

Individual specialization and temporal consistency in resource use by olive ridley sea turtles (*Lepidochelys olivacea*)

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Abstract

During ontogenetic development, several types of marine vertebrates commonly switch their habitats and resources used. Stable isotopes of carbon and nitrogen in bone collagen in lines of arrested growth in humeri of adult olive ridley sea turtles (*Lepidochelys olivacea*) were analysed to detect habitat use and dietary shifts over time. Adult turtles from northeastern Brazil undergo a marked ontogenetic shift at approximately 17 years old, which is within the range of estimates of age at sexual maturity, when individuals recruit from oceanic waters to coastal waters to breed. After this period, however, some individuals seem to inhabit continental shelf waters instead of returning to offshore areas. Young adults (12 to 18 years old) and older adults (19 to 23 years old) showed similar degrees of individual specialization based on both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. Nonetheless, older adults displayed less variable carbon and nitrogen values over time than did young adults, suggesting consistent use of the same feeding grounds as the turtles age. Overall, adults form a generalist population with specialist individuals. Isotopic niches and potential prey contributions are consistent with this classification, reinforcing the high plasticity of habitat use by olive ridleys. The individual variability and variable habitats used make olive ridleys susceptible to fisheries bycatch in neritic and pelagic habitats, where shrimp trawl and pelagic longline fisheries occur, respectively. Therefore, the year-round cycle of this species indicates the need for actions to be taken in both coastal and offshore areas to reduce adult mortality and achieve effective conservation.

Introduction

High individual variation in resource use may lead to individual specialization, i.e., individuals using small subsets of the resources used by the population (Bolnick et al. 2003). This phenomenon is widespread and has been demonstrated in invertebrate and vertebrate taxa (Bolnick et al. 2003). Changes between habitats and resources used could occur at different temporal scales, for instance, along the annual cycle, as well as over longer intervals, resulting from ontogenetic changes (Bolten 2003). Marine turtles are well known to recruit to coastal areas after a long period of pelagic offshore habitat use during the first years of life (Wyneken et al. 2013), although some species or individuals could commute between offshore and continental shelf areas (Turner Tomaszewicz et al. 2015).

The olive ridley sea turtle (*Lepidochelys olivacea*) is the most abundant sea turtle species worldwide (Reichert 1993). However, this species is listed as vulnerable on the global Red List (IUCN 2021). In addition, it is the most oceanic among sea turtle species, which, coupled with limited funding for research in comparison to that available for other species, makes it one of the least studied sea turtle species. Olive ridley sea turtles spend all juvenile stages in oceanic waters (Plotkin 2010), and in the western Atlantic Ocean, they mature at approximately 17 years old (Petitet et al. 2015), while in the eastern Pacific Ocean, they mature at approximately 13 years old (Zug et al. 2006). Then, this species is recruited to coastal waters for nesting. Adults can be either oceanic or neritic during the nonnesting period (Plotkin 2010) or use both habitats in variable proportions. In the population nesting in northeastern Brazil, three post-nesting migration patterns have been described: moving to oceanic waters, moving northwards along the Brazilian coast to neritic waters, and moving southward, e.g., to the Rio de Janeiro coast (Silva et al. 2011; Santos et al. 2019). Therefore, this species shows high individual variation in habitat use and diet. Whether individuals choose strategies and use them consistently throughout their lives or use variable strategies remains to be elucidated.

Individual specialization is evaluated by total niche width (TNW), that is, the variance in the type or size of all prey captured by the population, which can be partitioned into two components: the within-individual component (WIC), i.e., the average variance of resources found within individuals' diets, and the between-individual component (BIC), defined as the variance among individuals (Bolnick et al. 2003). Therefore, individual variation is large when the BIC encompasses a large proportion of TNW and the WIC/TNW ratio is small (Bolnick et al. 2003). However, the WIC/TNW ratio measures the degree of individual specialization, with values near 0 indicating specialist individuals, while values near 1 indicate generalist individuals (Bolnick et al. 2002).

In addition to individual specialization, temporal consistency can be evaluated by WIC values over time (Vander Zanden et al. 2013). As WIC measures the variance within each individual, a specimen sampled at several timepoints and having a high WIC value did not show temporal consistency over time (Vander Zanden et al. 2013). Nitrogen and carbon stable isotope values, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, respectively, have been used to infer diet and habitat use of animals (Fry 2006). Biological materials that retain the isotopic signature assimilated from their food during synthesis and are inert or have long turnover periods provide an alternative to the recapture and resampling of individuals, an option frequently unfeasible. Temporal consistency and individual specialization over time have thus been measured by using stable isotopes in the baleen of whales (Schell et al. 1989), whiskers of otters and seals (Newsome et al. 2009), teeth of fur seals (Albernaz et al. 2017), sea turtle scutes (Vander Zanden et al. 2010, 2013; Pajuelo et al. 2016), and humeri of loggerhead (*Caretta caretta*) and Kemp's ridley (*Lepidochelys kempii*) sea turtles (Snover et al. 2010; Avens et al. 2013; Ramirez et al. 2015). However, there is currently no study about stable isotope analysis in olive ridley sea turtle humeri.

Values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are mainly used to infer habitat or trophic level, respectively, because the former increase by approximately 1‰ between the food and its consumer, while the latter increase on a scale of 3 – 5‰ at each trophic level (Peterson and Fry 1987; Post 2002). Thus, the variances of these stable isotopes between and within individuals have been used to characterize populations: specialist populations,

generalist populations with generalist individuals, and generalist populations with specialist individuals (Bearhop et al. 2004; Fig. 1a – c in Vander Zanden et al. 2013). Specialist populations occupy narrow isotopic niches with low TNW, and individuals show temporal consistency over time and consequently low WIC; generalist populations with high TNW may be composed of generalist individuals who have low temporal consistency and high isotopic variance within individuals and consequently high WIC; and finally, specialist individuals from a generalist population exhibit high temporal consistency and low isotopic variance over time and consequently low WIC (Vander Zanden et al. 2013).

Based on stable isotope analysis (SIA) of scutes, the population of adult male and female loggerheads (*Caretta caretta*) from the North Atlantic Ocean has been classified as a generalist population with specialist individuals (Vander Zanden et al. 2010; Pajuelo et al. 2016). The juvenile loggerheads resident in estuarine waters along North Carolina have been found to demonstrate consistency in their selection of resources over time and were specialized in resource use relative to the population, although the population utilizes a narrow range of resources (Hall et al. 2015). Similarly, adult green sea turtles (*Chelonia mydas*) from a nesting beach in Costa Rica have also been demonstrated to form a generalist population with specialist individuals based on SIA of scutes (Vander Zanden et al. 2013). Finally, olive ridley turtles from the eastern Pacific Ocean and from the Indian coast have been classified as generalist populations by stable isotopes from epidermal tissue and dietary studies, respectively (Behera et al. 2014; Peavey et al. 2017). Therefore, we hypothesize that adult olive ridleys from northeastern Brazil should most likely be classified as a generalist population, with young adults being more generalist with low temporal consistency and older adults being specialists with high temporal consistency (as shown in Fig. 1c from Vander Zanden et al. 2013).

