




Loggerhead Sea Turtles Hand-Reared in Captivity: Isotopic Insights into Their Inherent Dietary Variation

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How to cite this paper: Mejía-Guarnizo, B.N., Polo-Silva, C.J., Jauregui-Romero, G.A. and Delgado-Huertas, A. (2024) Loggerhead Sea Turtles Hand-Reared in Captivity: Isotopic Insights into Their Inherent Dietary Variation. *Open Journal of Ecology*, **14**, 435-454.

<https://doi.org/10.4236/oje.2024.145026>

Received: April 2, 2024

Accepted: May 28, 2024

Published: May 31, 2024

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Abstract

Stable isotope analysis is a widely used method for gathering ecological insights into the diet and feeding habitats of various species. While captive studies often limit lethal sampling and differ from wild conditions, they offer valuable insights into inherent isotopic variations among individuals, which are often assumed to reflect differences between natural populations. In the Sea Turtle Conservation Program, loggerhead turtle hatchlings from different nests were fed. Necropsies were conducted on turtles that died during this period, obtaining bone fragments for analysis. We evaluated the isotopic variation of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) in bone tissue across six turtle nests ($n = 66$ samples) and assessed differences in Straight Carapace Length (SCL, $n = 71$ samples). Using SIBER and nicheROVER in R, we calculated niche width and overlap, while the simmr package determined primary prey assimilation. Despite feeding the hatchlings the same prey, we observed variations in nitrogen isotope assimilation between nests. Nests 4 and 6 had a niche width $>1.8\text{‰}$, indicating consistent consumption frequencies across all prey and $>70\%$ niche overlap with other nests. In contrast, nests 1 and 2 showed a narrower niche width ($<0.3\text{‰}$) and minimal overlap, suggesting specialization on specific prey. Comparing SCL, no significant diet differences were found between groups, nor a correlation between SCL and isotopes. The mixture model results indicated that *Mugil* sp. constituted the primary diet component ($>40\%$) across all groups. This study demonstrates how factors like competition or prey preference can influence the assimilation of diet, even when the source remains constant (inherent variation).

Keywords

Stable Isotopes, *Caretta caretta*, Head-Starting, Nests, Straight Carapace Length

1. Introduction

Loggerhead turtles (*Caretta caretta*), like other marine turtle species, exhibit remarkable longevity and undergo slow growth, characterized by a life cycle that includes natal philopatry, male-mediated gene flow, and extensive long-distance migrations, among other features, leading to complex population structure patterns [1]. Found in tropical and subtropical regions, these turtles nest along coastlines influenced by warm currents and undertake extensive migrations for breeding and feeding, inhabiting nearly all the world's ocean basins [2]. In Colombia, they nest on both the Caribbean and Pacific coasts, exhibiting variations in reproductive and feeding behaviors [2] [3]. Their migratory routes between feeding and nesting sites span thousands of kilometers and have been extensively documented [1].

Diet analysis offers valuable insights, allowing researchers to observe individuals across various life stages and habitats, providing insights into food preferences essential for establishing conservation strategies [4]. Recently, diverse approaches, such as stable isotopes, have been employed to study the foraging ecology of loggerhead sea turtles [5]. Stable isotope analysis of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) has emerged as a prevalent method to determine trophic status and trace the origins of nutrient resources for wildlife populations. This technique has been applied to trophic ecology studies, analyzing samples from animal tissues to investigate their diets over different timeframes [6] [7] [8]. The method relies on the fact that the carbon and nitrogen in an animal's body derive directly from its food, metabolic pathways, and tissue synthesis, meaning the isotopic composition of a tissue reflects its diet [9]. Stable isotope values can be influenced by factors such as food source, growth rate, metabolism, and environmental conditions [10] [11] [12].

Stable isotope analysis (SIA) quantifies the enrichment of heavier isotopes relative to lighter ones through an organism's diet [13] [14]. The extent of stable isotope enrichment in an organism's body depends on individual metabolic rates and the tissue analyzed [10] [15]. Discrimination factors can vary due to factors such as life stage, environment, nitrogenous waste excretion form, taxon, species, tissue type, diet quality, and isotopic composition [16] [17]. A commonly accepted diet-tissue discrimination value for nitrogen ($\delta^{15}\text{N}$) is 3.4‰ [10] [18]. $\delta^{13}\text{C}$ values typically show smaller variations compared to $\delta^{15}\text{N}$ values, leading to less pronounced trophic shifts in $\delta^{13}\text{C}$ values as nutrients move through the food web [15]. For instance, the discrimination factor in sea turtle bone tissue ranges from ~2‰ to 6‰ for both carbon and nitrogen, sometimes varying based on the feeding area [19] [20] [21].

Most studies utilize stable isotopes to investigate the diet and habitat use of species using specimens captured in the wild [4] [22] [23] [24] [25]. However, various intrinsic factors can lead to differences or changes in values when comparing populations or groups of organisms. In sea turtles, for instance, turnover rates in tissues can vary based on diet type, tissue type, and life stage [8] [9] [26]. Therefore, understanding the isotopic incorporation patterns in species studied under captive conditions is essential for a more accurate analysis of data from wild specimens, preventing potential overestimations in interpretations [11].

Conservation programs and research centers housing sea turtles, such as hawksbill (*Eretmochelys imbricata*), olive ridley (*Lepidochelys olivacea*), green (*Chelonia mydas*), and loggerhead turtles, provide them with *ad libitum* diets consisting of fish, vegetables, creeping beach plants, macroalgae, or squid [27] [28]. These diets have also been employed to feed hatchlings and juveniles of *C. caretta* in the Sea Turtle Conservation Program (ProCTMM). This approach has sparked significant interest in investigating these feeding patterns using stable isotope techniques to determine if these assimilation processes are occurring. Additionally, researchers are exploring whether maternal feeding cues from the natural environment persist during the turtles' initial months of life.

Studying the diet of loggerhead sea turtles, informed by their prey and access to it, enhances the precision of interpreting isotopic analysis results. Research conducted under human care offers valuable insights into the relationship between diet, tissue isotopic composition, and the impact of variables such as nest origin (a maternal genetic factor), size, and age on stable isotope values. While human intervention can affect aspects of stable isotope studies in animals like sea turtles, it's not necessarily the primary influencing factor. Studying animals in human care provides a controlled environment to investigate food sources and feeding processes, especially for species with complex life cycles. This approach allows for comparisons, shedding light on how various factors can influence stable isotope values.

The current study examines the isotopic variations of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) in juvenile loggerhead sea turtles housed in the ProCTMM incubation program. These turtles originate from nests located on various nesting beaches in the Colombian Caribbean region. We analyze isotopic differences in bone tissue among different nests and track changes as the turtles grow. The primary aim is to understand the feeding processes and prey assimilation in a group with potential access to identical food sources. Crucially, stable isotope studies on animals in human care offer insights into early-life variation, which can be highly beneficial for understanding these turtles' development.

