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ORIGINAL PAPER

High habitat use plasticity by female olive ridley sea turtles (*Lepidochelys olivacea*) revealed by stable isotope analysis in multiple tissues

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Abstract The marine habitat use of olive ridley sea turtles (*Lepidochelys olivacea*) from northeastern Brazil was analyzed via stable isotope analysis (SIA). Blood (red blood cells and serum), epidermis and scute samples from 46 nesting females were collected for SIA of carbon (δ^{13}C) and nitrogen (δ^{15}N) to infer the habitats used at distinct time windows. Such approach is possible because each tissue reflects consumer's diet at different time scales due to different tissue turnover time. Prey representative of both neritic and oceanic realms was used as endpoints. Differences in the residence time of δ^{13}C and δ^{15}N among samples indicated a shift from oceanic feeding grounds to neritic habitats before nesting or effects of prolonged fasting on stable isotope values. However, two individuals seemed to have used neritic feeding habitats for longer timespans before the nesting period. Stable isotope mixing models demonstrated high individual variability, suggesting the variable use of non-breeding grounds. Moreover, serum indicated that olive ridleys might feed during the nesting season, most likely opportunistically on discards from trawl fisheries. Finally, through correlations of stable isotope values among tissues, this study provides equations for the conversion and adequate comparison between values from different tissues. Therefore, the habitats used by olive ridley sea turtles from Brazil are vast, encompassing both oceanic and neritic habitats, where they encounter pelagic longline and trawl fisheries, respectively. The high individual variability in the population results in turtles experiencing distinct and variable threats during their annual cycle.

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Introduction

Understanding the ecology, demography and evolutionary biology of migratory species depends on identifying the connections among the habitats they use during their entire life cycle (Rubenstein and Hobson 2004). Especially for threatened migratory species, knowledge regarding habitat connectivity is essential, as threats faced in non-breeding areas or along the migratory route may affect their demography. This knowledge can allow the formation of inferences regarding how populations respond to climate change, incidental capture and habitat degradation (Hobson and Norris 2008).

The habitat use of sea turtles has been studied based on genetics, tracking-device technologies, mark-recapture methods and stable isotope analysis (SIA) (Morreale et al. 2007; Ceriani et al. 2014). Stable isotopes of carbon (δ^{13}C) and nitrogen (δ^{15}N) are used to study migratory connectivity (Hobson and Norris 2008). Because distinct isotopic landscapes occur in nature, it is possible to infer the movement patterns of individuals that travel between them

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(Rubenstein and Hobson 2004; Hobson and Norris 2008). Each habitat has a pattern of $\delta^{13}C$ and $\delta^{15}N$ values at the base of the food web that is mirrored upward through the food web to top predators (Post 2002). However, values of $\delta^{13}C$ and $\delta^{15}N$ change to each trophic level; the former change at the scale of 1‰ between a consumer and its food source, while the latter increases by 3–5‰; such values are called the trophic discrimination factor (TDF) (Peterson and Fry 1987; Post 2002). Therefore, due to its lower variability, $\delta^{13}C$ is used to infer habitats used during tissue synthesis, while $\delta^{15}N$ is used as a proxy for trophic level position due to its higher level of increase across the food web (Post 2002).

Thus, by sampling tissues with distinct half-lives (Vander Zanden et al. 2015) from the same individuals, SIA allows the understanding of resource utilization at multiple temporal scales (Martínez del Rio et al. 2009). Isotopic signatures are maintained at the time of tissue synthesis either permanently, in metabolically inert tissues such as feathers, hair and nails, or temporarily, in metabolically active tissues such as blood, skin and some bone components as collagen. Because each tissue has a specific average residence time of $\delta^{13}C$ and $\delta^{15}N$, i.e., the time required for integrating dietary input that varies from days to months or even years, each tissue reflects past time periods. Therefore, habitats, diet contribution and trophic levels at different time periods before sampling can be inferred (DeNiro and Epstein 1978, 1981; Hobson 1999). In summary, tissues with short half-life (e.g., serum) reflect a habitat used, or food ingested, more recently; tissues with long half-life (e.g., red blood cells - RBC in ectotherms) reflect the diet or location from an older time period. Moreover, these inferences may be analyzed by stable isotope mixing models (SIMMs), which study the contributions of different food sources to the diet of a consumer (Phillips et al. 2014).

In sea turtles, there are only a few studies about residence time and TDFs of $\delta^{13}C$ and $\delta^{15}N$ in tissues with different half-lives. The review on TDFs in Table 1 demonstrates that there is a single study on residence time of $\delta^{13}C$ and $\delta^{15}N$ in loggerhead juvenile sea turtles (*Caretta caretta*). It is well known that half-life of ^{13}C is inversely correlated to the degree of metabolic rate of a tissue. For instance, Reich et al. (2008) demonstrated that plasma solute has the lower residence time, followed by RBC, epidermis and scutes, while for $\delta^{15}N$, scute has the shortest residence time, followed by plasma solute, RBC and epidermis (Reich et al. 2008). TDF values are key input values in SIMMs (Bond and Diamond 2011); thus, the scarcity of available values could be a limitation for isotopic modeling.

Seven of the eight sea turtle species are listed as threatened on the IUCN Red List (IUCN 2015). These reptiles utilize distinct foraging and reproduction areas that often occur far from each other. The olive ridley sea turtle (*Lepidochelys olivacea*) is the most abundant sea turtle worldwide (Plotkin 2007) and is highly migratory, with post-hatchling and juvenile stages occurring in oceanic waters, and mature individuals recruiting to coastal environments for nesting (Plotkin 2007). After nesting, turtles migrate

Table 1 Overview of residence time and discrimination factors of $\delta^{13}C$ and $\delta^{15}N$ from serum, red blood cells (RBC), epidermis and scute tissues from sea turtles

Tissue	*Caretta caretta* juvenile[a] $n = 12$		*Chelonia mydas* adult[b] $n = 30$	*Chelonia mydas* juvenile[b] $n = 40$	*Chelonia mydas* juvenile[c] $n = 8$	*Dermochelys coriacea* juvenile[d] $n = 7$
	Residence time (days)	Discrimination factor (‰)	Discrimination factor (‰)	Discrimination factor (‰)	Discrimination factor (‰)	Discrimination factor (‰)
$\delta^{13}C$						
Serum/Plasma	39.6 ± 9.1	−0.38 ± 0.21	0.24 ± 0.61	1.16 ± 0.56	−0.12 ± 0.08	−0.58 ± 0.53
RBC	40.1 ± 3.4	1.53 ± 0.17	0.30 ± 0.58	0.51 ± 0.56	−1.11 ± 0.17	0.46 ± 0.35
Epidermis	46.1 ± 8.9	1.11 ± 0.17	1.62 ± 0.61	1.87 ± 0.56	0.17 ± 0.08	2.26 ± 0.61
Scute	50.9 ± 13.14	1.77 ± 0.58	–	–	–	–
$\delta^{15}N$						
Serum/Plasma	22.5 ± 5.1	1.50 ± 0.17	4.17 ± 0.41	4.06 ± 0.37	2.92 ± 0.08	2.86 ± 0.62
RBC	36.3 ± 3.4	0.16 ± 0.08	2.48 ± 0.35	2.36 ± 0.37	0.22 ± 0.08	1.49 ± 0.76
Epidermis	44.9 ± 3.1	1.60 ± 0.07	4.04 ± 0.44	4.77 ± 0.40	2.80 ± 0.31	1.85 ± 0.50
Scute	16.2 ± 2.3	−0.64 ± 0.09	–	–	–	–

[a] Reich et al. (2008)

[b] Vander Zanden et al. (2012)

[c] Seminoff et al. (2006)

[d] Seminoff et al. (2009)

back to their feeding grounds. However, there may be individual variability in residence time at the nesting beaches before and between nesting periods. There are reports of females mating during migration to the neritic zone, which may reduce their residence time in the neritic habitat previous to egg laying (Kopitsky et al. 1999).

