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Geographic Variation in *Opisthonema oglinum* (Lesueur, 1818) in the Southeastern Brazilian Bight Inferred from Otolith Shape and Chemical Signatures

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Abstract: The thread herring *Opisthonema oglinum* (Lesueur, 1818) is a small pelagic fish distributed in the western margin of the Atlantic Ocean from the United States to Argentina. It is a target species for diverse commercial fisheries, including the Brazilian industrial purse seine fleets that operate in the Southeastern Brazilian Bight. To investigate the geographic variation in the thread herring populations in this fishing ground, sagittal otoliths were collected from two areas: Rio de Janeiro (RJ: 23°04' S, 44°03' W) and Santa Catarina (SC: 26°05' S, 48°18' W). Otolith shape analyses and multi-elemental signatures were statistically evaluated using elliptical Fourier descriptors and elemental/Ca ratios. Remarkable differences in the thread herring otoliths between the two areas were found. The previous scenario in which the thread herring constitutes a single panmictic population in the Atlantic Ocean is now debatable. The implications of these results in terms of rational fisheries management for this species are highlighted.

Keywords: small pelagic fish; purse seine; Brazil; natural tags; elliptical Fourier descriptors; geochemical signatures

Key Contribution: Otolith shape and chemistry evidenced a remarkable geographic variation in *Opisthonema oglinum* individuals caught in an area of highest abundance in the Southeastern Brazilian Bight, where it is one of the most important target fish species for the industrial purse seine fleets. The dataset suggests a metapopulation structure composed of different population units which should be managed accordingly.

1. Introduction

Many freshwater, brackish, and marine fish species are important halieutic resources worldwide, sustaining a myriad of fisheries, both artisanal and industrial [1]. The sustainable and rational management of fisheries [2] implies a correct knowledge of the spatial pattern of the exploited fish species [3,4]. Diverse factors promote a heterogeneous spatial pattern of fish species in their distribution areas, namely some environmental constraints that usually drive phenotypic responses [5,6]. These phenotypic responses include a set of behavioral, morphological, and life history traits [6–8]. Thus, geographic variation in fisheries resources is somewhat expected and constitutes a key issue for fisheries management, such as the establishment of fishing closed areas and allowed catches, among other guidelines [4,9,10].

Different natural tags can be assessed to identify the geographic variation in fishes at different spatial and temporal scales, including the use of otoliths [11–13]. Otoliths are paired structures located in the inner ear of teleostean fishes that detect sound and water balance. There are three pairs (*lapilli*, *sagittae*, and *asteriscii*) associated with three otolithic organs (*utricle*, *sacculus*, and *lagena*, respectively) [14]. They are metabolic inert structures made of calcium carbonate that grow continuously, and within the structure, a set of minor and trace elements that replaces calcium in the aragonite matrix could reflect the environment where a fish lived [15–17]. It is well known that otolith shape and chemistry may vary within species due to several factors, such as fish growth, feeding regime, ontogeny, and habitat, among others [18–20]. Thus, otoliths are suitable tools to evaluate individual phenotypic geographic variations at the stock, population, or subpopulation level, which requires appropriate sampling designs, methodological approaches, and study goals [9,10,12]. The *sagitta* is usually the largest and thus the most used in previous studies, although the other otoliths are also useful and informative for these purposes [21–25].

In the case of small pelagic fishes, studying population structure and dynamics is quite complex since these species are usually widespread, show schooling behavior, and present huge mobility, in addition to their biomass being highly variable in short periods of time [26–29]. This is the case of the Atlantic thread herring, *Opisthonema oglinum* (Lesuer, 1818) (Clupeiformes, Clupeidae), a species distributed in the western Atlantic Ocean from the United States to Argentina. Inside its distribution area, the thread herring is a remarkable fishery resource, and there are many studies concerning different aspects of its biology and ecology, including age and growth [30–33], reproductive biology [34,35], trophic ecology [36,37], and seafood quality and processing [38,39], among others. These studies took place in the thread herring major fishing grounds, including the United States (North Carolina to Florida coast) [40–42], the Gulf of Mexico and the Caribbean Sea [34,43–46], and some areas off the Brazilian coast, where the species distribution is heterogeneous [47,48].

The thread herring is most abundant in the Southeastern Brazilian Bight (SEBB, 22° S–29° S), an area of 150,000 km² that is 1000 km long, which supports the highest fishing productivity in the Brazilian coast [49,50]. The industrial purse seine fishery is focused on three major species, namely *Sardinella brasiliensis*, *O. oglinum*, and *Chloroscombrus chrysurus*, which, during the period of 2017–2021, comprised 62% of the total purse seine landings [51–53]. Based on the former sources, the average landings from the purse seine fleets during this period attained 65,876.19 tones, 34% corresponding to *S. brasiliensis*, 22% to *O. oglinum*, and 6% to *C. chrysurus*. The relative importance of these three species on purse seine landings varies according to the resource's availability, showing some inter-annual oscillations (Figure 1). This scenario has been previously documented for the Brazilian sardine purse seine fishery, notably in relation to *Scomber japonicus* and *Trachurus lathami* as alternative species [54–57], although in the last years, *O. oglinum* has become the main alternative species when sardines are scarce. In general, this is a common situation for all small pelagic fishes worldwide [27,29].