2. Material and Methods

2.1. Study Area

Beach monitoring was conducted in the Los Cocos-Don Diego sectors, situated

near the city of Santa Marta in the northern region of the Magdalena department, Colombia (**Figure 1**). In this area, newly hatched turtles were collected from nests corresponding to the 2017-2018 nesting seasons between April and August. These nesting periods fall between the minor rainy season (May-June) and the minor dry season (July-August), which are characterized by unpredictable rainfall intensity and wind direction [29].

The beaches in this sector provide ideal conditions for sea turtle reproductive processes. Nesting events continue to be recorded on the Don Diego beaches, predominantly by loggerhead turtles, and to a lesser extent by green and hawksbill turtles [29].

2.2. Obtaining Sea Turtles for Human Care

During the nesting seasons, the ProCTMM team, in collaboration with trained community technicians from local fishing associations, conducts night patrols and beach monitoring. They implement management measures approved by the relevant environmental authorities, including relocating nests threatened by local hazards to designated “temporary corrals” set up each season. A portion of the hatchlings from these nests is collected and transferred to Mundo Marino de Santa Marta Aquarium’s facilities in El Rodadero, Santa Marta. Here, they are reared in the closed systems of the “ProCTMM Turtle Farm” before being reintroduced to their natural environment for repopulation.

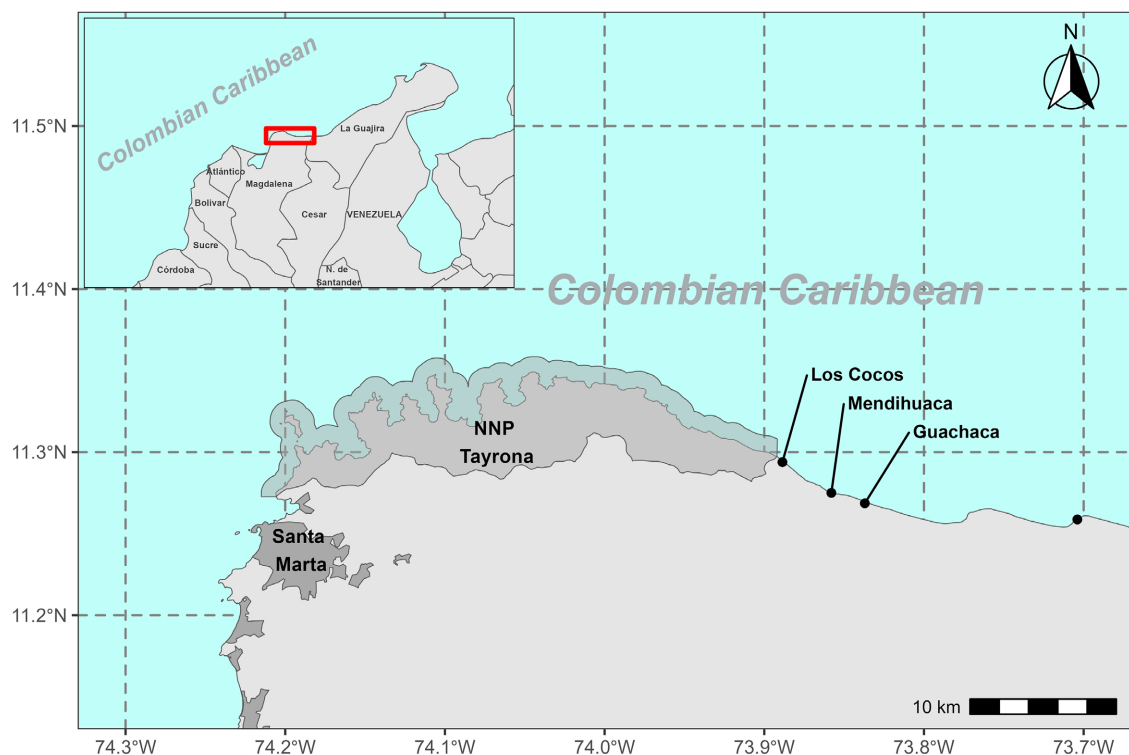


Figure 1. The study site encompasses nesting beaches in the Los Cocos, Mendihuaca, Guachaca, and Don Diego sectors of the Magdalena department in the Colombian Caribbean. The upper left image displays the study region’s location near Santa Marta city and the Tayrona National Natural Park.

Hatchlings and juvenile turtles are fed twice daily *Ad libitum* with portions of locally sourced fish species, including *Opisthonema oglinum*, *Mugil incilis* and *Scomberomorus brasiliensis* from the Scombridae family, as well as anchovies from the Engraulidae family. Their diet is supplemented with shrimp (*Litopenaeus vannamei*), *Loligo* spp., and *Callinectes* spp. This feeding regimen is maintained until approximately 10 months when they are reintroduced to their natural habitat.

2.3. Tissue Sample Collection

Deaths occurring during rearing are subjected to necropsies to obtain tissue samples. Bone tissue samples, specifically from the acromion process and coracoid bone, were collected from 66 individuals across six different nests.

Following the method described by Newsome *et al.* (2006) [30], the soft tissue was removed from the bone samples and stored in Eppendorf tubes. The tissue was demineralized, releasing collagen by adding 0.5 N hydrochloric acid (HCl) until fully covered, and then cooled to 5°C for 15 hours. The acid supernatant was subsequently extracted and dried. To conduct the necessary washes, a chloroform-methanol-water solution (2:1:0.8) was added. Samples were centrifuged at 2200 rpm for 15 minutes; this step was repeated three times to ensure sample cleanliness. Samples were then dried in an oven at 40°C for 24 hours. Afterward, 0.1 N HCl was added and left for 24 hours to preserve the collagen. Once the acid was removed, samples were dried again in an oven at 40°C for 48 hours.

The dried samples were pulverized using a mortar and pestle, weighed on an analytical balance (between 0.6 - 1 mg maximum), and placed in 8 × 5 mm tin capsules. These capsules, labeled and coded, were sent to the Stable Isotope Laboratory at the Zaidín Experimental Station (CSIC, Granada, Spain) for isotopic signal analysis. The carbon and nitrogen isotopic composition of vertebral collagen was determined using a Carlo Erba NA 1500 NC elemental analyzer coupled with a ConFlo III interface to a Delta Plus XP mass spectrometer (EA-IRMS; ThermoQuest).

