.30 | 9.1 ± 1.10 | Fantle et al. (1999) |
| Eastern oyster *Crassostrea virginica* | 31.4 | 12 | −19.1 ± 1.09 | 7.9 ± 0.59 | J. Nifong unpubl. data |
| Gastropods | | | | | |
| Atlantic moon snail *Neverita duplicata* | 38.1 | NA | −15.4 | 11.8 | Woodland et al. (2011) |
| Whelk *Busycon* sp. | 34.8 | 10 | −17.0 ± 0.70 | 9.4 ± 0.57 | Wallace et al. (2009) |
| Channeled whelk *Busycon canaliculatum* | 31.4 | NA | −15.5 | 8.7 | Peterson and Howarth (1987) |
| Queen conch *Strombus gigas* | 23.7 | NA | −10.0 | 2.9 | Stoner and Waite (1991) |
| Star snail *Lithopoma tectum* | 24.8 | 5 | −11.2 ± 0.10 | 4.3 ± 1.10 | Behringer and Butler (2006) |
| | 24.6 | 5 | −11.6 ± 1.20 | 4.2 ± 0.03 | Behringer and Butler (2006) |
| Chelicerate | | | | | |
| Horseshoe crab *Limulus polyphemus* | 37.5 | 1 | −13.2 | 10.3 | Knoff et al. (2001) |
| | 34.8 | 10 | −17.0 ± 1.31 | 11.6 ± 0.46 | Wallace et al. (2009) |
| | 34.8 | 9 | −17.0 ± 0.60 | 13.3 ± 0.90 | Snover et al. (2010) |
| Crustaceans | | | | | |
| Blue crab *Calinectes sapidus* | 38.8 | 3 | −16.6 ± 0.80 | 11.2 ± 0.60 | Fantle et al. (1999) |
| | 37.5 | 6 | −14.6 ± 0.50 | 11.5 ± 2.4 0 | Knoff et al. (2001) |
| | 37.0 | 9 | −16.0 | NA | Pruell et al. (2003) |
| | 34.8 | 4 | −16.3 ± 1.65 | 9.3 ± 0.38 | Wallace et al. (2009) |
| | 34.8 | 7 | −16.6 ± 0.50 | 11.2 ± 0.90 | Snover et al. (2010) |
| | 31.4 | 23 | −15.8 ± 1.03 | 10.0 ± 0.85 | J. Nifong unpubl. data |
| Spider crab *Libinia emarginata* | 34.8 | 11 | −17.9 ± 1.33 | 10.7 ± 0.48 | Wallace et al. (2009) |
| *Libinia dubia* | 34.8 | 5 | −17.6 ± 1.60 | 12.6 ± 1.10 | Snover et al. (2010) |
| Mysid shrimp *Neomysis americana* | 38.1 | NA | −19.2 | 11.2 | Woodland et al. (2011) |
| Mantis shrimp *Squilla empusa* | 37.0 | 6 | −18.6 ± 0.56 | 12.6 ± 0.43 | Buchheister and Latour (2011) |
| | 37.0 | 4 | −18.5 ± 0.20 | 13.4 ± 0.23 | Buchheister and Latour (2011) |
| | 37.0 | 6 | −18.7 ± 0.29 | 13.8 ± 0.36 | Buchheister and Latour (2011) |
| White shrimp *Penaeus* sp. | 31.4 | NA | −17.0 | 9.6 | Peterson and Howarth (1987) |
| | 31.4 | 11 | −15.9 ± 0.60 | 8.8 ± 0.63 | J. Nifong unpubl. data |
| Pink shrimp *Farfantepenaeus duorarum* | 25.0 | 4 | −13.7 ± 0.93 | 5.4 ± 0.50 | Harrigan et al. (1989) |
| | 25.0 | NA | −14.8 ± 0.50 | 8.4 ± 0.90 | Macko et al. (1984) |
| | 24.9 | 96 | −12.1 ± 0.30 | 5.4 ± 0.21 | Fry et al. (1999) |
| Spiny lobster *Panulirus argus* | 24.8 | 60 | −10.0 ± 2.10 | 5.2 ± 1.70 | Schwamborn and Criales (2000) |
| | 24.8 | 5 | −12.0 ± 0.70 | 7.4 ± 0.20 | Behringer and Butler (2006) |
| | 24.6 | 5 | −12.6 ± 0.50 | 7.5 ± 0.20 | Behringer and Butler (2006) |