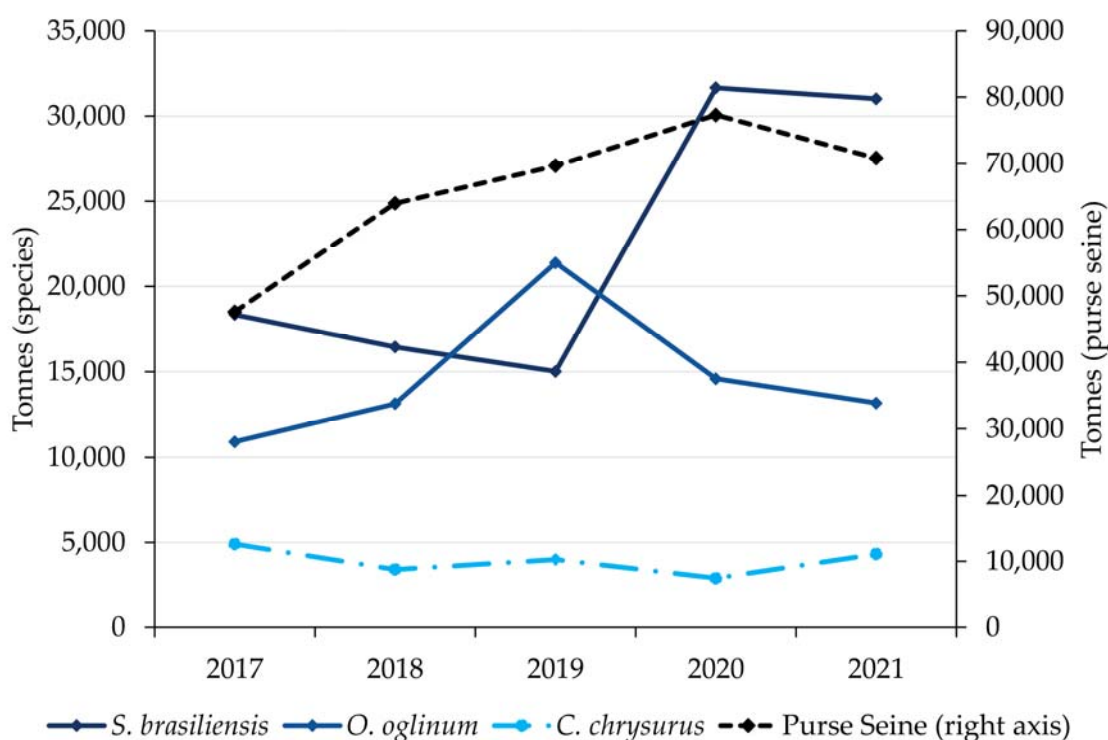


Figure 1. Industrial landings in the Southeastern Brazilian Bight (22° – 29° S) for the three major target species (*Sardinella brasiliensis*, *Opisthonema oglinum*, *Chroloscombrus chrysurus*) and total catches for the purse seine fleet.

Recently, *O. oglinum* was sampled in seven locations along the Brazilian coast (approximately $00^{\circ}30'$ S, $48^{\circ}30'$ W to $27^{\circ}30'$ S, $48^{\circ}30'$ W), and the population structure was analyzed using mtDNA [58]. This former study suggests a single and homogeneous group in the whole area for the species, a typical result for small marine pelagic fishes, suggesting a panmictic population. However, this does not necessarily mean that regional population units do not really exist since the large-scale genetic flow of the marine pelagic fish species seems to be sufficient to prevent the detection of spatial (mtDNA) genetic heterogeneity [59].

This study aimed to evaluate *O. oglinum* geographic variation in its most abundant area in the Southwestern Atlantic using alternative tools. As a small pelagic fish, it was hypothesized that even in a relatively homogenous oceanographic area (22° – 29° S) the thread herring can present a heterogeneous distribution [6,28]. The objective of this study was to assess, for the first time, using otolith analyses (shape and chemical signatures), the population structure of this species in the Brazilian major fishing ground (Rio de Janeiro and Santa Catarina coastal area).

2. Materials and Methods

2.1. Study Area

The Southeastern Brazilian Bight (SEBB: 22° – 29° S, Figure 2) is characterized by a continental shelf extending up to 230 km, and a unique hydrodynamic pattern in terms of thermal (T) and salinity (S) gradients [60,61]. Based on hydrodynamic differences, it is possible to recognize the inner (<50 m depth), the mid- (50 < 100 m), and the outer (100 < 200 m) continental shelf [60]. Three water masses predominate in the area: the Coastal Water (CW, variable T, $S < 34$); the Tropical Water (TW, $T > 20^{\circ}\text{C}$, $S > 36.40$), and the South Atlantic Central Water (SACW, $T < 20^{\circ}\text{C}$, $S < 36.40$). The Brazil Current (BC) transports these water masses southward in the area [61]. Two upwelling systems (Cape Frio and Cape of Santa Marta Grande) and biogeochemical fronts (mixing boundaries between adjacent water masses) also play an important role in the productivity of the continental shelf [50,60]. Mainly during the autumn–winter, the area experienced intrusions of the

Brazilian Coast Current (BCC) flowing from southern Brazil northward up to 25° S and eventually 23° S, transporting productive and cold waters (15° – 23° °C) [50,62]. Principally, during the spring–summer, SACW sub-superficially resurges into the continental shelf, enriching the area. In the Rio de Janeiro area, runoff of freshwater and brackish waters in the continental shelf is due to the Guanabara Bay and the East Fluminense Lagoon Systems [63,64]. Between $24^{\circ}40'$ and $25^{\circ}40'$ S, apports are due to the Cananéia–Iguape lagoon system and the Paranaguá Estuarine Complex [65,66]. The area of Santa Catarina presents a narrow continental shelf and follows the general oceanographic features described for the whole area. These processes make the SEBB the most productive area of the Brazilian coast [50,60,67].