2.4 Stable Isotope Analysis

Stable isotope values are expressed using the delta notation, and were calculated with the following formula number one:

$$\delta = \left[\left(\frac{R \text{ sample}}{R \text{ standard}} \right) - 1 \right] \times 1000 \quad (1)$$

R_{sample} y *R_{standard}*, represent the heavy and light fractions of each isotope in the sample and standard, respectively. The ¹³C:¹²C ratio is denoted as δ³C, while the ¹⁵N:¹⁴N ratio is represented as δ⁵N [31]. Commercial carbon dioxide (CO₂) and atmospheric nitrogen (N₂) served as the internal standards for isotopic analysis due to their abundance, affordability, and high isotopic purity [32]. δ³C values were analyzed using standards of −30.63‰ and −11.65‰ (V-PDB), while δ¹⁵N values used standards of −1.0‰ and +16.0‰. Isotopic measurements were conducted with an accuracy of ±0.1‰ for both elements. Carbon measurements are reported relative to the V-PDB standard (Vienna-PDB),

while nitrogen measurements utilize the AIRE standard (atmospheric nitrogen) [19]. Reference gases and standards, with varying C:N ratios and isotopic compositions, were recalibrated against International Reference Materials (USGS-24 and IAEA-C6 for carbon; IAEA-N1, IAEA-N2, and IAEA-N3 for nitrogen).

The lipid content in tissue can influence $\delta^{13}\text{C}$ values when the C:N ratio exceeds 3.5 [33]. For samples with a higher ratio than this threshold, the lipid effect on $\delta^{13}\text{C}$ values was corrected using the equations (number two) recommended for aquatic animals:

$$\delta^{13}\text{C}_{\text{normalized}} = \delta^{13}\text{C}_{\text{original}} - 3.32 + 0.99 \times \text{C} : \text{N} \quad (2)$$

2.5. Data Analysis

To assess the normality of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, we used the Shapiro-Wilks test, and for homoscedasticity, the Barlett test was employed. Differences in $\delta^{15}\text{N}$ values between nests were evaluated using an Analysis of Variance (ANOVA) model, and pairwise comparisons were assessed using Tukey's Honest Significant Differences Method. For $\delta^{13}\text{C}$ comparisons, the Kruskal-Wallis test was utilized [34]. Regarding size comparisons, the Kruskal-Wallis test was applied to both isotopes. Additionally, a linear regression was conducted to determine if a significant relationship existed between size and isotopic values.

The isotopic niche width was calculated using the Stable Isotope Bayesian Ellipses in R (SIBER) package (version 2.1.9) [35]. The area of the convex polygons is sensitive to sample size; therefore, we used isotopic ellipses (SEA) for comparative purposes. SEAs were corrected for sample size (SEAc) to mitigate potential biases arising from differences in sample sizes between nests. The SEAc encompasses approximately 40% of the data with a 95% credibility interval [35].

For overlap analysis, we utilized the NicheROVER package from the R program (version 1.1.2) to estimate isotopic niches—a 95% probability region based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic values of bones. This method quantifies the probability of an individual from one group occupying the isotopic niche of another group [36]. We conducted 1000 runs with a probability level of ≥ 0.95 . NicheROVER offers directional estimates of niche overlap in multidimensional space and allows for unique bivariate projections of the niche region as ellipsoids. This visualization aids in examining geometry and overlap patterns. The overlap metric calculates paired comparisons in both directions, providing the probability that an individual belongs to a specific species. This method's directional estimates are considered more robust for niche characterization than traditional methods that use percentages to measure overlap. It accounts for data uncertainty through a Bayesian framework, avoids assuming a uniform distribution of individuals within the niche region, and is insensitive to sample size, reducing variations in the niche region and overlap [36] [37].

Carbon source utilization was studied using the "simmr" package in R (version 0.5.1.216) [38]. Simmr employs mixing models through both Markov Chain Monte Carlo (MCMC) algorithms and the faster Fixed Form Variational Bayes

(FFVB) to quantify the relative contribution of sources to the diet of loggerhead turtles. We operated under the assumption that the main prey items, supplied *ad libitum*, would offer a reliable integrated representation of the isotopic variability in the base of the food web they represent over time and space [9] [39] [40]. These prey items (Table 1) were collected from the same study site (Santa Marta region) for another study [41].

3. Results

3.1. Isotopic Variation between Nests

A total of 66 bone tissue samples were collected from *C. caretta* specimens. The groups formed are detailed in Table 1, showing the respective number of individuals. Each group represents a nest from the nesting beaches, some potentially belonging to the same mother due to the possibility of multiple clutches laid during the nesting season. Nitrogen isotope values ranged widely between 7.89‰ and 11.27‰ (mean 9.41‰ \pm 0.63‰), while carbon values varied between -19.65‰ and -17.22‰ (mean -18.02‰ \pm 0.55‰).

Average values for each group are presented in Table 2, revealing that individuals were primarily fed by species with low $\delta^{13}\text{C}$ values (-18.82‰ to -17.86‰). Moreover, it's presumed that these prey items provided a moderately high trophic level diet for the turtles, based on literature values (9.02‰ to 10.02‰). Groups 4 and 6 showed the widest ranges in their values. Conversely, groups 1 and 2 displayed narrower intervals for both isotopes. Specifically, group 4 had a slightly more distinct carbon isotope value compared to the others. Group 5 consumed prey with higher $\delta^{15}\text{N}$ values (>10‰) than the other groups, which ranged between 9‰ - 9.6‰.

Table 1. Mean carbon and nitrogen isotope values of prey from the Santa Marta region served as carbon sources in the Bayesian mixture models.

Presa	Mean $\delta^{15}\text{N}$	SD $\delta^{15}\text{N}$	Mean $\delta^{13}\text{C}$	SD $\delta^{13}\text{C}$	Reference
<i>Ophistonema oglinum</i>	9.1	0.51	-17.15	0.38	
<i>Mugil</i> sp.	7.24	0.51	-21.83	0.38	Garzón-Peña (2018)
Scombridae	8.39	1	-17.38	1	
Engraulidae	10.21	1	-18.18	1	

Table 2. Average carbon and nitrogen isotope values for loggerhead turtles (*Caretta caretta*) are presented for each nest. N indicates the number of samples, while SD denotes the standard deviation.

Nest	N	Mean $\delta^{15}\text{N}$ ‰ \pm SD	Mean $\delta^{13}\text{C}$ ‰ \pm SD
1	5	9.02 \pm 0.30	-17.90 \pm 0.34
2	8	9.38 \pm 0.40	-17.86 \pm 0.33
3	30	9.21 \pm 0.47	-17.97 \pm 0.52
4	5	9.62 \pm 0.89	-18.82 \pm 0.72
5	9	10.07 \pm 0.68	-17.7 \pm 0.39
6	9	9.55 \pm 0.78	-18.17 \pm 0.65

The medians for carbon isotopes were largely similar across nests, except for nest 4, which showed an isolated, asymmetrical data distribution. Nests 2 and 3 displayed a more symmetrical distribution. Additionally, nests 4, 3, and 5 exhibited greater dispersion, with all nests, except for 4 and 5, showing atypical data. For nitrogen isotopes, the medians across all nests were comparable, except for nests 5 and 6. Most nests displayed an asymmetric distribution, except for nests 1 and 5.