Olive ridley sea turtles are commonly found stranded dead in their nesting beaches in northeastern Brazil, with both sexes represented, including adult females with fully formed eggs (Castilhos et al. 2011). Olive ridley sea turtles interact strongly with shrimp trawl fisheries, which is the main threat to this species in neritic waters of the state of Sergipe (Silva et al. 2011), where the largest nesting aggregation in Brazil occurs (Silva et al. 2007). Moreover, longline fisheries threaten olive ridley turtles in oceanic waters, where large numbers of adults and juveniles are incidentally captured (Sales et al. 2008). Despite the high mortality of adult olive ridleys in fisheries, this species is also highly threatened by marine debris in both neritic and oceanic waters (Yagmour et al. 2021). Thus, the identification of individual specialization, intrapopulation variability in habitat use and temporal consistency in this population may be useful for inferring individual differences in susceptibility to bycatch in fisheries in distinct areas and over the life cycle.

Thus, the present study aims to identify habitat use and dietary shifts from stable isotope analysis of lines of arrested growth (LAG) from olive ridley sea turtle humeri. Sequential samples from an individual generate a trajectory by year, allowing the evaluation of the degree of individual specialization (WIC/TNW ratio) and temporal consistency (WIC). In addition, a stable isotope mixed model was built to evaluate the contributions of oceanic and neritic dietary sources and infer the habitat use of the population and individuals to complement the analyses of individual specialization and temporal consistency.

Methods

Sample collection

Humeri of olive ridley sea turtles were obtained from a previous study at the southern coast of Alagoas and the coast of Sergipe in northeastern Brazil between 2009 and 2011 (Petitet et al. 2015). Samples were obtained along 173 km of beach, between 10°31'S and 11°25'S, which was monitored by the *Fundação Projeto Tamar* and the *Fundação Mamíferos Aquáticos* (FMA). Pirambu is the main nesting area, a high-energy beach with a narrow continental shelf (~ 20 km) located in the tropical zone with warm temperatures and dry summers (Silva et al. 2007). The coast of Sergipe state is the main Brazilian area for reproduction of solitary olive ridley sea turtles, where there are ~ 7000 nests per year with increased numbers over the years (Silva et al. 2007).

All turtles sampled had curved carapace length (CCL) recorded, measured from the nuchal notch to the posterior end of the posterior marginal. Only turtles in apparently good health, i.e., lacking tumours, were sampled. Humeri samples ($n = 68$) were processed for a skeletochronological study (Petitet et al. 2015). For the present study, a subset of 20 olive ridley humeri was analysed. Before sampling each bone section for skeletochronological analysis, a 1-mm thick section was taken for SIA.

Based on Colman et al. (2014), potential neritic prey for olive ridley sea turtles were collected in the study area from shrimp trawling bycatch. Neritic prey consisted of crustaceans and demersal fishes. Isotopic values from two types of jellyfish (Schyphozoa and Hydrozoa) that occur in the South Atlantic Ocean, from Dodge et al. (2011) and González-Carman et al. (2014), were chosen as references for oceanic prey.

Stable Isotope Analysis

Whole humerus sections and prey muscle were lipid-extracted using a Soxhlet apparatus with a 2:1 solvent mixture of chloroform and methanol during a cycle of 4 h for bone collagen and 2 cycles of 10 h for prey muscle (Medeiros et al. 2015; Post et al. 2007). Then, the samples were

dried at 60°C in an oven for 24 – 48 h to remove the residual solvent. Prey muscles were ground into powder, and 0.7 mg of each sample was loaded into a tin capsule for further analysis. For humerus sections, a stereoscopic microscope was used to identify the LAGs in the untreated humerus sections with the stained humerus section as a guide (Avens et al. 2013). When a LAG was identified, the largest amount of sample over the LAG circumference was manually collected with a low-power micromotor with a 0.2-mm thick drill. Before the next LAG sampling, the humerus section and the drill were rinsed with distilled water and dried in an oven at 60°C for 30 minutes. Each sample was loaded into a sterilized silver capsule, further acidified by 10% HCl using the “drop-by-drop” technique (Jacob et al. 2005) until no gas bubbles were produced (Medeiros et al. 2015), and dried in an oven at 60°C.

All samples were analysed by a continuous-flow isotope-ratio mass spectrometer (CF-IRMS, Thermo Finnigan Delta Plus XP, Bremen, Germany) coupled to an elemental analyser (Costech ECS 4010, Milan, Italy) at the Stable Isotope Laboratory at Washington State University, School of Biological Sciences, Pullman, Washington, USA. Stable isotope ratios were expressed in δ notation as parts per thousand (‰) deviation from the international standards for Vienna Pee Dee Belemnite limestone (carbon) and atmospheric air (nitrogen), as in Eq. 1:

$$\delta^{13}C \text{ or } \delta^{15}N (\text{‰}) = \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1$$

1

where R_{sample} and R_{standard} are the corresponding ratios of heavy-to-light isotopes ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) in the sample and standard, respectively.

Statistical analysis

Each LAG in a sea turtle represents 1 year of age, and although this has not been validated in olive ridley sea turtles, it has in the closest relative, Kemp’s ridley sea turtle (Snover and Hohn 2004). A Bayesian regression model was applied to infer whether age has a positive or negative effect on $\delta^{13}C$ and $\delta^{15}N$ values, which also accounted for random, individual effects. Temporal consistency and degree of specialization were measured by the within-individual component (WIC), between-individual component (BIC) and total niche width (TNW) (Bolnick et al. 2003). These indices were calculated from the variances of $\delta^{13}C$ and $\delta^{15}N$ values among LAGs, as in Vander Zanden et al. (2013). The WIC is a measure of temporal consistency, while the WIC/TNW ratio is a measure of individual specialization (Bolnick et al. 2003). A Bayesian multilevel regression model (Bürkner 2017) was also used to analyse the variance within and between individuals to calculate proxies for WIC and BIC values. The mean of the standard deviation of the intercept was used as a proxy of BIC, and sigma (σ) was used for WIC; the sum of these two proxies corresponds to the TNW. The general model is written as:

