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Foraging ecology of the critically endangered hawksbill sea turtle in the Gulf of Guinea

Sara Vieira [a,b,c,*], Betânia Ferreira-Airaud [a,b,c], Vânia Baptista [b], Manjula Tiwari [d], Rita Castilho [b,c,e], Maria A. Teodósio [b,c]

[a] Associação Programa Tatô, Avenida Marginal 12 de Julho, Ilha de São Tomé, Cidade de São Tomé, Democratic Republic of Sao Tome and Principe
[b] Centro de Ciências do Mar (CCMAR), Universidade do Algarve, Campus de Gambelas, Faro, 8005-139, Portugal
[c] Universidade do Algarve, Campus de Gambelas, Faro, 8005-139, Portugal
[d] Ocean Ecology Network, California, USA
[e] Pattern Institute, Faro, 8005-222, Portugal

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ABSTRACT

Understanding the ecological roles of critically endangered species is essential for effective conservation planning. This study investigates the foraging ecology and nutritional condition of the hawksbill sea turtle (*Eretmochelys imbricata*) in São Tomé Island, a key foraging ground in the Gulf of Guinea. We integrated stable isotope analyses of epidermal tissues with RNA/DNA ratios to assess habitat use, trophic position, and physiological status across life stages. Thirty hawksbill turtles (juveniles and adults) were sampled during in-water surveys conducted between 2021 and 2022 using minimally invasive techniques. Prey samples were also collected for isotopic baselines.

Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) values revealed significant ontogenetic shifts, with adults occupying broader isotopic niches. While sponges remained the dominant food source at both stages, adults exhibited greater dietary diversity, including red algae and tunicates. Juveniles showed higher spatial and temporal fidelity, suggesting stronger residency patterns. Estimated trophic positions ranged from 2.57 to 2.79, consistent with secondary consumers. RNA/DNA ratios indicated higher metabolic activity in juveniles and males, while lower values in females likely reflect reproductive metabolic suppression.

These findings represent the first integrative assessment of hawksbill turtle foraging and nutritional condition in the region. The study provides critical baseline data on one of the most genetically isolated and endangered hawksbill populations worldwide. This approach enhances understanding of their ecological function and supports the development of targeted conservation actions that account for life-stage–specific needs, contributing to adaptive management and long-term recovery of this critically endangered population.

1. Introduction

In recent decades, large marine vertebrates have experienced severe population declines, often exceeding 50%, due to cumulative anthropogenic pressures (McCauley et al., 2015). Conservation efforts for these species are particularly challenging due to their wide distribution ranges, complex life stage traits, and exposure to multiple human-induced threats (Sequeira et al., 2019). Despite their high mobility, many species predictably aggregate in specific areas during key life stages for foraging, breeding, and/or nesting. These aggregation sites may be shaped by dynamic oceanographic processes or correspond to fixed coastal features that provide critical ecological functions (Sequeira et al., 2025; Shimada et al., 2021; Siegwalt et al., 2020).

Among marine vertebrates, sea turtles are highly migratory species that spend most of their lives at sea, undertaking movements related to foraging, mating, and long-distance migration. While nesting sites have traditionally received the greatest conservation attention due to their strong site fidelity (Siegwalt et al., 2020), growing evidence indicates that individuals also exhibit long-term fidelity to foraging grounds (Shimada et al., 2021). As such, the protection of these habitats is

* Corresponding author. Associação Programa Tatô, Avenida Marginal 12 de Julho, Ilha de São Tomé, Cidade de São Tomé, Democratic Republic of Sao Tome and Principe.
E-mail address: saralexvieira@gmail.com (S. Vieira).

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increasingly recognized as essential to support conservation across all life stages (Dalleau et al., 2019; Dunbar et al., 2025).

Among the most threatened sea turtle species, the hawksbill turtle (*Eretmochelys imbricata*) has experienced an estimated 80% decline in global nesting abundance over the last century and is classified as Critically Endangered by the IUCN Red List (Meylan and Donnelly, 1999; Mortimer and Donnelly, 2008). In West Africa, the Eastern Atlantic population is considered one of the ten most endangered Regional Management Units (RMUs) worldwide (Wallace et al., 2025), highlighting the urgent need for detailed ecological research to inform conservation strategies. São Tomé and Príncipe host the last significant nesting aggregation in the region (Wallace et al., 2025; Ferreira-Airaud et al., 2024), comprising a genetically distinct and isolated population with low genetic diversity and heightened vulnerability (Monzón-Argüello et al., 2010, 2011). Recent estimates suggest that only 170 to 300 female hawksbills nest across both islands, with approximately 70% of nesting activity occurring on São Tomé (Ferreira-Airaud et al., 2024). Although legal protection was establish 2014, historical exploitation for their meat, eggs, and shell products has contributed substantially to the population' severe decline, and ongoing threats such as illegal harvesting and bycatch remain a concern (Ferreira-Airaud et al., 2022; Vieira et al., 2024).

Hawksbill turtles are widely distributed across tropical coastal waters and play a key ecological role in coral reef ecosystems, particularly through their feeding behavior. By selectively consuming reef-associated sponges, they influence benthic community structure and contribute to maintaining coral reef resilience (León and Bjorndal, 2002). Although traditionally considered dietary specialists, hawksbills are increasingly recognized as opportunistic feeders, consuming a variety of other organisms such as tunicates, bryozoans, mollusks, corals, and algae (León and Bjorndal, 2002; Baumbach et al., 2022; Berube et al., 2012; Carrión-Cortez et al., 2013; Meylan, 1988), suggesting that their foraging may be both directed and opportunistic. Understanding the trophic role of this species within coastal food webs is therefore essential to anticipate ecosystem responses to ongoing environmental pressures (León and Bjorndal, 2002).

Stable isotope analysis (SIA) is a widely used ecological tool that provides time-integrated insights into diet and habitat use through the measurement of naturally occurring stable isotope ratios, particularly nitrogen ($^{15}N/^{14}N$, reported as $\delta^{15}N$) and carbon ($^{13}C/^{12}C$, reported as $\delta^{13}C$) values relative to standard references. It is commonly applied to assess diet composition (Reynolds et al., 2023) and to quantify isotopic niches of sea turtles (Newsome et al., 2007). The isotopic niche is widely used as a proxy for the ecological niche, as $\delta^{13}C$ and $\delta^{15}N$ values provide an integrated representation of resource and habitat use. $\delta^{13}C$ values are typically used to infer sources of primary production and to distinguish among foraging habitats (e.g. inshore versus offshore or benthic versus pelagic systems), whereas $\delta^{15}N$ values increase predictably with trophic level, allowing estimation of an organism's relative position within the food web. However, these values can vary with environmental and spatial baseline conditions, particularly in tropical coastal areas, potentially complicating the interpretation of trophic relationship and leading to inaccurate inferences if not properly accounted for (Newsome et al., 2007). When analyzed together, $\delta^{13}C$ and $\delta^{15}N$ values provide a robust framework for characterizing isotopic niches and investigating trophic interactions and habitat use in marine organisms, including sea turtles (Reynolds et al., 2023; Newsome et al., 2007). Previous stable isotope studies have documented ontogenetic differences in isotopic niches in hawksbill turtles, including clear segregation between juvenile and adult individuals in West Africa (Ferreira et al., 2018), while broader analyses highlight dietary plasticity and trophic variability across life stages (Ramirez et al., 2023). In addition to SIA, monitoring an individual's nutritional condition can provide short-term insights into recent feeding activity within a study area. Biochemical indices such as the standardized RNA/DNA ratio (sRD) have proven effective in evaluating nutritional status, growth potential, and the overall physiological condition in marine organisms, including sea turtles and other species of marine megafauna (Alves et al., 2020; Chícharo and Chícharo, 2008; Vieira et al., 2014). The sRD is based on the principle that although DNA content remains relatively stable, RNA levels fluctuate with protein synthesis, thereby allowing the detection of recent feeding events over short time scales, often on the order of days, depending on species and environmental conditions (Chícharo and Chícharo, 2008). This approach has been applied across a range of marine taxa, including invertebrates and vertebrates such as fish, marine mammals, and sea turtles (Alves et al., 2020; Vieira et al., 2014; Morais et al., 2015; Meyer et al., 2012a). The sRD is influenced by developmental stage and is known to be species-specific (Chícharo and Chícharo, 2008).