The Kruskal-Wallis test for carbon values did not reveal significant differences ($X^2 = 10.39$, $p > 0.05$). In contrast, the ANOVA comparison for nitrogen isotopes indicated significant variations in the values ($F_{5,64} = 8.96$, $p \leq 0.05$). Tukey's multiple comparisons test for the nitrogen isotope (Table 2) identified differences between specific nests. Notably, nests 5 and 1 ($p = 0.021 < 0.05$) and nests 5 and 3 ($p = 0.0029 < 0.05$) showed significant distinctions in isotope assimilation, while other nest pairings did not display differences.

Based on SEAc values, nest 4 exhibited the widest isotopic range at 2.69‰^2 , followed by nests 6 (1.80‰^2) and 5 (0.78‰^2). The remaining nests demonstrated narrower data ranges, with values below 0.6‰^2 , and nest 1 recorded the smallest range at 0.20 (Figure 2).

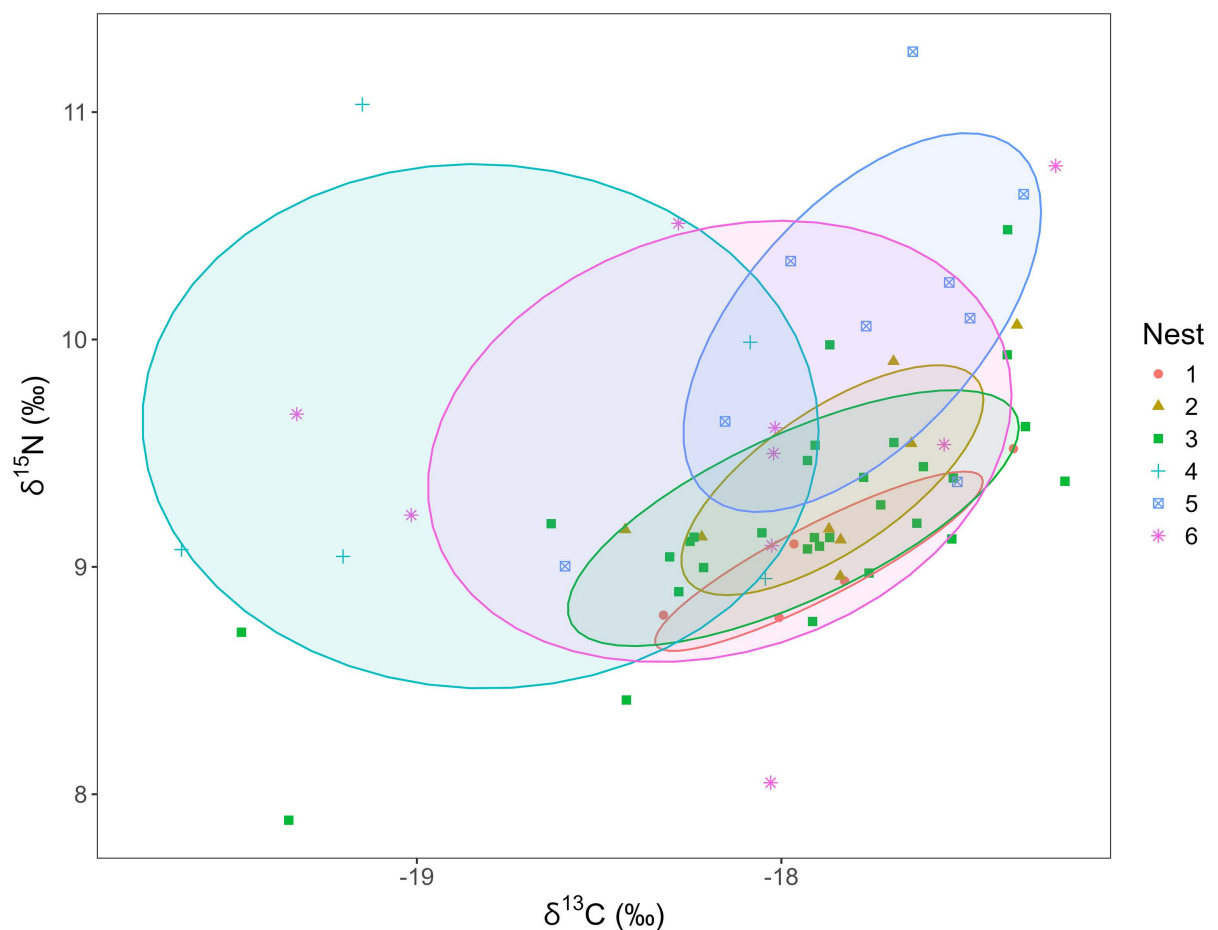


Figure 2. Isotopic niche (SEAc) for the six groups of loggerhead turtles (*Caretta caretta*) during the feeding process.

Table 3 presents the percentage (%) of isotopic overlap in paired comparisons of food assimilated across nests during rearing. Nest 1 had a 79% overlap with nest 2. However, when comparing the overlap of nest 2 with nest 1, it decreased to 34%. For nests 3 and 6, the overlap was 95%, indicating that nest 6's ellipse encompasses 95% of nest 3's ellipse. Conversely, the overlap from nest 6 to nest 3 was only 50%. Nest 6 exhibited high overlap percentages (>70%) with all other nests, followed by nests 7 and 4. Nest 5 showed minimal overlap with the other groups.

3.2. Isotopic Variation by Size (SCL)

For the size analysis, we considered 72 juvenile individuals grouped into six size intervals. Among the turtles sampled within the ProCTMM, the average straight carapace length (SCL) was 17.21 cm (S.D. = 1.58; range = 14 - 21 cm; N = 72). **Table 4** illustrates that most individuals had an SCL ranging from 15 to 18 cm.

The nitrogen isotope values ranged from 9.06 to 10.0‰ ($9.46 \pm 0.68\%$), while carbon isotope values ranged from -18.06 to -17.87% ($-17.99 \pm 0.58\%$). **Figure 3** and **Table 4** display the average values for each SCL class. The 18 - 19 cm group exhibited higher nitrogen isotopic ratios compared to other groups and displayed the largest deviations in terms of carbon isotopes, indicating this size range had the highest variance. Turtles exceeding 19 cm in size had lower nitrogen isotope values, suggesting a diet comprised of prey with lower trophic levels. Overall, minimal differences were observed in the isotopic ratios among groups, implying consistent dietary patterns regardless of size.