$$Y_i \sim D(f(n_i), \theta)$$

2

where Y_i is the response variable ($\delta^{13}C$ or $\delta^{15}N$) for each individual i through the linear combination of predictors transformed by the inverse link function f assuming a certain distribution D , which in this case, was from the Gaussian family, and with θ representing sigma (σ) for this distribution (Bürkner 2017). The linear predictor can generally be written as:

$$n_i = \beta X_i + v Z_i$$

3

In this equation, X and Z are the population-level and group-level design matrices, respectively, from the study data (age and identity of each LAG from each individual), and the coefficients β and v are the fixed and random effects, respectively, estimated along with σ (Bürkner 2017). Default priors were used for the model. For the index calculations (WIC, BIC and TNW), the sample was divided into two groups, one group with an age at sampling ranging between 14 and 18 years old (young adults) and another group with an age range between 19 and 23 years old (older adults). Kernel utilization density (KUD) was used to measure the isotopic niches to identify different age groups and the niche areas to compare among these groups (Eckrich et al. 2020). Points representing values of $\delta^{13}C$ and $\delta^{15}N$ were plotted within each polygon, and the niche size was estimated at 50% and 75% KUD contours; then, the overlap of the area for each group was calculated. The kernel method was chosen because it is free of the influence of grid size and placement. Furthermore, this analysis performed well with multimodal data and can provide estimates based on specified contours (Börger et al. 2006; Seaman et al. 1999). Therefore, KUD application was measured as parts per thousand (‰) (Eckrich et al. 2020).

Bayesian stable isotope mixed models (SIMM), MixSIAR GUI (Moore and Semmens 2008, Semmens et al. 2009, Stock and Semmens 2013), were used to estimate prey source contribution for a bone collagen tissue analysis based on the $\delta^{13}C$ and $\delta^{15}N$ values for each group as in KUD analysis. Moreover, all LAGs sampled for each individual were included as replicates to analyse intraindividual variation. The trophic

discrimination factor (TDF) for olive ridley sea turtle bone collagen is unknown. However, as a broad value averaged from different trophic webs, it is acceptable to assume that $\delta^{13}\text{C}$ values increase by approximately 1‰ between a consumer and its food source, while $\delta^{15}\text{N}$ values increase by 3 – 5‰ at each trophic level (Post 2002). The TDF used for SIMM in the present study, however, was from young juvenile loggerhead sea turtles ($\delta^{13}\text{C} = 1.11\text{‰} \pm 0.17$ and $\delta^{15}\text{N} = 1.60\text{‰} \pm 0.07$; Reich et al. 2008) due to the similar diets and habitats of loggerhead and olive ridley sea turtles (Bugoni et al. 2003; Colman et al. 2014), both with a juvenile oceanic phase based on gelatinous prey and a demersal diet based on fish and crustaceans (Bugoni et al. 2003; Bolten and Witherington 2003; Behera et al. 2014; Colman et al. 2014). Neritic prey (crustaceans and demersal fish species) and oceanic prey (jellyfish species) were used in mixed models. SIMM was not intended to infer the diet of olive ridley sea turtles but rather to assess the different contributions of oceanic vs. neritic food sources and, thus, complement inferences on the use of these two large marine habitats by turtles.

Frequentist statistical inference was used for KUD analysis, while the Bayesian framework (Ellison 2004) was used for the regression model, with the package 'brms' (Bayesian regression models using 'Stan'; Bürkner 2017) and for the SIMM, with the package MixSIAR GUI (Hopkins-III and Ferguson 2012). All analyses were performed with R software (R Core Team 2017), Stan (Carpenter et al. 2017; Stan Development Team 2017) and JAGS programs (Plummer 2013) to specify models and perform the Bayesian analysis (Gilks et al. 1994). Model diagnostics were based on leave-one-out cross-validation (LOO; Gelfand et al. 1992; Ionides 2008; Vehtari et al. 2017), in which the model is classified as good, ok, bad or very bad. Further diagnostics were also performed with the Rhat value, which gives information on the convergence of the algorithm (Rhat > 1 indicates the model is not well fitted).

Results

Olive ridley sea turtles sampled for humeri ranged in size from 58.0 to 77.0 cm CCL and in age between 14 and 23 years old (Petitet et al. 2015). Up to 5 LAGs from each specimen were drilled, resulting in 82 LAGs sampled for SIA. These LAGs represented back-calculated sizes between 47.57 and 76.96 cm CCL, and back-calculated ages ranged between 11 and 23 years old, based on these sizes (Petitet et al. 2015). Among the individuals sampled, 5 out of 20 were determined to be mature females due the presence of eggs formed in their oviducts, and the remainder of the sample ($n = 15$) was mostly within the size and age ranges of mature olive ridley sea turtles in the area (~ 62.5 cm CCL, Silva et al. 2007; 15–21 years, Petitet et al. 2015), which provided a clue regarding maturity, despite sex and maturation having not been determined.

The $\delta^{13}\text{C}$ values ranged from -20.96‰ to -11.94‰ (mean \pm SD = $-15.45 \pm 1.35\text{‰}$), and the $\delta^{15}\text{N}$ values ranged from 7.34‰ to 14.21‰ ($10.73 \pm 1.47\text{‰}$). The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values demonstrated segregation between two groups based on age (Fig. 1), which we classified as young adults (14–18 years) and older adults (19–23 years). For the young adults, $\delta^{13}\text{C}$ values had a greater range when compared with values in the older adults group (-20.96‰ to -11.94‰ and -17.98‰ to -12.64‰ , respectively; Figs. 1a & 2), while $\delta^{15}\text{N}$ values increased with age (Figs. 1b & 2), but the ranges were similar for all ages (young adults: 7.34‰ to 14.21‰ , mean = 9.86‰ ; older adults: 9.28‰ to 13.85‰ , mean = 11.32‰). The analysis using the Bayesian regression model indicated a positive influence of age on $\delta^{13}\text{C}$ values (mean age coefficient \pm SD: 0.31 ± 0.10) and on $\delta^{15}\text{N}$ values (mean age coefficient \pm SD: 0.32 ± 0.05) (Fig. 2; Table 1).

