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Interspecific and intraspecific comparison of the isotopic niche of shrimps targets of fishing in south-eastern Brazil

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Abstract

The study compares the isotopic niche $(\delta^{13}C-\delta^{15}N)$ of three species of penaeid shrimps (*Xiphopenaeus kroyeri, Artemesia longinaris* and *Litopenaeus schmitti*) that are targets of fishing in south-eastern Brazil. The two hypotheses raised are based on the niche theory, in which the coexistence between organisms that have similar dietary demands is possible due to trophic partitioning: (i) shrimp species that share the habitat have segregated isotopic niches; and (ii) stages of maturity and genders vary with the trophic habitat ($\delta^{13}C$) and/or trophic position ($\delta^{15}N$). In multispecific fishing grounds, the isotopic niches of the shrimp species were segregated or had low overlap, indicating trophic partitioning. The intraspecific comparison of $\delta^{13}C$ and $\delta^{15}N$ showed a similar trend in all species. For $\delta^{13}C$, the values were more enriched in adult individuals than in juveniles, but similar between males and females. For $\delta^{15}N$, adult individuals also had more enriched values, and males were more enriched than females. The results confirm the hypotheses raised, and the assumptions of niche theory apply to these penaeid shrimps.

Introduction

Niche differentiation is the process by which species and individuals develop different forms of use of the available resources (MacArthur, 1972). Considering feeding resources, competition influences interspecific and intraspecific trophic diversity, and niche overlap tends to be smaller due to trophic partitioning, allowing the coexistence of organisms that have similar dietary demands (MacArthur & Levins, 1967; Pianka, 1981). Trophic partitioning among morphologically similar consumers may also vary according to individual feeding preference, and prey availability, diversity and stability (Araújo *et al.*, 2011; Duarte *et al.*, 2017).

The analysis of stable isotopes of carbon (δ^{13} C) and nitrogen (δ^{15} N) in the consumer tissues complements the understanding of its trophic ecology from other approaches, such as analysis of digestive tract, observation of feeding behaviour in the environment, and morphological and functional analysis of the digestive tract (Newsome *et al.*, 2007, 2012; González-Ortegón *et al.*, 2021). The δ^{13} C values generally indicate the origin of feeding resources (oceanic or coastal; pelagic or benthic) and are used to recognize the trophic habitat of consumers, while δ^{15} N values are a measure of trophic position, especially useful when trophic ecology is not evaluated using the methods mentioned above (Cherel *et al.*, 2005; Fry, 2008; Ferreira *et al.*, 2020).

Layman *et al.* (2007) introduced ecomorphological metrics to summarize quantitative information from isotopic data to describe the trophic structure of a population or community. Subsequently, Jackson *et al.* (2011) developed the Bayesian approach to compare these metrics, allowing robust inferences about the isotopic niche of consumers. The stable isotopes provide quantitative information about the consumer's isotopic niche, which is associated with their feeding resources and trophic niche. Thus, the isotopic niche approach allows inferences on how consumers use the feeding resources available in their habitat (Layman *et al.*, 2007; Newsome *et al.*, 2007; Abrantes *et al.*, 2014).

Shrimps of the Penaeidae family play an important role in benthic communities because they are omnivorous secondary consumers that feed mainly on organic detritus and other invertebrates, providing energy to the upper trophic levels of both benthic and pelagic food webs (Abarca-Arenas *et al.*, 2007; Di Beneditto *et al.*, 2012). However, few studies have addressed the trophic relationships in shrimps using isotopic metrics (Willems *et al.*, 2016; Ji *et al.*, 2019; Ferreira *et al.*, 2020), and there is still a lack of information on how species and individuals interact with each other.

This study compares the isotopic niche of three species of penaeid shrimps that are targets of fishing in south-eastern Brazil to understand their trophic relationships both interspecific and intraspecific. The hypotheses raised are based on the niche theory, in which the coexistence between organisms that have similar dietary demands is possible due to trophic partitioning. The two hypotheses raised are as follows: (I) species that share the habitat (fishing



Fig. 1. Location of the six fishing ports in the states of Espírito Santo (ES) and Rio de Janeiro (RJ), south-eastern Brazil, where the shrimps were sampled.

ground) have segregated isotopic niches; and (II) stages of maturity (juvenile and adult) and genders (male and female) vary with the trophic habitat (δ^{13} C) and/or trophic position (δ^{15} N) to minimize intraspecific feeding overlap.

