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Trophic ecology of sympatric sea turtles in the tropical Atlantic coast of Brazil

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ABSTRACT

The Tropical Atlantic coast of Brazil is a hotspot area for multiple sea turtle species at all life stages. The multiple nearshore reefs and beaches, oceanic islands, and the only atoll in the south Atlantic Ocean, are suitable for year-round foraging, migration corridors, and nesting activities of five sea turtle species. Still, relatively few studies have assessed trophic niche among sympatric sea turtles which can provide a better understanding of how closely related species compete/partition the available resources. Using multiple biogeochemical tracers (i.e., nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) stable isotopes, and mercury (Hg)), we disentangled the trophic niches of four sea turtle species – the green turtle (*Chelonia mydas*), the loggerhead turtle (*Caretta*), the hawksbill turtle (*Eretmochelys imbricata*), and the olive ridley turtle (*Lepidochelys olivacea*) – co-occurring in nesting and foraging habitats along the northeastern coast of Brazil. We found interspecific differences in isotopic and contamination niches, as well as intraspecific niche variation associated with life stage. Differences in the estimation niche models associated to life-stage in *C. caretta* support the notion of ontogenetic shift in habitat and diet composition previously reported for this species. Oceanic habitat signatures were observed in juvenile green turtles and adult olive turtles, while nearshore habitat signatures were observed in adult hawksbill turtles.

1. Introduction

The Brazilian coast in the West Atlantic Ocean extends for more than 8000 km and is an important habitat for five species of sea turtle, including the Loggerhead turtle (*Caretta* Linnaeus, 1758), the Green turtle (*Chelonia mydas* Linnaeus, 1758), the Leatherback turtle (*Dermochelys coriacea* Vandelli, 1761), the Hawksbill turtle (*Eretmochelys imbricata* Linnaeus, 1766) and the Olive ridley turtle (*Lepidochelys olivacea* Eschscholtz, 1829) (Marcovaldi and Marcovaldi, 1999). The Northeastern coast of Brazil (lat. Long. ~2°S ~40°W to ~13°S ~38°W) is a known area for onshore and offshore foraging, migratory corridor, and nesting ground for all cited species (Lima et al., 2013; Marcovaldi and Marcovaldi, 1999).

Studies on foraging ecology and diet composition of sea turtles around the world have shown their important role in connecting oceanic and coastal food webs, especially by feeding on multiple trophic levels and occupying broad geographic ranges that includes both oceanic and coastal habitats (Figgener et al., 2019; Hamann et al., 2010). However, relatively few studies have assessed trophic niche among sympatric sea turtles species which can improve our understanding of how closely related species can partition common habitats and coexist with limited resources (Clyde-Brockway et al., 2022; Palmer et al., 2021; Wildermann et al., 2019). Furthermore, sympatry and syntopy are common in sea turtles with implications on their conservation and resilience to anthropogenic pressures (Hamann et al., 2010; Rees et al., 2016).

Sympatry is described here as multiple species with overlapping ranges, sharing a given habitat (syntopy), with implications on diet composition, habitat-use, and trophic ecology (Marko, 2008). Previous studies have shown that species living in sympatry can present various levels of diet plasticity which allow partitioning of food resources and reduces interspecific competition (Bezerra et al., 2021; Pantoja-Echevarría et al., 2022). These processes might explain differences in diet composition observed in sea turtle species in different habitats.

Sea turtle's diet varies across species and life stage. The Green turtle, *C. mydas*, is described as a generalist and opportunistic consumer that, depending on the geographical location and life stage, can rely on

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macroalgae, seagrass, and/or invertebrates (Bugoni et al., 2003; Nagaoka et al., 2012; Seminoff et al., 2021). The Loggerhead, *C. caretta*, are typically a generalist carnivore, with diet composed of mollusks and crustaceans, but also with variation in diet composition associated to foraging habitat and life stage (Blasi et al., 2018; Medeiros et al., 2019). Similarly, the Olive ridley turtle, *L. olivacea*, is known as a generalist carnivore, with diet composed of fish and crustaceans in adults (Colman et al., 2014) and of pelagic invertebrates in juveniles (Polovina et al., 2004). In contrast, the Hawksbill turtle, *E. imbricata*, are generally known to be an omnivore specialized in sponges, but also consuming tunicates, algae, and mangrove material (Martínez-Estévez et al., 2022; Reynolds et al., 2023). Therefore, in addition to prey availability, interspecific competition can be another factor in determining foraging behavior in sea turtles.

Stable isotope analysis (SIA), where the ratio of stable isotopes of selected elements (i.e., nitrogen ^{15}N/^{14}N, hereafter δ^{15}N; and carbon ^{13}C/^{12}C, hereafter δ^{13}C, relative to reference standards) has been used as a biogeochemical tool in ecological studies providing information to understand trophic dynamics of wild populations (Peterson and Fry, 1987; Post et al., 2007; Yeakel et al., 2016). Small changes in δ^{13}C, as carbon moves through food webs (enrichment of $\leq$1‰), reflect changes in sources of carbon and major pathways of energy transfer (Bouillon et al., 2011; Peterson and Fry, 1987), while δ^{15}N stepwise increase with each trophic step (~2‰–4‰) provides a framework where the δ^{15}N values of consumers, in relation to baseline δ^{15}N values of primary producers, reflect their trophic position, diet composition and can be used as a proxy of trophic niche (Hussey et al., 2010; Layman et al., 2007; Post, 2002). Similarly, the concentration of trace elements which biomagnifies through the food web, such as mercury (Hg), can be used as a dual proxy and/or a biogeochemical tool in ecological studies (Kiszka et al., 2015; Newman et al., 2011; Pinzone et al., 2019). Mercury is ubiquitous in marine ecosystems and diet is the most important route of uptake and accumulation in marine consumers (Hall et al., 1997). Because of this, Hg has been often used as a dietary tracer in many aquatic organisms, including seabirds (Thorne et al., 2021), marine mammals (Das et al., 2003; Peterson et al., 2015), fishes (Di Beneditto et al., 2013), elasmobranchs (Le Croizier et al., 2019; Pinzone et al., 2019), and sea turtles (Bezerra et al., 2015).