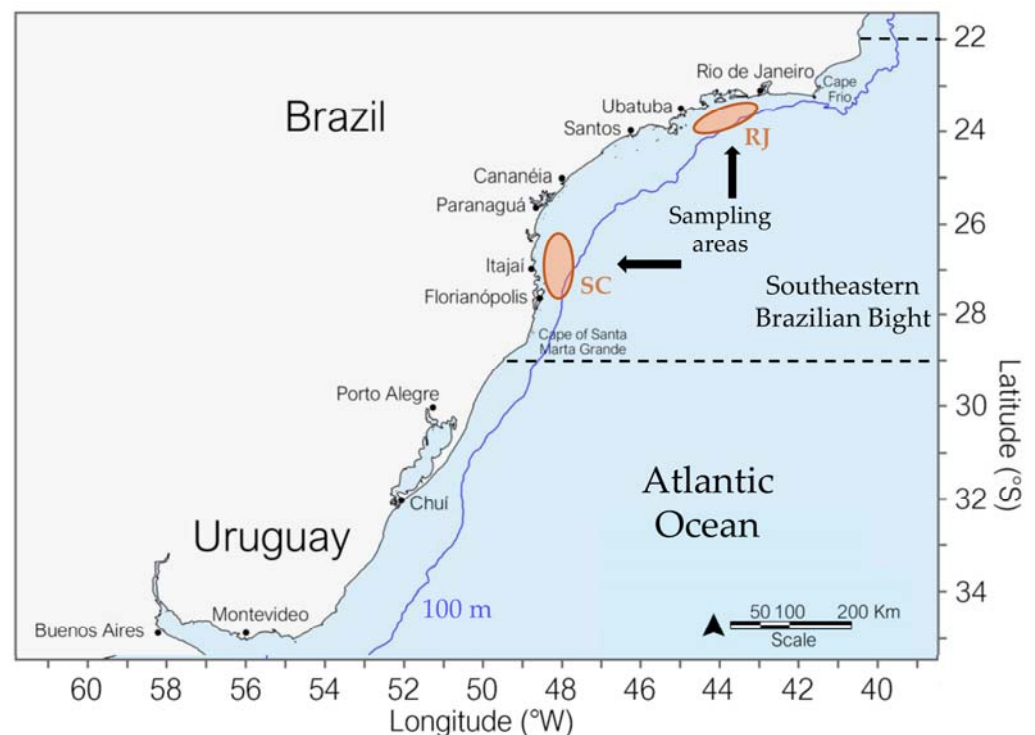


Figure 2. Southeastern Brazilian Bight area (dotted lines) in the Atlantic Ocean showing the main coastal cities, with the sampling areas in Rio de Janeiro (RJ) and Santa Catarina (SC) (fishing grounds) highlighted.

2.2. Biological Sampling

Fish samples of *O. oglinum* were obtained from the purse seine fleets in two distinct areas, Rio de Janeiro (RJ: $23^{\circ}04'$ S, $44^{\circ}03'$ W) and Santa Catarina (SC: $26^{\circ}05'$ S, $48^{\circ}18'$ W), between June and October 2011 (Figure 2). In the laboratory, each individual was measured (total length: TL, 0.1 mm), and the sagittal otoliths were carefully removed with a plastic tweezer. The otoliths were cleaned with ethanol 70% and distilled water, dried in a paper towel, and stored in plastic vials. To minimize ontogenetic influences and the sample size effect, a balanced sample of twenty-five specimens from each area comprising individuals in a restricted total length (227–254 mm, average of 240.0 mm for RJ and 238.8 mm for SC) and age (6–9 months old) range was used [68–70]. The age attribution for this sample was completed using otolith microstructural analysis [71].

2.3. Otolith Shape Analysis

Left sagittal otoliths were positioned with the *sulcus acusticus* oriented up and the rostrum oriented left on a dark background, and digital images were captured in full color (*jpeg) and 2560×1920 pixels using a stereomicroscope coupled to a camera with reflected light. Otolith shape was described with elliptical Fourier descriptors (EFD). The otolith

outlines were obtained using the ShapeR package in the R-project [72]. Firstly, the otolith images were transformed into grayscale, and then into black-and-white images using a threshold pixel value. These transformed images supported the outline capture. The pixel noise was removed by calculating a weighted moving average over three coordinate points. The Fourier variables were obtained and standardized in terms of size, rotation, and starting point. The first twelve harmonics that attained 98.5% of the cumulative power were used for shape reconstruction. During the standardization, the first three components were omitted, as well as the coefficients (eight) that presented an allometric influence. A total of 37 EFDs were used in further analyses.

2.4. Otolith Chemical Analysis

Right sagittal otoliths were cleaned in an ultrasonic bath for 5 min using ultrapure water (Thermo Scientific, Lab Tower EDI 15), followed by immersion in 3% analytical grade hydrogen peroxide (H_2O_2 , *v/v*) (Fluka Trace Select 30%) for 15 min to remove any adherent biological tissues. The otoliths were then rinsed with ultrapure 1% nitric acid (HNO_3 , *v/v*) (Fluka Trace Select 69%) for 10 s and triple-washed with ultrapure water for 5 min to remove the acid [73]. Finally, otoliths were stored in pre-decontaminated plastic tubes and allowed to dry overnight in a laminar flow hood [74]. The decontaminated otoliths were then weighed (OM_R , 0.00001 g) using an analytical balance, dissolved for 15 min in 100 μL of HNO_3 (Fluka Trace Select 69%), and then diluted with ultrapure water to a final volume of 5 mL [2% HNO_3 (*v/v*) and 0.02% TDS (*m/v*)] before stirring with a vortex [20].

Sixteen minor and trace elements (^{137}Ba , ^{111}Cd , ^{52}Cr , ^{59}Co , ^{65}Cu , ^7Li , ^{25}Mg , ^{55}Mn , ^{23}Na , ^{60}Ni , ^{208}Pb , ^{85}Rb , ^{121}Sb , ^{82}Se , ^{88}Sr , and ^{66}Zn), plus the calcium (^{44}Ca), were analyzed with Inductively Coupled Plasma Mass Spectrometry (ICP-MS) using an iCAP 227 TM Q 228 (Thermo Fisher Scientific, Bremen, Germany) instrument equipped with a concentric glass nebulizer, a Peltier-cooled baffled cyclonic spray chamber, a standard quartz torch, and a two-cone interface design (nickel sample and skimmer cones). Argon of high purity (99.9997%, Gasin II, Leça da Palmeira, Portugal) was used as the nebulizer and plasma gas. Qtegra™ software (Thermo Fisher Scientific, Bremen, Germany) was used for instrument control and data acquisition. The instrument was operated under the following conditions: RF power, 1550 W; argon flow rate, 14 L/min; auxiliary argon flow rate, 0.8 L/min; and nebulizer flow rate, 0.98 L/min. Indium (^{115}In), Scandium (^{45}Sc), Yttrium (^{89}Y), and Terbium (^{159}Tb) were monitored as internal standards.