Values are means ± SD. *Lat* latitude; *N*: sample size, *NA* not available

et al. 2009). Recently, Hatase et al. (2010) found differences in body size in adult female loggerheads ($N = 149$) related to differential foraging habitat use. Similarly, Zbinden et al. (2011) found that nesting loggerheads in the Mediterranean ($N = 58$) exhibited differences in body size and clutch size associated with geographically separated foraging areas. In the NWA, however, Hawkes et al. (2007), based on a limited sample size ($N = 12$), did not find any difference in fecundity measures (clutch frequency, clutch size, body size, remigration intervals, and inter-nesting intervals) between adult females using northern ($N = 9$) versus southern areas ($N = 3$). In this study, we found no differences in body size between turtles migrating to cool and highly productive waters of the MAB (Group 3, $N = 8$) and turtles migrating south to warm waters of the subtropical NWA (Group 4, $N = 3$), but our samples size for southern

turtles was small. Further systematic assessment of how differences in nutrient sources and environmental factors acting on nutrient availability, as well as differences in the concentration of pollutants, may shape the life history and health of loggerheads is crucial, if we want to understand changes in loggerhead population abundance in the Atlantic (Witherington et al. 2009).

Studies using satellite telemetry have shown that female NWA loggerhead turtles follow different migration patterns (Plotkin and Spotila 2002; Dodd and Byles 2003; Hawkes et al. 2007, 2011; Foley et al. 2008; Turtle Expert Working Group 2009) and show fidelity to foraging areas with unique environmental characteristics after the mating season (Hawkes et al. 2007, 2011). NWA adult males in this study use foraging grounds (Fig. 2) similar to those of NWA females (Hawkes et al. 2011), and the agreement found in our study between SI and satellite data suggest that males show site fidelity to these foraging areas. The similar patterns in the use of foraging areas and in the SI values observed between females and males in the NWA may indicate that adult males have similar foraging strategies–similar habitat use, foraging areas, and movement patterns–as those of adult female loggerheads in the NWA.

## Conclusions

In the present study, adult male loggerheads breeding in Florida revealed a geographic pattern in the SI values, which indicates that males use isotopically distinct geographic areas after the mating season. Therefore, SI may help identify foraging subpopulations within a breeding area and elucidate residency and migration patterns in sea turtles in the NWA. Moreover, by linking foraging grounds to breeding areas through SI analysis, we can begin to understand how distinct environmental factors in different foraging grounds affect the biology and ecology of loggerheads. The agreement between the isotopic signatures and post-mating movement patterns suggests a foraging site fidelity in male loggerheads that has been observed in adult females. Also, adult male loggerheads revealed a variation in $\delta^{13}C$ and $\delta^{15}N$ values similar to that observed in adult females, suggesting that males and females have similar foraging strategies. The use of additional markers in combination with isotopic signatures may help differentiate geographically separated areas with similar isotopic signatures. Understanding the temporal and spatial distribution of sea turtle populations is essential for the development of effective conservation and management strategies.

**Acknowledgments** We thank Capt. Lindsey Parker and the crew of the RV Georgia Bulldog, A. Segars, J. Byrd, and K. Mazzarella for invaluable support during fieldwork. The U.S. Fish and Wildlife Service, U.S. National Marine Fisheries Service, the National Fish and Wildlife Foundation, and the Knight Vision Foundation provided funding support for this project. For comments on earlier versions of the manuscript, we thank L.C. Majure and H. B. Vander Zanden. We also thank J. Curtis and the Stable Isotope Lab at the University of Florida for assistance with stable isotope analysis. We are grateful to H. B. Vander Zanden and J. Nifong for sharing unpublished data, and two anonymous reviewers for their comments. Turtle samples were collected in compliance with the National Marine Fisheries Service (Section 10(A)(1)(a) Permit #1540), Florida Fish and Wildlife Conservation Commission (Marine Turtle Permit #163) and the Institutional Animal Care and Use Committee of the University of Florida.