The concept of ecological niche is fundamental to understand species' roles in the food web. It is defined as a multidimensional space whose defining axes represent environmental and physical variables, including organisms' geographic range, distribution depth, temperature, salinity, etc. (Hutchinson, 1957). Therefore, ecological niches can be described by multiple characteristics of species (e.g., functional, morphological, physiological) and are used by ecologists to understand aspects of resource use, geographic distribution, and food web composition and structure (Chase and Leibold, 2003). Since stable isotope ratios in biological tissues of consumers derive from all trophic pathways, they can be used as trophic niche proxies (Layman et al., 2007). This approach allows to reconstruct consumers' isotopic niches and estimate associated quantitative metrics, such as isotopic niche ranges, total area of convex hulls, niche width using standard ellipse areas, and niche overlap allowing for inferences about trophic role, species interaction, diet composition, habitat use, and ontogenetic changes (Jackson et al., 2011; Layman et al., 2007; Newsome et al., 2007).

As sea turtles are an endangered species, it is important to employ non-invasive methods of sampling for biogeochemical tracers. In this sense, the carapace scutes, mainly composed of keratin, is an inert structure that retains a record of sea turtles' diet and habitat-use (Barrios-Rodríguez et al., 2023; Reich et al., 2007; Rodriguez et al., 2022; Vander Zanden et al., 2010; 2014). Scute sampling has been used on ecological and contamination studies on multiple sea turtle species and allows to investigate trophic patterns in these long-lived species (Bezerra et al., 2015; Vander Zanden et al., 2010).

Several studies have described the occurrence and isotopic variations of sea turtle species along the Brazilian coast. Most studies are of *C. mydas* and *C. caretta* species, but also of *L. olivacea*, from areas in the southern coast and northeastern coast of Brazil. Using carbon (δ^{13}C) and nitrogen (δ^{15}N) stable isotopes researchers have described many features of sea turtles' ecology, including the herbivory level and niche breadth variations in juvenile *C. mydas* from neritic foraging grounds (Di Beneditto et al., 2017; Gama et al., 2021), differences in foraging and habitat use associated with life stage in *C. caretta* (Medeiros et al., 2019), habitat-use plasticity in nesting L. olivacea (Petitet and Bugoni, 2017), and interspecific variation in isotopic composition associated with both habitat-use and diet (Filippos et al., 2021; Soares et al., 2021). In contrast, none have described trophic niche, using multiple biogeochemical tracers, of multiple sea turtle species co-occurring in NE Brazilian coast in the Western Equatorial Atlantic Ocean.

Our goal is to describe trophic niche of four sea turtle species inhabiting the northeastern coastal of Brazil in the Western Equatorial Atlantic Ocean, using carbon (δ^{13}C) and nitrogen (δ^{15}N) stable isotopes and total Hg (hereafter referred as Hg) as ecological tracers. Specifically, we ask the following questions (1) Do Sea turtle species co-occurring in tropical foraging grounds present overlapping isotopic niches? We hypothesize that sea turtle species sharing foraging habitats will present some degree of niche overlap but with differences in area size associated to species-specific feeding characteristics (i.e., generalist and specialist). (2) Do Sea turtle species co-occurring in nesting areas present overlapping isotopic niches? Considering that nesting turtles do not rely on nesting ground for food resources, estimation niche models should reflect their respective foraging grounds. Thus, we hypothesize that potential overlap among species could suggest a shared foraging area among them. (3) Do juvenile and nesting individuals of *C. caretta* differ in isotopic composition and Hg concentrations? We hypothesize that these groups will present similar isotopic composition as it relates to habitat carbon sources (i.e., δ^{13}C), but different δ^{15}N composition considering that food resource partitioning has been shown to be associated with life stage and habitat-use (Blasi et al., 2018). We also hypothesize that Hg concentrations should differ between these groups also as a result of different diet composition.

2. Materials and methods

2.1. Sample acquisition and processing

Sea turtle biological samples were obtained from 2009 to 2016 through a long-term sampling effort by the authors in collaboration with multiple non-governmental agencies, including *Fundação Projeto Tamar* (Bahia and Ceará Bases), *Instituto Verde-Luz*, and *Projeto Ecoassociados*. Hg concentrations and ratios of carbon and nitrogen stable isotopes compose a large database, including multiple tissues and species of sea turtles from the Northeastern coast of Brazil. From this long-term project, multiple graduate Theses were produced and data from selected species, tissues, and sites were previously published in the literature (Barrios-Rodríguez et al., 2023; Barrios et al., 2018; Bezerra et al., 2012, 2013, 2015; López-Castro et al., 2013; Rodriguez et al., 2019, 2020a). The present study, however, conducts an ecological analysis at a regional scale not presented elsewhere.

From this database, we selected adult individuals nesting in sites along the coast of Bahia (n = 18 for *C. caretta,* and n = 54 for *L. olivacea*), and Pernambuco (n = 44 for *E. imbricata,* and n = 4 for *L. olivacea*) (Fig. 1). We also selected juvenile individuals from foraging sites in Bahia (n = 26 for *C. mydas*), Ceará (n = 4 for *C. caretta,* and n = 32 for *C. mydas*), and Pernambuco (n = 4 for *C. mydas*). The criteria for classifying these juvenile individuals was a curvilinear carapace length smaller than 90 cm, which is below the size range of individuals nesting in the Northeastern coast of Brazil, according to Marcovaldi and Chaloupka (2007) for *C. caretta*, and Almeida et al. (2011) for *C. mydas*. (Fig. 1).

Samples were collected from random areas of the lateral region of the carapace by carefully scrapping the superficial layers, with a dissection

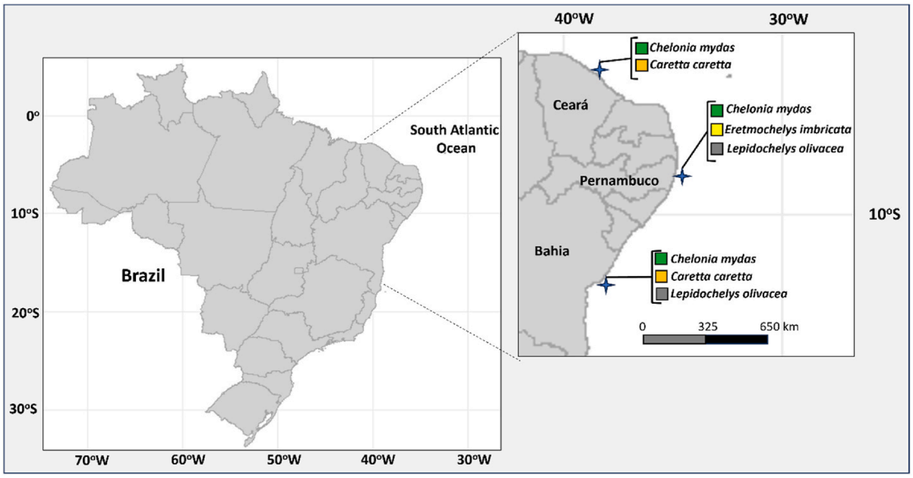

Fig. 1. Map of study area highlighting the sampling location of sea turtle species.