The otolith samples were analyzed in random order to avoid possible sequence effects. Procedural blanks and Certified Reference Material n° 22 “Fish Otolith” (NIES 22, National Institute for Environmental Studies, Japan) were similarly prepared for blank corrections, accuracy calculations, and quality precision for the analysis of selected trace elements in fish otoliths. The precision of individual elements was determined from the percentage of the relative standard deviation (RSD, %) of three replicate measurements and varied from 2% to 10%. The accuracy, expressed as a percentage of the recovery rate (RR, %), ranged between 85% and 109%. Both values (RSD and RR) were within the analytical accepted values (Dove et al. 1996: RSD:20% and RR 75–125%). The limit of detection (LOD, $\mu\text{g/L}$) were obtained from the individual calibration of the curves using the three sigma criteria: ^{137}Ba (0.049), ^{44}Ca (24.176), ^{111}Cd (0.008), ^{59}Co (0.103), ^{52}Cr (0.049), ^{65}Cu (0.240), ^7Li (0.100), ^{25}Mg (1.163), ^{55}Mn (0.012), ^{23}Na (1.787), ^{60}Ni (0.092), ^{208}Pb (0.007), ^{85}Rb (0.009), ^{121}Sb (0.005), ^{82}Se (1.024), ^{88}Sr (0.008), and ^{66}Zn (0.160). RSD ranged between 0.98%–249 and 3.49%. Trace elements consistently above the LOD (^{111}Cd , ^{121}Sb , ^{82}Se , and ^{66}Zn) were excluded from further analyses. Multi-elemental signatures (MESs), originally in μg element/L solution, were thereafter transformed to μg element/g otolith and finally to μg element/g calcium [75].

2.5. Statistical Analysis

Prior to performing statistical analyses, outliers of elemental ratios (element/Ca) were checked using a Grubb’s test and trunked, if needed [69]. Thereafter, they were

checked for normality (Shapiro–Wilk test) and homogeneity of variances (Levene’s test). Mn/Ca and Pb/Ca were $\log(x + 1)$ transformed to meet these assumptions. To ensure that site-specific differences in otolith chemistry were not confounded by otolith mass (OM_R), the relationship between elemental ratios and OM_R was evaluated using an analysis of covariance (ANCOVA), with OM_R as a covariate and area as a fixed factor. The effect of OM_R on otolith chemistry was thus removed by subtracting the product of the common within-group linear slope by OM_R [68]. This relationship was significant for Na/Ca, Cr/Ca, Cu/Ca, Li/Ca, Mn/Ca, and Pb/Ca ($p < 0.05$). After assumption checking, t -tests were used to explore the single differences in MES between the areas.

The EFD, MES, and EFD + MES datasets were analyzed using multivariate techniques as follows. The data were $\log(x + 1)$ transformed and subjected to a principal component analysis (PCA) using a variance–covariance matrix. The components that accounted for 95% of the total variance were selected to subsidize subsequent analyses. A hierarchical cluster analysis (HCA, Euclidian distance and Ward aggregation method) was used to verify the grouping power without prior knowledge of the original area of thread herring otoliths. The power to predict the areas was evaluated by applying a stepwise discriminant function analysis (DFA), whose accuracy was verified using the percentage of correct reclassification for the discriminant functions using a jackknifed (“leave one out”) matrix. The Doornik–Hansen statistics were calculated to verify the multivariate normality of each dataset [76]. Accordingly, significant differences were tested with a parametric multivariate analysis of variance (MANOVA, approximate F -statistic Pillai’s trace). Statistical analyses were performed based on theoretical and applied sources [59,77–81] using Systat v.13.2 software (SYSTAT Software Inc., San Jose, CA, USA), PAST 4.12, and R-Program packages. A significance level of 0.05 (α) was used in all statistical procedures.

3. Results

3.1. Otolith Shape Analysis

After running a PCA, nine components explained 95% of the total variance. The dendrogram produced using the HCA allowed us to identify four fish groups corresponding to two otoliths shapes (OS), one from Rio de Janeiro ($OS1$), two groups from Santa Catarina ($OS2$ and $OS4$, with some bias), and another group that represents a mix from the two areas but closer to RJ ($OS3$) (Figure 3a). $OS1$ represented an otolith shape typical of those from Rio de Janeiro, which was proportionally larger in height and more rounded and crenate than those in thread herring from Santa Catarina (Figure 4). In this OS , some individuals from SC were recorded, as well as the outlier group $OS2$. $OS4$ was characterized by otoliths proportionally longer in length and less crenate, which is typical of those from Santa Catarina (Figure 4). $OS3$ was defined as a mixing group with no clear pattern, being constituted both by individuals from RJ and SC equally. DFA presented a satisfactory percentage of reclassification (72% overall, 72% for Rio de Janeiro, and 72% for Santa Catarina). The Doornik–Hansen test indicated normality ($Ep = 4.527$, $p = 0.379$). The MANOVA revealed a significant difference between the areas ($F = 2.376$, $p = 0.02936$).