Table 3. Isotopic niche amplitude ($\%{}^2$) and percentage (%) of niche overlap among the six-loggerhead turtle (*Caretta caretta*) nests. SEAc: Amplitude corrected ellipse.

Grupo	1	2	3	4	5	6	SEAc ($\%{}^2$)
1	NA	79	98	75	66	97	0.20
2	34	NA	95	77	85	98	0.35
3	34	66	NA	75	67	95	0.56
4	5	13	26	NA	25	69	2.69
5	8	39	49	64	NA	89	0.78
6	11	31	50	75	53	NA	1.80

Table 4. Average values of carbon and nitrogen isotopes of the loggerhead turtle (*Caretta caretta*) for each SCL size. N = samples, μ = average and SD = standard deviation.

SCL (cm)	N	Mean $\delta^{15}N\%$ \pm SD	Mean $\delta^{13}C\%$ \pm SD
14 - 15	9	9.33 ± 0.68	-18.26 ± 0.55
15 - 16	18	9.40 ± 0.72	-17.87 ± 0.67
16 - 17	14	9.48 ± 0.57	-17.92 ± 0.34
17 - 18	14	9.41 ± 0.67	-17.99 ± 0.61
18 - 19	10	10.0 ± 0.68	-18.01 ± 0.81
>19	7	9.06 ± 1.00	-18.06 ± 0.44

When conducting the Kruskal-Wallis test for carbon values, no significant differences were observed ($X^2 = 3.72$, $p = 0.58 > 0.05$). Similarly, the comparison for nitrogen isotope values revealed no significant differences ($X^2 = 7.27$, $p = 0.20 > 0.05$).

Based on the isotopic width illustrated in **Figure 3** and the SEAc values provided in **Table 5**, Group 5 had the largest area, followed by Groups 2 and 1. In contrast, Group 3 occupied the smallest area. Despite these variations, all groups exhibited a comparable isotopic niche, suggesting significant overlap in resource utilization across different sizes. The percentage (%) of isotopic overlap in paired comparisons among SCL groups (**Table 5**) was high, indicating shared resource use among the groups. Notably, the least overlap was observed between the 16 - 17 cm group and both the 14 - 15 cm and 18 - 19 cm groups, with less than 30% of the isotopic niche area shared. This suggests that the primary differences in dietary patterns among juvenile turtles were between these size groups.

Regarding the linear relationship, there is insufficient evidence to suggest that nitrogen and carbon isotopes have a significant effect on the straight carapace length of loggerhead turtles ($p = 0.944$ and $p = 0.9190$, respectively). This implies that, based on this model, neither of the two isotopes significantly contributes to predicting size (**Figure 4**).

3.3. Contribution of Primary Carbon Sources to the Diet of Logger Head Turtles

The mixing model outputs illustrate the contribution of various prey to the diets of different nests (**Figure 5**) and size groups (**Figure 6**). Overall, *Mugil* sp. was the predominant contributor isotopically to the bone tissue of the turtles. Other prey such as *O. oglinum*, Scombridae, and Engraulidae were also present in the turtles' diets but in smaller proportions, accounting for approximately 25%.

Across the different nests, on average, *Mugil* sp. constituted about 40% of the turtles' diet, with proportions varying significantly among the samples. Nest 3 predominantly consumed this species (>70%) and exhibited the highest consumption of *O. oglinum* at 30%. In contrast, Nest 4 displayed the greatest variability in the consumption of this prey among its individuals.

Table 5. Isotopic niche amplitude (‰²) and percentage (%) of niche overlap among the six-loggerhead turtle (*Caretta caretta*) sizes. SEAc: Amplitude corrected ellipse.

SCL (cm)	14 - 15	15 - 16	16 - 17	17 - 18	18 - 19	>19	SEAc (‰ ²)
14 - 15	NA	80	26	64	73	43	1.20
15 - 16	65	NA	32	76	75	44	1.41
16 - 17	80	99	NA	98	92	64	0.26
17 - 18	69	94	45	NA	84	51	0.94
18 - 19	53	75	22	60	NA	19	1.79
>19	89	98	52	92	78	NA	0.50

Regarding size-based comparisons, smaller turtles (14 - 16 cm) consumed a larger proportion of *Mugil* sp., with less variability. Conversely, larger turtles (17 cm and above), while still predominantly consuming this prey, showed a decreased proportion and exhibited greater variability in prey contribution.