## References

Arendt MD, Segars AL, Byrd JI, Boynton JI, Whitaker JD, Parker L, Owens DW, Blanvillain G, Quattro JM, Roberts MA (2012a) Distributional patterns of adult male loggerhead sea turtles (*Caretta caretta*) in the vicinity of Cape Canaveral, Florida during and after a major annual breeding aggregation. Mar Biol. doi:10.1007/s00227-011-1793-5

Arendt MD, Segars AL, Byrd JI, Boynton JI, Schwenter JA, Whitaker JD, Parker L (2012b) Migration, distribution, and diving behavior of adult male loggerhead sea turtles (*Caretta caretta*) following dispersal from a major breeding aggregation in the Western North Atlantic. Mar Biol. doi:10.1007/s00227-011-1826-0

Barile PJ (2004) Evidence of anthropogenic nitrogen enrichment of the littoral waters of east central Florida. J Coast Res 20:1237–1245

Behringer DC, Butler MJ (2006) Stable isotope analysis of production and trophic relationships in a tropical marine hard-bottom community. Oecologia 148:334–341

Bjorndal KA, Meylan AB, Turner BJ (1983) Sea turtle nesting at Melbourne Beach, Florida, I. Size, growth and reproductive biology. Biol Conserv 26:65–77

Blanvillain G, Pease AP, Segars AL, Rostal DC, Richards AJ, Owens DW (2008) Comparing methods for the assessment of reproductive activity in adult male loggerhead sea turtles *Caretta caretta* at Cape Canaveral, Florida. Endang Species Res 6:75–85

Block BA, Dewar H, Blackwell SB, Williams TD, Prince ED, Farwell CJ, Boustany A, Teo SLH, Seitz A, Walli A, Fudge D (2001) Migratory movements, depth preferences, and thermal biology of Atlantic bluefin tuna. Science 293:1310–1314

Block BA, Teo SLH, Walli A, Boustany A, Stokesbury MJW, Farwell CJ, Weng KC, Dewar H, Williams TD (2005) Electronic tagging and population structure of Atlantic bluefin tuna. Nature 434:1121–1127

Bolker BM, Okuyama T, Bjorndal KA, Bolten AB (2007) Incorporating multiple mixed stocks in mixed stock analysis: 'many-to-many' analyses. Mol Ecol 16:685–695. doi:10.1111/J.1365-294x.2006.03161.X

Buchheister A, Latour RJ (2011) Trophic ecology of summer flounder in Lower Chesapeake Bay inferred from stomach content and stable isotope analyses. Trans Am Fish Soc 140:1240–1254

Carleton SA, Martínez del Rio C (2005) The effect of cold-induced increased metabolic rate on the rate of 13C and 15N incorporation in house sparrows (*Passer domesticus*). Oecologia 114:226–232

Cherel Y, Hobson KA (2007) Geographical variation in carbon stable isotope signatures of marine predators: a tool to investigate their foraging areas in the Southern Ocean. Mar Ecol-Prog Ser 329:281–287

Dodd CK Jr, Byles R (2003) Post-nesting movements and behavior of loggerhead sea turtles (*Caretta caretta*) departing from east-central Florida nesting beaches. Chelonian Conserv Biol 4:530–536

Evans SL, Anderson WT, Jochem FJ (2006) Spatial variability in Florida Bay particulate organic matter composition: combining flow cytometry with stable isotope analysis. Hydrobiologia 569:151–165

Fantle MS, Dittel AI, Schwalm SM, Epifanio CE, Fogel ML (1999) A food web analysis of the juvenile blue crab, *Callinectes sapidus*, using stable isotopes in whole animals and individual amino acids. Oecologia 120:416–426

Fennel K, Wilkin J, Levin J, Moisan J, O'Reilly J, Haidvogel D (2006) Nitrogen cycling in the Middle Atlantic Bight: results from a three-dimensional model and implications for the North Atlantic nitrogen budget. Global Biogeochem Cycles 20:1–14. doi:10.1029/2005gb002456

Foley AM, Schroeder BA, MacPherson SL (2008) Post-nesting migrations and resident areas of Florida loggerheads. In: Kalb H, Rohde A, Gayheart K and Shanker K (compilers) Proceedings of the twenty-fifth annual symposium on sea turtle biology and conservation. NOAA Tech Mem NMFS-SEFSC-582

Frick MG, Williams KL, Bolten AB, Bjorndal KA, Martins HR (2009) Foraging ecology of oceanic-stage loggerhead turtles *Caretta caretta*. Endang Species Res 9:91–97