Table 1

Statistical summary from Bayesian regression model applied to determine if age influences $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from lines of arrested growth in olive ridley sea turtles (*Lepidochelys olivacea*) from northeastern Brazil. The letter n indicates the number of lines of arrested growth sampled from 20 turtles. CI: confidence interval; SD: standard deviation; LOO: leave-one-out validation

Model	Variable intercept	Estimate	SD	95% CI	Rhat	LOO validation (Good + OK classifications)
$\delta^{13}\text{C} \sim \text{age}$ ($n = 82$)	Intercept	-21.01	1.76	-24.69 – -17.77	1.00	98.7%
	Age	0.31	0.10	0.13–0.52	1.00	
$\delta^{15}\text{N} \sim \text{age}$ ($n = 82$)	Intercept	4.96	0.94	3.09–6.80	1.00	97.7%
	Age	0.32	0.05	0.22–0.43	1.00	

Mean carbon and nitrogen WIC values, as a proxy for temporal consistency, were smaller for older adults (0.82 and 0.56, respectively) than for young adults (1.11 and 0.71, respectively) (Table 2). However, the higher WIC/TNW ratio for carbon values of older adults, as a proxy of individual specialization, may be masked by small BIC values among older individuals, indicating that this group has both low within-individual and interindividual variation in $\delta^{13}\text{C}$ values over time (Table 2). This is further supported by higher TNW values for the younger individuals than for the older ones for carbon (3.01 and 1.33, respectively). For nitrogen values, young adults and older adults had similar WIC/TNW ratios (0.32 and 0.40, respectively) and similar contributions of BIC values to TNW (68% and 60%, respectively). Isotopic niche width was larger for young adults than for older adults (8.38‰^2 for the 50% contour and 20.92‰^2 for the 70% contour, 3.78‰^2 for the 50% contour and 8.19‰^2 for the

75% contour, respectively; Table 2; Fig. 2), which corroborated TNW values (Table 1) for both groups (3.01 and 1.33, respectively, for carbon values; 2.26 and 1.43, respectively, for nitrogen values). Isotopic niche overlap was higher when comparing young vs. older groups (~ 51.3–56.0%) than when comparing older vs. young groups (~ 23.1–21.9%), depending on KUD inference criterion (Table 2; Fig. 3). Therefore, older adults seemed to be more consistent over time than young adults for both habitat (based on carbon) and trophic level (based on nitrogen). In addition, the individual specialization level was the same for both stable isotopes and for both groups, as the WIC/TNW ratio of carbon from older adults was masked by low BIC values (Table 2).

Table 2

Within-individual component (WIC), between-individual component (BIC), total niche width (TNW) and the ratio of WIC/TNW values calculated from the Bayesian multilevel regression model of carbon and nitrogen stable isotopes in lines of arrested growth in humeri of olive ridley sea turtles (*Lepidochelys olivacea*) from two different age groups in northeastern Brazil. Niche size and niche overlap calculated from kernel utilization density (KUD) at 50% and 75% contour levels. Niche overlap for each group (young and older adults) is shown as the percentage of resources used by the other group that are shared by both groups

Groups (age in years)	<i>n</i>	$\delta^{13}\text{C}$				$\delta^{15}\text{N}$				Niche size (‰ ²)		Niche overlap (%)	
		WIC	BIC	TNW	WIC/TNW	WIC	BIC	TNW	WIC/TNW	50%	75%	50%	75%
Young adults (14– 18)	8	1.12	1.89	3.01	0.38	0.71	1.56	2.27	0.32	8.38	20.92	51.3	56.0
Old adults (19– 23)	12	0.82	0.50	1.32	0.62	0.56	0.87	1.43	0.40	3.78	8.19	21.9	23.1

For the young adults, the greatest contribution was from jellyfish, followed by crustaceans and demersal fish (Table 3; Figs. 4 & 5). The older adult group showed the greatest mean contribution of crustaceans, but jellyfish made a higher contribution in younger individuals, while both jellyfish and crustaceans contributed more to the diets of older individuals (Table 3; Figs. 4 & 5). Potential prey contributions varied among specimens, which corroborated the BIC values for both carbon and nitrogen values (Table 2).

Table 3

Stable isotope mixed model (MixSIAR) results with predicted diet proportions (5th and 95th percentile) for each potential prey item compared to $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ mixture values for olive ridley sea turtles (*Lepidochelys olivacea*) in both groups (young adults, ID 1 to ID 8; and older adults, ID 9 to ID 20). Mean values are in parentheses. n = sample size. Values in **bold** indicate the prey items with the greatest dietary contributions

ID Turtle (n)	Jellyfish	Crustacean	Demersal fish
1 (4)	0.835–0.954 (0.904)	0.031–0.146 (0.077)	0.003–0.042 (0.018)
2 (4)	0.642–0.911 (0.793)	0.029–0.321 (0.158)	0.001–0.150 (0.049)
3 (4)	0.917–0.994 (0.967)	0.003–0.070 (0.025)	0.000–0.025 (0.008)
4 (4)	0.823–0.981 (0.914)	0.009–0.153 (0.064)	0.001–0.076 (0.023)
5 (4)	0.750–0.959 (0.868)	0.016–0.228 (0.103)	0.001–0.093 (0.029)
6 (4)	0.731–0.968 (0.873)	0.016–0.254 (0.109)	0.001–0.058 (0.018)
7 (5)	0.079–0.478 (0.263)	0.013–0.783 (0.293)	0.002–0.321 (0.080)
8 (4)	0.536–0.866 (0.723)	0.242–0.876 (0.613)	0.002–0.212 (0.074)
Young adults (total)	0.661–0.891 (0.799)	0.094–0.293 (0.186)	0.000–0.041 (0.014)
9 (4)	0.254–0.813 (0.603)	0.123–0.704 (0.352)	0.001–0.138 (0.044)
10 (4)	0.484–0.860 (0.710)	0.061–0.478 (0.241)	0.001–0.148 (0.049)
11 (4)	0.280–0.818 (0.618)	0.111–0.680 (0.337)	0.001–0.134 (0.045)
12 (4)	0.124–0.712 (0.456)	0.167–0.831 (0.476)	0.001–0.216 (0.068)
13 (4)	0.147–0.711 (0.466)	0.125–0.805 (0.446)	0.002–0.264 (0.088)
14 (4)	0.568–0.887 (0.755)	0.047–0.394 (0.199)	0.001–0.139 (0.046)
15 (4)	0.269–0.815 (0.607)	0.118–0.691 (0.350)	0.001–0.133 (0.043)
16 (4)	0.226–0.779 (0.561)	0.122–0.728 (0.381)	0.002–0.179 (0.057)
17 (4)	0.064–0.560 (0.298)	0.182–0.903 (0.589)	0.001–0.365 (0.113)
18 (4)	0.066–0.531 (0.279)	0.115–0.898 (0.527)	0.001–0.531 (0.194)
19 (4)	0.051–0.463 (0.230)	0.055–0.909 (0.414)	0.001–0.743 (0.356)
20 (5)	0.124–0.675 (0.433)	0.108–0.826 (0.458)	0.002–0.318 (0.109)
Old adults (total)	0.245–0.652 (0.484)	0.286–0.685 (0.490)	0.000–0.097 (0.026)

Discussion

In the present study, ontogenetic shifts in the diet and habitat use of olive ridley sea turtles in northeastern Brazil were elucidated. Each sample from each LAG was considered an integration of information from throughout that given year, thus reflecting the “averaged” diet and habitat based on stable isotope values for that time interval. Therefore, the analysis of sequential LAGs should detect potential shifts in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values across interval of one-year long (Avens et al. 2013, 2020). We found that there is an ontogenetic shift at approximately 17 years of age, which is within the estimated range of age at sexual maturity (ASM) for this population (Petitet et al. 2015).

