Otolith shape can be used as a tool to infer population connectivity among individuals of *Larimus breviceps* at Southwestern Atlantic

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Abstract

Otoliths are an excellent tool for analysing the pattern of habitat use between adults and juveniles and connectivity between fish populations. *Larimus breviceps* is a species belonging to the family Sciaenidae, which has an important role in the marine food chain, as it is one of the most abundant and frequent species in the bycatch of coastal shrimp fisheries in Brazil. The present study aimed at comparing the otolith shape of specimens collected in three different Brazilian coastal areas: Sergipe (SE), northeastern region; São Paulo (SP), southeastern region; and Paraná (PR), southern region. In a laboratory, 88 otoliths were extracted, photographed, and the contour was analysed by the wavelet method (32 from SE, 28 from SP, and 28 from PR). The otolith contours varied between sampling sites. Linear discriminant analysis correctly reclassified 60.23% otoliths by the sampled sites, with the best reclassifications occurring in SE (62.5%), followed by PR (60.71%) and SP (57.14%). Multivariate analysis of variance also evidenced significant differences in contours among the sampling sites ($F = 2.3$; $P < 0.005$). Thus, two morphotypes of otoliths were found for *L. breviceps*: one from Sergipe (northeastern Brazil) and the second one from southeastern–southern Brazil, indicating connectivity between the populations off São Paulo and Paraná, to be confirmed by future genetic studies.

Introduction

The Brazilian continental shelf presents a relative stability in physical and chemical parameters (Castro and Miranda, 1998; Rossi-Wongtschowski and Madureira, 2006; Mahiques *et al.*, 2010). Despite the stability, this environment presents a high biodiversity (Rossi-Wongtschowski and Madureira, 2006) due to high connectivity between the estuarine and shelf ecosystems for some fish species (Ibañez *et al.*, 2017; Soeth *et al.*, 2019; Kikuchi *et al.*, 2021). Thus, this leads to high functional, physiological, and morphological plasticity for some species (Mai *et al.*, 2014; Avigliano *et al.*, 2017).

Otoliths are metabolically inert structures composed of calcium carbonate, mainly precipitated in the form of aragonite and countless chemical elements (Cadrin and Friedland, 1999; Campana, 1999; Schulz-Mirbach *et al.*, 2019). The precipitation of calcium carbonate is regulated by hormones and influenced by environmental factors such as temperature and salinity (Popper and Fay, 2011). The morphology of otoliths is complex, being influenced by growth parameters (Xiong *et al.*, 2015), which could be related to morphological and morphometric variations such as distinct growth rates in the same population (Tuset *et al.*, 2019), first maturation (Carvalho *et al.*, 2020), and physiological stress (Holmberg *et al.*, 2018). It is possible to describe patterns of habitat use by using ontogenetic variations in the otolith shape (Carvalho *et al.*, 2015; Bot *et al.*, 2020). Conversely, widely distributed species may have different otolith morphotypes, as observed for *Micropogonias furnieri* (Santos *et al.*, 2017) and *Trachurus picturatus* (Vasconcelos *et al.*, 2018).

The Sciaenidae family is composed by 270 species with a wide range of sizes (10–200 cm) (Chao, 1978; Chao *et al.*, 2015). Most of them live in shallow water (<50 m) (Odell *et al.*, 2017), with long or short life cycles of up to 31 years (Waggy *et al.*, 2006; Cardoso and Haimovici, 2011; Morat *et al.*, 2017). Several species of Sciaenidae are commercially exploited and show complex migratory patterns (Albuquerque *et al.*, 2012; Childs *et al.*, 2015). In the Southwestern Atlantic Ocean, the annual landings of sciaenids represent 22% of the total marine landings on the Brazilian coast (Chao *et al.*, 2015). *Larimus breviceps* (Cuvier, 1830) is a demersal species widely distributed in the Central and Southwestern Atlantic (from Costa Rica to Santa Catarina in Brazil) (Vianna and Almeida, 2005; Cattani *et al.*, 2011). It has benthophagous habits and can attain up to 31 cm in total length (TL) (Santos *et al.*, 2021a; Froese and Pauly, 2023). The size at first maturity is known only for northeastern Brazil (11 cm TL,

according to Santos *et al.*, 2021b). It has an important role in the food chain as prey of mammals and seabirds (Beneditto, 2017; Miotto *et al.*, 2017), and it is an abundant and frequent species of the bycatch of the coastal fisheries in Brazil, such as beach seine (Vianna and Almeida, 2005; Passarone *et al.*, 2019) and shrimp trawling (Barreto *et al.*, 2018). This study aims at verifying the existence of any distinction in the shape of *L. breviceps* otoliths that may represent distinct morphotypes or stocks in three areas of the Brazilian coast. Thus, the results of this study can be used as a basis for future policies towards the management of different fish stocks.