The migratory connectivity of loggerhead sea turtles has been extensively studied using SIA in Japan, the North Atlantic, the Mediterranean and the North Pacific (Hatase et al. 2002; Revelles et al. 2007; Vander Zanden et al. 2016; Turner Tomaszewicz et al. 2017). However, habitat use of olive ridley sea turtles has previously been studied only via satellite telemetry of adults and juveniles (Polovina et al. 2004; Whiting et al. 2007; Plotkin 2010; Silva et al. 2011; Chambault et al. 2016). On the coast of French Guiana, after nesting, olive ridleys remain over the continental shelf in areas with high availability of food resources due to the eddies formed by the North Brazil retroflection, an area characterized by low turbulence and high micronekton biomass (Chambault et al. 2016). In the Pacific Ocean off the coast of Costa Rica, olive ridley adults migrate long distances, but without fidelity to any feeding ground (Plotkin 2010), while juveniles exhibited a habitat use of oceanic waters at 8–31°N at a temperature range of 23–28 °C (Polovina et al. 2004). In Australia, this species also migrates long distances and uses several habitats such as coastal areas, the continental shelf and the continental slope, after reproduction (Whiting et al. 2007). In Brazil, Silva et al. (2011) demonstrated a variable pattern in post-nesting migration for this species: after nesting, some individuals migrate back to oceanic feeding grounds, while others migrate to neritic feeding grounds.

Olive ridley sea turtles are known to be opportunistic, carnivorous and generalist feeders during their entire life cycle (Polovina et al. 2004; Colman et al. 2014). Colman et al. (2014) demonstrated the predominance of fish in the diet of adult olive ridleys at Pirambu Beach, northeastern Brazil in Atlantic Ocean, whereas along the Pacific coast of Mexico, for adults, crustaceans and fish were the predominant food items (Montenegro-Silva et al. 1986). For juveniles, salps and pyrosomes were the most important foods in oceanic waters of the Pacific Ocean (Polovina et al. 2004).

Olive ridley sea turtles utilize several different types of habitats, including oceanic and neritic waters, where they face distinct threats (Silva et al. 2011). In oceanic waters of the Atlantic Ocean, juvenile and adult olive ridley sea turtles are incidentally captured by pelagic longline fisheries targeting tuna, swordfish and sharks (Sales et al. 2008). In neritic waters adjacent to nesting beaches as well as in distant feeding grounds, olive ridleys are drowned in shrimp trawl nets (Silva et al. 2010; Di Beneditto et al. 2015). In the study area (Fig. 1), the number of adult olive ridleys found stranded dead has increased in recent years (Castilhos et al. 2011), which may affect the persistence of the local population.

The present study aims to infer the habitats used by nesting female olive ridley sea turtles during the non-breeding period in the western Atlantic Ocean. Presumably, SIA of tissues with long turnover periods (e.g., scutes and RBCs) will reflect contributions to the diet in older periods, predominantly from oceanic, but also from neritic waters. And tissues with short half-life (e.g., serum) will reflect contributions to the diet in recent period, only for neritic waters, assuming that turtles ingest food during this period. RBCs, serum, epidermis and scutes have different average residence time of $\delta^{13}C$ and $\delta^{15}N$ (see review in Table 1), and each tissue may indicate whether a particular olive ridley turtle inhabited oceanic or neritic habitats during the internesting period or only immediately before nesting and where they may remain during the non-breeding period. Habitat use was inferred based on $\delta^{13}C$ and $\delta^{15}N$ values from tissues with different half-life, representing different time windows before nesting, from weeks to months. In addition, SIMM was used to determine the diet contribution of potential sources and habitats at these different time scales, using potential neritic prey as endpoint of neritic habitats, and gelatinous prey as endpoint for oceanic habitat.

Methods

Study site

Sampling was conducted at Pirambu Beach, on the central coast of Sergipe State, northeastern Brazil (Fig. 1). Pirambu is a high-energy beach with a narrow continental shelf that is located in the tropical zone and has warm temperatures and a dry summer (Silva et al. 2007). In 1982, TAMAR-ICMBio (the Brazilian Sea Turtle Conservation Program) established a research station in this area to monitor the nesting activity of four sea turtle species: olive ridley, loggerhead, green (*Chelonia mydas*) and hawksbill (*Eretmochelys imbricata*) (Marcovaldi and Marcovaldi 1999). In Sergipe, olive ridleys nest mainly at Pirambu Beach, which shows higher numbers of olive ridley nests compared to nests of other sea turtle species and to adjacent beaches (Silva et al. 2007). Olive ridleys are known to perform arribadas, in which thousands of females emerge simultaneously to lay their eggs (Pritchard 2007), but in the study area, only solitary nesting occurs, with two clutches per female, in average, during each nesting season (Silva et al. 2007). The nesting season occurs between September and March, with small numbers of turtles nesting year-round (Silva et al. 2007). The number of nests has increased since

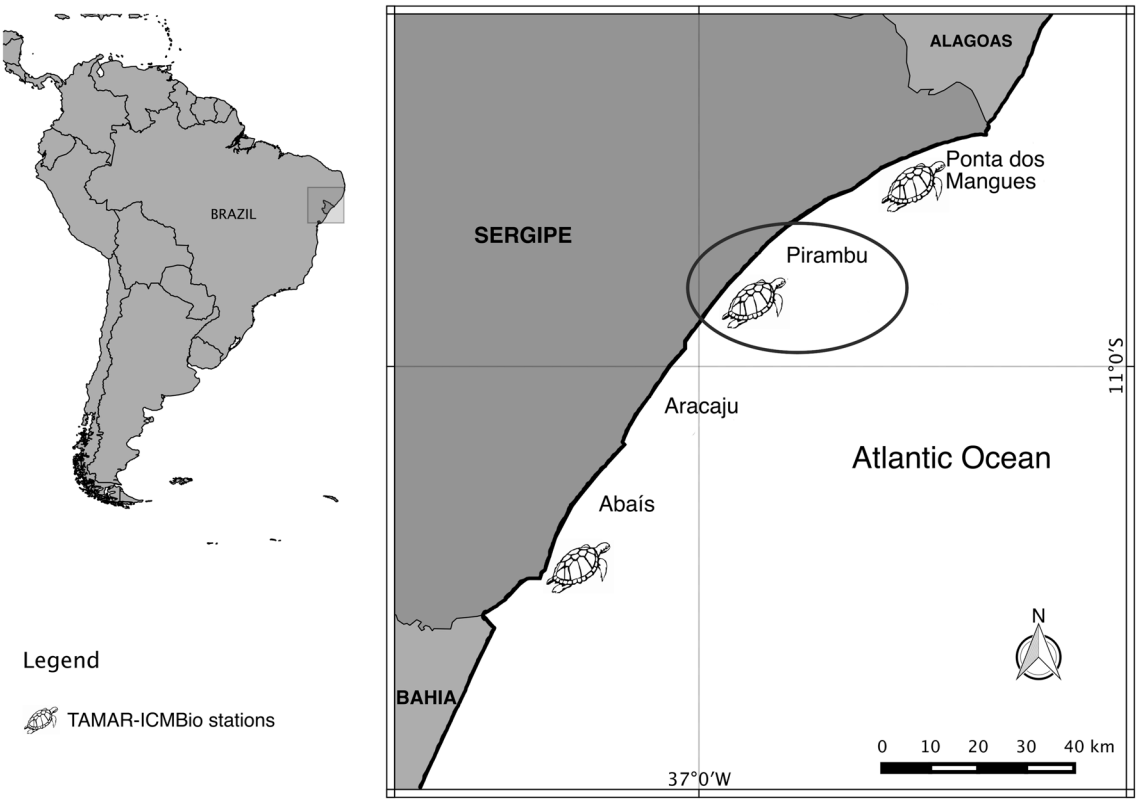

Fig. 1 Sampling location of olive ridley (*Lepidochelys olivacea*) nesting females at Pirambu Beach, Sergipe State, Brazil (indicated by a *black circle*). Turtles and names indicate other TAMAR stations, where nesting of olive ridley turtles also occurs

1998, 16 years after the beginning of TAMAR-ICMBio activities (Silva et al. 2007).