Young adults experience a wider range of habitats than do older adults, while there is a slight difference in trophic position between age groups, which suggests that younger individuals occupied the broadest niche, as shown by the greater variation in carbon than in nitrogen values. This interpretation indicates that older adults are more consistent over time in habitats used than are young adults, which is in line with the high variation in $\delta^{13}\text{C}$ values for younger adults and with the observation of lower WIC values for $\delta^{13}\text{C}$ in older adults than in young adults (WIC = 0.82 and 1.11, respectively). The youngest turtles could be in a phase when they learn where they have to go to forage and develop, thus consequently visiting more habitats than old adults do, and may ingest a variety of food items they find (Snover et al. 2007). Subadult olive ridleys from the Mexican Central Pacific population appear to use oceanic waters, as indicated by the carbon values in epidermal tissue (Carpenna-Catoira et al. 2022). In other vertebrate groups, juveniles are also less selective in feeding than adults because they have to grow fast to minimize predation risk (Snover et al. 2007). Although isotopic nitrogen varied more with age than carbon did, there were small variations among individual trajectories, which suggests that older animals are slightly more consistent in resource use than younger animals. However,

the nitrogen WIC values for both groups (young and older adults) indicated consistency in trophic position over the years sampled (0.71 and 0.56, respectively). The explanation for this pattern is related to the age group to which they belong; all animals sampled were in the adult phase, and some were sexually mature (Silva et al. 2007; Petit et al. 2015). As expected, they invest in prey with high nutritional values, directed towards the energetic cost of reproduction, unlike juvenile turtles that invest in growth (Araújo et al. 2011). Moreover, a consistency in $\delta^{13}\text{C}$ values seems to be established from 17 years old onwards, when they mature (Petit et al. 2015). ASM is the time when olive ridley turtles migrate to coastal waters to mate and nest (Plotkin 2010); thus, recruitment to the breeding population seems to be accompanied by changes in diet and habitat after spending the entire immature phase in oceanic waters. However, the life cycle of olive ridley sea turtles is more complex because after nesting, they show variation in migratory strategies, as reported in Santos et al. (2019) with satellite telemetry of the same population examined in this study. These researchers demonstrated that some turtles move to feeding areas in northern Brazil and others migrate to feed in the southeast, while other individuals move to oceanic waters towards the west coast of Africa (Mauritania, Senegal, Guinea Bissau, Guinea and Sierra Leone) (Silva et al. 2011; Santos et al. 2019), which makes it difficult to infer the habitat use of this species. This species has the same complex life cycle in the eastern Pacific Ocean (Morreale et al. 2007; Plotkin 2010; Guzman et al. 2019). These studies corroborate the high variation in $\delta^{13}\text{C}$ values found, as each sample is an average of the entire year, and could explain the high degree of individual variation among younger individuals, which was reflected in high BIC-to-TNW ratio values (~ 62%). Moreover, the wide range of habitats at different latitudes experienced by the olive ridley sea turtle population from northeastern Brazil could potentially explain the high variation in $\delta^{13}\text{C}$ values, as well as the $\delta^{13}\text{C}$ values from the epidermal tissue of loggerhead sea turtles sampled at various latitudes in the northern Atlantic Ocean (Pajuelo et al. 2012). On the other hand, there was no significant variation in carbon from plasma and red blood cells of the loggerhead sea turtle population in North Carolina or from epidermal tissue of the olive ridley sea turtle population in the Mexican Central Pacific sampled at similar latitudes, between neritic and oceanic waters (McClellan et al. 2010; Carpena-Catoira et al. 2022), which reinforces the influence of latitude on carbon values. Therefore, the temporal consistency shown by the older adults probably results from the accumulated experience of finding the best feeding areas every year, after and between nesting seasons, demonstrating that older individuals are more specialist than younger individuals.

The high interindividual variation among younger and smaller individuals is consistent with tracking data (Santos et al. 2019), which has demonstrated that the largest and intermediate-sized turtles migrate to southern and northern Brazil, respectively, while smaller turtles migrate to oceanic waters. This is also in line with the enrichment of $\delta^{15}\text{N}$ with age demonstrated in the oldest individuals, as this group migrates to feeding areas with high primary productivity from the upwelling southeast of Brazil and discharge of the Amazon River in northern Brazil. Moreover, this migration pattern has also been detected in nesting and inter-nesting olive ridley females in French Guiana and Indonesia (Chambault et al. 2016; Fukuoka et al. 2022). Beyond the constancy in trophic position, the Brazilian population demonstrated high interindividual variation in nitrogen, explained by a high percentage of BIC within TNW for both groups (68% and 60%), which corroborates tracking data and the diverse feeding grounds of this species with differences in prey items.

The isotopic niche of older adults was narrower than that of young adults, which was reflected in TNW values for carbon (1.33 and 3.01, respectively) and nitrogen (1.43 and 2.26, respectively). The level of individual specialization indicated by $\delta^{15}\text{N}$ values was higher than that for $\delta^{13}\text{C}$. Although young adults had slightly higher levels of individual specialization as indicated by $\delta^{13}\text{C}$ than did older individuals, the level of individual specialization indicated by $\delta^{15}\text{N}$ was similar for both groups (0.32 and 0.40). Even after recruitment, they may not change trophic level if isotopic values at the food web baseline are similar, as expected given homogeneous isoscapes in northeastern Brazil (McMahon et al. 2013). Green and adult loggerhead sea turtles studied by Vander Zanden et al. (2013) and Pajuelo et al. (2016) also had similar levels of specialization for $\delta^{15}\text{N}$, but $\delta^{13}\text{C}$ seems to indicate higher specialization than found for olive ridley sea turtles in the current study. Notwithstanding, adult loggerhead and green sea turtles forage mostly near the coast, while olive ridley sea turtles forage in oceanic waters in addition to neritic foraging grounds (Silva et al. 2011; Santos et al. 2019). These are two marine realms with contrasting $\delta^{13}\text{C}$ values, with wide variation in latitude (McClellan et al. 2010; McMahon et al. 2013), where turtles migrate along 30 degrees of latitude (Santos et al. 2019). Therefore, the area of overlap by the young group of the older group's niche is ~ 56%, as their niche is wider than the niche of the oldest turtles.