knife, avoiding the skin and dermis tissues (Barrios-Rodríguez et al., 2023). A sub set of samples (26 juvenile *C. mydas* individuals) were collected using a 6 mm biopsy punches also from the lateral region of the carapace (see López-Castro et al. (2013) for methodological details) which included not only superficial layers (older diet records) but also deeper/newer ones (relatively more recent diet records). For these samples, we took an average of isotopic values from all layers as, according to López-Castro et al. (2013), no differences in isotopic values were observed among scute layers. All samples were washed with deionized water in ultrasound baths, freeze-dried following homogenization using mortar and pestle, and stored in glass containers until analysis.

All procedures for wildlife handling and sampling were carried out following the Brazilian environmental legislation, under the authorization of the System of Authorization and Information in Biodiversity - SISBIO, Licenses numbers 21693–1 to 21693–9, 66837 and 66088 from the Ministry of the Environment and Natural Resources (IBAMA/ICMBio) of Brazil.

2.2. *Biogeochemical tracer analysis*

Total mercury (Hg) concentrations were quantified in about 0.5 g sub-sample, in duplicate, digested in 10 mL of concentrated HNO_3 in a microwave oven (MARS XPRESS – CEM), 400–800 W at 200 °C for 30 min followed by the addition of 1 mL of H_2O_2 and dilution to 100 mL with ultra-pure water (<3 μS), followed by quantification in a cold vapor atomic absorption spectrophotometer (CV-AAS NIC RA-3). Standard Reference Materials – SRMs were analyzed simultaneously with every sample batch and with certified Hg concentration of 61 ± 3.6 ng g^{-1} (NIST 2976), 610 ± 30 ng g^{-1} (ERM BB422) and 340 ± 40 ng g^{-1} (BCR 060). An overall recovery of 96.3 ± 8.7 % was obtained for Hg concentrations and the detection of limit (LOD), calculated according to USEPA (2000), was 0.34 ng Hg g^{-1}. Elemental (C and N) and isotopic composition ($\delta^{13}C$ and $\delta^{15}N$) were determined by weighing approximately 1 mg of dry sample into tin capsules and analyzing with a continuous-flow isotope-ratio mass spectrometer (Delta V Advantage, Thermo Scientific, Germany) coupled to an elemental analyzer. Results are expressed in the conventional delta (δ) notation relative to Pee Dee Belemnite for $\delta^{13}C$ and atmospheric N_2 for $\delta^{15}N$, according to equation (1).

$$\delta = \left(\left[R_{sample} = R_{standard}\right] - 1\right) \times 1000 \tag{1}$$

where R_{Sample} and $R_{Standard}$ are the corresponding ratios of rare to common isotopes ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) in the sample and international standards, respectively (Peterson and Fry, 1987).

2.3. *Statistical analysis*

Data processing and statistical analyses were performed using R Studio (V. 2022.07.1 Build 554). To examine normality of variables and regression residuals we used a Kolmogorov–Smirnov test. We first grouped our data by species to test for differences in isotopic composition ($\delta^{13}C$ and $\delta^{15}N$) and Hg among sites, for juvenile *C. mydas* (Bahia - BA, Ceara - CE, and Pernambuco - PE) and adult *L. olivacea* (BA and PE), and then, we pooled the data from all sites and grouped it by species and, for *C. caretta,* we also included life stage groups (adults and juveniles). These tests were performed using the non-parametric Kruskal-Wallis (KW) test followed by a post-hoc pairwise comparison using Wilcoxon rank sum exact test, with adjusted p values using Holm correction. Statistical significance was set at 0.05. We tested for correlations between $\delta^{15}N$ and $\delta^{13}C$, as well as these variables with animal size (curved carapace length – CCL) and Hg using Pearson and Spearman tests.

Using the Stable Isotope Bayesian Ellipses (SIBER) package we calculated isotopic niche space metrics (e.g., Total area (TA), standard ellipse area corrected for small sample size (SEAc), and $\delta^{13}C$ and $\delta^{15}N$ ranges) for each species-life stage group (i.e., *C. caretta* adult – Cc_A, *C. caretta* juvenile – Cc_J, *C. mydas* juvenile – Cm_J, *E. imbricata* adult – Ei_A, and *L. olivacea* adult – Lo_A). Overlaps among niches were calculated using the "maxLikOverlap" function (Jackson et al., 2011). Standard ellipses were also constructed using $\delta^{13}C$–Hg and $\delta^{15}N$–Hg pairs to provide complimentary information on species' trophic niches, referred here as contamination niche (Pinzone et al., 2019).

3. Results

3.1. *Biogeochemical tracers (C, N, and hg) description*

The four sea turtle species occurring in the NE coast of Brazil (Fig. 1) presented large variation of $\delta^{15}N$ values, ranging from 5.1‰, in an adult *E. imbricata*, to 15.3‰, in an adult *L. olivacea*, and of $\delta^{13}C$ values, ranging from −20.2‰, in a juvenile *C. mydas*, to −13.7‰, in an adult *E. imbricata* (Table 1 and Fig. 2). Total Hg varied from 3.5 ng g^{-1}, in an adult *E. imbricata*, to 8513.6 ng g^{-1}, in an adult *L. olivacea* (Table 1).

For L. *olivacea,* differences between sites were not significant for $\delta^{15}N$ (Kruskal-Wallis, H = 1.22; df = 1, n = 58, p = 0.27), $\delta^{13}C$ (Kruskal-Wallis, H = 3.8; df = 1, n = 58, p = 0.07), Hg (Kruskal-Wallis, H = 0.159; df = 1, n = 58, p = 0.69), and animal size (CCL) (Kruskal-Wallis, H = 0.019; df = 1, n = 58, p = 0.89) (Table S1). Therefore, we pooled data from both sites for this species. Similarly, for *C. mydas*, we found no differences in $\delta^{13}C$ (Kruskal-Wallis, H = 3.09; df = 2, n = 62, p = 0.213), and Hg (Kruskal-Wallis, H = 4.54; df = 2, n = 33, p = 0.103) (Table S1).