Materials and methods

Study area

L. breviceps specimens were acquired in three localities along the Brazilian coast (Figure 1). The sampled specimens from northeastern Brazil were obtained from the commercial catches of shrimp trawlers based in Aracaju, state of Sergipe (10°55′41.07″S–37°02′34.08″W) (Figure 1A). Northeastern Brazil is characterized by bottom water temperatures ranging between 25.5 and 29.6°C (Cardoso and Haimovici, 2011), being considered an oligotrophic environment (Heileman, 2009). This coast is subjected to a marked period of high precipitation in the austral winter, with an annual precipitation varying between 1000 and 1500 mm (Ekau and Knoppers, 1999).

In the continental shelf of the southeastern region, the specimens were collected by gillnetters in the coast of the state of São Paulo (Peruíbe: 24°19′2″S–46°59′44″W; and São Sebastião: 23°45′40″S–45°24′44″W) (Figure 1B). In the coast of the state of Paraná, in southern Brazil, a subtropical environment, the specimens were collected by gillnetters in shallow coastal areas dominated by waves (Pontal do Paraná: 25°35′43.91″S–48°22′23.74″W; and Matinhos: 25°49′30.80″S–48°31′48.30″W) (Figure 1C). Southeastern–southern Brazil has lower temperature (sometimes below 21°C) and higher productivity, influenced by the constant nutrient input from estuaries (Rossi-Wongtschowski and Madureira, 2006; Lessa *et al.*, 2018) and by the intrusion of

cold waters across the shelf (Central South Atlantic Water) with higher precipitation in the summer (Oliveira *et al.*, 2018). Its hydrography has wind and ocean currents as the main forces acting on the dynamics of the continental shelf, influencing the process of upwelling and intrusion of colder, nutrient-rich water masses that occur in the austral summer (Araújo and Gasalla, 2022). A water mass resulting from the mixture of coastal waters coming from the La Plata River, reinforced by the Patos Lagoon flow (Subtropical Shelf Water, SSW), flows over the platform extending to southeastern Brazil, being intensified by winds from the south quadrant in the winter. On the contrary, in the summer, the SSW converges with the coastal branch of the Brazilian Current, carrying tropical oligotrophic waters (Silveira *et al.*, 2000). This implies an alternation of these water masses on the continental shelf of southeastern and southern Brazil, which favours the larval dispersal of several fish resources, both northwards and southwards (Porcaro *et al.*, 2014).

Sample processing

After sampling, fish specimens were taxonomically identified, measured in TL (in cm, from the snout to the margin of the tail), and weighed in total weight (in g). Their sex was characterized macroscopically based on Vazzoler (1996). Only adults of *L. breviceps* were used with a TL ranging between 13.8 and 20.0 cm in Sergipe (SE), 19.2 and 24.8 cm in São Paulo (SP), and 16.5 and 24.6 cm in Paraná (PR). All specimens used in the analyses presented length above the length at first maturity (Silva *et al.*, 2015; Santos *et al.*, 2021b). The sagitta otoliths were extracted from each fish, cleaned, packed dry, and numbered according to the geographic location.