Sampling methods

During the reproductive season, TAMAR-ICMBio staff performs standard night patrols covering 12 km of beach at Pirambu, looking for female sea turtles and their nests. In November 2013, during the early part of the nesting season, whose peaks occur in December–January (Silva et al. 2007), in partnership with TAMAR-ICMBio, serum, RBC, epidermal and carapace samples of female olive ridley sea turtles were collected for SIA. Sampling began as soon as the turtle initiated egg laying, as nesting desertion due to disturbance does not occur in this population once egg laying starts. However, because sampling occurred during nesting, some tissues could not be collected as turtles finished laying eggs and returned to the ocean. The curved carapace length (CCL) of each turtle was measured from the nuchal notch to the tip of the longest posterior marginal scute using flexible tape measures (±0.1 cm) (Bolten 1999), and sampling was only performed using females with a healthy appearance, i.e., no tumors (Jones et al. 2016). Blood samples (3 ml) were collected with a 25 × 0.7 mm needle and syringe via the lateral cervical sinus and were transferred to non-heparinized containers. At the end of monitoring, whole blood was separated into serum and RBC by centrifugation (5000 rotations per minute—RPM—over 10 min), and the samples were then frozen. Epidermis samples were collected from the right shoulder, between the neck and the front flipper using a sterile scalpel. Carapace samples were collected from the first left scute in two places, one from the inner edge (anterior) and another from the outer edge (posterior), representing the oldest and youngest tissues, respectively (Reich et al. 2007; Fig. S1).

During the same period of turtle sampling, potential prey items inferred by the dietary study of Colman et al. (2014) were collected in the same area. Prey items were obtained from the bycatch of shrimp fisheries in the study area and from the stomach contents of four olive ridley sea turtles that were found stranded dead at Pirambu Beach and necropsied. External layers of prey tissue were removed, and parts not reached by enzymes were collected for SIA. Prey items that were classified as neritic include muscle tissue from the spider crab (*Libinia ferreirae*), box crab (*Calappa sulcata*), brachyuran crab (*Hepatus pudibundus*), clock crab (*Persephona lichtensteinii*), purse crab

(*Persephona punctata*), blue crab (*Callinectes* sp.), two species of shrimp from the Caridae family and seven species of fish from Sciaenidae family. As a proxy for oceanic prey, we used isotopic values from jellyfish (*Velella velella*) that were stranded and collected from Trindade Island, Brazil. This island is located at the eastern end of the sea mountain chain Vitória-Trindade, 1160 km from mainland Brazil, and samples collected at this place are assumed to represent isotopic values of oceanic prey. This jellyfish feeds mostly on zooplankton (Mianzan and Girola 1990; Purcell et al. 2015 and references therein) while the oceanic salps eaten by Pacific Ocean olive ridley turtles (Montenegro-Silva et al. 1986) are filter-feeders relying mostly on phytoplankton (Hereu et al. 2010), and large jellyfishes feed on higher trophic levels (Fleming et al. 2015). Thus, *V. velella* seems to be at intermediate trophic levels among other gelatinous organisms, and thus represents well oceanic pelagic prey potentially ingested by olive ridleys.

Tissue samples were rinsed with distilled water, and in all tissues, except blood (serum and RBC), the lipids were then extracted to remove the influence of the ^{13}C-depleted values of lipids (Post et al. 2007). The lipids were extracted using a Soxhlet apparatus with a 2:1 solvent mixture of chloroform and methanol (Medeiros et al. 2015); one cycle of 4 h was used for scute samples, and two cycles of 10 h were used for prey muscle and sea turtle epidermis. The samples were then dried at 60 °C in an oven for 24–48 h to remove the residual solvent, while serum and RBCs were lyophilized for 8 h, and then all tissues were ground into powder. Serum was the only tissue in our study that had C:N ratios >3.5, indicating that its high lipid content may alter δ^{13}C values (Post et al. 2007). Therefore, 10 serum samples were lipid-extracted as described above for other tissues and were then prepared for SIA. This procedure aimed to provide an equation for normalization between lipid-extracted and non-extracted serum samples. The lipid-extracted and non-extracted samples were then compared using a Bayesian paired *t* test to determine whether there was a difference in the δ^{13}C values (see "Results").

SIA

For each of the samples from potential prey items and turtles, approximately 0.7 mg was loaded into a sterilized tin capsule and then analyzed using a continuous-flow isotope-ratio mass spectrometer (CF-IRMS, Thermo Finnigan Delta Plus XP, Bremen, Germany) coupled to an elemental analyzer (Costech ECS 4010, Milan, Italy) at the Stable Isotope Laboratory of Washington State University, School of Biological Sciences, Pullman, Washington, USA. Stable isotope ratios are expressed in δ notation as parts per thousand (‰) deviation from the international standards Vienna Pee Dee Belemnite limestone (carbon) and atmospheric air (nitrogen) as in Eq. 1:

$$\delta X\left(^{0}/_{00}\right) = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}}\right), \quad (1)$$

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

A Bayesian paired *t* test (Kruschke 2015) was used to test for significant differences between lipid-extracted and non-extracted serum samples and between anterior and posterior scute samples. A Bayesian variance test (ANOVA) was also applied to compare δ^{13}C and δ^{15}N values among all tissues analyzed.

Linear regressions were conducted for the δ^{13}C and δ^{15}N values among all tissues collected to provide a tissue-to-tissue conversion (Vander Zanden et al. 2014). These conversions are useful because scute and epidermis samples can be easily collected with minimum stress to turtles without affecting the nesting behavior, health or physiological status of the individuals (Bjorndal and Bolten 2010; Vander Zanden et al. 2014). Moreover, blood samples require immediate centrifugation and freezing, which can present logistical challenges for sampling in remote places where electricity is not available (Vander Zanden et al. 2014). Pearson's correlation test was applied to the linear regressions fitted among tissues.

SIMM in IsotopeR (Hopkins-III and Ferguson 2012) was used to estimate the relative contributions of different sources to the diets of female olive ridley sea turtles. Sampling of turtles and prey occurred in November, and because some olive ridley females recruit to coastal zones around September to reproduce, the assumption was that serum reflected the recent diet and therefore that serum may reflect the contribution of the neritic habitat to the diet, just before nesting (Silva et al. 2007; Reich et al. 2008). The TDF used for SIMM in the present study was from early juvenile loggerhead sea turtles (Reich et al. 2008) (Table 1) due to the similar diets and habitats of loggerhead and olive ridley sea turtles (Bugoni et al. 2003), 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). Reich et al. (2008) determined the residence times and TDF of the epidermis, scutes, RBC and serum based on diets with different protein/lipid proportions. For the analysis of the contributions of potential prey items to the diet assimilation in different olive ridley tissues, the items were grouped into crustaceans (crab and shrimp species), demersal fish (all fishes from Sciaenidae family) and jellyfish, with the first two groups representing

neritic prey (higher δ^{13}C values) and the last group representing oceanic, gelatinous prey (lower δ^{13}C values) (Post 2002; Bugoni et al. 2010).

All statistical inferences were performed within a Bayesian statistical framework (Ellison 2004; Clark 2005). We selected this approach because in Bayesian analysis, estimates of unknown parameters are given as probability distributions denoted 'posteriors' (Gelman et al. 2003), which provides a useful framework to include sources of uncertainty, variability and even prior information (Clark 2005; Hooten and Hobbs 2015). We used non-informative priors for all estimated parameters and models fitted. Samples for the posterior distributions were drawn by Markov Chain Monte Carlo (MCMC) simulation methods (Gelman et al. 2003). In contrast to conventional hypothesis tests and *P* values, the Bayesian paired *t* test provides direct probability statements about the values of interest and the highest (posterior) density intervals (HDIs) covering the 95% most likely values. The odds ratios are obtained by dividing the probability that the difference is greater than or equal to zero by the probability that it is lower than zero, indicating the relative plausibility of both hypotheses. For example, an odds ratio above 20 indicates strong evidence in favor of a positive difference, while an odds ratio below 1/20 (0.05) indicates strong evidence to the contrary (Kruschke 2015). In addition, for Bayesian ANOVA analysis, Bayes Factor (BF) values indicate how many times in the simulation a given difference is likely to occur under the alternative or the null hypothesis.