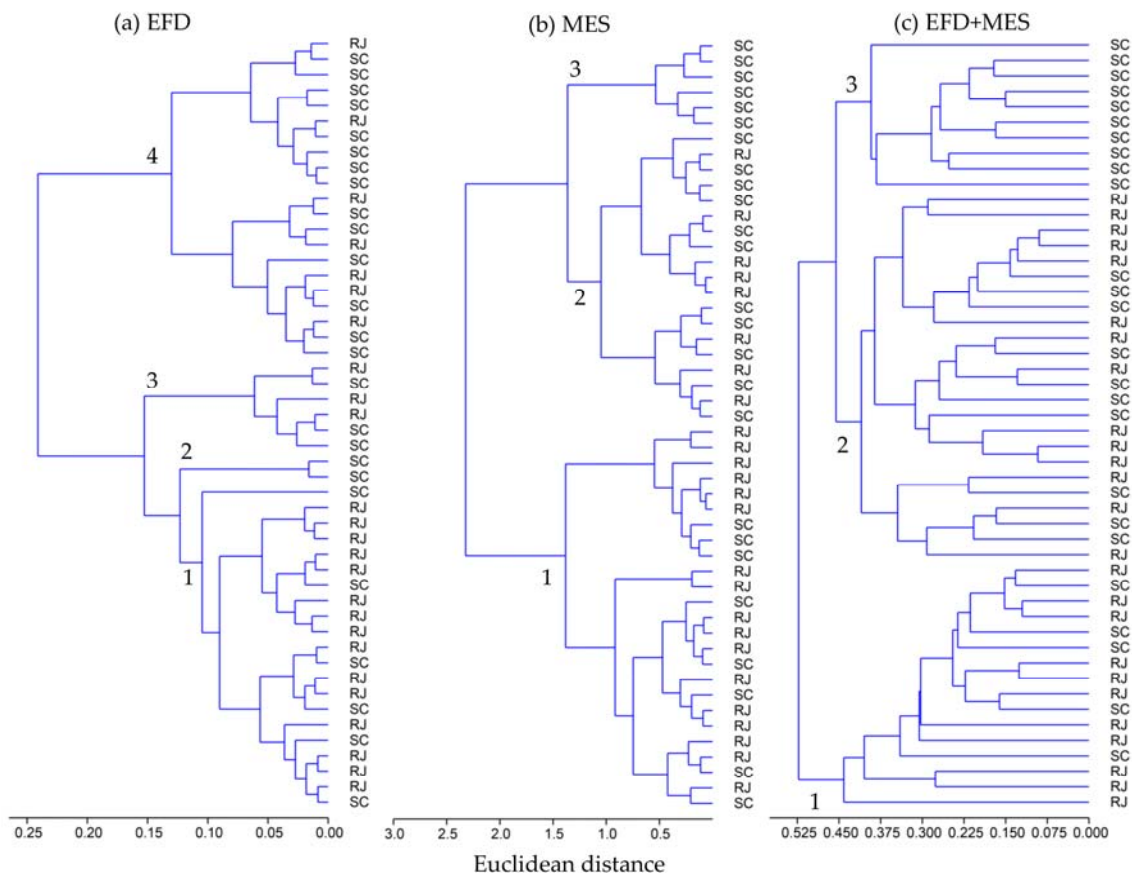


Figure 3. Dendrograms highlighting groups (arabic numbers) corresponding to the otolith shapes (a), multi-elemental signatures (b), and otolith shape + multi-elemental signatures (c) of *Opisthonema oglinum* from the Southeastern Brazilian Bight (22°–29° S) (for more details, see result’s section).

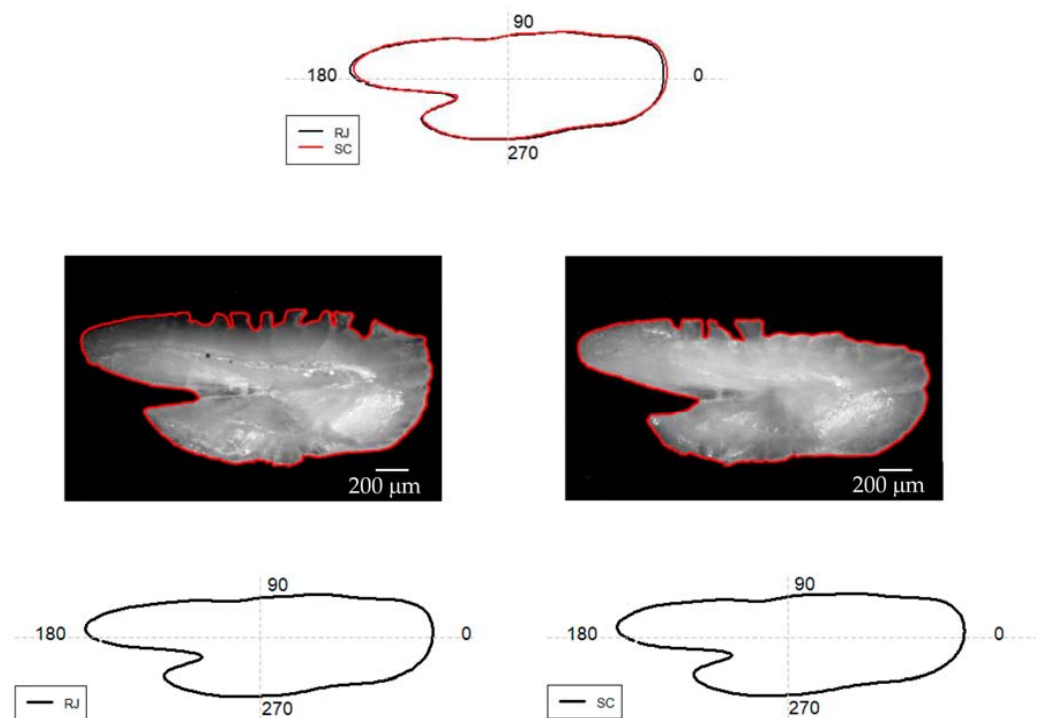


Figure 4. Images and outlines of the two otolith shapes in *Opisthonema oglinum* from the Southeastern Brazilian Bight (22°–29° S).

3.2. Otolith Chemical Analysis

Opisthonema oglinum otoliths did not present differences between the two areas when individually analyzed for the most multi-elemental signatures, except for Na/Ca, Mg/Ca, and Mn/Ca (Figure 5). The PCA resulted in seven components that explained 95% of the total variance. The HCA dendrogram identified three fish groups of chemical signatures: one from Rio de Janeiro, with some bias (CS1), a second mixing group (CS2), and a third strictly from Santa Catarina (SC) (Figure 3b). The multi-elemental signatures combined in each area characterize the groups of each area (Figure 5). MES presented a higher percentage of re-classification of DFA than EFD (76% overall, 80% for Rio de Janeiro, and 72% for Santa Catarina), which was supported by a remarkable difference between the MES from Rio de Janeiro and Santa Catarina (MANOVA, $F = 4.807$, $p = 0.000486$; multivariate normality $E_p = 13.77$, $p = 0.467$).