SIMM also demonstrated differences in habitats used between young and older adults. Gelatinous prey made a major contribution to the diet of young individuals, most likely because they had been in oceanic waters in previous years (Santos et al. 2019). Although some older individuals also showed major contributions from jellyfish, the greatest contribution on average for the entire group was crustacean prey. Older adults, most likely mature individuals, may forage in neritic areas and eventually travel to areas off the continental shelf, which is narrow in northeastern Brazil. Colman et al. (2014) demonstrated that demersal fish and crustaceans had great importance in olive ridley diets in the study area, based mainly on dead stranded adults. All older individuals who showed jellyfish prey contributions also displayed, at similar values, crustacean prey contributions, while the oldest individuals exhibited major contributions from crustacean prey. Furthermore, these latter turtles were from the older adult group, ranged in age from 20 and 23 years old and were probably mature sea turtles (Petit et al. 2015). Moreover, the 5 mature females were in this group, with jellyfish and crustacean prey contributions together or crustacean prey contributions alone predominating. This result is consistent with that for mature individuals, which demonstrated a major contribution from jellyfish in scute tissues (Petit and Bugoni 2017), which reflects, in ectotherms, the diet and location from an earlier time period. Thus, the crustacean contribution found in mixed models

may be from mature turtles that had migrated to neritic foraging grounds after nesting and stayed there until the next nesting season based on the migration pattern of the largest turtles in the same area (Santos et al. 2019). This scenario was demonstrated from the same population with serum tissue analysis of nesting olive ridley sea turtles, reflecting a major contribution from demersal fish and prey with high nutritional value such as crustaceans (Petitet and Bugoni 2017). Moreover, olive ridley females from French Guiana and Indonesia dove for food, from which it was deduced that they were feeding at the bottom (Chambault et al. 2016; Fukuoka et al. 2022), probably on demersal prey items as inferred from the oldest individuals in this study.

Post-nesting migration patterns generate high levels of interindividual variation in nitrogen values in both age groups, as corroborated by the low WIC/TNW ratio values of this stable isotope. However, for carbon values, the young adults had higher interindividual variation, which corroborated the low WIC/TNW ratio, while older adults had low variation between individuals and low within-individual variation. This could be masked by the high WIC/TNW ratio values in the oldest individuals (Vanden Zanden et al. 2013). Santos et al. (2019) showed that the largest individuals migrate to southeastern and northern Brazil; thus, together with lower WIC and lower BIC values for this group and with the analysis of individual trajectories of isotopic lines, older adults had a moderate degree of individual specialization for carbon. Therefore, in both groups, the WIC/TNW ratios for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were closer to 0, rather than 1, suggesting a moderate level of individual specialization (Bolnick et al. 2002). Due to high variability in migration patterns among individual adult olive ridley sea turtles (Silva et al. 2011; Santos et al. 2019), they seem to specialize eventually because they migrate to different habitats with different resources available. Moreover, migration to varied areas may decrease intraspecific competition, increasing individual specialization due to low densities (Araújo et al. 2011). In addition, olive ridley sea turtles from coastal India and the eastern Pacific Ocean have also been classified as generalist populations based on studies of diet and stable isotopes ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) from epidermal tissue, respectively (Behera et al. 2014; Peavey et al. 2017). The current study adds novelty regarding individual specialization over time based on sequential samples from individuals.

Conclusions

This study demonstrated that olive ridley sea turtles nesting in northeastern Brazil are better classified as a generalist population with specialist individuals; the population is heterogeneous, composed of groups of individuals with distinct diets using a range of habitats during the nonnesting period. Stable isotopes confirm previous results from different nonbreeding foraging grounds used by this heterogeneous population. However, each sampled LAG integrates a full year of habitat use, and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values also reflect a mixture of neritic and oceanic habitats from different latitudes. Olive ridley sea turtles can migrate between these habitats for nesting or between neritic habitats with different isotopic values throughout the year (Silva et al. 2007). In addition to the variation demonstrated, consistency was detected in habitat as well as in food items, which varied among individuals but remained consistent from approximately 17 years of age onwards. Variable migration patterns of olive ridley sea turtles increase threats to this species, with shrimp trawl fisheries near nesting beaches, shrimp and finfish trawlers all along the Brazilian continental shelf, and longline fisheries in oceanic waters (Sales et al. 2008; Silva et al. 2010). In addition to fisheries, olive ridley sea turtles are also impacted by marine debris in both oceanic and neritic waters (Yaghmour et al. 2021) and by the changing character, irregular occupation and lighting of the coast. Therefore, it is essential to better understand the year-round cycle of this species to support conservation plans and decrease adult mortality.

Declarations

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Conflict of Interest The authors declare that they have no conflicts of interest.

Availability of data and material Data are available upon request and will be deposited in IsoBank in the future.

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Author contributions RP collected samples with support from JCC; RP prepared humerus samples, performed stable isotope analysis and conducted data analysis under the supervision of LB. RP wrote the first version; all authors reviewed and contributed to the final version of the manuscript.