Otolith contour analysis

The right otolith was photographed and the otolith length (OL, in mm) and otolith height (OH, in mm) were measured from these images (Figure 2A). The wavelet function was used to define the otolith contour (Parisi-Baradad *et al.*, 2010; Sadighzadeh *et al.*, 2014) (Figure 2B). The wavelet is the result of the expansion of
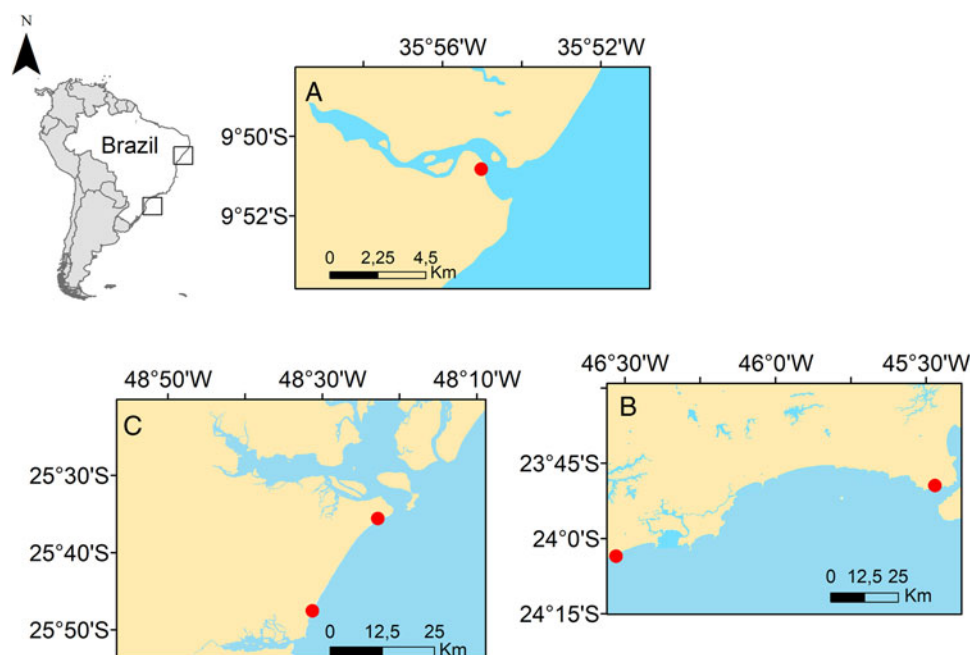

Figure 1. Sampling sites of *L. breviceps*: (A) Aracaju – Sergipe, northeastern Brazil; (B) São Sebastião and Peruíbe – São Paulo, southeastern Brazil; and (C) Pontal do Paraná and Matinhos – Paraná, southern Brazil.
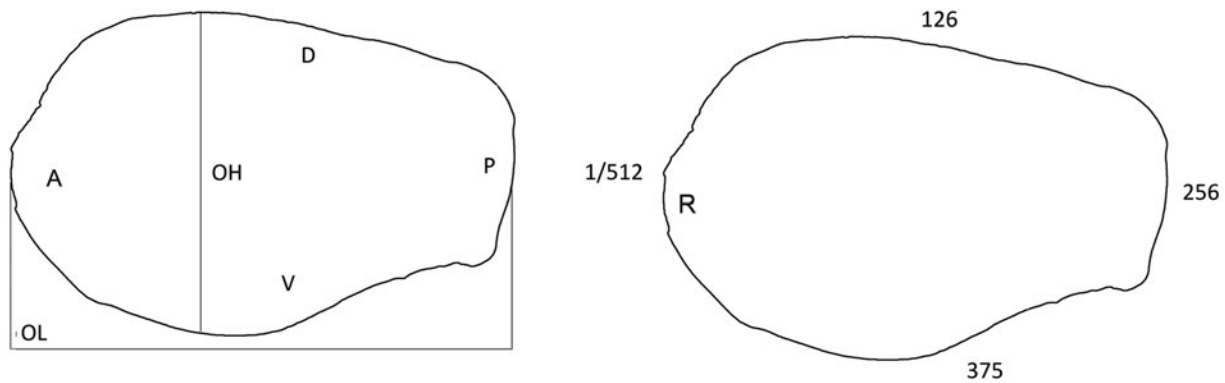
Figure 2. (A) Otolith sagitta of *L. breviceps*. R, rostrum; A, anterior; D, dorsal; P, posterior; V, ventral region of the otolith; OL, otolith length; OH, otolith height. (B) Otolith contour using 512 equidistant points.

Table 1. Mean and standard deviation of fish TL, OL, and OH of *L. breviceps* by location and '*n*' number of specimens analysed in Sergipe (SE), northeastern Brazil, in São Paulo (SP), southeastern Brazil, and in Paraná (PR), southern Brazil

States	*n*	TL (cm)	OL (mm)	OH (mm)
SE	32	16.45 ± 1.52	9.87 ± 0.73	6.41 ± 3.28
SP	28	21.82 ± 1.57	12.57 ± 0.84	7.93 ± 4.02
PR	28	21.84 ± 1.51	12.28 ± 1.04	7.84 ± 3.96

a signal in a family of functions representing expansions and translations of a mother function, i.e.: $\Psi s(x) = 1/s\Psi(\varphi/s)$, where Ψ is a function with local support in a limited amplitude on the abscissa axis; φ lowers the step filter; and s is a scale parameter (Mallat, 1991). A total of 512 points, with equidistant coordinates from each otolith, were extracted with the rostrum as the contour origin (Parisi-Baradad et al., 2010). The fourth and fifth wavelets are more appropriate for identifying stocks or populations, as they describe the contour of the otoliths more sensitively (Sadighzadeh et al., 2014). The image processing was performed using AFORO (http://aforo.cmima.csic.es/) (Parisi-Baradad et al., 2010).