Fry B, Mumford PL, Rubble MB (1999) Stable isotope studies of pink shrimp (*Farfantepenaeus duorarum* Burkenroad) migrations on the southwestern Florida shelf. Bull Mar Sci 65:419–430

Goericke R, Fry B (1994) Variations of marine plankton $\delta^{13}C$ with latitude, temperature, and dissolved $CO_2$ in the World Ocean. Global Biogeochem Cycles 8:85–90

Graham BS, Koch PL, Newsome SD, McMahon KW, Aurioles D (2010) Using isoscapes to trace the movements and foraging behavior of top predators in oceanic ecosystems. In: West JB, Bowen GJ, Dawson TE, Tu KP (eds) Isoscapes: understanding movement, pattern and process on earth through isotope mapping. Springer, New York, pp 299–318

Harrigan P, Zieman JC, Macko SA (1989) The base of nutritional support for the gray snapper (*Lutjanus griseus*): an evaluation based on combined stomach content and stable isotope analysis. Bull Mar Sci 44:65–77

Hatase H, Takai N, Matsuzawa Y, Sakamoto W et al (2002) Size-related differences in feeding habitat use of adult female loggerhead turtles *Caretta caretta* around Japan determined by stable isotope analysis and satellite telemetry. Mar Ecol Prog Ser 233:273–281

Hatase H, Sato K, Yamaguchi M, Takahashi K, Tsukamoto K (2006) Individual variation in feeding habitat use by adult female green sea turtles (*Chelonia mydas*): are they obligately neritic herbivores? Oecologia 149:52–64

Hatase H, Omuta K, Tsukamoto K (2010) Oceanic residents, neritic migrants: a possible mechanism underlying foraging dichotomy in adult female loggerhead turtles (*Caretta caretta*). Mar Biol 157:1337–1342

Hawkes LA, Broderick AC, Coyne MS, Godfrey MH, Godley BJ (2007) Only some like it hot—quantifying the environmental niche of the loggerhead sea turtle. Diversity Distrib 13:447–457. doi:10.1111/J.1472-4642.2007.00354.X

Hawkes LA, Witt MJ, Broderick AC, Coker JW, Coyne MS, Dodd M, Frick MG, Godfrey MH, Griffin DB, Murphy SR, Murphy TM, Williams KL, Godley BJ (2011) Home on the range: spatial ecology of loggerhead turtles in Atlantic waters of the USA. Diversity Distrib 17:624–640. doi:10.1111/j.1472-4642.2011.00768.x

Hays GC, Broderick AC, Godley BJ, Luschi P, Nichols WJ (2003) Satellite telemetry suggests high levels of fishing-induced mortality in marine turtles. Mar Ecol-Prog Ser 262:305–309

Hobson KA, Piatt JF, Pitocchelli J (1994) Using stable isotopes to determine seabird trophic relationships. J Anim Ecol 63:786–798

Hopkins-Murphy SR, Owens DW, Murphy TM (2003) Ecology of immature loggerheads on foraging grounds and adults in internesting habitat in the eastern United States. In: Bolten AB, Witherington BE (eds) Loggerhead sea turtles. Smithsonian Institution Press, Washington, pp 79–92

IUCN (2011) IUCN red list of threatened species, version 2011.2. http://www.iucnredlist.org. Accessed 6 Feb 2012

Knoff AJ, Macko SA, Erwin RM (2001) Diets of nesting Laughing Gulls (*Larus atricilla*) at the Virginia Coast reserve: observations from stable isotope analysis. Isot Environ Healt S 37:67–88

Lamb K, Swart PE (2008) The carbon and nitrogen isotopic values of particulate organic material from the Florida Keys: a temporal and spatial study. Coral Reefs 27:351–362

Lemons GE, Eguchi T, Lyon BN, LeRoux R, Seminoff JA (in press) Effects of blood anticoagulants on stable isotope values ($\delta^{13}C$ and $\delta^{15}N$) of sea turtle blood tissue: implications for studies at remote field sites. Aquatic Biol. doi:10.3354/ab00397

Limpus CJ, Miller JD, Parmenter CJ, Reimer D, McLachlan N, Webb R (1992) Migration of green (*Chelonia mydas*) and loggerhead (*Caretta caretta*) turtles to and from eastern Australian rookeries. Wildl Res 19:347–358

MacKenzie KM, Palmer MR, Moore A, Ibbotson AT, Beaumont WRC, Poulter DJS, Trueman C (2011) Locations of marine animals revealed by carbon isotopes. Sci Rep 1:21. doi:10.1038/srep00021.