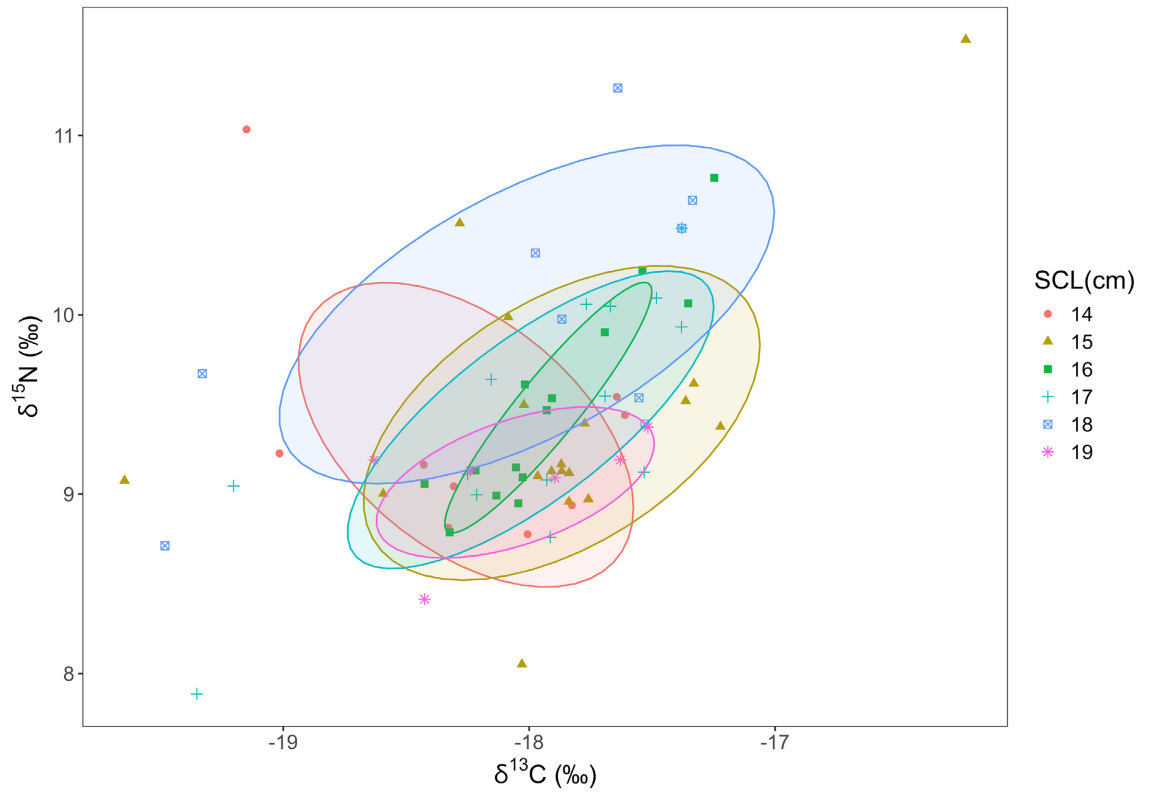
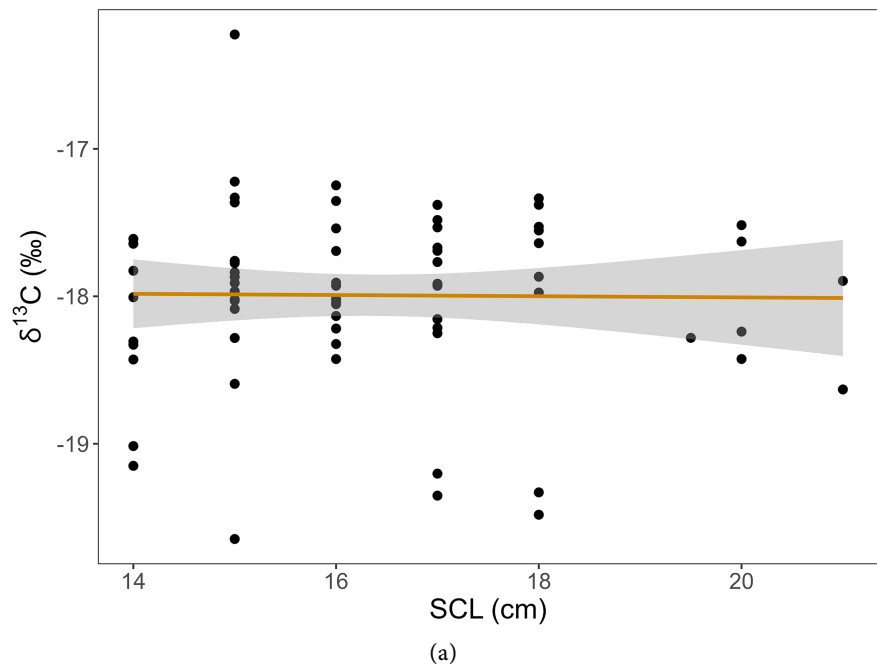


Figure 3. Isotopic niche for the six groups of SCL of loggerhead turtles (*Caretta caretta*) during the feeding process.



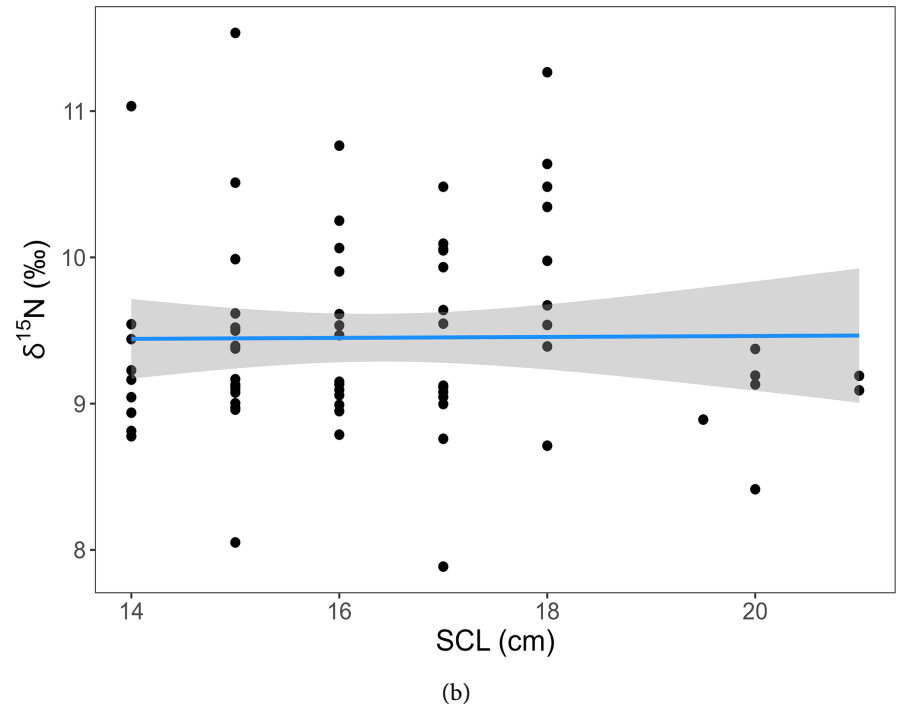


Figure 4. Linear regressions depicting size-related trends in carbon (a) and nitrogen (b) isotope ratios of loggerhead turtles are shown. Non-significant relationships are represented by solid lines, accompanied by their respective 95% confidence intervals (shaded area). Additionally, the equations and adjusted coefficients of determination (R^2) for the linear models are provided.