All analyses were performed using R software (R Core Team 2014) and the JAGS program [http://mcmc-jags.sourceforge.net (Accessed 4 February 2015)] to specify models and perform the Bayesian analysis (Gilks et al. 1994). The package used for the paired *t* test was BayesianFirstAid, BayesFactor was used for the ANOVA analysis, and IsotopeR was used for SIMMs (Hopkins-III and Ferguson 2012).

Results

A total of 46 adult female olive ridley sea turtles were sampled, of which 39 individuals had the complete set of tissues sampled, ranging in size from 64.0 to 76.0 cm CCC (mean ± SD = 71.4 ± 3.10 cm).

After lipids were extracted, all serum samples had C:N ratios <3.5. The Bayesian paired *t* test provided strong evidence that the lipid-extracted and non-extracted serum samples differed in both δ^{13}C and δ^{15}N values. The mean paired difference of δ^{13}C values was −1.6‰, with a credibility interval (CrI) of −1.9 to −1.2‰ and an odds ratio of 0.001. The mean paired difference of δ^{15}N values was −0.26‰, with a CrI of −0.40 to −0.11‰ and an odds ratio of 0.002. Thus, all other serum δ^{13}C values were corrected by a linear regression generated using these values (Fig. 2), while the original δ^{15}N values were used without mathematical normalization. Despite a minor difference between the lipid-extracted and non-extracted δ^{15}N values, this difference was within the analytical error of the equipment used, based on repeated measures of internal laboratory standards acetanilide, corn and keratin (for δ^{13}C SD ± 0.06; for δ^{15}N SD ± 0.26).

The scute samples provided weak evidence of a difference between the anterior and posterior samples (mean paired difference = −0.03‰, CrI = −0.12 to 0.07‰, odds ratio = 0.31 for δ^{13}C values; mean paired

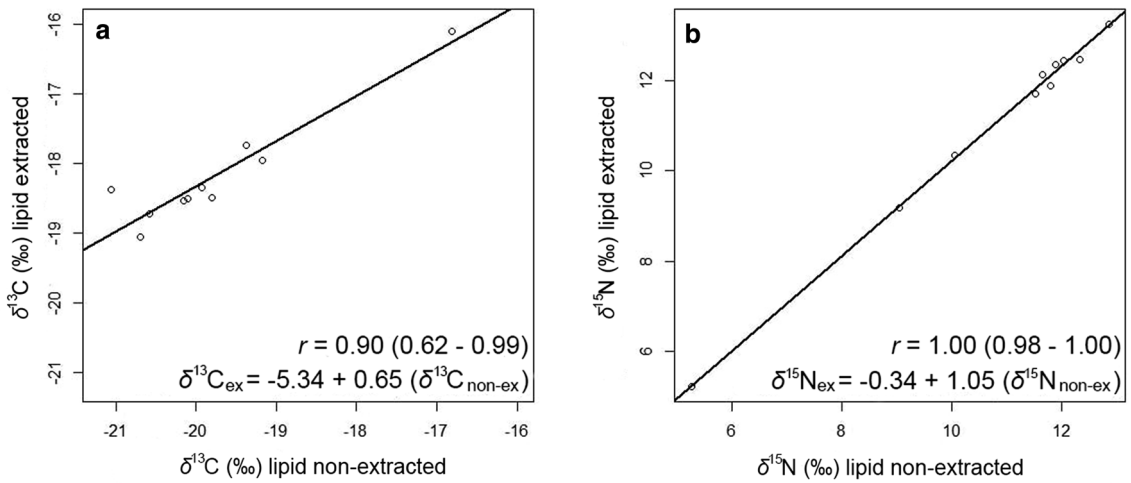

Fig. 2 Linear regressions between pairs of δ^{13}C values (**a**) and between pairs of δ^{15}N values (**b**) of lipid-extracted and non-extracted serum samples. *Equations* inside the graphics indicate the relationship between samples with and without lipids. *Ex* extracted lipids, *Non-ex* non-extracted lipids, *r* is the Bayesian First Aid Pearson's correlation coefficient

difference = 0.06‰, CrI = −0.07 to 0.19‰, odds ratio = 0.83 for δ^{15}N values); therefore, we used the mean value between scute values for all analysis.

Values of δ^{13}C showed the following pattern: RBC < serum < scute < epidermal tissue (Tables 2, S1; Fig. 3), which corroborates the results from the MCMC simulation ANOVA. For δ^{13}C, the Bayes factor (BF) was the highest (4.93) and had a posterior probability of 88%, indicating that tissues differed from each other in 88% of the simulation values (Table S1; Fig. 3b). For δ^{15}N values, the pattern was scute < RBC < epidermis < serum tissue (Tables 2, S1; Fig. 3), which was corroborated by the MCMC simulation ANOVA (Table S1; Fig. 3b). For δ^{15}N, ANOVA also showed the highest BF of 5.99 and a posterior probability of 85% (Table S1; Fig. 3b).

All linear regressions of the δ^{15}N values and δ^{13}C values resulted in high correlation (i.e., r values >0.7), with the correlations between the δ^{15}N values being even higher than those between the δ^{13}C values (Figs. 4, 5). Values of δ^{15}N did not differ between the various tissues despite epidermal tissue having the lowest Pearson's correlation coefficient (r = 0.76–0.90) among all the tissues (Fig. 5). For δ^{13}C values, the epidermis also had the lowest r (r = 0.42–0.55) compared to the other tissues (Fig. 4).

Stable isotope values of prey samples are presented in Table S2 and all values for individual turtles and each tissue in Table S3. The SIMM with values from RBC and epidermal samples, representing months before, demonstrated that the greatest contribution was from jellyfish, followed by

Table 2 δ^{13}C and δ^{15}N stable isotope values (mean ± standard deviation) from serum, red blood cells (RBCs), epidermis and scute tissues of olive ridley (*Lepidochelys olivacea*) females sampled at Pirambu, Sergipe State, Brazil

Tissue	*n*	δ^{13}C (‰)	δ^{15}N (‰)
Serum	46	−18.25 ± 0.56 (−19.56 to −16.27)	11.68 ± 1.65 (5.22–14.67)
RBCs	46	−18.39 ± 0.66 (−20.24 to −16.35)	10.06 ± 1.52 (4.04–13.34)
Epidermis	43	−16.56 ± 0.74 (−17.90 to −14.86)	10.83 ± 1.27 (6.41–13.67)
Anterior scute	40	−17.95 ± 1.14 (−22.61 to −15.60)	9.70 ± 1.56 (4.89–12.71)
Posterior scute	40	−17.81 ± 0.85 (−19.89 to −15.65)	9.64 ± 1.67 (4.45–12.60)

Values in parentheses are the range of δ^{13}C (‰) and δ^{15}N (‰); *n* is the number of individuals sampled