Despite the ecological importance of hawksbill sea turtles in the Gulf of Guinea, in-water ecological studies in the region remain scarce (Ferreira-Airaud et al., 2022). To date, only one study has been conducted in São Tomé and Príncipe, revealing isotopic niche segregation between juvenile and adult hawksbills on Príncipe Island (Ferreira et al., 2018). However, no similar efforts have been made on São Tomé Island, even though its surrounding waters are known to be inhabited by juveniles, adults, and sub-adults year-round (Ferreira-Airaud et al., 2022). Given potential differences in habitat characteristics and resource availability between the islands, investigating foraging ecology in São Tomé may provide further insight into ontogenetic shifts and habitat use in this population.

This study aims to investigate how habitat use, trophic ecology, and nutritional condition vary across life stages in hawksbill sea turtles from São Tomé Island using an integrative approach combining in-water capture data, SIA and RNA/DNA ratios. Juvenile turtles inhabiting shallow coastal zones are generally considered residents, whereas adults occurring in the same areas may represent a mixture of resident and migratory individuals. Consequently, potential habitat and dietary partitioning between life stages is expected and can be inferred from their isotopic signatures. To investigate these ecological dynamics, this study employs SIA, a powerful method for reconstructing short-term dietary patterns and estimating trophic position by examining carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) values (Haywood et al., 2019). In addition to assessing potential dietary shifts and trophic levels between juvenile and adult hawksbill turtles, we also evaluate the nutritional condition of individuals using the sRD. By integrating isotopic and biochemical indicators, this study provides new insights into the ecological strategies of this critically endangered population. These findings establish acritical baseline for addressing key knowledge gaps and supporting evidence-based conservation strategies aimed at promoting population recovery.

2. Materials and methods

2.1. Study area

São Tomé and Príncipe is a small equatorial island nation in the Gulf of Guinea (0.263584° N, 6.602234° E), composed of two main volcanic islands, São Tomé (857 km^2) and Príncipe (139 km^2), and several smaller islets (Ceríaco et al., 2022). Part of the Cameroon Volcanic Line, the archipelago lies in an oligotrophic oceanic zone, with São Tomé hosting about 96% of the country's 215,000 inhabitants (Morais et al., 2015). Its narrow continental shelf spans roughly 450 km^2 above the 200 m isobath and supports a mosaic of coastal habitats, including rocky reefs, rhodolith beds, macroalgae, and seagrass meadows. Shallow shelves characterize the northeastern coast of São Tomé, whereas the southern coast is deeper and more exposed to wave action. The climate alternates between a long rainy season (September–May, with a short dry spell in December–January) and a dry, cooler season known locally as "Gravana" (June–August), shaped by the Inter-Tropical Convergence Zone (Ceríaco et al., 2022).

One sampling site was selected based on prior studies and its inclusion in the long-term capture-mark-recapture program developed by

Programa Tatô (Ferreira-Airaud et al., 2022) (Fig. 1). This site, located between the southern coast of São Tomé Island and Rolas Islet, consists of rocky reefs and platforms covered with macroalgae, primarily *Polysiphonia* spp. and *Dyctiota* spp. (Hancock et al., 2018).

2.2. In-water surveys

In 2017, Programa Tatô, a local non-governmental organization, initiated a long-term in-water tagging and recapture program to monitor sea turtle foraging habitats. The present study used data collected through this program between February 2018 and June 2025. Weekly snorkel-based surveys of consistent duration (3-4 h) were conducted in the sampling site, with the GPS location of each turtle sighting recorded using a handheld device. Individuals were visually detected by experienced observers and manually captured by free-diving during daylight hours, typically when observed resting beneath rocky ledges or feeding on the seabed (Hancock et al., 2018).

Upon capture, the minimum curved carapace length (CCL_{min}; notch to notch) of each sea turtle was measured using a flexible measuring tape to the nearest 0.1 cm, following the protocol outlined by Bolten (Bolten et al., 1999). Inconel tags (National & Tag Co., Style 681) were applied to both front flippers, and tag numbers were recorded for all previously marked individuals. GPS coordinates of each capture location were recorded to support the analysis of spatial and temporal patterns. A subset of captured turtles was subsequently sampled for SIA and sRD, as described in Section 2.3. After data and sample collection, turtles were released at their original capture sites.

Underwater habitat mapping was carried out between November 2020 and March 2021, down to a maximum depth of 25 m, using a combination of in situ freediving surveys and satellite imagery analysis, as outlined in Cowburn (2018). Data were collected along predefined transects at 5 depth intervals (5, 10, 15, 20, and 25 m), resulting in 290 sampling points. At each point, a ~10 m diameter section of the seabed was filmed using a GoPro 12, and the substrate was later classified into one of four categories: Sand, Rhodoliths, Rock, or Coral. Habitat classifications were refined by integrating field observations, satellite data, and local ecological knowledge, and final habitat units were manually mapped in QGIS.