Table 1
Median and interquartile range (IQR) of δ^{13}C and δ^{15}N isotope values, Total Hg, and animal size (curvilinear carapace length) of four sea turtle species occurring in the Northeastern coast of Brazil.

Species	n	size (cm)	δ^{13}C (‰)			δ^{15}N (‰)			Total Hg (ng.g^{-1} dry weight)		
			Median ± IQR	Min	Max	Median ± IQR	Min	Max	Median ± IQR	Min	Max
Caretta (Adult)	18	99.4 ± 4.4	−16.1 ± 1.1	−18.8	−13.8	10.7 ± 4.8	6.3	14.3	124.3 ± 361.5	10.1	1672.0
Caretta (Juvenile)	4	73.4 ± 8.1	−17.7 ± 1.6	−18.6	−14.9	7.2 ± 3.0	5.4	8.8	364.3 ± 82.23	242.7	434.8
Chelonia mydas (Juvenile)	62	38.5 ± 8.5	−17.9 ± 1.9	−20.2	−13.9	9.2 ± 2.1	5.6	11.8	340.2 ± 557.9 (n = 33)	7.8	1244.6
Eretmochelys imbricata (Adult)	44	90.7 ± 4.5	−16.5 ± 0.5	−17.3	−13.7	6.4 ± 1.7	5.1	11.5	10.4 ± 18.1 (n = 42)	3.5	88.6
Lepidochelys olivacea (Adult)	58	70.9 ± 3.5	−18.2 ± 0.9	−19.5	−14.3	9.9 ± 3.2	6.8	15.3	581.8 ± 569.9	39.9	8513.6

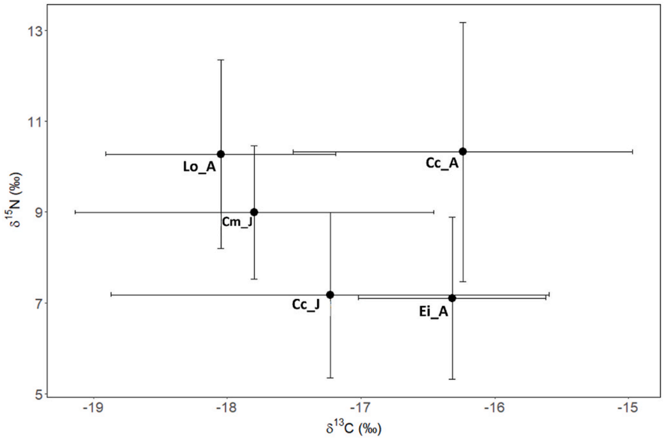

Fig. 2. Isotopic space of sea turtle species in the Northeastern coast of Brazil. Cm_J – Juvenile *Chelonia mydas* (n = 62); Cc_J – Juvenile *Caretta* (n = 4); Cc_A – Adult *Caretta* (n = 18); Ei_A – Adult *Eretmochelys imbricata* (n = 44); Lo_A – Adult *Lepidochelys olivacea* (n = 58).

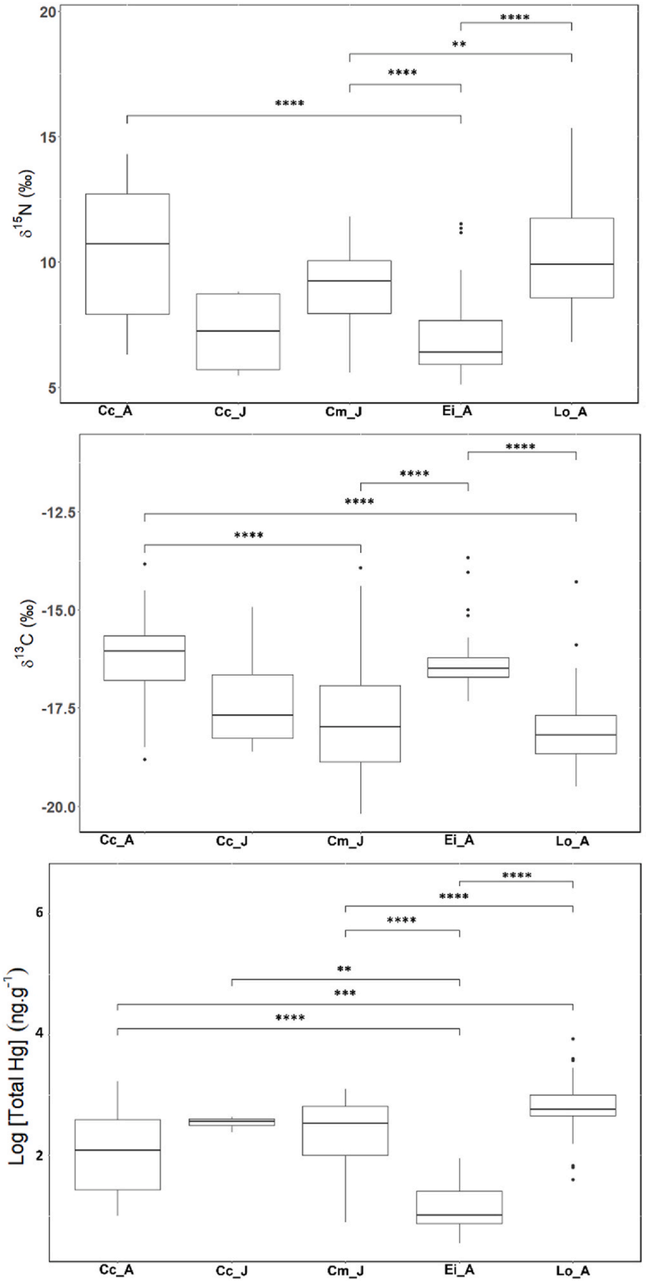

Fig. 3. Variation of biogeochemical tracers (Hg, δ^{13}C, δ^{15}N) in sea turtle species sampled in the in the Northeastern coast of Brazil. **p ≤ 0.01; ***p ≤ 0.001; ****p ≤ 0.0001.

In contrast, animal size (CCL) differed among sites (Kruskal-Wallis, H = 10.5; df = 2, n = 62, p = 0.005) and was larger in PE compared to BA and CE (Post-hoc Wilcoxon rank p = 0.006). δ^{15}N values also differed among sites (Kruskal-Wallis, H = 8.67; df = 2, n = 62, p = 0.01) and it was lower in PE compared to BA (Post-hoc Wilcoxon rank p = 0.021) but not different than CE (p = 0.190), while BA and CE did not differ (p = 0.06) (Table S1). Considering that geographical distances among sites are within the distribution range of these populations we pooled data from all sites and examined variations among species and life stages (for *C caretta* only).