Macko SA, Entzeroth L, Parker PL (1984) Regional differences in nitrogen and carbon isotopes on the continental shelf of the Gulf of Mexico. Naturwissenschaften 71:374–375

Martínez del Rio C, Wolf BO (2005) Mass balance models for animal isotopic ecology. In: Starck MA, Wang T (eds) Physiological and ecological adaptations to feeding in vertebrates. Science Publishers, Enfield, pp 141–174

McClellan CM, Braun-McNeill J, Avens L, Wallace BP, Read AJ (2010) Stable isotopes confirm a foraging dichotomy in juvenile loggerhead sea turtles. J Exp Mar Biol Ecol 387:44–51. doi:10.1016/J.Jembe.2010.02.020

McKinney RA, Oczkowski AJ, Prezioso J, Hyde KJW (2010) Spatial variability of nitrogen isotope ratios of particulate material from Northwest Atlantic continental shelf waters. Estuar Coast Shelf S 89:287–293. doi:10.1016/J.Ecss.2010.08.004

Michener RH, Kaufman L (2007) Stable isotope ratios as tracers in marine food webs: an update. In: Michener RH, Lajtha K (eds) Stable isotopes in ecology and environmental science, 2nd edn. Blackwell Publishing, Malden, pp 238–282

Minagawa W, Wada E (1984) Stepwise enrichment of $^{15}N$ along food chains: further evidence and the relation between $\delta^{15}N$ and animal age. Geochim Cosmochim Acta 48:1135–1140

Montoya JP (2007) Natural abundance of $^{15}N$ in the marine environment. In: Michener RH, Lajtha K (eds) Stable isotopes in ecology and environmental science. Blackwell Publishing, Malden, pp 176–201

Montoya JP, Carpenter EJ, Capone DG (2002) Nitrogen fixation and nitrogen isotope abundances in zooplankton of the oligotrophic North Atlantic. Limnol Oceanogr 47:1617–1628

Newsome SD, Tinker MT, Monson DH, Oftedal OT, Ralls K, Staedler MM, Fogel ML, Estes JA (2009) Using stable isotopes to investigate individual diet specialization in California sea otters (*Enhydra lutris nereis*). Ecology 90:961–974

Owens DW, Ruiz GJ (1980) New methods of obtaining blood and cerebrospinal fluid from marine turtles. Herpetologica 36:17–20

Pajuelo M, Bjorndal KA, Alfaro-Shigueto J, Seminoff JA, Mangel JC, Bolten AB (2010) Stable isotope variation in loggerhead turtles reveals Pacific-Atlantic oceanographic differences. Mar Ecol-Prog Ser 417:277–285

Peterson BJ, Howarth RW (1987) Sulfur, carbon, and nitrogen isotopes used to trace organic matter flow in the salt-marsh estuaries of Sapelo Island, Georgia. Limnol Oceanogr 32:1195–1213

Plotkin PT, Spotila JR (2002) Post-nesting migrations of loggerhead turtles *Caretta caretta* from Georgia, USA: conservation implications

for a genetically distinct subpopulation. Oryx 36:396–399. doi:10.1017/S0030605302000753

Post D (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83:703–718

Post DM, Layman CA, Arrington DA, Takimoto G, Quattrochi J, Montana CG (2007) Getting to the fat of the matter: models, methods, and assumptions for dealing with lipids in stable isotope analyses. Oecologia 152:179–189

Pruell RJ, Taplin BK, Cicchelli K (2003) Stable isotope ratios in archived striped bass scales suggest changes in trophic structure. Fisheries Manag Ecol 10:329–336

R Development Core Team (2009) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. www.R-project.org

Ragland JM, Arendt MD, Kucklick JR, Keller JM (2011) Persistent organic pollutants in blood plasma of satellite-tracked adult male loggerhead sea turtles (*Caretta caretta*). Environ Toxicol Chem. doi:10.1002/etc.540

Reich KJ, Bjorndal KA, Bolten AB (2007) The 'lost years' of green turtles: using stable isotopes to study cryptic lifestages. Biol Lett 3:712–714