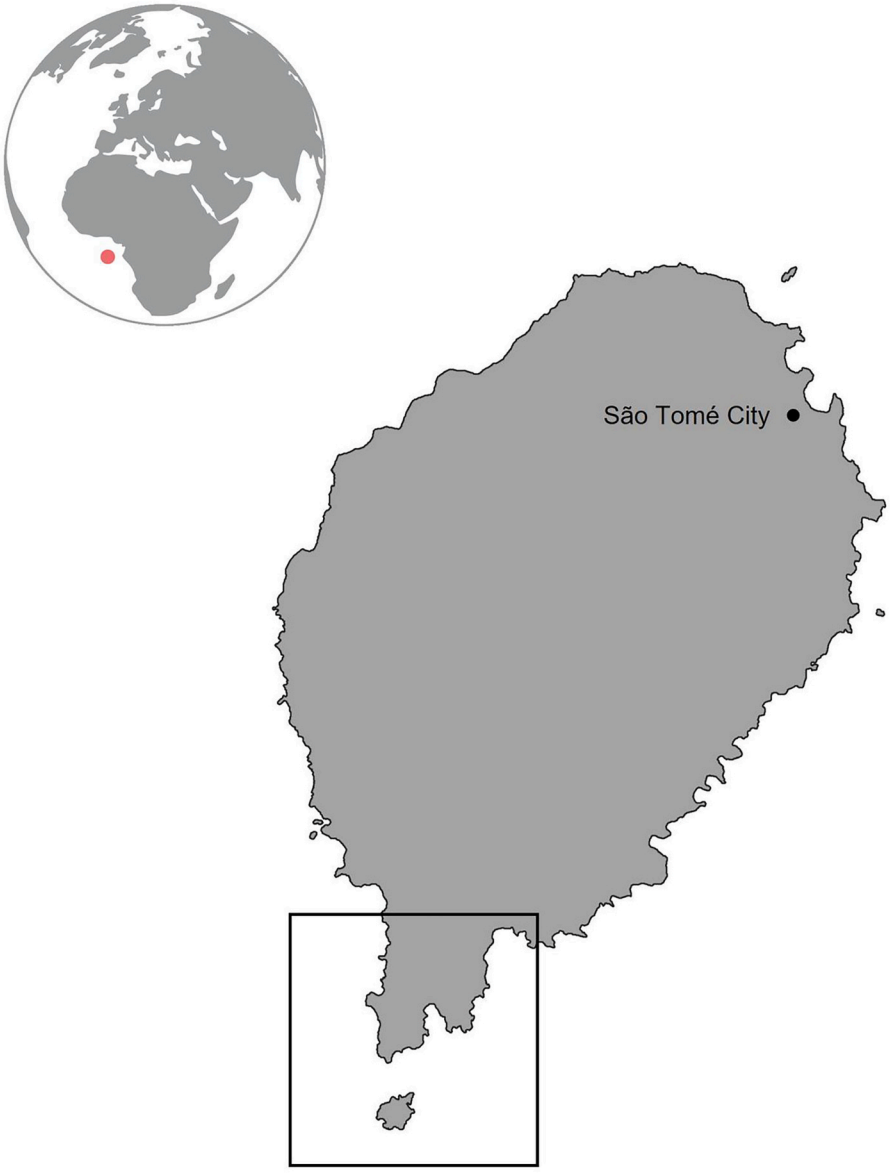

Fig. 1. Geographic location of the study area on São Tomé Island, situated within the Gulf of Guinea in the eastern Atlantic Ocean.

2.3. Sea turtle tissue sample collection

A total of 30 hawksbill turtles (*Eretmochelys imbricata*) were opportunistically non-invasively sampled around Rolas Islet between 8 October 2021 and 23 December 2022. Before release—within 10 min of capture—a small skin biopsy of the top epidermal layer was taken from the trailing edge of the rear flipper using a sterile razor scalpel; one sample was preserved in 96% ethanol, and the other in RNA lock reagent for laboratory processing. Although some studies suggest that ethanol preservation may alter $\delta^{13}C$ and $\delta^{15}N$ values in muscle tissue of fish and invertebrates (Kaehler and Pakhomov, 2001; Ruiz-Cooley et al., 2011), prior research has shown no significant impact on epidermal samples from sea turtles (Barrow et al., 2008). Furthermore, any preservation effect is likely to be species-specific and unrelated to storage time (Kiszka et al., 2014). Since all samples underwent identical treatment, isotopic comparisons remain valid and reliable.

2.4. Prey item collection

Vegetation and animal items (hereafter referred to as prey items) were selected based on direct field observations of feeding activity during free-diving surveys, complemented by information provided by local spearfishers on commonly consumed prey. (Table 1, Table 2). Items observed to be actively consumed by turtles were collected by free diving. Sampling sites were chosen to represent ecologically meaningful habitats that overlap with the known turtle foraging areas.

Patches of macroalgae were identified along a predefined transect (10–15 m), and sampling points were determined using a stratified random approach to minimize collection bias. From the center of each randomly selected patch, 3 to 5 blades were gathered, ensuring that the specimens were mature and representative of the dominant vegetation. Additionally, two samples each of tunicates, zoanthids, and sponges were collected opportunistically within the same area, prioritizing the most commonly encountered taxa. For tunicates, internal muscle-like tissues and body walls were dissected, avoiding the cellulose-rich outer tunic. In zoanthids, soft polyp tissue, including oral discs and tentacles, was carefully removed, excluding the basal attachment material. Sponge samples consisted of the outer ectosome and inner mesohyl, with care taken to avoid siliceous spicules. All specimens were thoroughly rinsed to eliminate sand, epibionts, and detritus, then preserved in 96% ethanol in the field. In the lab, samples were dried at 60 °C before isotopic analysis.

Zooplankton samples were collected using two types of plankton nets with different mesh sizes: a 500 μm net, targeting mesozooplankton and macrozooplankton, towed horizontally; and a 100 μm net, targeting microplankton, towed vertically, at the surface of each foraging site, with three replicates per site and per season (dry and rainy), to establish the isotopic baseline of the local marine food web. All samples were preserved in 96% ethanol, as freezing was not a viable option during fieldwork.

Table 1
Putative prey item categories collected for stable isotope analysis. The common name is given when the species was not identified.

Phylum	Family	Category	Species
Porifera		Sponge	*Demospongiae* spp.
Chordata	Ascidiacea	Tunicate	*Didemnidae* spp.
Cnidaria	Sphenopidae	Zoanthid	*Palythoa* spp.
Rhodophyta	Florideophyceae	Red algae	*Polysiphonia* spp.
Ochrophyta	Phaeophyceae	Brown algae	*Dictyota* spp. *Sargassum* spp.

Table 2
Mean (±SD) $\delta^{13}C$ and $\delta^{15}N$ values of putative prey items used in the mixing models.

Diet item	Mean $\delta^{13}C$	SD $\delta^{13}C$	Mean $\delta^{15}N$	SD $\delta^{15}N$
Sponge	−18.20	1.08	8.13	1.14
Tunicate	−20.41	1.43	5.51	1.54
Zoanthid	−18.32	3.80	3.72	2.23
Red algae	−20.63	0.17	5.82	0.51
Brown algae	−16.24	0.21	3.91	0.48

2.5. Stable isotopes analysis

Sea turtle tissue samples were rinsed with deionized water, dried at 60 °C for at least 48 h, and ground into a fine powder. Lipid extraction was not conducted, as previous research has shown that this procedure does not significantly affect the stable isotopic values of sea turtle epidermis tissue (Bergamo et al., 2016; Post et al., 2007; Zanden et al., 2012).

Potential prey items were identified to the lowest possible taxonomic level, dried at 60 °C (≥48 h), and powdered. Zooplankton was sorted under a stereomicroscope into major taxonomic groups and dried at 60 °C for 24 h.

Stable isotope ratios were measured using a Thermo Delta V Advantage IRMS (CIIMAR, University of Porto), calibrated with international reference materials IAEA-N-1 ($\delta^{15}N = +0.4‰$), IAEA-NO-3 ($\delta^{15}N = +4.7‰$), and IAEA-N-2 ($\delta^{15}N = +20.3‰$); and a two-point calibration for carbon with USGS-40 ($\delta^{13}C = -26.39‰$) and USGS-24 ($\delta^{13}C = -16.05‰$). Isotopic compositions are reported in delta notation (δ) as parts per thousand (‰), relative to VPDB (for carbon) and AIR (for nitrogen), using the formula $\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000$, where X is ^{13}C or ^{15}N, and R represents the ratio of heavy to light isotope. Analytical precision, based on replicate analyses of reference standards, was ±0.1‰ for both $\delta^{13}C$ and $\delta^{15}N$ values.