Median δ^{15}N values and interquartile range (IQR) of *C. mydas, E. imbricata,* and *L. olivacea* were 9.2 ± 2.1‰; 6.4 ± 1.7‰; and 9.9 ± 3.2‰, respectively. Median values and IQR of *C. caretta* adult and juvenile individuals were 10.7 ± 4.8‰ and 7.2 ± 3.0‰. Values for δ^{15}N differed significantly among groups (Kruskal-Wallis, H = 57.3; df = 4, n = 186, p < 0.001), and was lower in *E. imbricata* compared to all other groups (Post hoc Wilcoxon, p < 0.001), except *C. caretta* juvenile group (p = 1) (Fig. 3). Values for δ^{15}N were significantly higher in *L. olivacea* compared to *C. mydas* (Post hoc Wilcoxon, p = 0.01), and no difference was found between *C. caretta* (both groups) and *C. mydas* (Post hoc Wilcoxon, p > 0.21), and between *C. caretta* (both groups) and *L. olivacea* (Post hoc Wilcoxon, p > 0.10) (Fig. 3). Values for δ^{15}N did not differ between juvenile and adults of *C. caretta* (Post hoc Wilcoxon, p = 0.38).

Median and IQR values for *C. mydas, E. imbricata,* and *L. olivacea* were −16.5 ± 0.5‰; −18.2 ± 0.9‰ and −18.0 ± 0.9‰, respectively. Median values and IQR of *C. caretta* adult and juvenile individuals were −16.1 ± 1.1‰ and −17.7 ± 1.6‰, respectively. Values for δ^{13}C differed significantly among groups (Kruskal- Wallis, H = 71.3; df = 4, n = 186, p < 0.001) (Fig. 3). Pairwise comparisons showed that δ^{13}C values in adult and juvenile individuals of *C. caretta* did not differ (p = 1), and *L. olivacea* and *C. mydas* presented δ^{13}C values significantly lower compared to *E. imbricata* (Post hoc Wilcoxon, p < 0.001). Values for δ^{13}C did not differ between *C. caretta* (both groups) and *E. imbricata* (p > 0.58), and between *L. olivacea and C. mydas* (p = 0.82), while δ^{13}C values in *C. caretta* (adult) were significantly higher compared to *C. mydas* ($p < 0.001$) and *L. olivacea* ($p < 0.001$) (Fig. 3).

Total Hg, in the present study, is being used as biogeochemical tracer to help understanding trophic ecology of the studied sea turtles. Therefore, only Hg levels of individuals with stable isotope measurements were included. Refer to Barrios-rodriguez et al. (2024) for a detailed discussion of Hg contamination in sea turtles from our study area. Median and IQR values of *C. mydas*, *E. imbricata,* and *L. olivacea* were 340.2 ± 557.9 ng g^{-1}; 10.4 ± 18.1 ng g^{-1}; and 581.8 ± 569.9 ng g^{-1}, respectively (Table 1). Total Hg concentrations differed significantly among groups (Kruskal- Wallis, $H = 96.9$; $df = 4$, $n = 155$, $p < 0.001$) (Fig. 3). Pairwise comparisons showed that Total Hg concentrations in adult and juvenile individuals of *C. caretta* did not differ (Post hoc Wilcoxon, $p = 0.66$), and these two groups are not different than *C. mydas* ($p = 0.70$). *L. olivacea* presented the highest Hg concentrations ($p < 0.001$) among all groups, except compared to *C. caretta* juvenile ($p = 0.09$). *E. imbricata* presented the lowest Hg concentrations ($p < 0.01$) among all groups.

We observed a weak, but significant, correlation between δ^{13}C and δ^{15}N values for *E. imbricata* ($t = 4.7$, $df = 42$, p-value <0.001, $r = 0.58$), and *L. olivacea* ($t = 3.4$, $df = 56$, p-value $= 0.001$, $r = 0.42$) (Fig. S1). For all other groups no significant correlation between these variables was observed. A moderate and significant correlation between δ^{15}N and animal size was observed for *L. olivacea* only ($t = 3.8$, $df = 56$, p-value <0.001, $r = 0.46$) (Fig. S2). Weak significant correlations between δ^{13}C and animal size were observed for *C. mydas* ($t = 2.6$, $df = 60$, p-value $= 0.012$, $r = 0.32$), and *L. olivacea* ($t = 2.4$, $df = 56$, p-value $= 0.019$, $r = 0.31$) (Fig. S2). For L. *olivacea* the correlation between these variables was weak, but significant, and positive ($t = 2.15$, $df = 56$, p-value $= 0.036$, $r = 0.28$). A moderate significant and positive correlation between δ^{15}N and Hg was observed for *L. olivacea* only ($t = 5.4623$, $df = 56$, p-value <0.001, $r = 0.59$) (Fig. S3). Similarly, a significant and positive correlation between δ^{13}C and Hg was observed for *L. olivacea* only ($t = 2.23$, $df = 56$, p-value $= 0.02$, $r = 0.28$) (Fig. S3).

3.2. Isotopic and contamination niches variation

Sea turtle species inhabiting the NE coast of Brazil differed on niche width of isotopic and contamination niches. Adult Individuals of *C. caretta* presented the largest SEAc in all estimation models (δ^{13}C vs δ^{15}N; Hg vs δ^{15}N; Hg vs δ^{13}C; Table S2). In general, SEAc presented the following decreasing order: *C. caretta* > *C. mydas* > *L. olivacea* > *E. imbricata,* in all models. The exception was for the SEAc (Hg vs δ^{15}N and Hg vs δ^{13}C models) of juvenile individuals of *C. caretta* that presented the smallest areas (Table S2). Overlap of isotopic niches were high between *E. imbricata* and *C. caretta* species and between *C. mydas* and *C. caretta*. The isotopic niche of *E. imbricata* presented 58.9% and 32.4% overlap with the isotopic niches of juvenile and adult *C. caretta* individuals, respectively (Fig. 4). The isotopic and contamination niches of *C. mydas* overlapped by 15.2%, 93.3% and 91.1% with *C. caretta* niches in the δ^{13}C vs δ^{15}N, Hg vs δ^{15}N and Hg vs δ^{13}C models, respectively (Fig. 4). In contrast, contamination niches of *E. imbricata* were completely disassociated from contamination niches of all other sea turtle species. The exception was a small (5.7%) overlap with the contamination niche of adult *C caretta* individuals (Hg vs δ^{13}C model) (Fig. 4). The isotopic niche and contamination niches of *L. olivacea* overlapped largely with those of *C. mydas* in all estimation models. Overlapping areas between these species represented 52.5%, 43%, and 58.1% of *L. olivacea* niches in the δ^{13}C vs δ^{15}N, Hg vs N and Hg vs δ^{13}C models, respectively.