Materials and methods

Sampling

The shrimps were sampled in six fishing ports in south-eastern Brazil, located at states of Espírito Santo and Rio de Janeiro (Figure 1). The choice of fishing ports was defined by their representativeness in regional landings. *Xiphopenaeus kroyeri* (Heller, 1862), known as Atlantic seabob shrimp, was sampled in the six fishing ports. The Argentine stiletto shrimp (*Artemesia longinaris* Bate, 1888) and the southern white shrimp (*Litopenaeus schmitti* (Burkenroad, 1936)) were sampled in two fishing ports. The choice of the species sampled in each fishing port was based on their presence in the landings, verified *in situ*. Juvenile and adult individuals of both genders are captured in local fisheries (Fernandes *et al.*, 2011, 2014; Eutrópio *et al.*, 2013) and were sampled for this study.

The fisheries were done with bottom trawl net in coastal waters around the fishing ports, between 1–3 nautical miles from the coastline and 5–30 m deep (Ferreira & Di Beneditto, 2021). Shrimp species are caught simultaneously during bottom trawl. Samplings were performed between June and August 2018, immediately after landing. In the ports of Conceição da Barra, Vitória and Atafona (Figure 1), fishing is focused on *X. kroyeri*. In Anchieta, Farol de São Tomé and Macaé (Figure 1), fishing is multispecific, with more than one target species in the landings.

For the analysis of δ^{13} C and δ^{15} N, 120 individuals of each species were sampled to represent the local stocks (30 adult males, 30 juvenile males, 30 adult females and 30 juvenile females). After sampling, each shrimp was identified at the species level and categorized according to the stage of maturity and gender, considering the morphology of the primary and secondary sexual traits. In males, the presence of gonopores in the fifth pair of pereiopods and the copulatory organ (petasma, which is fused only in adult individuals) were observed (Costa et al., 2003). The females were recognized by the gonopores in the third pair of pereopods and by the presence of telic situated ventrally between the fourth and fifth pair of pereopods (Costa et al., 2003). Gonads chromatic feature is the visual method to determine the maturation stage of the ovaries in penaeid shrimps (Brown & Patlan, 1974, Dumont & D'Incao, 2004; Peixoto et al., 2018). The developing or developed adult females have voluminous and olive-coloured ovaries, and the spawned females exhibit flaccid ovaries with a white and translucent colour.

Isotopic analyses of carbon (δ^{13} C) and nitrogen (δ^{15} N)

In the laboratory, the abdominal muscle of each shrimp was removed, stored in a dry and sterile plastic tube, frozen $(-20^{\circ}C)$, lyophilized and homogenized in fine powder in a mortar and pestle. The exoskeleton and internal organs, such as gills, gonads, hepatopancreas and intestine, were removed before storage to prevent the analysis of tissues with different metabolic rates, compromising the isotopic interpretation.

Samples of 0.4 mg of muscle tissue (dry weight) were analysed to determine the isotopic composition in a Delta V Advantage interface Conflo IV, mass spectrometer (Thermo Scientific, Germany) coupled to the elemental analyser Flash 2000 at the Laboratório de Ciências Ambientais of Universidade Estadual do Norte Fluminense Darcy Ribeiro. The reference values for carbon and nitrogen isotopic analyses were Vienna Pee Dee Belemnite (VPDB) and atmospheric N2, respectively. The samples were analysed together with analytical blanks and urea analytical standards (VAT Analysentechnik -330802174; CH_4N_2O Mw = 60, C = 20%, N = 46%) with certified isotopic compositions ($\delta^{13}C = -39.89\%$ and $\delta^{15}N = -0.73\%$). Analytical control was performed every 10 samples using a certified isotopic standard (Elemental Microanalysis Protein Standard OEA): δ¹³C = -26.98% and $\delta^{15}N = +5.94\%$. The analytical reproducibility was based on triplicates for every 10 samples: $\pm 0.3\%$ for $\delta^{15}N$ and $\pm 0.2\%$ for δ^{13} C. The results were expressed in parts per thousand (%).

Data analysis

All data analyses were performed in the R program (R Core Team, 2021), assuming an a priori error of 5% ($\alpha = 0.05$). The assumptions of normality and homoscedasticity were tested by the Shapiro–Wilk and Levene tests, respectively.