$\delta^{13}C$ and $\delta^{15}N$ values of all putative prey items used in the mixing models are presented in the mixing models are presented in Table 2 to support the interpretation of dietary estimates and assess source distinctiveness.

2.6. Determination of nucleic acids, concentrations, and ratios

Three indices were used to assess nutritional condition: standardized RNA:DNA ratio (sRD), DNA/mg, and RNA/mg per tissue, to evaluate physiological status across life stages. Quantification was performed according to the modified protocols of Caldarone et al. (2001) and Esteves et al. (2000), applied to vertebrate muscle tissue (Olivar et al., 2009). Tissue samples were chemically and mechanically homogenized, and nucleic acids quantified using fluorescence analysis with Gel Red. Fluorescence was measured on a Biotek Synergy HT plate reader (Ex: 365 nm, Em: 590 nm). Endogenous fluorescence was negligible and excluded. After the initial measurement, samples were incubated with RNase A at 37 °C for 30 min. RNA content was estimated by subtracting DNA-only fluorescence from the total signal. Concentrations were determined using standard curves of *u*-phagus DNA (0.25 μg μL^{-1}) and *E. coli* 16S–23S RNA (4 μg μL^{-1}) (Roche), with an average RNA/DNA fluorescence slope of 2.84 ± 0.20. sRD values were calculated using this slope and a reference slope of 2.4 (Caldarone et al., 2006).

2.7. Data analyses

We calculated CPUE as the sum of the number of sea turtles captured per hour of underwater survey time. Juvenile (J < 60 cm CCL) and adult (A > 70 cm CCL) hawksbills were grouped based on their size. Although the minimum sizes for mature turtles were defined as CCL >60 cm for females (minimum size observed for nesting females at São Tomé Island (Ferreira-Airaud et al., 2024);), this study adopted a stricter

classification. Individuals between 60 and 70 cm were excluded to ensure a clear separation between juveniles and adult groups, as individuals become reproductively mature at this size range (Witzell, 1983).

Spatial use patterns were analyzed separately for each life stage using two complementary methods. Minimum Convex Polygons (MCPs) were calculated in QGIS-LTR (QGIS Development Team, 2024) to estimate the overall extent of occurrence for juveniles and adults. Additionally, Kernel Density Estimation (KDE) was applied to identify core use areas (50%, 75%, and 90% isopleths), applying the default bandwidth based on Silverman's Rule of Thumb, which is appropriate for non-tracked animal location data (Wilcox and Wilcox, 2022).

Analyses were conducted using R-studio (v2025.09.1 (Posit team, 2025);). Given that the spatial behavior of hawksbill females in the region has been thoroughly described by Ferreira-Airaud et al. (2024), our spatial analyses focused exclusively on juvenile and male turtles to avoid duplication and provide new insights into these less characterized groups. Recapture rate was calculated as the proportion of individuals with multiple sightings (Schofield et al., 2018). Spatial and temporal fidelity were assessed by calculating the linear distance (km) and time interval (days) between consecutive sightings using geodesic distance functions from the geosphere package in R.

Stable isotope data ($\delta^{13}C$ and $\delta^{15}N$ values) were tested for normality using the Shapiro-Wilk test. All life stages met the assumption of normality ($p > 0.05$), validating the use of parametric analyses. For $\delta^{13}C$ values, Shapiro-Wilk test results were: Juveniles ($W = 0.919$, $p = 0.126$), Males ($W = 0.834$, $p = 0.117$), and Females ($W = 0.972$, $p = 0.906$). For $\delta^{15}N$ values, results were: Juveniles ($W = 0.921$, $p = 0.132$), Males ($W = 0.929$, $p = 0.575$), and Females ($W = 0.941$, $p = 0.671$).

For zooplankton samples with C: N ratios exceeding 3.5, $\delta^{13}C$ values were adjusted for lipid content using mass-balance correction approach. Corrections for zooplankton followed the equation proposed by Smyntek et al. (2007); Eq. (5)):

$$\delta^{13}C_{corr} = \delta^{13}C_{bulk} + 6.3 \times [(C:N_{bul} - 4.2) \ / \ C:N_{bulk}] \quad (1)$$

Where $\delta^{13}C_{bulk}$ and $C{:}N_{bulk}$ represent the stable carbon isotope values and atomic carbon-to-nitrogen ratio measured in the non-extracted zooplankton sample, and $\delta^{13}C_{corr}$ is the lipid-corrected stable carbon isotope value. In addition, $\delta^{13}C$ and $\delta^{15}N$ values of zooplankton were adjusted to account for preservation in ethanol, with corrections of +0.4‰ and −0.6‰, respectively (Feuchtmayr and Grey, 2003).

The trophic position (TP) of hawksbill turtles was estimated using the scaled isotopic framework developed by Hussey et al. (2014), which considers the asymptotic enrichment of $\delta^{15}N$ values across trophic levels. TP was determined according to the following equation:

$$TP = \left(\log\left(\delta^{15}N_{lim} - \delta^{15}N_{zooplankton}\right) - \log\left(\delta^{15}N_{lim} - \delta^{15}N_{turtles}\right)\right) \ / \ k + TP_{zooplankton} \quad (2)$$

where $\delta^{15}N_{lim}$ is the theoretical upper limit of $\delta^{15}N$ in top consumers, derived as $-\beta_0/\beta_1$, with $\beta_0 = 5.92$ and $\beta_1 = -0.27$. The $\delta^{15}N_{zooplankton}$ represents the stable nitrogen isotope values of the baseline organisms, in this case, the mean of different zooplankton groups assumed to occupy trophic level 2. The $\delta^{15}N_{turtles}$ represents the measured isotopic value for each turtle. The rate constant k, representing the enrichment rate of $\delta^{15}N$ per trophic level, was calculated as:

$$k = -\log\left(\beta 0 - \delta^{15}N_{lim} \ / \ -\delta^{15}N_{lim}\right) \quad (3)$$

As no significant differences were found between males and females in $\delta^{15}N$ values (ANOVA: $p = 0.094$), both sexes were grouped as "adults" for trophic position estimates.

Isotopic niche parameters were investigated through Stable Isotope Bayesian Ellipses (SIBER v2.1.7 (Jackson et al., 2011);). The total area (TA) was computed as the convex hull encompassing all isotopic values in the $\delta^{13}C$–$\delta^{15}N$ biplots, along with the small-sample corrected standard ellipse area (SEAc) to account for sample sizes below 50 (Jackson et al., 2011; Layman and Post, 2008). Bayesian Standard Ellipse Areas (SEAB) were also estimated using Markov Chain Monte Carlo (MCMC) simulations, incorporating uniform priors and equal likelihoods across iterations. This Bayesian approach provides a more reliable estimation under conditions of low sample size and the presence of potential outliers (Jackson et al., 2011). Niche overlap between groups was assessed by comparing the posterior distributions of the ellipses.