4. Discussion

In general, isotopic composition and Hg concentration in scute samples can integrate a long-term record of diet and foraging habitat of sea turtles (from at least 0.8 years in juvenile individuals to a maximum of 6.5 years in adult individuals) (Barrios-Rodríguez et al., 2023; López-Castro et al., 2014; Vander Zanden et al., 2013). However, these diet records vary with depth of keratin layer and scute location in the carapace (e.g., Central region vs. Lateral region) for *C. mydas* and *C. caretta* (López-Castro et al., 2013; Reich et al., 2007), and *E. imbricata* (Houtan et al., 2023), with superficial layers representing older records

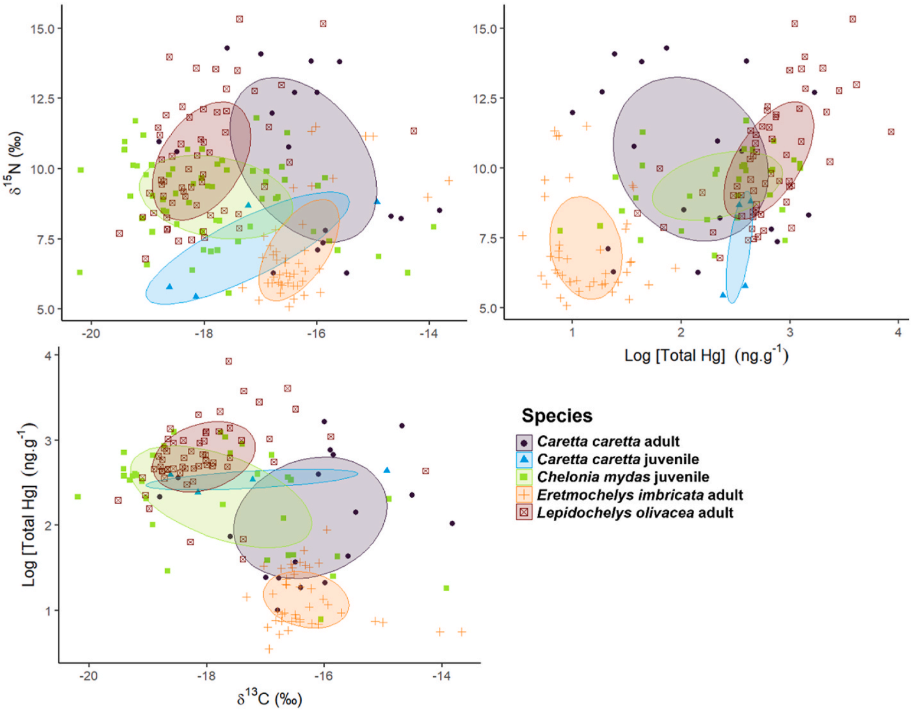

Fig. 4. Isotopic niche (δ^{15}N vs. δ^{13}C) and contamination niches (Hg vs. δ^{15}N and Hg vs. δ^{13}C) of sea turtle species from the Northeastern coast of Brazil.

compared to deeper layers. Therefore, to reduce this variability is important that scute sampling is standardized.

In the present study, we collected the majority of scute samples opportunistically by scrapping the superficial layers of the lateral region of the carapace, therefore our results integrate the older diet record of individuals rather than the most recent. However, because of the uneven sloughing of superficial carapace material among individuals (López-Castro et al., 2014; Vander Zanden et al., 2013), these records might not represent the same time period for all sampled individuals which contributes to the variability observed in the estimation niche models.

Many studies have described the isotopic composition and/or Hg concentrations of sea turtle species from the Southwest Atlantic Ocean (Agostinho et al., 2021; Bezerra et al., 2015; Di Beneditto et al., 2017, 2019; Gama et al., 2021; Medeiros et al., 2019; Rodriguez et al., 2020b) demonstrating the importance of this region as foraging grounds of multiple sea turtle species. In contrast, only recently researchers have described the trophic niche of sympatric sea turtle species using biogeochemical tracers (Chandelier et al., 2023; Clyde-Brockway et al., 2022; Figgener et al., 2019; Moorehouse et al., 2023; Silver-Gorges et al., 2023; Weber et al., 2023), and only a few focusing in populations from the NE of Brazil in the Western South Atlantic Ocean (Filippos et al., 2021; Soares et al., 2021). The niche area, estimated using SEAc, represents the breadth of foraging in sympatric sea turtle species and is influenced by differences in diet and habitat use of each species, as well as food-web diversity and habitat isotopic composition and environmental Hg concentrations.

Adult individuals of *C. caretta* presented the widest niche in all estimation models reflecting their generalist feeding behavior. A similar behavior was also reported by Vander Zanden et al. (2010) in a group of adult *C. caretta* individuals from the North Atlantic. The isotopic niche model for this species presented a wide range of δ^{13}C and δ^{15}N values (Fig. 4). *C. caretta* individuals nesting in Brazil have been shown to migrate from and to multiple foraging habitats along the northeastern coast of Brazil (Marcovaldi et al., 2010). These authors have found that all studied nesting adults would travel thousands of kilometers across multiple suitable habitats until arriving in a chosen area and staying for over a year or until the next nesting migration (Marcovaldi et al., 2010). Assuming that individuals are constantly feeding during these migrations it is plausible that they incorporate the isotopic signature of prey from the multiple sites, as well as their chosen long-term foraging site which would produce the observed large variation and wide niche. This interpretation is corroborated by the large variation in Hg concentrations in this group which could reflect the spatial variability of Hg accumulation in the biota along the Brazilian coast (Costa et al., 2012). In contrast, smaller contamination niche areas were observed for juvenile individuals of *C. caretta* which is a result of the low variability in Hg concentrations in this group (Table 1 and Fig. 3) and is consistent with individuals feeding on prey from the same foraging site.