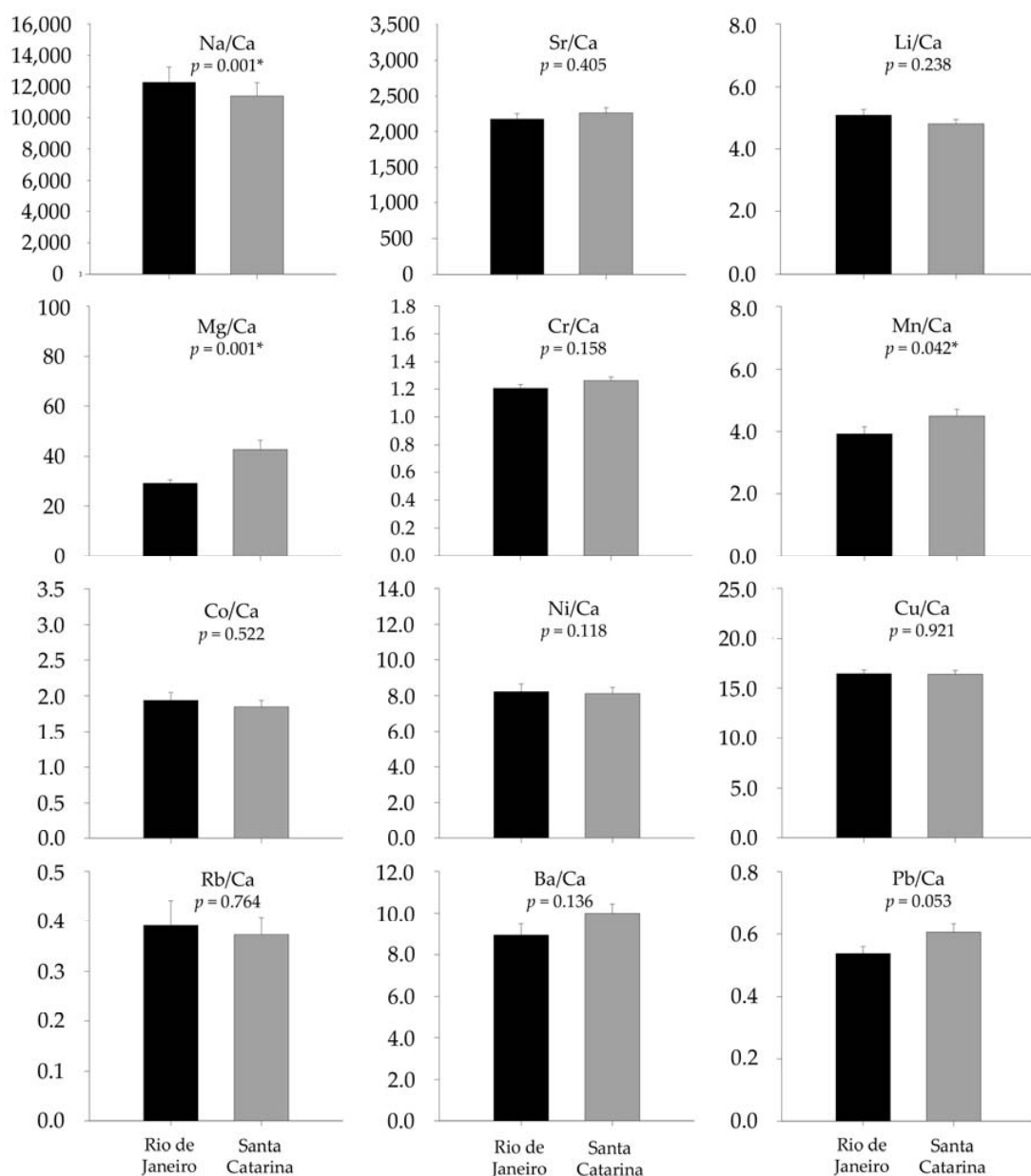


Figure 5. Comparison of the element/Ca ratios for the whole otoliths in *Opisthonema oglinum* from the Southeastern Brazilian Bight (22°–29° S) between Rio de Janeiro and Santa Catarina. Data are presented as mean values ± standard errors. The asterisks (*) mean a significant difference between areas (Student *t*-test, $p < 0.05$).

3.3. Otolith Shape and Chemical Analyses Combined

The integrative approach (MES + EFD) supported the geographic variation in thread herring otoliths. Seven principal components accounted for 95% of the explanation. The dendrogram from the HCA followed the same trend as that presented in the MES HCA, with a fish group from Rio de Janeiro (OS-CS1, with some bias), a mixing group (OS-CS2), and an exclusive group from Santa Catarina (OS-CS3) (Figure 3c). In this case, the number of individuals in the Santa Catarina group increased in relation to the MES analysis. The percentages of reclassification in the DFA were highest in relation to the EFD and MES analyses (78% overall, 84% for Rio de Janeiro, and 72% for Santa Catarina). The data presented multivariate normality ($E_p = 13.29$, $p = 0.5039$), and a remarkable difference between areas was detected (MANOVA, $F = 6.163$, $p = 5.45 \times 10^{-5}$).

4. Discussion

The otolith shape analyses and geochemical signatures evidenced geographic variation in *O. oglinum* from the Southeastern Brazilian Bight. Regional environmental conditions inside the study area are potential drivers for these differences. Rio de Janeiro coastal waters are close to highly productive areas in a relatively extensive continental shelf, including the Guanabara Bay, the East Fluminense Lagoon Systems, and the Cape Frio upwelling, whereas Santa Catarina inshore waters are in a less productive oceanographic area [67]. These distinct environmental conditions could influence fish feeding and growth, thus producing otolith proportionally larger in height and longer in length from Rio de Janeiro and Santa Catarina, respectively. This could also somewhat explain the higher Na/Ca and lower Mg/Ca and Mn/Ca ratios found in Rio de Janeiro, although most element/Ca ratios did not show any particular geographic variation. Moreover, all the natural tags combined showed a remarkable difference between the individuals from both areas. Thus, EFD and MES appear to be high-resolution proxies for geographic variation in *O. oglinum* from the Southeastern Brazilian Bight.