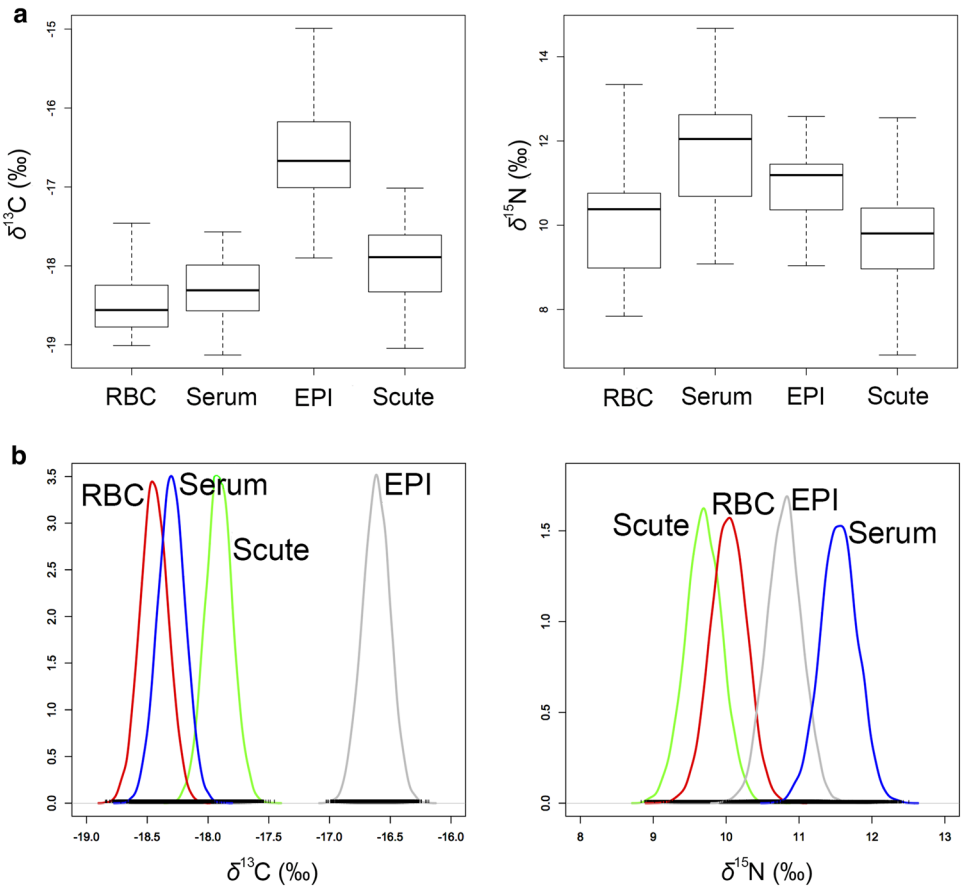

Fig. 3 **a** δ^{13}C and δ^{15}N values from tissues sampled. The *horizontal black line* indicates the median value, the *box* indicates the quantiles of 25 and 75%, *dashed lines* indicate extreme values. **b** Posterior probability of Markov Chain Monte Carlo (MCMC) simulation from ANOVA analysis of each tissue sampled. *RBC* red blood cell, *EPI* epidermis

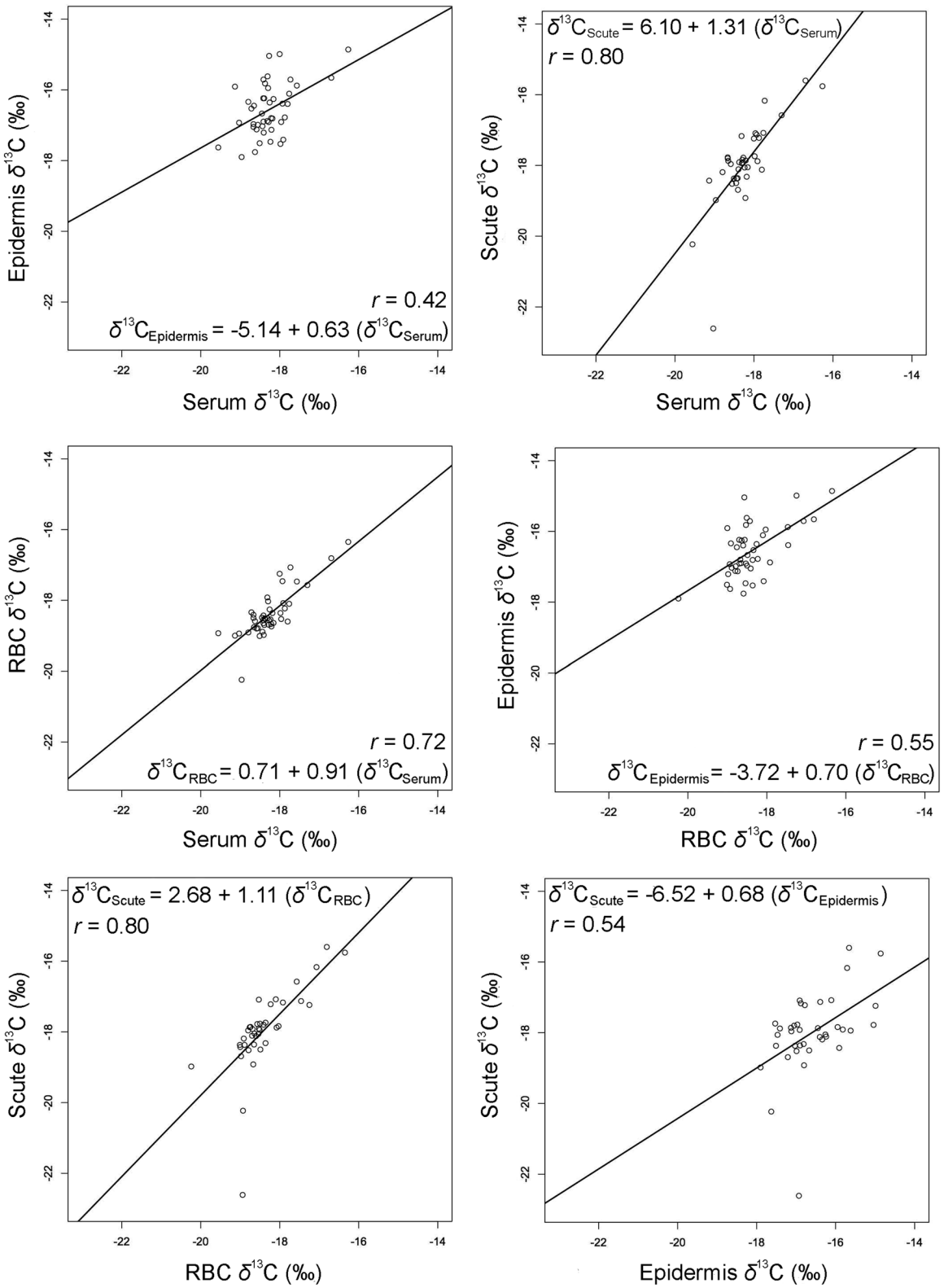

Fig. 4 Linear relationships among $\delta^{13}C$ values of tissues from olive ridley sea turtles (scute, epidermis, serum and red blood cells - RBCs). The regression equation and the Bayesian First Aid Pearson's correlation coefficient (r) are provided inside each graph