To verify the first hypothesis that shrimp species that share the habitat have segregated niches, the fishing ports considered were those with multispecific fishing: Anchieta (X. kroyeri and L. schmitti), Farol de São Tomé (X. kroyeri and A. longinaris), and Macaé (X. kroyeri, A. longinaris and L. schmitti). The isotopic niche breadth is based on the position of individuals in the δ^{13} C- δ^{15} N space (Layman *et al.*, 2007; Jackson *et al.*, 2011), calculated from the function of stable isotope Bayesian ellipses in the R program (Stable Isotope Bayesian in R - SIBER) (Jackson et al., 2011; Parnell et al., 2013; R Core Team, 2021). The area of the standard ellipse, which represents the isotopic niche width, is based on the centroid of the group and sized with the chance of including 40% of subsequently sampled data. The area of each standard ellipse was compared probabilistically with the posterior Bayesian distributions, calculating the proportion of ellipses for group 1 which is greater than that for group 2 (Jackson et al., 2011). The percentage of overlap of the area of the standard ellipses is the measure of isotopic niche overlap between species. To analyse how the values of $\delta^{13}C$ and $\delta^{15}N$ varied among the shrimp species in the multispecific fishing ports, one-way ANOVA and a posteriori Tukey's test were used.

To verify the second hypothesis that stages of maturity and genders vary in relation to the trophic habitat and/or trophic position to minimize intraspecific feeding overlap, two-way ANOVA was used. This test isolates the effects of each factor (stage of maturity and gender) separately, and measures the effect of the interaction between them.

Results

Interspecific comparison

The isotopic niche overlap between shrimp species was absent or low (Figure 2). The percentage of overlap of the area of the standard ellipses in Anchieta (*X. kroyeri vs L. schmitti*) was 34% (Figure 2A); in Farol de São Tomé (*X. kroyeri vs A. longinaris*) was absent; and in Macaé, it was 9% between *A. longinaris* and *L. schmitti* and absent in the comparisons involving *X. kroyeri*. Niche segregation was mainly supported by *X. kroyeri*, which showed more enriched values of δ^{13} C compared with the other species (Figure 2, Table 1).



Fig. 2. δ^{13} C and δ^{15} N values of shrimp species from multispecific fishing ports in south-eastern Brazil (A: Anchieta; B: Farol de São Tomé; C: Macaé). The Triangle, lozenge and circle represent *Xiphopenaeus kroyeri*, *Artemesia longinaris* and *Litopenaeus schmitti*, respectively. The rows represent the data ellipses (40% confidence interval) for the isotopic niches.

Intraspecific comparison

The values of δ^{13} C differed significantly between maturity juvenile and adult individuals in all species, with higher values in adults (two-way ANOVA, F = 103.49, df = 1, $P = 2 \times 10^{-16}$) **Table 1.** Mean and standard deviation (SD) of δ^{13} C and δ^{15} N in shrimp species from six fishing ports in the states of Espírito Santo (ES) and Rio de Janeiro (RJ), south-eastern Brazil

Fishing port Species	δ^{13} C (‰) Mean ± SD	δ^{15} N (‰) Mean ± SD	anova δ ¹³ C	Tukey post hoc $\delta^{13}\text{C}$	anova δ ¹⁵ n	Tukey post hoc $\delta^{15}N$
Conceição da Barra (ES)						
X. kroyeri	-17.6 ± 0.4	10.7 ± 0.3				
Vitória (ES)						
X. kroyeri	-16.4 ± 0.7	11.0 ± 0.7				
Anchieta (ES)						
X. kroyeri	-16.0 ± 0.6	11.1 ± 0.3	F = 22.319	X. kroyeri > L. schmitti	F = 15.076	X. kroyeri > L. schmitti
L. schmitti	-16.7 ± 1.3	10.9 ± 0.2	$P = 3.97 \times 10^{-6}$	$P = 4 \times 10^{-6}$	<i>P</i> = 0.0001	<i>P</i> = 0.0001
Atafona (RJ)						
X. kroyeri	-16.5 ± 0.3	11.6 ± 0.3				
Farol de São Tomé (RJ)						
X. kroyeri	-16.4 ± 0.3	11.1 ± 0.3	F = 485.35	X. kroyeri > A. longinaris	F=198.01	X. kroyeri > A. longinaris
A. longinaris	-17.4 ± 0.4	11.6 ± 0.2	P = 2.2 × 10 ⁻¹⁶	$P = 2.2 \times 10^{-16}$	$P = 2.2 \times 10^{-16}$	$P = 2.2 \times 10^{-16}$
Macaé (RJ)						
X. kroyeri	-17.4 ± 0.4	11.7 ± 0.3				
A. longinaris	-18.1 ± 0.3	11.4 ± 0.2	F = 325.5	X. kroyeri > A. longinaris > L. schmitti	F = 29.93	X. kroyeri > A. longinaris < L. schmitti
L. schmitti	-18.2 ± 0.2	11.6 ± 0.2	$P = 2 \times 10^{-16}$	P<0.01	$P = 9.65 \times 10^{-13}$	<i>P</i> < 0.0009

(Figure 3A). The exception was *A. longinaris* in Farol de São Tomé, with juveniles more enriched in δ^{13} C. Meanwhile, no significant difference was found in the three species comparing gender males and females (two-way ANOVA, *F* = 1.491, df = 1, *P* = 0.22) (Figure 3A). No interactions were detected between maturity and gender factors (two-way ANOVA, *F* = 0.38, df = 1, *P* = 0.68).