The mechanisms behind the otolith shape determination remain poorly known, but they are related to exogenous (environmental) and endogenous (physiological) factors [13,82,83]. Regarding the environment, highly productive areas tend to modulate otolith morphotypes as a result of the combination of temperature, salinity, and food availability, which enhances growth rates and favors intense feeding behavior [25,84,85]. In the SEBB, diverse species present otolith morphotypes related to the Rio de Janeiro area, such as *Sardinella brasiliensis* [86], *Isopisthus parvipinnis* [87], and *Merluccius hubbsi* [88], among others, and the same is observed for the thread herring. This is a common pattern for the main fisheries resources in SEBB [49], evidencing a general trend on a macro spatial scale.

Endogenous factors also modulate the otolith shape, whose complexity increases with age [89]. The use of thread herrings 240 mm long and 6–9 months old indicated otoliths are well-differentiated just after first maturity, which occurs at 190 mm and 5 months old [35,71]. Differences in individual growth appear after sexual maturity [71]; thus, geographic differences in the otolith growth parameters are expected to occur in the selected individuals. The current results confirm a previous observation that the otolith shape can be used to evaluate geographic variation even before the otolith “adult” pattern would be completely acquired [70]. There is no ontogenetic description (by size/age classes) for thread herring otolith shape, although in longer/older individuals (310 mm, ~two years old), the sagitta is more dentate [71,90]. This was probably the source of bias in the EFD analyses, which were less accurate in relation to MES and EFD + MES, presenting the most between-areas mixing (HCA), the smallest percentage of reclassification (DFA), and the highest p -value in the MANOVA, even being significant. Notwithstanding, the EFD is an up-to-date approach used to successfully study the spatial discrimination of fish groups, including small pelagic fishes [13,91–94].

Regarding the MES, knowledge about the incorporation mechanism for the minor and trace elements in fish otoliths is still limited to a few elements [95]. The general process of assimilation involves absorption from the water via the gills and intestine; thus,

elements enter the blood and are transported to the inner ear, where they pass by the endolymph and are incorporated into the otolith [15,95,96]. Water temperature and salinity, feeding regime, and environmental gradient concentrations are the major exogenous factors that affect the chemical composition (and shape) of otoliths [97–99]. Nevertheless, minor and trace elements found in the aragonite matrix also result from endogenous processes, including some structural otolith-bound proteins [95]. Recently, it was suggested that only those elements resulting from the salt-fraction of the endolymph (e.g., ^{88}Sr , ^7Li , ^{11}B , ^{24}Mg , ^{39}K , ^{55}Mn , ^{138}Ba), not bound to proteins, are useful for identifying individuals from distinct geographic areas [95]. Among them, five were studied here (Sr/Ca, Li/Ca, Mg/Ca, Mn/Ca, Ba/Ca), and two indicated significant differences between areas (Mg and Mn) as described below.

Sr/Ca and Ba/Ca are positively and negatively related to salinity, respectively [100–102]. Thread herrings from Rio de Janeiro are in an area characterized by the water masses formerly described (Section 2.1) and by three fronts as follows [cf. 50]. The Cape Frio Upwelling Front (CFUF) flows southwestward, mainly in the summer, transporting nutrients from the Cape Frio upwelling system. The Bottom Thermal Front (BTF) separates the inner and mid-shelf (50 m depth), and the Surface Haline Front (SHF) separates the mid- and outer shelf and boundaries among the CW, TW, and SACW. In Santa Catarina, these three water masses are present as well as the BTF and SHF, with winter intrusions of the BCC. The MES observed for Sr/Ca, Ba/Ca, and Mg/Ca can be associated with this set of environmental features related to 6–9 months of thread herring life in these areas. A higher Sr/Ca ratio in SC can result from the BCC intrusions, whilst the lower ratio in RJ results from the warmer oligotrophic habitat experienced during late summer, autumn, and winter. During these seasons, the continental shelf does not receive SACW intrusions and fronts oscillate less [50,60]. Ba is also linked to terrestrial run-off and freshwater/river discharge in estuaries [103] and up-welling phenomena [104]. Ba/Ca differences, with a higher ratio in RJ, are clearly explained by the runoff from the Guanabara Bay and the East Fluminense Lagoon Systems. However, these differences (Sr/Ca and Ba/Ca) in otoliths were not large enough to be statistically valid.

Mg/Ca is positively related to temperature and tends to increase with intense feeding activity [105,106]. A lower average value in Rio de Janeiro suggests the influence of cold waters transported by the Cape Frio Upwelling Front (CFUF) in this area [50]. The ratios observed can also be related to feeding activity. The thread herring presents great trophic adaptability, consuming a wide range of prey, both benthic and pelagic [44,107]. Copepods, diatoms, and other prey are common in its diet, and it is sustained with items that occupy lower trophic levels. These are typical organisms susceptible to local environmental changes that take place in the SEBB [50]. Considering that the individuals analyzed here came from the most recent spawning season (summer, November 2010 to February 2011), they probably experienced an intense feeding activity due to the winter enrichment provided by the BCC intrusion [50,62].

Several studies have included Mn as an environmental indicator for estuarine habitats since its concentrations tend to decrease with distance from coastlines [102,108,109]. Mn appears also to be related to somatic growth, diet, maternal influence, and low oxygen conditions [102,106,110]. Herein, only trophic transference could explain the Mn ratios and their higher values in SC, as there were no clear effects to support other considerations.

Similar to other minor elements, Na is a physiologically regulated element required for metabolic reactions and processes associated with growth and reproduction [111]. However, its concentration in fish otoliths may suggest geographical and habitat-specific differences [112], distinct geological characteristics of the resident waters [113], and anthropogenic contamination of the water masses [87,114]. Contamination seems to be the most probable explanation for the higher ratio in Rio de Janeiro, where the thread herring fishing ground is influenced by Guanabara Bay, the most polluted coastal ecosystem in Brazil [115].