Dietary contributions were estimated using the MixSIAR Bayesian mixing model (MixSIAR v3.1.12 (Stock and Semmens, 2016);), implemented in JAGS. Brown algae was excluded from the final model due to negligible posterior contribution and limited source identifiability. Due to substantial isotopic overlap between tunicates and red algae, these sources were combined a posteriori to improve source identifiability in the mixing model, following Stock et al., 2018 (Stock et al., 2018). The model used $\delta^{13}C$ and $\delta^{15}N$ values from consumer tissues and potential dietary sources. Since trophic discrimination factors (TDFs) have not been experimentally estimated for hawksbill turtles, we followed the approach used by Sanchez et al. (2024) and applied values derived from loggerhead turtles (*Caretta caretta*): 2.62 ± 0.34‰ for $\delta^{13}C$ values and 1.54 ± 0.12‰ for $\delta^{15}N$ values (Reich et al., 2008). MCMC sampling used 300,000 iterations, 200,000 burn-in iterations, thinning of 100, and 3 chains. Model convergence was assessed using the Gelman–Rubin diagnostic ($\widehat{R}$), with 13 of 56 parameters >1.01, but only 2 exceeding 1.05 and 1 above 1.1 (resid.prop (Sequeira et al., 2019) = 1.15; deviance = 1.22), which are acceptable for complex hierarchical models. The remaining parameters exhibited strong convergence, with most values close to 1.00. Geweke diagnostics revealed that only 1 variable in Chain 1 was outside the ±1.96 range (~2%), compared with 14 and 24 in Chains 2 and 3, respectively. Despite slightly elevated values for some variables, the overall diagnostic patterns indicate sufficient convergence and mixing across chains, thereby supporting reliable inference from the posterior distributions.

To control for the effect of body size on nutritional condition, we examined the correlation between curved carapace length (CCL) and the standardized RNA: DNA ratio (sRD). No significant correlation was observed between body size and sRD values ($r = -0.13$, $p > 0.05$).

Since critical sRD threshold values have not yet been established for sea turtles — i.e., reference points to determine whether individuals are in good or poor nutritional condition — a percentile-based method was applied to assess nutritional condition, following the approach of Alves et al. (2020) and Meyer et al. (2012b). Under this method, average sRD values near the 75th percentile are interpreted as indicative of good nutritional condition, suggesting the animal has likely fed within the last 1 to 3 days. Conversely, values near the 10th percentile are considered indicative of poor nutritional condition. The sRD data were tested for normality using the Shapiro-Wilk test ($p > 0.05$), validating the use of non-parametric analyses to assess statistically significant differences ($p < 0.05$) between groups.

3. Results

3.1. In-water surveys

Between February 5, 2018, and June 23, 2025, a total of 113 sightings of hawksbill sea turtles were recorded as part of the Programa Tatô in-water monitoring program, in a total of 272.5 h of survey time with 0.41 sea turtles/hour (range 0.33–0.50 individuals per hour of survey time). Rough estimates of density (as surveys were not intensive) ranged from 1 to 2 individuals per hectare, assuming 1 ha per survey unit.

Targeted efforts resulted in the hand capture of 95 individuals. Among these, 50 were juveniles, and 45 were adults. Regarding adult sex determination, 31 individuals were classified as males and 14 as females.

The recapture rate among juveniles was 23.5%, higher than in males

(13.6%). Juveniles also showed strong spatial fidelity, with a median recapture distance of 0.21 km. In contrast, males exhibited a broader movement pattern, with a median recapture distance of 1.00 km. Temporal fidelity also differed between groups: the median time between consecutive observations was 195.5 days for juveniles (ranging from 8 to 1109 days), compared to 337.0 days for males (ranging from 28 to 1145 days). Habitat use analysis revealed similar spatial preferences between juvenile and adult individuals. The majority of sightings for both life stages occurred over rocky substrates, accounting for 58.0% of adult and 59.3% of juvenile observations. Rhodolite beds were also commonly

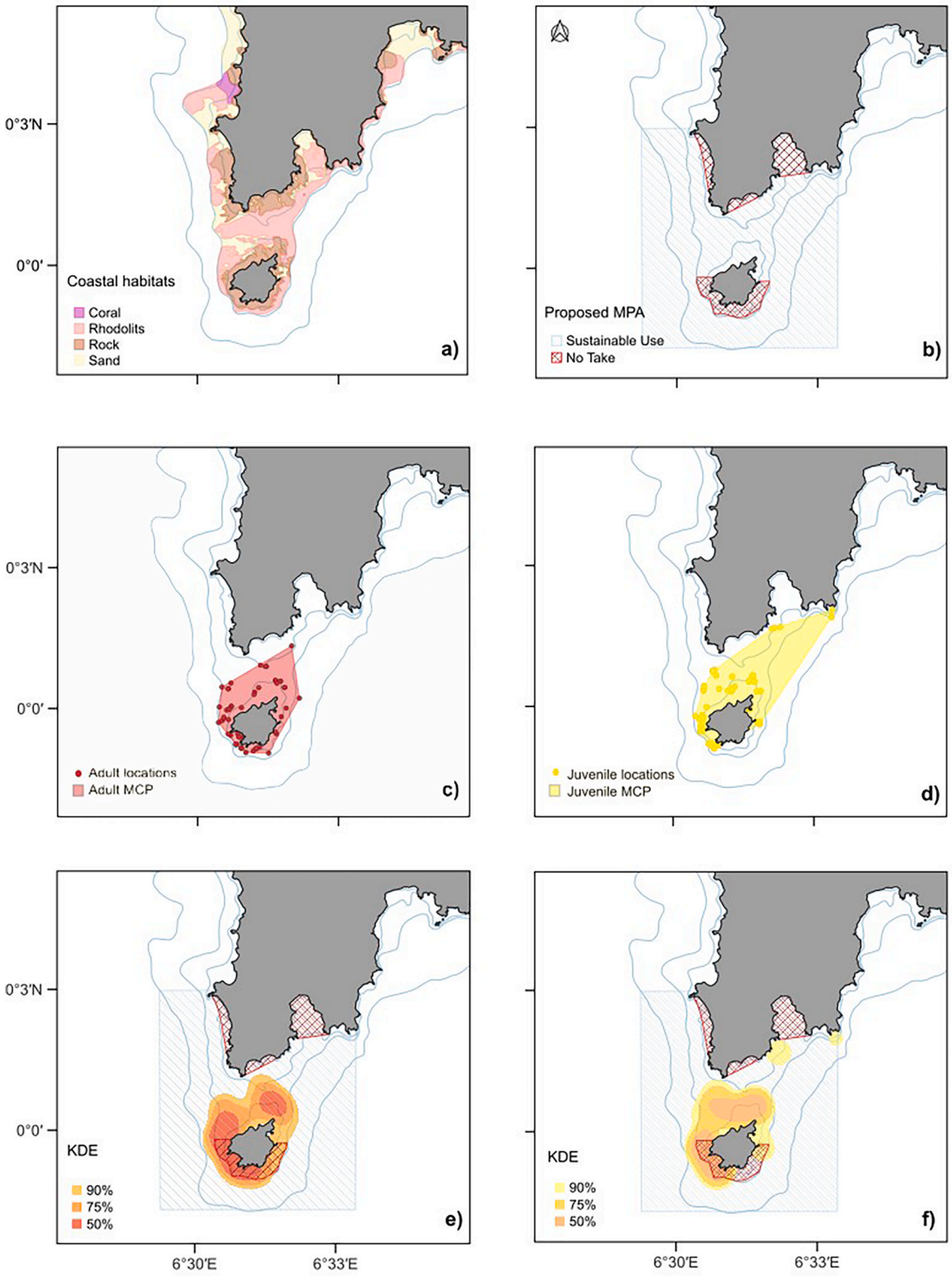

Fig. 2. (a) Marine coastal habitats of the study area (source: Vieira et al. *in press*); (b) Proposed Marine Protected Areas (MPAs) location of the south of São Tomé, highlighting the no take zone and the sustainable use area (source: 4th co-management assembly of the project establishment of a network of MPAs in São Tomé and Príncipe in a shared management approach managed by the consortium Oikos, FFI, Fundação Príncipe and Marapa, April 20, 2022); Minimum convex polygon of adults (c) and juveniles (d) hawksbill turtles; Kernel Density Estimations (KDEs, 50, 75, and 90%) of adults (e) and juveniles (f) hawksbill turtles.