Isotopic niche of juvenile *C. caretta* presented a small overlap (19.3%) with adult individuals of the same species. That could reflect the difference in feeding strategies between these groups. The lower, but non-significant, δ^{15}N in juveniles compared to adults seems to confirm that in this area juveniles feed at lower trophic levels, as previously suggested for populations in Brazilian areas (Bugoni et al., 2003; Medeiros et al., 2019). In contrast, we observed, for several adult individuals, δ^{15}N values in the same range of juveniles (Fig. 4), but the overall range in δ^{15}N were larger in adults compared to juveniles which suggest the former can feed on preys at multiple trophic levels (Medeiros et al., 2019). The absence of differences in δ^{13}C between these reflect the large variability of δ^{13}C values seems to suggest the utilization of areas with multiple carbon sources for both juvenile and adults. Values of δ^{13}C in foraging grounds located offshore can be lower compared to nearshore coastal areas (Costa et al., 2020; Michener and Kaufman, 2007). Alternatively, δ^{13}C-depleted values, as observed in most juvenile individuals, can also suggest feeding in a macroalgae-based food-web, which is a characteristic of coastal areas in the States of Bahia and Ceará, where these juveniles were sampled (Bezerra et al., 2015). The estimated recruitment size for juveniles in the southern Brazilian coast range from 55.7 to 77.9 cm of curvilinear carapace length (Monteiro, 2017), thus classifying the individuals from the present study as recently transitioning from oceanic to neritic coastal areas which explain the large variability in δ^{13}C.

It is worth noting that the juvenile *C. caretta* group in the present study is composed of only four individuals and, thus, might not reflect the isotopic and Hg variability in this population. Juvenile and adult *C. caretta* individuals inhabit neritic habitats and forage on benthic organisms, including mollusks, crustaceans and coelenterates, and even small proportions of fish (Medeiros et al., 2019; Palmer et al., 2021). Such variation in trophic level of prey characterizes these animals as trophic generalist and explains the large range of δ^{15}N values, and Hg concentrations observed in the present study. Regarding the δ^{13}C values for this species, variation in baseline isotopic composition is likely the most important factor explaining the observed large variation. Nesting *C. caretta* in this region migrate to and from multiple foraging grounds along the northeastern and southern Brazilian coast and, thus, spatial variation in baseline isotopic values is likely substantial (Soares et al., 2021). The same large variation was also observed for *L. olivacea* which also originates from multiple foraging grounds with different isotopic baseline composition (Echevenguá et al., 2023; Petitet and Bugoni, 2017).

The positive correlation of δ^{15}N with CCL (Fig. S2), observed in *L. olivacea*, is consistent with a shift in foraging behavior associated with animal growth. Larger individuals of this species seem to be feeding on prey with higher trophic levels, which is also associated with an increased incorporation and accumulation of Hg, as suggested by the observed positive correlation between δ^{15}N and Hg (Fig. S3). Similarly, ontogenetic shifts in foraging habitat also seem to be occurring in these nesting *L. olivacea* individuals, as indicated by the significant correlation between δ^{13}C and CCL (Fig. S3). We found that larger individuals presented enriched δ^{13}C values compared to smaller individuals, which could be an indication of a shift towards coastal habitats presenting enriched δ^{13}C carbon sources (e.g., POM) compared to oceanic habitats (Figueiredo et al., 2020). This shift towards coastal habitats is followed by an increase in trophic levels of prey as suggested by the positive correlation between δ^{13}C and δ^{15}N observed in *L olivacea*, as well as in *E. imbricata*. Similar results was observed in freshwater turtles where the positive correlation between δ^{13}C and δ^{15}N was interpreted as supporting the use of multiple foraging habitats with different carbon sources (Hopkins et al., 2013). In contrast, Vacca et al. (2023) have shown that, for a neritic population of *C. mydas*, the shift towards coastal foraging habitats (enriched δ^{13}C carbon sources) were followed by a decrease in δ^{15}N values, which reflects the well-known process of shifting from an oceanic-omnivorous to coastal-herbivorous diet in this species. A similar relationship was also observed in the present study, although the relationship between δ^{13}C and δ^{15}N in *C. mydas* was marginally non-significant ($p = 0.054$; Fig. S1).

The isotopic niche of adult individuals of *E. imbricata* presented the smallest areas compared to other species (Table S1). Contamination niches for this species were also the smallest when comparing juvenile and adults of each sea turtle species. This result is in agreement with a specialized diet commonly reported for this species, consisting mostly of sponges and small proportions of animal and plant matter (Carneiro-Proietti et al., 2012; Martins et al., 2020). In addition, the narrow range, and relatively low levels of Hg observed for *E. imbricata* can indicate high selectivity of prey and a diet composed of low trophic level organisms.

There is no information regarding foraging area location of adult individuals of *E. imbricata* in Brazil (Marcovaldi et al., 2012) and the relatively small niche areas observed in the present study might indicate a single (or spatially restricted) foraging ground for the majority of sampled individuals. Satellite-tracking of nesting *E. imbricata* in Brazil suggests that these individuals migrate short distances from breeding grounds to potential foraging areas located along the eastern coast of Brazil within coastal reef ecosystems (Marcovaldi et al., 2012). *E. imbricata* presented the highest δ^{13}C values which suggest foraging in nearshore/coastal areas (Riccialdelli et al., 2010). The observed smaller isotopic and contamination niches can also be a result of small home ranges which has been reported previously for adult *E. imbricata* individuals from the same area (Marcovaldi et al., 2012). Adult *E. imbricata* individuals presented no overlap with *L. olivacea* and juvenile *C. mydas* individuals in all estimation models which is also in agreement with feeding nearshore rather than offshore and oceanic foraging grounds (Da Silva et al., 2011; Di Beneditto et al., 2019; Petitet and Bugoni, 2017). The absence of trophic niche overlap between *E. Imbricata* and *C. mydas* has been documented previously in a trophic niche study using stomach content analysis (Martins et al., 2020).