The other elemental ratios that were analyzed (Li/Ca, Cr/Ca, Co/Ca, Ni/Ca, Cu/Ca, Rb/Ca, Pb/Ca) showed no significant statistical differences between areas. These results somewhat confirm that these ratios are not good proxies to evidence geographic variation [95]. Nonetheless, there are diverse cases in which these ratios (together with the others formerly discussed) played an important role in detecting geographic variation [100,101,116–118]. Li was previously reported as a reliable geographic indicator [99]. Cr and Co were found in otolith cores of *Gadus morhua*, which were related to different spawning areas and early development [118], but this is an issue that cannot be addressed with a bulk otolith analysis. Pb and Cu were suggested as bioindicators coupled to tissue analyses [87,119], and they are also positively correlated with coastal habitats [120]. Cu/Ca followed this trend with a higher average in RJ (close to Guanabara Bay), but variation was found for Pb. For Ni, it recently was demonstrated that it is not incorporated in the otolith via diet [121], herein remaining inconclusive. Rb is usually associated with less saline aquatic environments [87], which is the case in Rio de Janeiro.

Nevertheless, the otolith MES were robust enough to sustain some geographic variation in *O. oglinum* from the Southeastern Brazilian Bight. The statistical results from the HCA, DFA, and MANOVA were stronger in relation to EFD, i.e., an exclusive group of individuals from SC, a higher percentage of reclassification, and a lower *p*-value, respectively. The significance level was highest in the EFD + MES analyses, in which the best separation was acquired. The highest power to differentiate thread herrings between RJ and SC was obtained by combining EFD + MES. The otolith “identity” from SC was higher probably due to the relative environmental constancy/stability in comparison to RJ, where the coastal runoff and biogeochemical fronts change the continental shelf conditions.

The current results confirm that *O. oglinum* presents geographic variation, suggesting a metapopulational structure in the SEBB. Previous DNA analysis comprising the whole Brazilian coast indicated that the thread herring could be a single and homogeneous population unit with high intrapopulation genetic variation [58]. Indeed, several studies failed to show spatial structuring in high-mobile marine pelagic fish species using classic molecular approaches. This was the case for *S. brasiliensis* in the Southeastern Brazilian Bight [56] and for *Trachurus picturatus* in the NE Atlantic [59]. Both species were initially considered to be a single panmictic population. However, complimentary phenotypic approaches, such as shape and chemical analyses of otoliths, revealed a clear metapopulational structure for *S. brasiliensis* [86,122] and *T. picturatus* [83,100,101].

The metapopulation diagnostic for *O. oglinum* found in this study is reinforced by its occurrence in coastal areas along the SEBB. The thread herring is always present in fish assemblages, despite some seasonal variations ([107,123–129], *inter alia*). These works focused on regional/local environments that indicate inshore–offshore displacements of thread herring, which were influenced by its preference by warmer waters [45,46]. Thread herring larvae are also common in ichthyoplankton along continental shelves [43,130], supporting its inshore–offshore displacements. Latitudinal migrations could lead to the mixing of groups of *O. oglinum*, but this hypothesis seems to be unlikely, according to the datasets from the last pelagic surveys using hydroacoustic in the study area, which date back to 1995, 2008, 2009, and 2010 [56,131]. Together with other clupeids, the thread herring is a typical coastal ecotype, recorded up to ~80 nautical miles from the coastline and ~50 m depth (inner continental shelf) [131]. In the summer of 2008 (January/February), *O. oglinum* was recorded in the whole area (in the marine areas in the cities of Rio de Janeiro, Ubatuba, Santos, Cananéia, Itajaí, and Florianópolis and in the Cape of Santa Marta Grande, see Figure 2 for reference) [132]. In the spring of 2008 (November) and 2009 (October), *O. oglinum* was not recorded during the surveys despite the abundance of other related species such as *S. brasiliensis*, *S. japonicus*, and *C. chrysurus* [133,134]. In the summer of 2010 (March), the thread herring was also scanty [135]. These absences could be explained by the occurrence of *O. oglinum* in shallow and coastal areas, out of the survey range area [133–135], thus supporting inshore–offshore displacements and disregarding latitudinal migrations.

For management purposes, stocks can be defined as homogeneous groups that possess intrinsic biological features (growth and mortality rates, reproductive biology) and that can be exploited independently [11]. Stock is an administrative concept, and the definition of stock depends on the life history parameters that can be used to differentiate groups, supported with a holistic approach [9,91]. This approach implies that different methodologies must be applied, and consistent results must be attained [10]. Many fish stocks are defined according to geographic boundaries, life history traits, demographic characteristics, and economic and/or political importance. This means that the complex spatial structure of fish populations, together with their migration routes and connectivity patterns, is frequently forgotten, which can lead to an overexploitation scenario [4,136]. In this way, a proper stock definition for *O. oglinum* in the area must encompass not only the current results but a set of distinct methods applied to samples obtained both from scientific surveys and commercial landings.

Finally, the bulk otolith approach (i.e., the entire fish life cycle before capture) used in this study, although valuable, does not allow us to infer where and when those regional differences were acquired [101]. Thus, it remains unknown if they are related to different natal signatures, revealing distinct spawning grounds, or if they are acquired later in life, after recruiting to the different harvesting regions. Nevertheless, the relatively short life cycle (close to ~2 years) of *O. oglinum*, and the use of individuals just after the first maturity at 6–9 months of age, address this limitation. In the case of small pelagic fish that present high mobility, such as the thread herring, a more accurate sample design for stock identification must consider the spatial gradient and include the temporal perspective, ensuring synoptic sampling in all areas during each period of sampling [28]. The combined use of the three otolith pairs can also contribute to refining the current diagnostic [21–25].

5. Conclusions

Opisthonema oglinum presents geographic variation due to a metapopulation structure in the Southeastern Brazilian Bight. The results of this study recorded a significant phenotypic geographic variation regarding the otolith shape and multi-elemental signatures of the thread herring. These natural tags suggest that this species is not a single homogeneous group in the study area. However, more data from scientific surveys, fisheries statistics, and biological and ecological studies are needed to support this finding.

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