used, representing 26.0% of adult and 30.5% of juvenile sightings. Sandy habitats were the least used, comprising only 16.0% of adult and 10.2% of juvenile records. A chi-square test confirmed that these differences were not statistically significant ($\chi^2 = 0.92$, df = 2, p = 0.632), indicating no evidence of habitat partitioning between life stages. The Bhattacharyya Affinity (BA) matrix indicated a high degree of spatial overlap between males and females (BA = 0.9928), suggesting that both sexes occupy nearly identical areas. In contrast, a moderate overlap was observed between adults and juveniles (BA = 0.6424), indicating partial spatial segregation between life stages.

Minimum Convex Polygon (MCP) estimates showed that juveniles occupied a larger area (12.72 km^2) (Fig. 2c) compared to adults (8.71 km^2) (Fig. 2d), which overlapped by 100% with the proposed Marine Protected Area (MPA) (Fig. 2e and f).

3.2. Isotopic niche and diet

The CCL of juveniles varied from 33 to 56 cm (42.2 ± 5.4; n = 18), and the CCL of adults ranged between 70 and 84 cm (76.8 ± 4.5; n = 12, 6 females and 6 males). $\delta^{13}C$ values ranged from −17.81 to −14.84‰ (−15.96 ± 0.83) for juveniles and from −21.88 to −16.03‰ (−16.03 ± 1.73) for adults. A one-way ANOVA revealed significant differences in $\delta^{13}C$ values among life stages (F = 12.15, p < 0.001), with juveniles exhibiting significantly higher $\delta^{13}C$ values than adults. Post-hoc comparisons indicated that both males and females differed significantly from juveniles (Males vs Juveniles: F = 22.82, p < 0.001; Females vs Juveniles: F = 7.39, p = 0.014), while no significant difference was observed between males and females (F = 0.34, p = 0.572).

Regarding $\delta^{15}N$ values, these largely overlapped among groups, ranging from 8.37 to 10.99‰ (mean ± SD; 9.59 ± 0.87) in juveniles and from 8.05 to 12.24‰ (10.39 ± 1.06) in adults. No significant overall differences in $\delta^{15}N$ values were detected among life stages (ANOVA: F = 2.59, p = 0.094). However, pairwise comparison revealed that adult males exhibited significantly higher $\delta^{15}N$ values than juveniles (F = 5.61, p = 0.027). In contrast, no significant differences were observed between females and juveniles (F = 0.53, p = 0.476) or between males and females (F = 0.34, p = 0.573).

Isotopic niche metrics revealed clear differences between life stages. Adults exhibited a markedly broader isotopic niche (SEAc = 6.66), compared to juveniles (SEAc = 2.53). These results suggest that adults exploit a wider range of trophic resources or feeding habitats, indicating greater dietary variability (Table 3).

Dietary composition differed between life stages, although sponges remained the predominant food source across both groups (Fig. 3). Juveniles exhibited a greater estimated reliance on sponges (66.0%) compared to adults (40.2%). In contrast, adults showed a more diverse dietary composition, with higher substantial contributions from both sponges and the combined of red algae and tunicates (34.6%), suggesting broader dietary flexibility. Juveniles displayed lower estimated contributions from this combined source (13.5%). Zoanthids contributed moderately to the diet of both life stages (8.0% in adults and 4.6% in juveniles), with overlapping credible intervals indicating no clear difference in their relative importance between juveniles and adults (Fig. 3).

The isotopic niche overlap between juveniles and adults was 35.01%, supporting partial niche differentiation across life history stages (Fig. 4).

Overall, the estimated trophic position of hawksbills using the scaled isotopic model by Hussey et al. (Schofield et al., 2018) indicated that juveniles occupied a mean TP of 2.57 ± 0.22, while adults exhibited a higher mean TP of 2.79 ± 0.29.

Table 3
Standard ellipse area (SEA) and convex hull area (TA) for juveniles and adult hawksbill sea turtles at São Tomé Island. SEAc: SEA corrected.

Size class	TA	SEA	SEAc
Juveniles	5.86	2.38	2.53
Adults	15.15	6.06	6.66

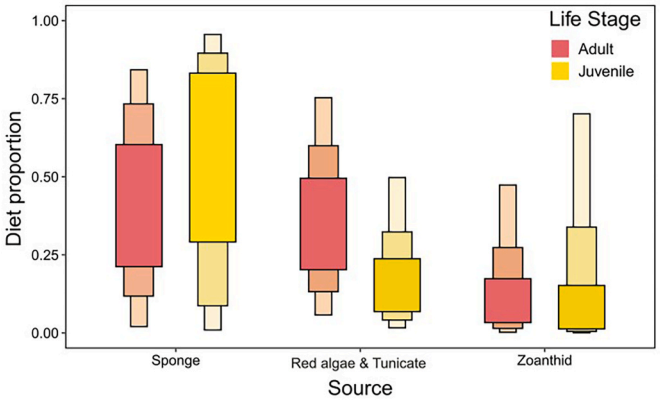

Fig. 3. Potential contribution of common diet items to the diet of juveniles and adult's hawksbill sea turtles in São Tomé Island, with credible intervals represented by shaded boxes of varying intensity, with the darkest shade indicating the 50% interval, a lighter shade indicating the 75% interval, and the lightest shade indicating the 100% interval, as determined by the MixSIAR Bayesian mixing model. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

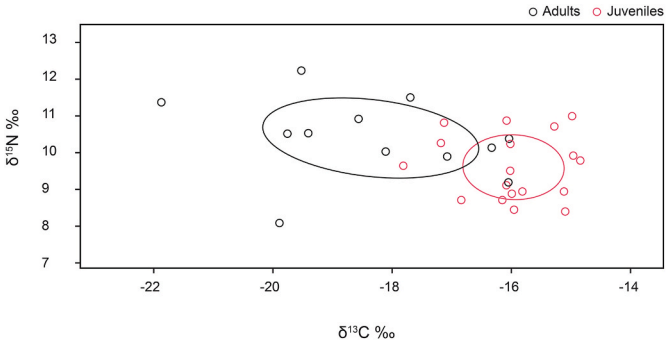

Fig. 4. Standard ellipse area corrected (SEAc) produced by SIBER, indicating the trophic niches occupied by the distinct life stages of hawksbill sea turtles in São Tomé Island. Open circles represent individual $\delta^{13}C$–$\delta^{15}N$ values.