In general, the values of δ^{15} N varied significantly between stages of maturity (two-way ANOVA, F = 53.02, df = 1, $P = 6.09 \times 10^{-13}$) and genders (two-way ANOVA, F = 51.62, df = 1, $P = 1.20 \times 10^{-12}$) (Figure 3B). No interactions were detected between maturity and gender factors (two-way ANOVA, F = 0.48, df = 1, P = 0.61). Adult individuals were more enriched than juveniles, and males had more enriched values than females. The exceptions were *X. kroyeri* in Conceição da Barra and *A. longinaris* in Farol de São Tomé, where there was no significant difference between both stages of maturity (F = 0.486, df = 1, P = 0.48 for *X. kroyeri*, F = 0.087, df = 1, P = 0.76 for *A. longinaris*) and genders (F = 0.121, df = 1, P = 0.72for *X. kroyeri*, F = 0.061, df = 1, P = 0.80 for *A. longinaris*).

Discussion

Interspecific comparison

The interspecific comparison of the isotopic niche of coexisting shrimp species corroborated the first hypothesis raised in the study. The results support the assumption of niche theory that species that share habitats and have similar feeding demands tend to have segregated niches with low overlap (MacArthur & Levins, 1967; Pianka, 1981). Trophic partitioning among shrimps, inferred by stable isotopes, has already been recorded as a strategy to minimize the possible effects of interspecific competition in other decapod crustaceans (Cummings *et al.*, 2011) and other animal taxa (Alfaro *et al.*, 2006; Hyodo, 2015; Figgener *et al.*, 2019).

The isotopic niche segregation was mainly supported by the more enriched values of δ^{13} C in X. kroyeri. The distribution pattern of this species justifies the difference. Castilho et al. (2008) analysed the abundance of eight species of shrimp in southeastern Brazil in relation to environmental variables, including X. kroyeri, A. longinaris and L. schmitti. The authors found that the occurrence of X. kroyeri was limited in waters with temperatures below 28°C and beyond 15 m depth, suggesting that the species is more abundant in and dependent on warmer and shallower waters than other species. Values of $\delta^{13}C$ are more enriched in shallow coastal waters of the benthic environment (Fry, 2008), which is the preferred habitat of X. kroyeri. Typical values for benthic microalgae reported in the literature range between -12 and -20‰ (Bouillon et al., 2011). The benthic environment is consistently more enriched in δ^{13} C than its pelagic counterpart (~7‰) due to isotopic fractionation (France, 1995). This benthopelagic difference can be reflected in shrimp δ^{13} C values, and thus the microalgae and phytoplankton can be one of the main primary sources of resources for these species (Fry, 2008). Isotopic analysis proves to be a powerful tool to distinguish between benthic and pelagic food sources for coastal animals.

The greatest dispersion of shrimps along the δ^{15} N axis, illustrated in Figure 2, suggests that the individuals have high food plasticity. The isotopic results showed the feeding plasticity of penaeid shrimps, which was already verified in previous studies with digestive tract analysis (Boschi, 1969; Branco & Moritz Junior, 2001; Albertoni *et al.*, 2003; Spanjersberg *et al.*, 2006; Willems *et al.*, 2016).

The density of individuals of any exploited population by commercial fishing must be high in each fishing ground to maintain the viability of the economic activity (King, 2007). Food availability is only one of the features for the maintenance of shrimp populations. Other environmental features, such as type of sediment, salinity, depth and water temperature are also determinant or limiting to the establishment of the species (Gulland & Rotschild, 1981).



Fig. 3. δ¹³C and δ¹⁵N values of stages of maturity (juvenile and adult) and genders (male and female) of the shrimp species from six fishing ports in south-eastern Brazil. Horizontal lines in the box indicate median of boxplot. (F.A., adult female; F.J., juvenile female; M.A., adult male; M.J., juvenile male; CBarra, Conceição da Barra; FST, Farol de São Tomé).