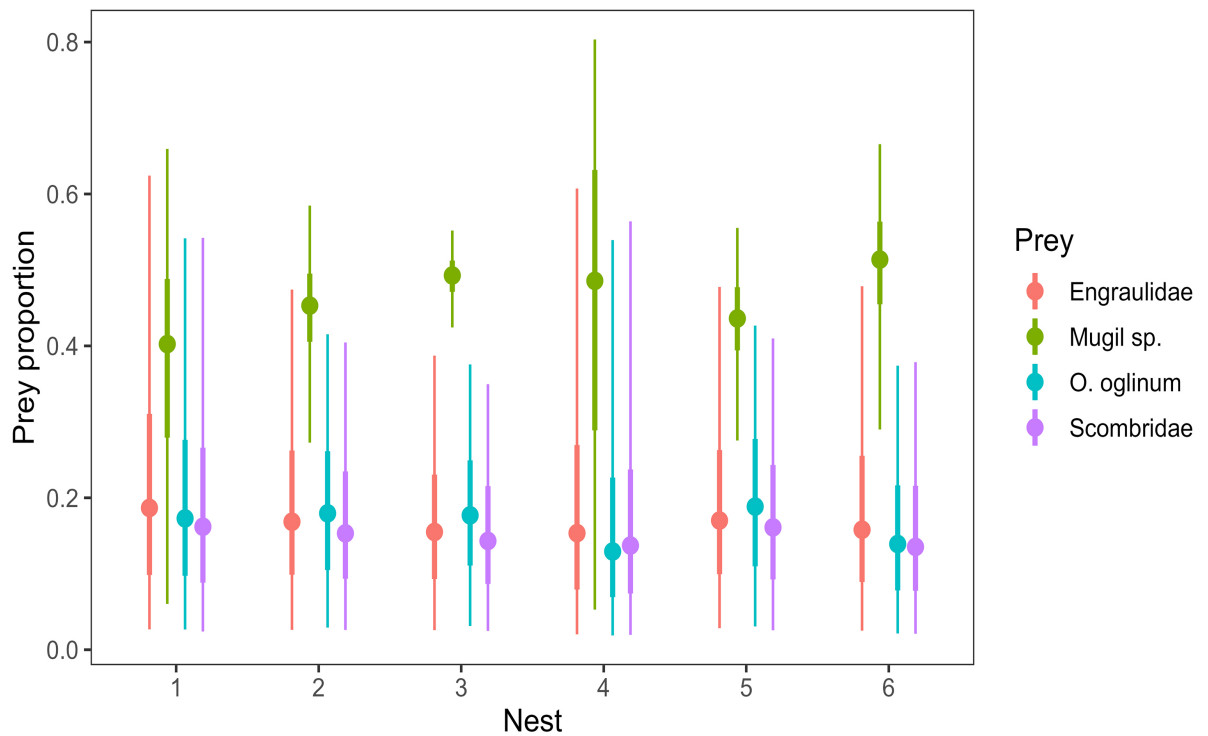


Figure 5. Contribution of the different prey supplied *Ad libitum* to loggerhead turtles among nests. Clean line: 95% confidence interval. Dark line: 50% confidence interval.

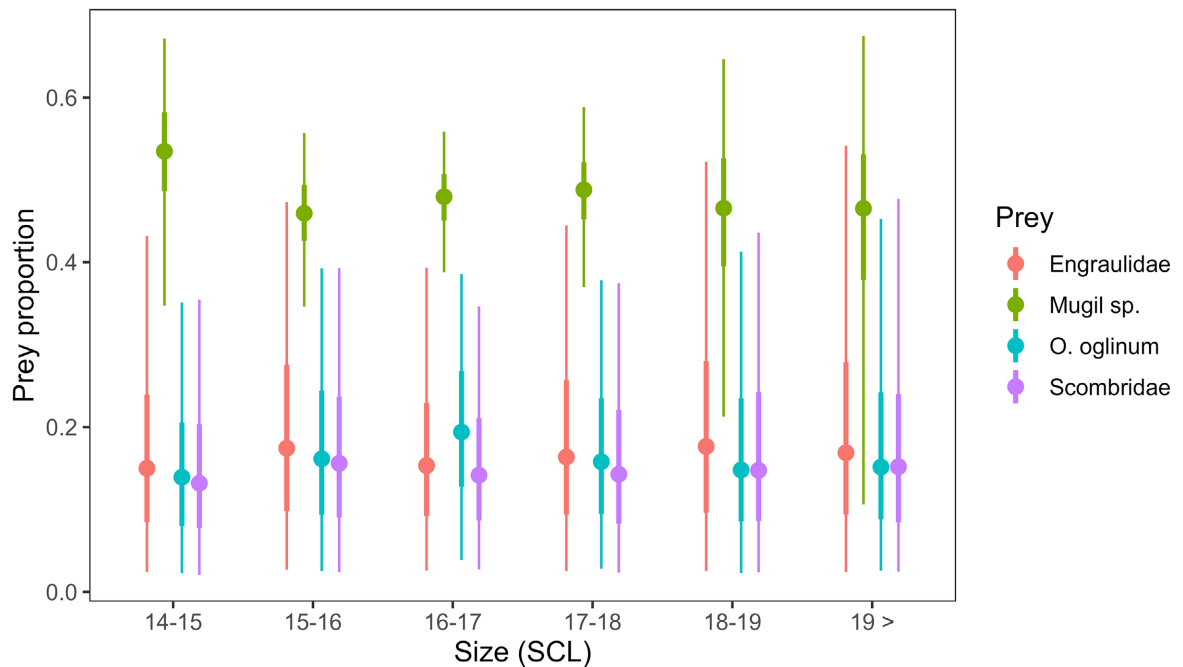


Figure 6. Contribution of the different prey supplied *Ad libitum* to loggerhead turtles among size (SCL). Clean line: 95% confidence interval. Dark line: 50% confidence interval.

4. Discussion

Based on the isotopic analyses conducted across the studied nests, no significant differences were observed in carbon isotope values, reflecting the consistent source of the food supplied. This consistency was expected given that all nests were provided the same prey *Ad libitum*. However, variations in nitrogen isotope values were evident, leading to distinct groupings, particularly in nests 2 and 5. These groups showed minimal isotopic overlap with each other.

Several factors could contribute to these differences, including intrinsic variability among individuals within each nest, variations in nutrient assimilation pathways, and age at death [42]. Additionally, individual factors like access to food, competition based on attributes such as strength, size, vitality, and prey preferences can influence food consumption [9].

In a study on bone tissue of *C. caretta*, 11 specimens found dead on the coasts of Northern Cyprus and southern Turkey displayed an average isotope $\delta^{15}\text{N}$ of $20\text{‰} \pm 0.2\text{‰}$ (range 13.1‰ to 26.4‰) and carbon $\delta^{13}\text{C}$ of $-14.16\text{‰} \pm 0.2\text{‰}$ (range -17.5‰ to -11.4‰) in individuals ranging from 23 to 79 cm [22]. These values differ from those found in our study, where nitrogen averaged $9.45\text{‰} \pm 0.2\text{‰}$ and carbon averaged $-17.99 \pm 0.58\text{‰}$. These discrepancies could be attributed to the turtles grazing in different geographical areas and the sampled individuals being predominantly adults, which would place them at higher trophic levels due to their varied diet encompassing both herbivores and carnivores in their natural environment.

In the results presented for *C. caretta*, differences were observed between nests despite having the same prey availability and feeding frequency. These variations

could stem from the genetic diversity among individuals in each nest, potentially originating from different mothers foraging in distinct geographical areas, with their isotopic signals persistently reflected in the bone [43] [44]. The intra-tissue variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values among juveniles from the same clutch may be attributed to inherent differences in stable isotope values, such as variations in physiology and metabolism. These differences can lead to variations in isotopic values even when individuals grow in the same environment and consume the same resources [45]. A study on green turtles found that inherent variations in stable isotope values differed among tissues in both juveniles and adults [9].