3.3. Nutritional condition

Nutritional condition across the life stages of hawksbill sea turtles was evaluated using the sRD, which revealed significant differences among groups (H = 9.57, p = 0.0084). Percentile-based analysis revealed distinct patterns of metabolic activity among life stages. Juveniles exhibited a mean sRD of ~1.73, with a wide distribution ranging from approximately 0.96 (10th percentile) to 3.37 (90th percentile). The mean exceeded the median, indicating a right-skewed distribution and suggesting that some individuals may have experienced periods of accelerated growth or recent intensive feeding. This pattern reflects considerable variability in growth and nutritional condition, likely linked to differences in individual feeding performance and physiological development. Males showed the highest mean sRD (~1.9) and a narrower percentile range, indicating more homogeneous metabolic activity. The close alignment between the mean and median suggests a stable, symmetric distribution, consistent with a relatively uniform nutritional condition typical of a metabolically stable life stage. In contrast, females had the lowest mean sRD (~0.8), with the mean and median values closely aligned and all percentiles clustered at lower levels. This points to a generally lower metabolic activity and limited variability compared to juveniles and males. These patterns were

supported by pairwise comparisons. A Mann-Whitney test revealed a significant difference between males and females ($p = 0.009$), suggesting sex-related variation in nutritional status. No significant difference was detected between juveniles and males ($p = 0.415$), whereas juveniles differed significantly from females ($p = 0.007$). These results suggested that females may exhibit a distinct physiological profile, while males are more similar to juveniles (Fig. 5).

4. Discussion

Using an integrative approach combining stable isotope analysis, habitat use, and nucleic acid-based indicators, this study examines the ecological strategies of hawksbill turtles in the coastal waters of São Tomé Island. Despite occupying the same shallow coastal habitats, hawksbill turtles exhibit pronounced ontogenetic differences in habitat use, trophic ecology, and nutritional condition. Juveniles show strong site fidelity and higher nutritional condition, while adults exploit a broader isotopic niche and occupy higher trophic positions, reflecting more flexible foraging strategies. Together, these results highlight the importance of life stage-specific processes in shaping population dynamics and conservation implications.

Habitat use analysis revealed no significant spatial partitioning between juvenile and adult hawksbill turtles in São Tomé Island's shallow waters, with both life stages predominantly associated with rocky substrates and rhodolite beds. This pattern is consistent with previous studies showing strong associations between hawksbills and hard-bottom habitats that provide reliable prey availability (León and Bjorndal, 2002; Meylan, 1988). Despite this overlap, our results indicate ontogenetic differences in spatial fidelity, with juveniles exhibiting stronger site fidelity and higher recapture rates than males. Similar patterns have been documented in other regions, where juveniles occupy reef-associated habitats with restricted movement ranges (Berube et al., 2012; Carrión-Cortez et al., 2013). These development habitats may provide ecological advantages, including stable resource availability and reduced predation risk, but may also increase vulnerability to localized disturbances, particularly in coastal regions where reef habitats may be impacted by sedimentation from terrestrial runoff and erosion, as well as broader stressors such as coral bleaching (Berube et al., 2012; Briggs et al., 2024).

Stable isotope analysis further revealed niche partitioning between life stages, with adults exhibiting broader resource use. Lower $\delta^{13}C$ values in adults suggest greater use of more offshore and deeper waters,

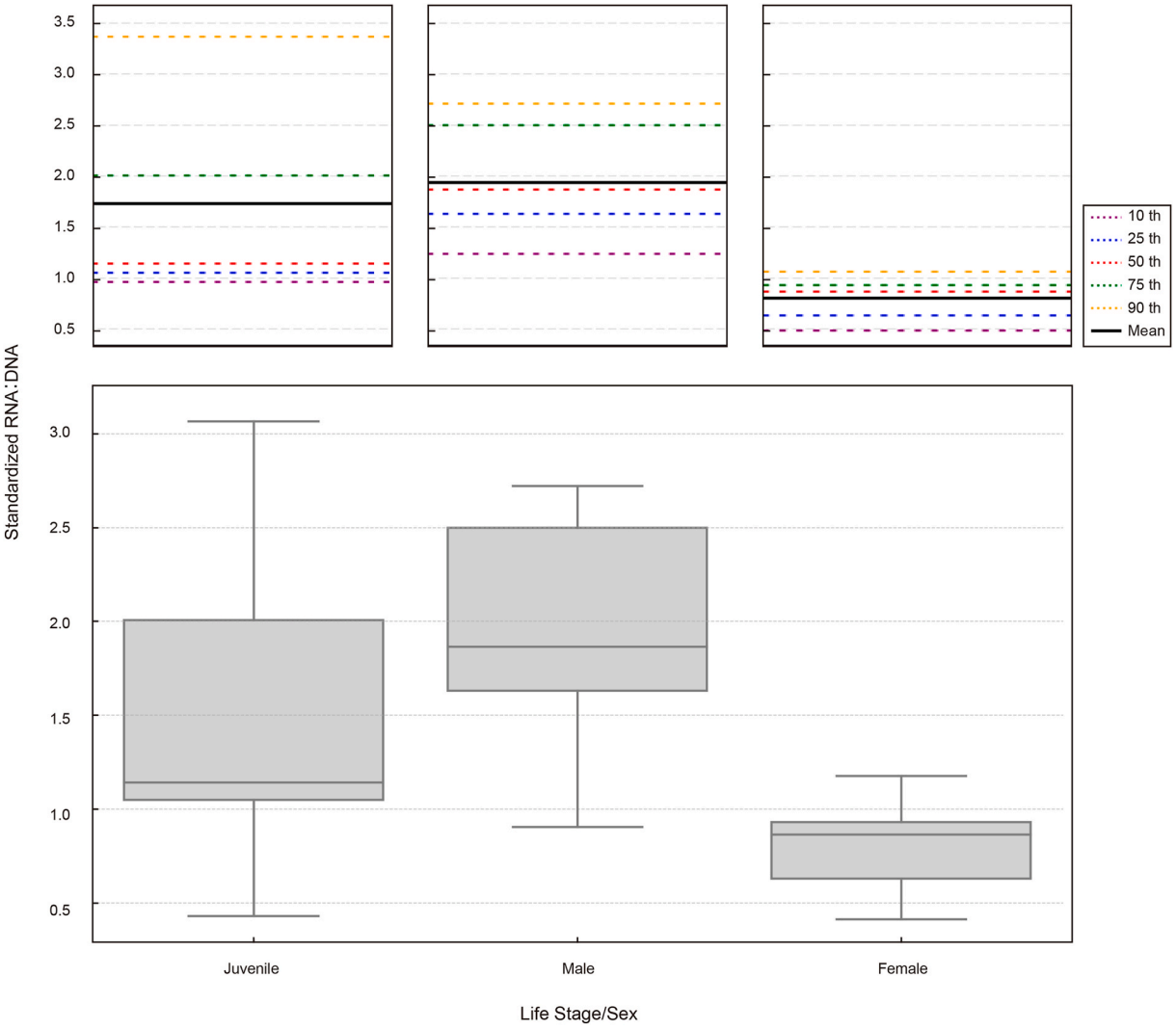

Fig. 5. (a) Percentile approach of the standardized RNA/DNA of juveniles (CCL <60 cm; n = 18) and adults (CCL >70 cm; n = 12; 6 male and 6 females) hawksbill sea turtles at São Tomé Island; colored dashed lines indicate percentile thresholds (10th, 25th, 50th, 75th and 90th percentiles), and the black line indicates the mean. Groups with mean values closer to the 75th percentile and farther from the 10th percentile are interpreted as having better nutritional condition; (b) Standardized RNA/DNA ratio for juvenile and adults' hawksbill sea turtles at the study area; boxplots summarize the distribution of sRD values for each group, with the central line indicating the median, the box the interquartile range, and the whiskers the data spread.

whereas higher $\delta^{13}C$ values in juveniles are consistent with a stronger association with nearshore and shallow habitats (Hill et al., 2006; Michener et al., 2007; Nerot et al., 2012). This pattern is further supported by the limited presence of adults in shallow coastal areas (Ferreira-Airaud et al., 2022). Similar patterns were noted in Príncipe Island (Ferreira et al., 2018), and a positive correlation between size and $\delta^{13}C$ values in the Gulf of California further indicates ontogenetic habitat shifts (León and Bjorndal, 2002; Reynolds et al., 2023).