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Figures

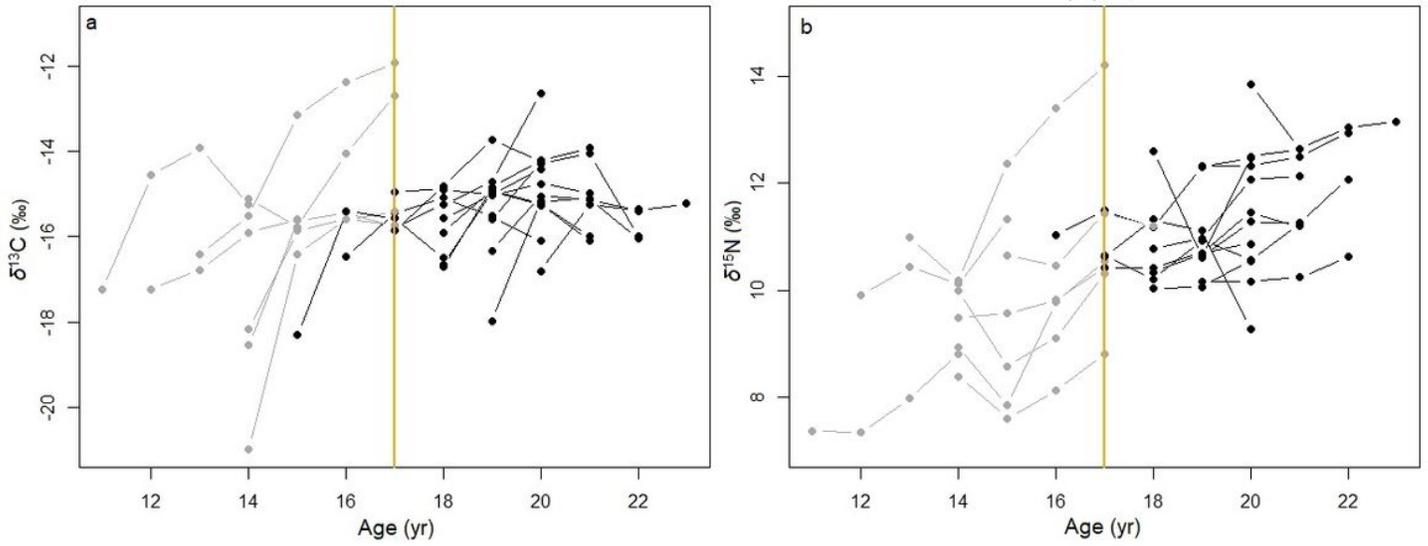


Figure 1

Values of $\delta^{13}\text{C}$ (a) and $\delta^{15}\text{N}$ (b) for each line of arrested growth (LAG) sampled from olive ridley sea turtle (*Lepidochelys olivacea*) humeri. Each trajectory represents an individual, and each LAG represents an age from this individual

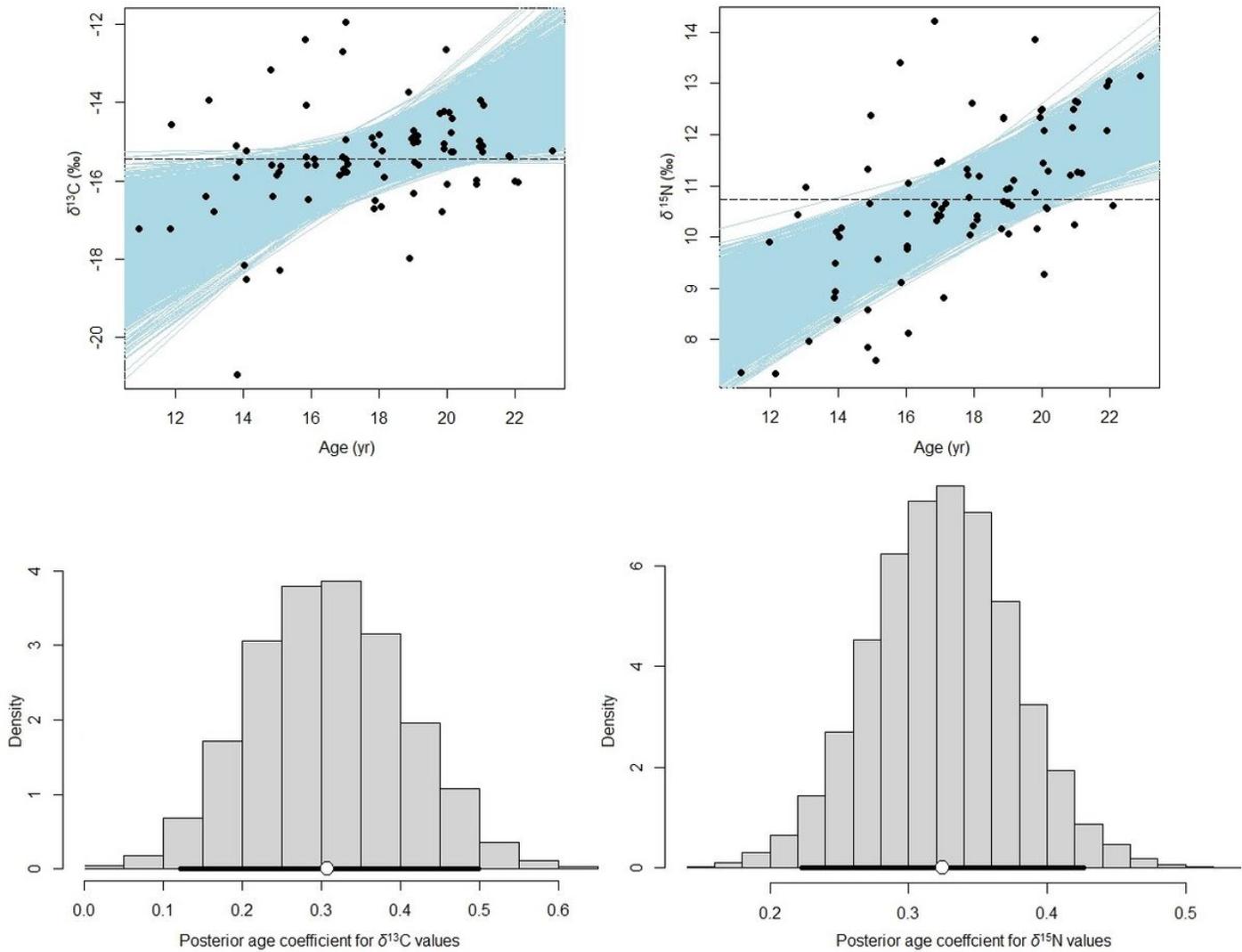


Figure 2

Bayesian regression models of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values on age, which indicate a positive influence of age on both carbon and nitrogen in bone tissue of olive ridley sea turtles (*Lepidochelys olivacea*) from northeastern Brazil. Black dots are the lines of arrested growth sampled. Under each regression graph is the corresponding posterior distribution for each age coefficient

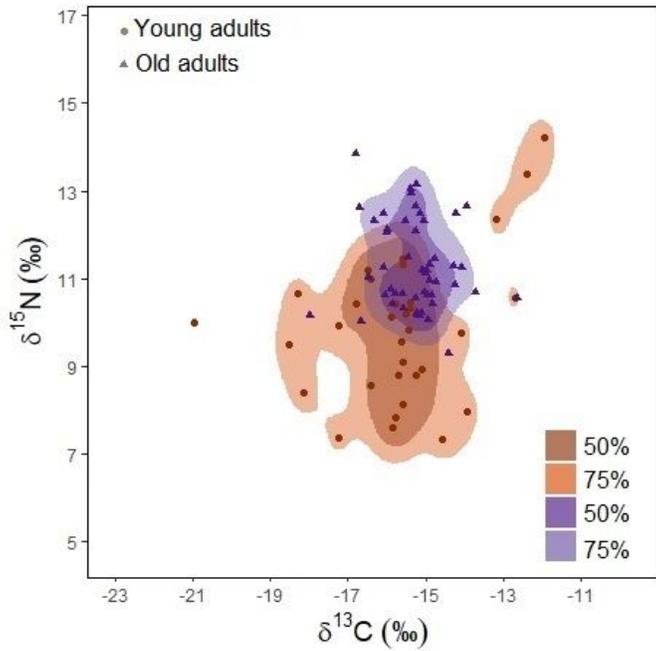


Figure 3

Isotopic niches of two age groups of olive ridley sea turtles (*Lepidochelys olivacea*) from KUD analysis. Young adults (red circles) occupy significantly greater niche area than do older adults (purple triangles). Red and purple shadows represent 50% and 75% credibility intervals for each age group, respectively