The results indicated no correlation between the size of the individuals and their isotopic values, aligning with previous studies suggesting that as sea turtles age, their trophic level and feeding area remain relatively stable [8] [22]. The variations in nitrogen isotopes observed at the individual level are likely intrinsic to each nest or size group. Smaller organisms often grow at a slower rate due to both genetic predisposition and physical limitations that restrict their food access, leading to differences among the evaluated groups [27].

For instance, a study described a comparable situation when examining growth rates and size at sexual maturity in *Chelonia mydas*, a closely related species. Under controlled tank conditions, they found that differences arose from variations between individuals or dietary preferences, such as the consumption of specific types of prey. These differences in growth rates, age, and other physiological and health factors can impact the diet assimilated in the tissues of sea turtles [2].

In contrast, a study on green turtles (*Chelonia mydas*) revealed that as turtles grow larger, they tend to feed at higher trophic levels [22]. However, this study also found no correlation between individual size, ranging from 23 to 79 cm, and the $\delta^{15}\text{N}$ isotopic signatures in bone collagen [22]. These findings align with our observations in *C. caretta*. Our research exclusively focused on juvenile turtles, with sizes smaller than those examined by Godley *et al.* Surprisingly, we found no significant differences among these smaller size groups, nor did we identify a clear relationship between isotopic data and straight carapace length.

Other studies on various sea turtle species similarly found no relationships between body size and the two isotope ratios, suggesting that loggerhead turtles may not exhibit size-related differences in foraging habitat use [46]. These findings, along with previous research, imply that ontogenetic habitat shifts in sea turtles are facultative, resulting in polymorphic life histories [46]. Additionally, these results may indicate that bone collagen, at least in this species and possibly in sea turtles overall, may not provide integrated dietary information over extended periods, approaching the lifespan of the individual, as suggested for other groups [47] [48].

The observations apply to loggerhead turtles and other sea turtle species for several reasons. Firstly, sea turtles have extended maturation periods, with estimates ranging from at least 9 to 14 years in leatherbacks, 19 to 27 years in greens, and over 20 years in loggerhead turtles [49]. As reptiles, turtles likely ex-

perience skeletal growth during these maturation phases and possibly beyond, involving ongoing remodeling and metabolic processes of skeletal elements. Consequently, bone collagen is expected to reflect dietary preferences over an intermediate timeframe, potentially filling in gaps when other information is unavailable [49]. Moreover, physical wear on the shell's outer surface suggests that this protein serves as an indicator of medium-term (6 - 12 months) dietary influences. Notably, the most significant dietary variations have been observed in juvenile organisms due to their body growth and utilization of different isotopic gradients [48] [50]. However, our study exclusively focused on juveniles under human care, representing a closely matched age class. Thus, the lack of differences observed was anticipated due to the narrow size range evaluated.

Barnes *et al.* [42] indicated that inherent variations among individuals raised on a controlled diet often account for a substantial portion of the variation observed in wild organisms. Given that these inherent changes are influenced by species, life history stages, and environmental factors, it is essential to quantify specific isotope variations in certain tissues for stable isotope studies to yield insights into trophic status and niche breadth of a population [9] [51]. Following this approach, they found no significant differences in the variance of $\delta^{15}\text{N}$ between laboratory and field animals, drawing from 53 observations of diverse aquatic and terrestrial organisms ranging in size from copepods to polar bears. However, the authors observed greater variation in carbon fractionation ($\delta^{13}\text{C}$) in laboratory-reared animals compared to their wild counterparts, based on 103 observations from their own research and the literature. Thus, the results obtained in our study, conducted under human care conditions, may offer insights into the inherent isotopic variations of *C. caretta* in natural settings. Consequently, it could be inferred that, despite turtles, and specifically *C. caretta*, having similar dietary habits, their tissue assimilation of these diets may differ due to factors such as population origin (genetic), prey selection, and individual size.

Turtles generally prefer to consume high-quality prey, bypassing those with lower nutritional value. As food availability decreases, they broaden their selection to include species with lower nutritional content but greater abundance to supplement their diet [7] [52]. In the controlled feeding environment of the breeding program, turtles selectively consume certain prey. Our study's mixture models revealed a consistent preference across all evaluated groups for *Mugil* sp., with *O. oglinum* being consumed to a lesser extent.

Additionally, a hierarchical behavior was observed, reflecting dominance and territoriality among individuals. This behavior manifests as one turtle displacing another to claim its space, especially evident during anticipated feeding times or when feeding schedules were introduced. Given these observations, it is reasonable to suggest that the behavior exhibited by *C. caretta* under human care in the ProCTMM program could influence the dietary assimilation into their tissues. This behavior underscores that, irrespective of their nesting origin or size, these turtles consistently prioritize certain food types over the available options.

5. Conclusions

No significant differences were observed in carbon isotope values across nests, likely due to the uniform food source provided by the ProCTMM program, sourced from the nearby Colombian Caribbean region. However, variations in nitrogen isotopes were evident, influenced by factors such as competition, stress levels, and individual food preferences. No significant differences in isotopic values were detected among different size groups (SCL), nor was there a discernible relationship between these variables. This suggests that the isotopic assimilation into the bone tissue of *C. caretta* is not influenced by individual size, potentially because all turtles are within the same juvenile age category. Given that these animals are only a few months old, maternal dietary influences from their natural environment may still be present in the analyzed tissue, capturing information from months to years.

Interestingly, among the supplied prey, *Mugil* sp. was predominantly assimilated across various nests and sizes of turtles. This suggests a preference for this species or its greater representation in the bone tissue.

Acknowledgements

This research is developed within the framework of the ProCTMM and is part of the Research Group Dynamics and Management of Marine-Coastal Ecosystems (DIMARCO) Category A1 of Colciencias/Minciencias, with the endorsement of the Regional Autonomous Corporation of Magdalena (CORPAMAG) as Environmental Authority of relevance to the sector. This study was part of the internal research project of the Universidad Jorge Tadeo Lozano entitled “isotopic analysis and evaluation of the genetic variability of the caguama turtle (*Caretta caretta*), disposed to rising and introduction processes in the Colombian caribbean, stage II”. To Luis Garzon for dissecting all the turtles to obtain bone tissue. To Leidy Hernández for collaborating with the processing of the stable isotope samples.

Data Availability Statement

The data presented in this study are available on request from the corresponding author.

Credit Authorship Contribution Statement

Brenda N. Mejía-Guarnizo: Conceptualization, Methodology, Formal analysis, Investigation, Writing-original draft, Visualization. Carlos J. Polo-Silva: Conceptualization, Methodology, Writing-review & editing, Supervision. Aminta Jau-regui-Romero: Conceptualization, Writing-review & editing, Supervision, Project administration, Funding acquisition. Antonio Delgado-Huertas: Investigation, Resources.

Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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