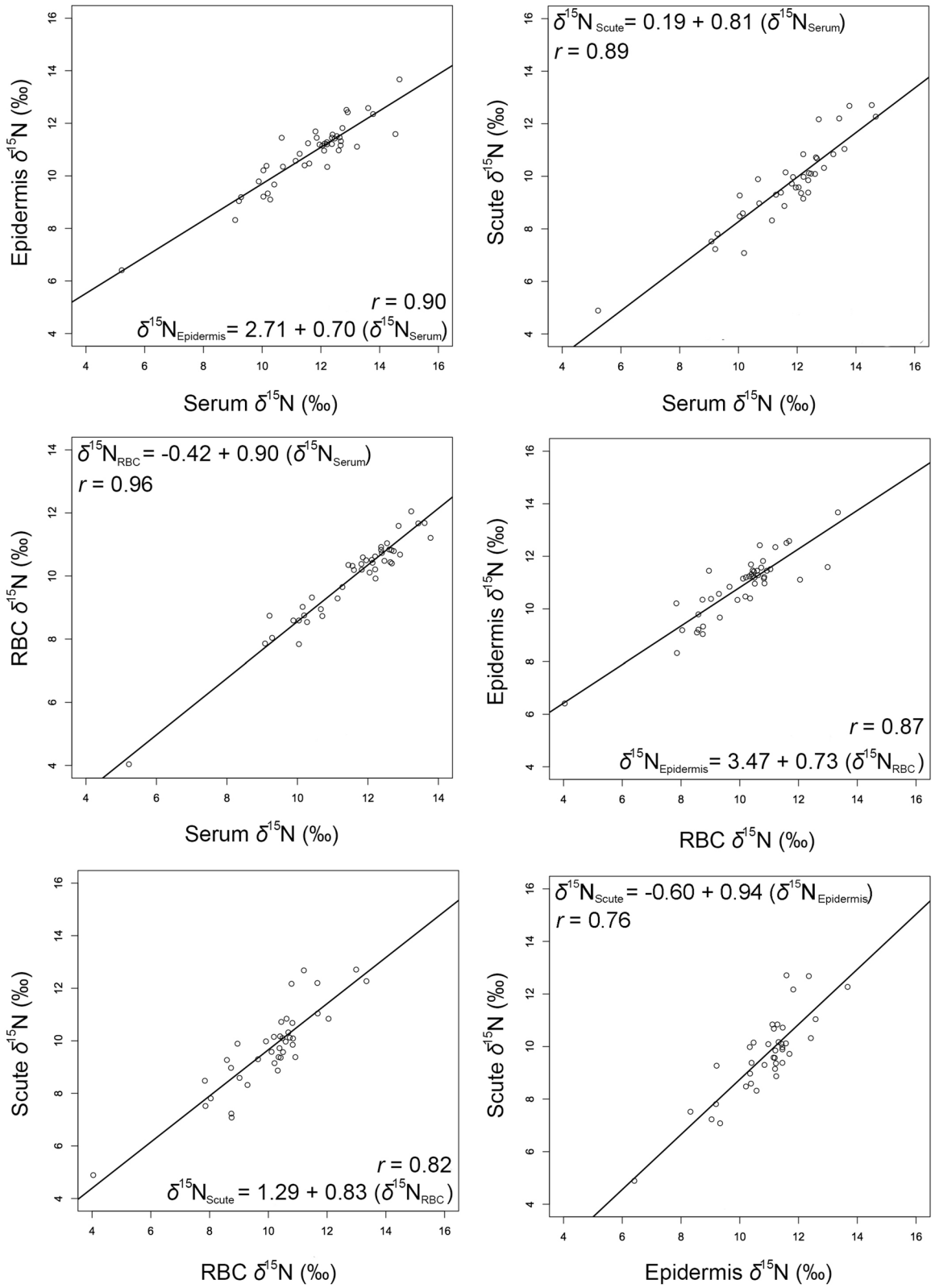

Fig. 5 Linear relationships among $\delta^{15}N$ values of tissues from olive ridley sea turtles (scute, epidermis, serum and red blood cells - RBCs). The regression equation and the Bayesian First Aid Person's correlation test (*r*) are provided inside each graph

Table 3 Dietary contributions of different sources for female olive ridley sea turtles (*Lepidochelys olivacea*) from Pirambu, Sergipe State, Brazil

Tissue	Jellyfish		Demersal fish		Crustacean	
	Mean (%)	CrI (%)	Mean (%)	CrI (%)	Mean (%)	CrI (%)
RBCs	81	37–100	19	14–62	0	0–1
Epidermis	54	39–70	45	29–60	0	0–7
Scute	20	0–47	79	49–100	2	0–8
Serum	4	0–40	95	60–100	0	0–1

CrI credibility interval, *RBCs* red blood cells

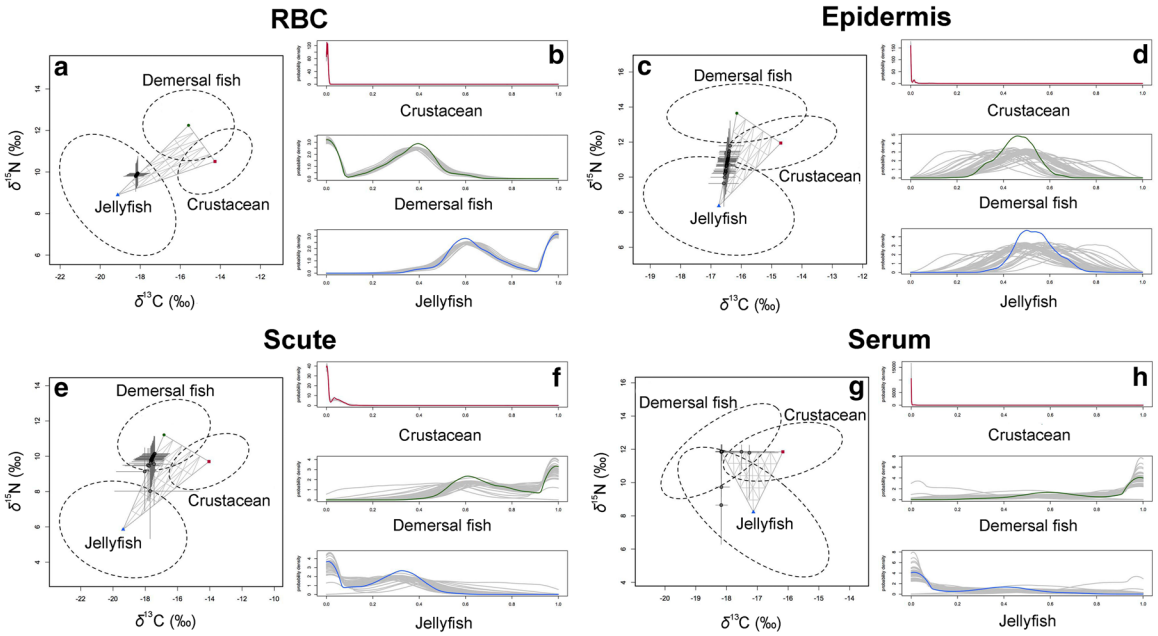

Fig. 6 Estimated stable isotope values (δ^{13}C, δ^{15}N) (**a**, **c**, **e** and **g**) for red blood cells (RBCs), epidermis, scute and serum, respectively, from olive ridley sea turtles (*Lepidochelys olivacea*) and the proportional dietary contributions (expressed as marginal posterior distributions) of different potential sources: jellyfish (*blue triangle*), demersal fish (*green circle*) and crustacean (*pink square*) (**b**, **d**, **f** and **h**). *Gray lines* indicate each individual sampled, and the *colour line* in the middle is the mean diet contribution in **b**, **d**, **f** and **h**

demersal fish, with a negligible contribution of crustaceans (Table 3). Scute and serum samples (weeks to a few months previous to sampling) showed that the greatest contribution was from demersal fish, followed by jellyfish, with a negligible contribution from crustaceans (Table 3). Although most individuals exhibited this pattern, some individuals showed different dietary compositions (individual lines are visible in Fig. 6).

Discussion

The simultaneous measure of δ^{13}C and δ^{15}N values in several tissues of the same olive ridley turtles provided a clear picture of habitats used months and weeks before nesting, as well as the individual variability within the population nesting on northeastern Brazilian beaches.

Methodological considerations

Serum samples demonstrated moderate lipid contents, and most samples had C:N ratios <3.5 after proper extraction using chloroform:methanol, allowing for the mathematical normalization of δ^{13}C values (Fig. 2). Chloroform:methanol solution had been widely used and recommended for lipid extraction before stable isotope analysis, as it remove both polar and nonpolar lipids (Sotiropoulos et al. 2004; Medeiros et al. 2015). However, lipid extraction also increased the δ^{15}N values. Marine fish and elasmobranch muscle δ^{15}N values also increased after lipid extraction with the same solvent used in this study (Logan et al. 2008; Hussey et al. 2012). Nevertheless, the average increase in δ^{15}N values in lipid-extracted samples is within the range of analytical error (~0.26‰) and is much lower than biologically meaningful differences under most

circumstances, such as in changes between trophic levels, for which such values are expected to vary 3–5‰ (Peterson and Fry 1987). However, several studies did not find any alteration in δ^{15}N values after lipid extraction using a chloroform:methanol solution (e.g., Arrington et al. 2006; Medeiros et al. 2015). Therefore, because some samples in the current study showed increases of up to 0.50‰ and because the differences between the groups being compared are small, lipid extraction should be undertaken carefully, e.g., using the same procedure for all samples. Furthermore, because the results of lipid extraction studies vary, we encourage a close look to the lipid content of samples, based on C:N ratios. We also encourage an analysis whether differences between groups is expected to be much higher than the error associated with lipid content or the lipid extraction protocol. Such procedures would indicate the better approach and the limitations of conclusions, in a case-by-case basis.