Xiphopenaeus kroyeri was the only species sampled in the six fishing ports, indicating that both availability of feeding resources and other environmental features are adequate for maintaining their fishing stocks. Conversely, *A. longinaris* prefers areas with colder water (Costa *et al.*, 2005), and above 22°S (i.e. north of the port of Farol de São Tomé) there is no record of this species in landings. *Litopenaeus* *schmitti* preferentially inhabits sandy bottom (Boos *et al.*, 2016), with larger particle size than fine sand, silt and clay, characteristic of coastal areas with strong fluvial influence. This would explain, for example, the absence of the species in the port of Atafona, which is influenced by the Paraíba do Sul River, the largest river input in south-eastern Brazil (Souza *et al.*, 2010).

Intraspecific comparison

The second hypothesis that there is variation in the trophic habitat and/or trophic position of juvenile and adult individuals, and males and females to minimize feeding overlap, was confirmed. In general, the same trends were noted for the three shrimp species. Differences between stages of maturity were observed for δ^{13} C and δ^{15} N. The most enriched (less negative) values of δ^{13} C in adults and less enriched (more negative) in juveniles may indicate feeding activity mainly associated with benthic environment and water column, respectively (Fry, 2008).

The less enriched values of $\delta^{15}N$ in juveniles may be related to the size (and trophic position) of the prey consumed. The feeding habits of the three shrimp species were never analysed at the six fishing ports considered by this study. However, previous studies done in other areas and based on digestive tract analysis showed that for X. kroyeri (Cortés & Críales, 1990; Branco & Moritz-Júnior, 2001; Willems et al., 2016) and A. longinaris (Boschi, 1969; Spanjersberget al., 2006), there is a difference in the size of prey consumed by juveniles (smaller prey) and adults (larger prey). As crustaceans develop and undergo morphological and physiological changes, their prey capture skills and nutritional needs are altered (Dall et al., 1990). Additionally, there are studies with A. longinaris (Gimenez et al., 2002) and L. schmitti (Lemos et al., 2002) that showed variations in digestive enzymes between juveniles and adults. This represents variations in their food metabolism, which most likely interferes with the selection of consumed resources.

The results showed that the trophic habitat (δ^{13} C) was shared between genders, but the values of δ^{15} N varied (males > females). This finding partially diverges from previous studies based on the digestive tract analysis (Boschi, 1969; Cortés & Críales, 1990; Branco & Moritz-Júnior, 2001; Spanjersberg *et al.*, 2006; Willems *et al.*, 2016), which found males and females sharing the feeding resources. In this case, as well as for juveniles and adults, the range of δ^{15} N values was not large enough to define a trophic level (trophic enrichment of 1.4‰ or higher, according to McCutchan *et al.*, 2003). The difference in δ^{15} N between males and females can be explained by the size of prey consumed, as assumed for juveniles and adults.

Besides differences in the size of prey consumed, other possible explanations for the intraspecific difference between genders regarding the δ^{15} N values should be considered. The efficiency of $\delta^{15}N$ as trophic marker is sensitive to the nutritional status of the consumer and quantitative and qualitative differences in food intake and assimilation (Hobson et al., 1996; Jennings et al., 2002; Das et al., 2003). In experimental tanks with Litopenaeus vannamei, Moss & Moss (2006) tested the effects of gender and body size on food acquisition time. Bardera et al. (2020), in a study with the same species, compared the pattern of feeding activity between males and females. The results of both studies indicated that even with a smaller body size compared with females, which is a morphological feature of all penaeid shrimps (Dall et al., 1990), males showed a competitive advantage in the time of food acquisition, ingesting greater quantities in the same time interval. These differences in feeding behaviour could explain the variations in the $\delta^{15}N$ values among genders, as recorded in the study.

Conclusion

The isotopic niche of the penaeid shrimps targeted by fisheries in south-eastern Brazil and their isotopic composition (δ^{13} C and δ^{15} N) showed interspecific and intraspecific trophic partitioning, respectively. Therefore, the results are in accordance with the assumptions of niche theory. Meanwhile, the isotopic niche

model ($\delta^{13}C \times \delta^{15}N$) is a simplified 2D geometry representing only a part of the species' real niche. As discussed in Shipley & Matich (2020), to represent a more realistic and multidimensional niche space, such as described by Hutchinson (1957), additional niche axes will need to be considered, including habitat, time, ratio size and inter-individual differences.

The utilization of stable isotopes as an indirect measure of the trophic ecology of consumers, such as the penaeid shrimps, was supported by the results of this study. The partitioning of trophic resources, along with other environmental factors, contributes to the maintenance of these shrimp stocks for exploitation by extractive fishing.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/S0025315422000558.

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Author contributions. Keltony de Aquino Ferreira: Conceptualization, Sampling, Methodology, Investigation, Formal analysis, Writing. Ana Paula Madeira Di Beneditto: Conceptualization, Funding acquisition, Writing, Adriane Cristina Araújo Braga: Writing – review.

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

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