Niche areas of juvenile individuals of *C. mydas* largely overlapped with adult individuals of *L. olivacea* in all estimation models (Fig. 4). The isotopic niche of *L. olivacea* in the present study is characteristic of a population with an oceanic habitat, but the large variability among individuals suggests that neritic habitats are also important for part of this population. Previous studies have shown that *L. olivacea* can travel thousands of kilometers to their nesting site and that this population in particular is composed of individuals foraging in areas of northeast Brazil (State of Maranhão), southeast Brazil (States of Rio de Janeiro, São Paulo, Paraná, and Santa Catarina), and, across the Atlantic Ocean, off the coast of multiple West Africa countries (Da Silva et al., 2011; Santos et al., 2019). Petitet and Bugoni (2017) estimated a greater contribution of demersal fishes for the isotopic signature of a *L. olivacea* nesting population from the same area, which explain most individuals in the present study presenting high δ^{15}N and low δ^{13}C values (Fig. 4). In general, *L. olivacea* diet is composed of benthic fish and crustaceans (Colman et al., 2014), but diet plasticity occurs especially in nesting populations (Petitet and Bugoni, 2017). The overlap of isotopic and contamination niches of *L. olivacea* nesting population with juvenile individuals of *C. mydas* in the present study suggests these groups can feed in the same foraging habitat at some point of each species life cycle, potentially sharing prey resources.

Juvenile individuals of *C. mydas* are known to feed on oceanic areas before recruiting to the neritic habitat nearshore (Reich et al., 2007; Villa et al., 2017). The recruitment to coastal populations in the Southern Atlantic Ocean, occurs at around 30 cm–40 cm of body size (Arthur et al., 2008; Lenz et al., 2017; Reich et al., 2007). This suggests the population sampled in the present study has recently shifted from oceanic to coastal habitats. The exception would be the four individuals sampled in Pernambuco which have an average body size of 60 cm, and thus are considered long-term residents of the neritic habitat. That would explain the wide variation in isotopic composition and relatively large isotopic and contamination niche areas, as some individuals can still present the oceanic signature (e.g., δ^{13}C-depleted, and δ^{15}N-enriched values) while others reflect the isotopic composition and Hg accumulation from coastal foraging. We found some individuals of *C. mydas* presenting δ^{13}C-depleted (<-19‰) values suggesting the feeding on macroalgae-based food webs which has been previously reported for the same population (Bezerra et al., 2015). Alternatively, low δ^{13}C values can also reflect foraging at adjacent oceanic areas as isotopic signatures of particulate organic matter and zooplankton are very carbon depleted (Figueiredo et al., 2020). López-Castro et al. (2013) have shown that neritic *C. mydas* populations from other areas in the Western Atlantic Ocean have connections with multiple oceanic habitats prior to recruiting to coastal areas which explain the mixed isotopic signatures found in the present study for this species.

High values of dietary overlap within a guild of sympatric predators would suggest that prey are not a limiting factor in the environment (Vaudo and Heithaus, 2011). Non-overlapping ellipses between sympatric species suggest the presence of resource partitioning between those species either in basal resources supporting diets, foraging locations or specific prey (e.g., Burkholder et al., 2011; Matich et al., 2011). However, the presence of overlapping ellipses does not necessarily suggest shared patterns of resource use between species. In the case of complex habitats with multiple carbon sources and many available prey resources, multiple distinct patterns of resource consumption can result in similar stable isotope signatures (Matich et al., 2011).

Our results provide a detailed overview of trophic niches of sympatric sea turtle species sharing and/or partitioning the same habitat. We found that adult individuals of *L. olivacea* had similar isotopic signatures to juvenile individuals of *C. mydas*, suggesting these species share the same habitat during different stages of their life cycle. Although sharing the same habitat, we found that these species are not competing for food resources because they are clearly feeding on different prey as evidenced by the separated contamination niches and much greater Hg concentration in *L. olivacea* compared to *C. mydas*. Another important finding is the complete separation of *E. imbricata* trophic niche from all other studied species. These adult individuals feed very low in the food web and in coastal habitats not utilized by juvenile *C. mydas* and *C. caretta* individuals or adult *L. olivacea* and *C. caretta* individuals. In addition, the contamination niches of *E. imbricata* corroborate the idea of these individuals utilizing unique habitats with little contamination of Hg. Finally, the distinct isotopic and contamination niches between juvenile and adult *C. caretta* individuals is another evidence of the ontogenetic shift in habitat and diet composition previously reported for this species.

4.1. Limitations and recommendations

Comparisons of isotopic values between different sea turtle species can be challenging due to differences in tissue-prey isotopic discrimination factor (TDF). The trophic discrimination factor represents the isotopic difference between prey and the consumer's tissue and is reported to be associated with life stage, tissue type, and species (Vander Zanden et al., 2012). The commonly accepted TDF for carbon ranges from 0 to 1‰ (DeNiro and Epstein, 1978; Peterson and Fry, 1987), while for nitrogen the value of 3.4‰ is more commonly used (Post, 2002). Sea turtle specific TDFs have been estimated for different tissues in *C. mydas* and ranges from -0.38‰ to 1.77‰ for carbon, and -0.64‰–1.60‰ for nitrogen (Reich et al., 2008), In another study, the estimated TDF for skin tissue of *C. mydas* was 0.17 ± 0.03‰ and 2.80 ± 0.11‰ for carbon and nitrogen, respectively (Seminoff et al., 2006). For *C. caretta* the estimated TDF for scute was 1.77 ± 0.58‰ and 1.65 ± 0.12‰ for carbon and nitrogen, respectively (Reich et al., 2008). Therefore, TDF variation can confound the interpretation of isotopic differences across species. In the present study, the observed differences in isotopic composition were most of the time larger than reported TDFs for sea turtles which support the ecological relevance of our results.

The lack of baseline data for stable isotopes in primary producers across our study area certainly limits our interpretations of isotopic niche differences among species. This information is key to understand how much of isotopic variation reflects trophic niche of sea turtles, and not spatial variation in isotopic composition. In compiled database of isotope data from Brazilian coastal marine areas, isotope values of multiple macroalgae species from selected sites within our study area (lat. Long. ~2°S ~40°W to ~13°S ~38°W) vary from -30.7‰ to -5.7‰ (-17.3 ± 4.7‰) for δ^{13}C, and from 2.7‰ to 9.0‰ (5.3 ± 1.8) for δ^{15}N. Therefore, we recommend that future studies include isotope composition of primary producers to help disentangling factors that contribute to isotopic niche of sea turtles.

CRediT authorship contribution statement

Moises F. Bezerra: Writing – original draft. **Cesar A. Barrios-Rodriguez:** Writing – review & editing, Investigation, Formal analysis. **Carlos E. Rezende:** Writing – review & editing, Resources, Methodology. **Melania C. López-Castro:** Writing – review & editing, Data curation. **Luiz D. Lacerda:** Writing – review & editing, Validation, Resources.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2024.106406.

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