We provided tissue-to-tissue equations for the conversion of δ^{13}C and δ^{15}N values among tissues. These equations could allow comparisons between studies measuring stable isotopes in different tissues, in cases they had been synthesized from the same pool of nutrients, i.e., reflect a comparable time window. This is probably the case for some tissues, e.g., epidermis and scute, but not others, such as serum and scute (Table 1). This consistency in correlations could also be maintained if a consumer has a constant diet throughout the year, which could be the case for some turtles but not others. In all these cases correlations essentially measure differences in metabolic pathways among tissues. Alternatively, a lack of correlation between tissues would indicate a switch in diet, in addition to metabolic routing. Values of δ^{13}C among tissues also showed high correlations, but these were lower than for the δ^{15}N values between tissues, suggesting that olive ridley sea turtles may move interchangeably between habitats or switch diets frequently, resulting in tissues with different half-life representing different habitats or diets. Alternatively, different metabolic routing used for tissue synthesis may result in the distinct assimilation of isotopes, depending on the protein composition of each tissue synthesized, as well as the protein content of prey (Martínez del Rio et al. 2009).

Habitat use

Studies using SIA in olive ridley sea turtles tissues or attempting to infer their habitat use in the Atlantic Ocean during non-breeding and breeding periods, using intrinsic markers, are not available for comparison. The stable isotope values of δ^{13}C and δ^{15}N in various tissues indicated the use of neritic and oceanic habitats, similar to those demonstrated by satellite telemetry for the same population (Silva et al. 2011).

Olive ridley turtle undergoes long migrations during adulthood; thus, tissues may show different isotopic values, especially in terms of δ^{13}C, as turtles move between habitats with distinct isotopic signatures (Hobson and Norris 2008; Hoffman 2016). Adult olive ridleys nesters in northeastern Brazil may migrate to post-nesting feeding grounds in oceanic waters in the central Atlantic or to neritic waters over the continental shelf. A third individual strategy may be to spend some time in neritic feeding grounds and then migrate to the open ocean (Silva et al. 2011). Reis et al. (2010) reported 23 olive ridley sea turtles stranded dead on the Rio de Janeiro coast between August 2005 and November 2009. One specimen had been previously tagged when nesting at Pirambu Beach (our study site), which may suggest that some individuals remain in neritic waters over the continental shelf during the non-nesting period. Similarly, Guimarães et al. (2017) reported 21 olive ridley turtles captures over the continental shelf of Rio de Janeiro State by commercial trawlers. In contrast, Sales et al. (2008) showed that adult olive ridleys intensively use oceanic waters between 5°N and 5°S and along the continental shelf of northeastern Brazil in the western Atlantic Ocean. In the eastern tropical Pacific Ocean, adults displayed no fidelity to specific feeding habitats and were classified as nomadic (Plotkin 2010). This pattern differs from loggerhead sea turtles from North Atlantic, which have strong fidelity to non-breeding areas (Hall et al. 2015; Vander Zanden et al. 2016). Overall, the diet of olive ridleys is poorly known in the Atlantic Ocean (e.g., Colman et al. 2014; Di Beneditto et al. 2015) and has been limited to studies of large juveniles and adults. At this phase individuals are more prone to maintain foraging consistency after the juvenile period, relying on the same areas and prey, as demonstrated for green sea turtles (Vander Zanden et al. 2013). The few dietary studies of olive ridley have all reported similar prey items: demersal fishes, crustaceans and gelatinous prey (Montenegro-Silva et al. 1986; Colman et al. 2014; Di Beneditto et al. 2015). However, these studies are based on stranded turtles, which may not be representative of the diet of oceanic turtles. In the tropical waters of the Pacific Ocean where stomach contents of olive ridleys were sampled offshore, it was demonstrated that adults and juveniles have similar diets, based mostly on jellyfish and ctenophores, and share the same habitat (Kopitsky et al. 2001). Despite limitations of using a few samples of a single gelatinous prey (i.e., *V. velella*) as indicator of the oceanic environment, because the prey chosen is at intermediate trophic level between salps and large-sized jellyfish, one would expect that stable isotope values of salps would provide an indication of even more intense use of oceanic environments by olive ridleys. Otherwise, if we had measured stable isotope values in cnidarians that rely on fish for food, it would indicate a lower number of turtles

as inhabitants of oceanic habitats, but would not radically change the main conclusion of the current study.

Values of δ^{15}N showed high correlations among the different tissues (Fig. 5). Although δ^{15}N values may be a good proxy for trophic level, interpretation is difficult if the baseline values of each habitat are unknown. Moreover, in highly migratory species such as olive ridley sea turtles, it is more difficult to interpret δ^{15}N values (Martínez del Rio et al. 2009). McMahon et al. (2013) showed limited differences in copepod zooplankton δ^{15}N values in a vast region off northeastern Brazil, but because neritic samples were not included in their study, the neritic–oceanic gradient remains poorly defined. Although our sampling included several tissues with different half-lives, the interpretation of changes in habitats, and which habitat each δ^{15}N value refers to is challenging. In addition, some factors may influence both δ^{13}C and δ^{15}N values, such as metabolic processing, macronutrient routing, biochemical composition, and differential fractionation during assimilation (Martínez del Rio et al. 2009; Vander Zanden et al. 2014), which influence tissue half-lives in growing turtles (Reich et al. 2008).

Each tissue reflects the olive ridley diet for different time periods due to different residence times of carbon and nitrogen, but these data in adult sea turtles have not been measured, as shown in Table 1. RBCs, epidermis and scutes of tortoises and juvenile sea turtles reflect the foraging grounds at least 4–7 months prior to sampling (Brace and Altland 1955; Hamann et al. 2003; Seminoff et al. 2007; Reich et al. 2010; Ceriani et al. 2014; Prior et al. 2016). Moreover, in reptiles, RBCs can persist for up to 11 months because they are nucleated, long-lived cells (Frische et al. 2001). In juvenile loggerhead sea turtles, RBCs had a residence time of 40 days for carbon (Reich et al. 2008), but the two diets used had similar δ^{13}C values, and thus the residence time may be higher. The lowest δ^{13}C value in RBCs presented here most likely represents the period during which olive ridleys were in oceanic waters (Bugoni et al. 2010). Opposite pattern was found for two individuals, which had higher δ^{13}C values for RBCs (−16.35 and −16.81‰) than the others, suggesting that they were most likely in neritic feeding grounds before nesting. In addition to RBCs, serum, scute and epidermal tissues also exhibited high δ^{13}C values for these two individuals. Although the majority of olive ridley adults migrate to oceanic waters after the nesting season, a small proportion of individuals forage in coastal waters (Reis et al. 2010; Santos et al. 2016), and the two individuals with higher δ^{13}C values may represent specimens from neritic non-breeding areas. The δ^{15}N values in these two specimens also differed markedly from the others, being the lowest values from all samples and tissues. Although there are reports of olive ridley sea turtles in Rio de Janeiro waters in southeastern Brazil, local upwelling occurs at this location, and depending on the N cycling, upwelling could result in prey with low δ^{15}N values. Thus, these two individuals with low δ^{15}N values were probably in feeding grounds on the Rio de Janeiro coast before moving to nesting grounds. However, alternative explanations, such as individuals feeding higher on the trophic chain in the oceanic environment, or remaining in patches of habitat with higher δ^{15}N values at the base of the food web, could not be ruled out.