Reich KJ, Bjorndal KA, Martínez del Rio C (2008) Effects of growth and tissue type on the kinetics of $^{13}C$ and $^{15}N$ incorporation in a rapidly growing ectotherm. Oecologia 155:651–663. doi:10.1007/S00442-007-0949-Y

Reich KJ, Bjorndal KA, Frick MG, Witherington BE, Johnson C, Bolten AB (2010) Polymodal foraging in adult female loggerheads (*Caretta caretta*). Mar Biol 157:113–121. doi:10.1007/S00227-009-1300-4

Reñones O, Polunin N, Goni R (2002) Size related dietary shifts of *Epinephelus marginatus* in a western Mediterranean littoral ecosystem: an isotope and stomach content analysis. J Fish Biol 61:122–137

Rooker JR, Secor DH, deMetrio G, Schloesser R, Block BA, Neilson JD (2008) Natal homing and connectivity in Atlantic bluefin tuna populations. Science 322:742–744

Schwamborn R, Criales MM (2000) Feeding strategy and daily ration of juvenile pink shrimp (*Farfantepenaeus duorarum*) in a South Florida seagrass bed. Mar Biol 137:139–147

Seminoff JA, Jones TT, Eguchi T, Jones DR, Dutton PH (2006) Stable isotope discrimination (delta C-13 and delta N-15) between soft tissues of the green sea turtle *Chelonia mydas* and its diet. Mar Ecol-Prog Ser 308:271–278

Seminoff JA, Jones TT, Eguchi T, Hastings M, Jones DR (2009) Stable carbon and nitrogen isotope discrimination in soft tissues of the leatherback turtle (*Dermochelys coriacea*): insights for trophic studies of marine turtles. J Exp Mar Biol Ecol 381:33–41. doi:10.1016/J.Jembe.2009.08.018

Seney EE, Musick JA (2007) Historical diet analysis of loggerhead sea turtles (*Caretta caretta*) in Virginia. Copeia 2007:478–489

Snover ML, Hohn AA, Crowder LB, Macko SA (2010) Combining stable isotopes and skeletal growth marks to detect habitat shifts in juvenile loggerhead sea turtles *Caretta caretta*. Endang Species Res 13:25–31. doi:10.3354/esr00311

Stoner AW, Waite JM (1991) Trophic biology of *Strombus gigas* in nursery habitats: diets and food sources in seagrass meadows. J Mollusk Stud 57:451–460

Suryan RM, Saba VS, Wallace BP, Hatch SA, Frederiksen M, Wanless S (2009) Environmental forcing on life history strategies: evidence for multi-trophic level responses at ocean basin scales. Progr Oceanogr 81:214–222. doi:10.1016/J.Pocean.2009.04.012

Thorrold SR, Latkoczy C, Swart PK, Jones CM (2001) Natal homing in a marine fish metapopulation. Science 291:297–299

Turtle Expert Working Group (2009) An assessment of the loggerhead turtle population in the western North Atlantic Ocean. NOAA Tech Mem NMFS-SEFSC-575

Vander Zanden HB, Bjorndal KA, Reich KJ, Bolten AB (2010) Individual specialists in a generalist population: results from a long-term stable isotope series. Biol Lett 6:711–714. doi:10.1098/Rsbl.2010.0124

Wallace BP, Avens L, Braun-McNeill J, McClellan CM (2009) The diet composition of immature loggerheads: insights on trophic niche, growth rates, and fisheries interactions. J Exp Mar Biol Ecol 373:50–57. doi:10.1016/J.Jembe.2009.03.006

Witherington B, Kubilis P, Brost B, Meylan A (2009) Decreasing annual nest counts in a globally important loggerhead sea turtle population. Ecol Appl 19:30–54

Woodland RJ, Secor DH, Wedge ME (2011) Trophic resource overlap between small elasmobranchs and sympatric teleost in Mid-Atlantic Bight nearshore habitats. Estuar Coast 34:391–404

Zbinden JA, Bearhop S, Bradshaw P, Gill B, Margaritoulis D, Newton J, Godley BJ (2011) Migratory dichotomy and associated phenotypic variation in marine turtles revealed by satellite tracking and stable isotope analysis. Mar Ecol-Prog Ser 421:291–302. doi:10.3354/Meps08871