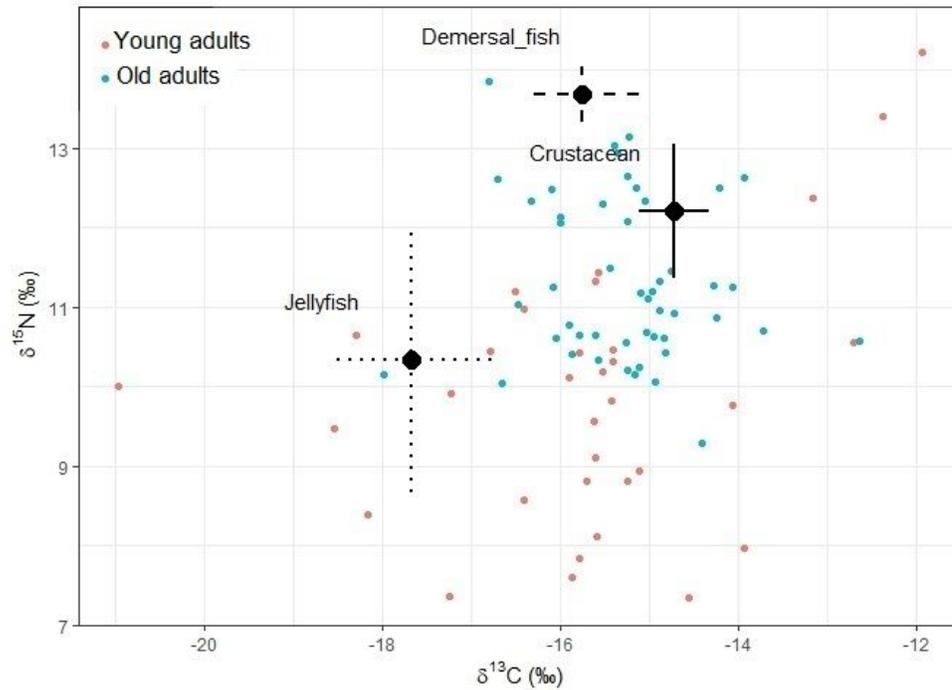


Figure 4

Isospace plot of potential prey items that contribute to the diets of olive ridley sea turtles (*Lepidochelys olivacea*) from northeastern Brazil. Red dots (young adults) and blue dots (older adults) refer to $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from lines of arrested growth from each individual sampled. Stable isotope values from jellyfish (Hydrozoa and Scyphozoa) prey are from Dodge et al. (2011) and González-Carman et al. (2014), respectively

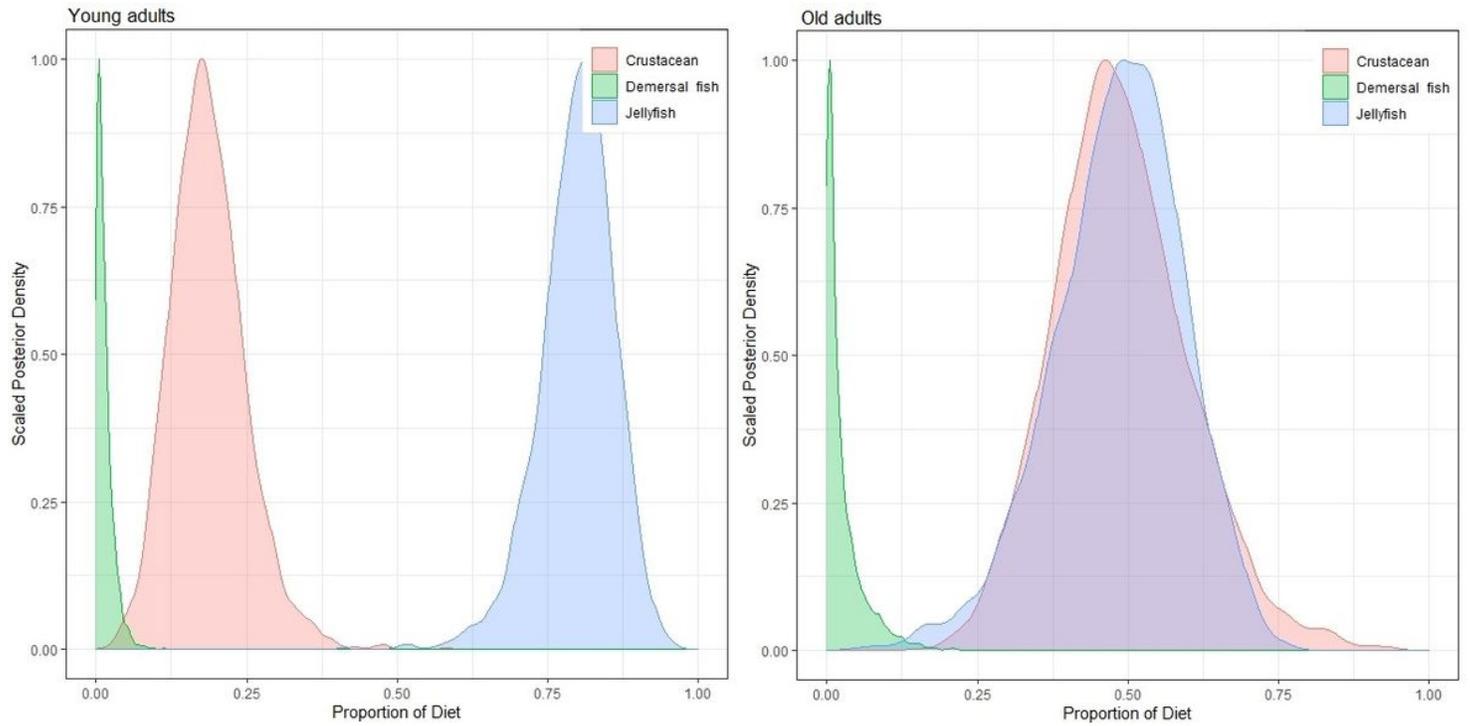


Figure 5

Proportions of potential food sources from MixSIAR analysis of olive ridley sea turtles (*Lepidochelys olivacea*) from northeastern Brazil. This graph demonstrates the mean contributions of potential prey for both groups, jellyfish for young adults and both jellyfish and crustaceans for older adults