Migration is a crucial component of the sea turtle life cycle and life history; these reptiles migrate in search of food resources, mates, nesting beaches or more optimal temperatures. Because these components are characteristics of each species, individual variability is expected in species with wide distributions (Morreale et al. 2007). Individual variability has been reported in numerous populations of vertebrates and invertebrates. In such situations, individuals use a small subset of the resource base of the population (Bolnick et al. 2003). Consequently, generalist populations may be formed by specialized individuals (Bolnick et al. 2003). In our study, SIMM analysis showed large variability between individuals for all tissues, but with a consistency for each individual, i.e., high values for a given tissue were followed by similar high values in other tissues (Table S3), as demonstrated by high correlations between tissues. These results make improbable that difference between isotopic values between tissues are due to differences between metabolic routing. Results seem indicate that turtles can migrate to breed from both neritic and oceanic habitats or that move between neritic and oceanic habitats during the period before nesting or during inter-nesting, resulting in considerable variation among tissues. An alternative non-exclusive explanation is that turtles originate from distinct non-breeding areas with different isotopic values. This scenario is consistent with the lower correlations among the δ^{13}C values of the tissues sampled, and corroborates previous data on tracking (Silva et al. 2011). Moreover, the RBCs, epidermis, scute and serum showed a gradual increase in δ^{13}C values, suggesting a habitat shift from oceanic to neritic habitats for reproduction in female turtles. Because RBCs reflect less recent periods than other tissues, jellyfish contributed 81%, while demersal fish contributed 19%. The contribution of demersal fish increased from the epidermis to scutes and serum in SIMMs, with the latter having the shortest residence time for nitrogen, but the longest for carbon (Reich et al. 2008; Table 1). Because serum reflects the most recent time period, it showed the greatest contribution of demersal fish, corresponding to the bulk of the population inhabiting neritic habitat during the nesting season.

Regarding values in scutes, the discrepant residence times from a single study make difficult to interpret when its synthesis occurred. If we assume that scutes had been formed

months before breeding, i.e., in non-breeding grounds, the SIMM indicating demersal items as main contributors is hard to explain for most individuals, which are supposed to use oceanic areas during this period. Therefore, SIMMs showed a marked switch in habitat use for feeding in olive ridley sea turtles immediately before and during reproduction. However, individual variability was again represented by some individuals still having oceanic isotopic signatures (~5% of the sample). The narrow shelf break near the nesting beaches may facilitate displacement to offshore waters immediately before nesting or during the inter-nesting period.

Female olive ridley turtles nest from 1 to 3 times each season, with ~22 days between clutches (Matos et al. 2011). Because our sampling occurred in November, it is unknown whether the samples corresponded to the first or second clutches. If they were first clutches, the sampled turtle was most likely in neritic waters for some time during courtship, mating, ovulation and oviductal egg development (Rostal 2007). Therefore, although sea turtles rarely invest in feeding during the nesting season, they are opportunistic and may therefore make use of discards from shrimp trawl fisheries (Carvalho 2007; Romero et al. 2008) or the presence of other prey in the vicinity of nesting beaches between laying events. Serum samples, reflecting the most recent diet likely when the turtles were breeding, showed the highest contribution of demersal fish (95%) and the lowest contribution of jellyfish (5%). This suggests that the sampled olive ridleys were most likely feeding during breeding. Colman et al. (2014) demonstrated the great importance of neritic items such as shrimps, crabs and demersal fishes, which are typically discarded by shrimp trawl fisheries, for olive ridley adults found stranded dead at Pirambu Beach. In addition, based on satellite tracking, Silva et al. (2011) demonstrated active movements during the inter-nesting period and suggested that reproductive females in Sergipe (Brazil) forage during nesting. Measurements of turtle body mass in successive nesting attempts for some turtles in the area also confirm that they are feeding between laying events (Castilhos and Tiwari 2006). However, Goldberg et al. (2013) suggested that hawksbill sea turtles do not forage during breeding based on hormone levels, despite it was demonstrated that hawksbill turtles may feed opportunistically during breeding (Witzell 1983), similar to olive ridley sea turtles (Colman et al. 2014). Vitellogenesis in sea turtles occurs approximately 4–6 months before migration for nesting (Rostal et al. 1998), and turtles then undergo several steps in preparation for nesting. Therefore, if there is no easily available prey, turtles most likely do not eat for a long time during migration and nesting. Because egg reproduction requires high levels of energy consumption, fasting turtles can mobilize their own protein stores as energy sources during the nesting period, which may be an alternative explanation for the high δ^{15}N values found in serum. Food-deprived birds had been demonstrated to have higher δ^{15}N values in comparison to non-fasting birds (Hobson et al. 1993). Moreover, high δ^{15}N values were demonstrated in tail hair for fasting blue wildebeest (*Connochaetes taurinus*) in Africa (Rysava et al. 2016). Despite the vitellogenic period is well known, the food-deprived period before female nesting, the magnitude of food ingestion just prior and during nesting, and the exact arrival time of females sampled in nesting beaches is poorly defined. The scarcity of such information precludes inferences on foraging habitats based on SI values during the weeks to months previous to nesting.

Inferences on habitats used by sea turtles during the non-nesting period will benefit from further studies testing the consistency of individuals between years, i.e., if stable isotope values remain similar in tissues of each individual on a long time-scale (sensu Bolnick et al. 2003). Additionally, the use of SIA of other elements such as sulfur could improve definition of non-breeding foraging areas. Finally, the use of compound specific SIA (e.g., Bradley et al. 2016) could provide further evidences on the origin of nutrients allocated to reproduction (in the form of egg yolk, albumen and eggshell) and synthesis of different body tissues.

Implications for conservation

Here, based on stable isotopes from several tissues, we have demonstrated that olive ridley sea turtle breeding group in northeastern Brazil use a wide range of habitats, such as oceanic and neritic waters south and north of the nesting grounds. Therefore, this study confirms previous studies based on turtles stranded on the coast, incidental capture in fisheries, and satellite telemetry, both with small numbers of individuals ($n = 23$ stranded specimens Reis et al. 2010; $n = 21$ individuals captured Guimarães et al. 2017; $n = 10$ turtles tracked Silva et al. 2011). Stable isotope analysis in multiple tissues demonstrated that although the bulk of the population uses oceanic habitats during the non-breeding season, there is high individual variability. Thus, threats imposed by shrimp trawl fisheries adjacent to nesting areas (Silva et al. 2010), and finfish trawling in non-breeding areas (Guimarães et al. 2017) are in fact year-round problems for the portion of the population that remains over the continental shelf throughout the year, as trawling targeting shrimp and finfish occurs all along the Brazilian coast (Isaac et al. 2006). Furthermore, most individuals face the threat of incidental capture both in shrimp trawl nets during breeding and in pelagic longline fisheries in oceanic waters during the non-breeding period (Sales et al. 2008; Silva et al. 2011). Mitigating incidental capture by both trawling and longline fishery is essential, as turtles using both oceanic and neritic foraging strategies are important for

maintaining the population as well as for preserving the ecological plasticity of the population.

This species matures at approximately 16 years of age (Petitet et al. 2015), and although it is the most abundant sea turtle species globally (Plotkin 2007), the number of adults found stranded dead on the Sergipe coast has increased (Castilhos et al. 2011). Shrimp trawling is prohibited during only part of the nesting season and enforcement is precarious.

The SIA of serum showed that turtles most likely forage just before and during the breeding season and therefore that olive ridley sea turtles spend time in neritic waters before, during and after nesting. Stable isotope studies together with previous analyses based on satellite telemetry and stomach contents contribute to a better understanding of feeding behavior, migration and habitat use during a larger proportion of the life cycle of olive ridleys, including the poorly known non-breeding period. Conservation plans for this species in Brazil benefit greatly from such information. Bycatch mitigation measures for longline and trawl fisheries should continue to be the focus for conservation.

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Compliance with ethical standards

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

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Ethical approval This article does not contain any studies with human participants. All applicable international, national, and institutional guidelines for the care of animals found stranded alive were followed. We did not conduct experiments with animals.

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