In contrast, $\delta^{15}N$ values showed considerable overlap between adults and juveniles, suggesting broadly similar trophic levels, although a significant difference between adult males and juveniles may indicate subtle sex-related variation in resource use (Ramirez et al., 2023). Despite this overlap, isotopic niches metrics indicate greater trophic variability in adults, potentially reflecting access to a wider range of prey types or habitats (Ferreira et al., 2018). However, isotopic homogeneity in the Gulf of Guinea (Graham et al., 2010) may reduce the resolution of $\delta^{15}N$-based trophic differentiation, reinforcing the need for complementary approaches or larger sample sizes to detect finer-scale patterns.

Differences in trophic position and diet further support ontogenetic shifts in foraging strategy (Chatterji et al., 2022). Adults occupied a slightly higher trophic position ($TP \approx 2.79$) than juveniles ($TP \approx 2.57$), indicating a greater reliance on higher trophic level prey. While hawksbills are traditionally considered sponge specialists (Berube et al., 2012; Meylan, 1988), increasing evidence points to a greater dietary plasticity (León and Bjorndal, 2002; Carrión-Cortez et al., 2013; Ramirez et al., 2023; Stock et al., 2018; Bell, 2013). In this study, adults consumed a broader range of prey, including the combined group of red algae and tunicates, suggesting greater foraging flexibility potentially linked to increased mobility and reproductive energy demands. Given the low digestibility and limited energetic value of sponges (Auer et al., 2015), this dietary diversification may be necessary to meet metabolic requirements. Similar shifts towards alternative prey, including algae, have been documented in other regions, reinforcing the view that hawksbills exhibit flexible foraging strategies shaped by life stage, habitat, and prey availability (León and Bjorndal, 2002; Baumbach et al., 2022; Carrión-Cortez et al., 2013; Bell, 2013). However, the absence of comprehensive regional dietary studies and global stable isotope datasets for hawksbills and their prey limits broader ecological interpretations.

Nutritional condition, assessed through sRD, also varied among life stages and sexes. Higher sRD values in juveniles likely reflect elevated metabolic rates and protein synthesis associated with growth (Auer et al., 2015). Similarly, males exhibited higher sRD values than females, possibly due to lower energetic investment in reproduction and the ability to maintain some level of foraging during the breeding season (Hamann et al., 2002). In contrast, females showed consistently lower sRD values, likely reflecting the substantial energetic coast of reproduction, including egg production and prolonged fasting during nesting (Witzell, 1983; Richardson et al., 1999).

Male hawksbills have been observed to remain in the vicinity of nesting areas, as seen in Mona Island, Puerto Rico, and may be able to replenish energy reserves by opportunistic feeding during the breeding season (Van Dam et al., 2008). Although prey availability around nesting grounds is often limited, this capacity to forage locally, even intermittently, may help explain their higher sRD values relative to females. Still, due to habitat constraints and potential for competition, some males may also undertake short migrations post-breeding.

Although females in this study were sampled at sea and not directly observed nesting, the presence of mating scars suggested recent reproductive activity, supporting this interpretation. Like other sea turtles, hawksbills build up energy stores during extended foraging periods before migration and nesting. After reproduction, they return to distant, resource-rich foraging grounds to restore depleted reserves, a process that may take several years (Richardson et al., 1999). The mobilization of lipid and protein stores during nesting has been linked to marked declines in plasma triglycerides and total protein (Auer et al., 2015; Perrault et al., 2014). A reduced food intake during this period likely affects biochemical indicators, such as RNA and DNA concentrations (Chícharo and Chícharo, 2008).

Despite these insights, some limitations should be acknowledged. The relatively small sample size and uneven temporal sampling may constrain the detection of seasonal patterns. While stable isotope analysis provides valuable information on foraging ecology, it does not allow precise identification of prey species or recent dietary intake, which could be addressed through complementary approaches, such as stomach content analyses or DNA metabarcoding (Haywood et al., 2019). Moreover, prey availability and habitat quality were not directly assessed, despite their likely influence on foraging behavior and nutritional condition. Future research should integrate tracking data, repeated biochemical measurements, and habitat assessments, as well genetic analyses, to better understand population structure, foraging ecology and regional variability.

From a conservation perspective, the observed overlap between critical juvenile developmental and adult breeding habitats within the proposed marine protected area (MPA) boundaries suggests a strong foundation for spatial protection of this population during these life stages (Ferreira-Airaud et al., 2024). However, legal designation alone is insufficient. Without effective enforcement and regulation, key threats, such as illegal harvesting and bycatch, persist (Vieira et al., 2024; Perrault et al., 2014). These challenges are particularly critical given the strong site fidelity observed in individuals, which increases their vulnerability to localized impacts. Effective conservation will require context-specific management strategies that integrate functional ecological indicators and dynamic environmental data (Iacarella et al., 2021). To translate these strategies into practical action, specific measures – such as seasonal or gear-specific fishing restrictions – should be adopted, along with community-based monitoring initiatives, as those led by Programa Tatô, which foster local stewardship and improve compliance. Additionally, integrating biochemical tools such as stable isotope analysis and RNA/DNA ratios into long-term monitoring programs may also provide early-warning indicators of environmental change (Chícharo and Chícharo, 2008). Ultimately, this study provides essential baseline data to support adaptive, multi-scale-specific conservation strategies. By aligning spatial protection with informed and responsive management, São Tomé and Príncipe have a unique opportunity to safeguard one of the world's most genetically distinct and critically endangered hawksbill turtle populations (Wallace et al., 2025; Monzón-Argüello et al., 2011).

Ethics statement

The work was ethically approved by the Directorate of Environment and Climate Action, a national agency responsible for the overall coordination of the implementation of environmental actions and legislation in the country, including sea turtle protection legislation. Sea turtle tissue samples were imported to Portugal (University of Algarve) under the CITES permits n° 22ST000002/AC and 22ST000003/AC.

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work, the authors used ChatGPT to organize the content and improve the language of the manuscript. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

CRediT authorship contribution statement

Sara Vieira: Conceptualization, Formal analysis, Investigation, Methodology, Writing – original draft. **Betânia Ferreira-Airaud:** Investigation, Writing – review & editing. **Vânia Baptista:** Formal

analysis, Investigation, Methodology. **Manjula Tiwari:** Conceptualization, Supervision, Validation, Writing – review & editing. **Rita Castilho:** Formal analysis, Supervision, Validation, Writing – review & editing. **Maria A. Teodósio:** Conceptualization, Resources, Supervision, Validation, Writing – review & editing.

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.

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Data availability

The datasets supporting the findings of this study will be made publicly available in a trusted repository upon article acceptance. In the meantime, data are available from the corresponding author upon reasonable request.

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