A principal component analysis (PCA), based on the variance–covariance matrix, was applied to reduce wavelet functions without losing information (Tuset et al., 2015). The principal components (PCs) explaining most data variability were selected by the broken-stick method (Gauldie and Crampton, 2002). Subsequently, the effect of the allometry of fish size was removed using the residuals of the linear regression between the significant PCs and the OL. From these, a new PCA was run (Stransky and MacLellan, 2005) to check for variations in the otolith contour for each study site:

Sergipe, São Paulo, and Paraná. A linear discriminant analysis (LDA) was applied between sites to verify the correct percentage of otolith reclassification. A multivariate analysis of variance (MANOVA) was performed with the PCs without the effect of allometry, to check for differences in the shape of otoliths collected in those three states. All statistical analyses were performed using Past software version 4.03 (Hammer et al., 2001).

Results

A total of 88 otoliths of *L. breviceps* from Sergipe, São Paulo, and Paraná were analysed (Table 1). The reconstruction of the otolith contour using wavelets 4 and 5 showed high variability in the contour of the specimens from the three states. This variability was observed in the dorsal, ventral, and posterior regions. Wavelet 4 showed greater variation between Sergipe and São Paulo–Paraná in the anterior region of the otoliths (Figure 3A). Wavelet 5 presented variation between Sergipe and São Paulo–Paraná in all regions of the otoliths (Figure 3B).

The PCA showed high variability in the otolith shape (Figure 4). PC1 explained 97.6% and PC2 explained 1.7% of the otolith shape variability. Along PC1 more elongated otoliths are distributed with entire all margins, and on PC2 more rounded otoliths are distributed with entire all margins, whose anterior region presents a prominence and slight excisura. Otoliths of *L. breviceps* from SP and PR were more distributed along PC1 with more elongated otolith shape and those from SE were differentiated from them along PC2 with more rounded otoliths (Figure 4).

The LDA showed correct reclassification of 60.23% of all otoliths among sites. SE otoliths showed the highest reclassification
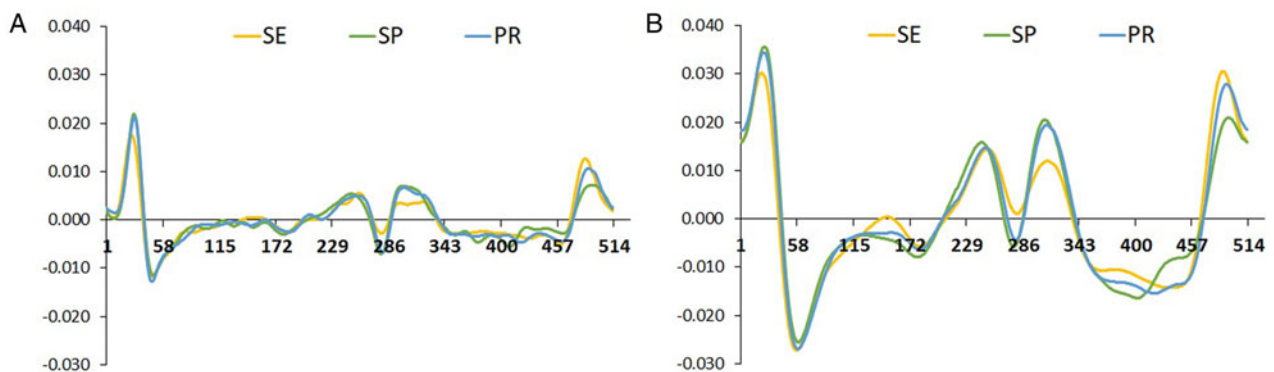

Figure 3. Contour decomposition of the sagitta otolith of *L. breviceps* collected in Sergipe (SE), northeastern Brazil, in São Paulo (SP), southeastern Brazil, and in Paraná (PR), southern Brazil: (A) wavelet 4 and (B) wavelet 5.
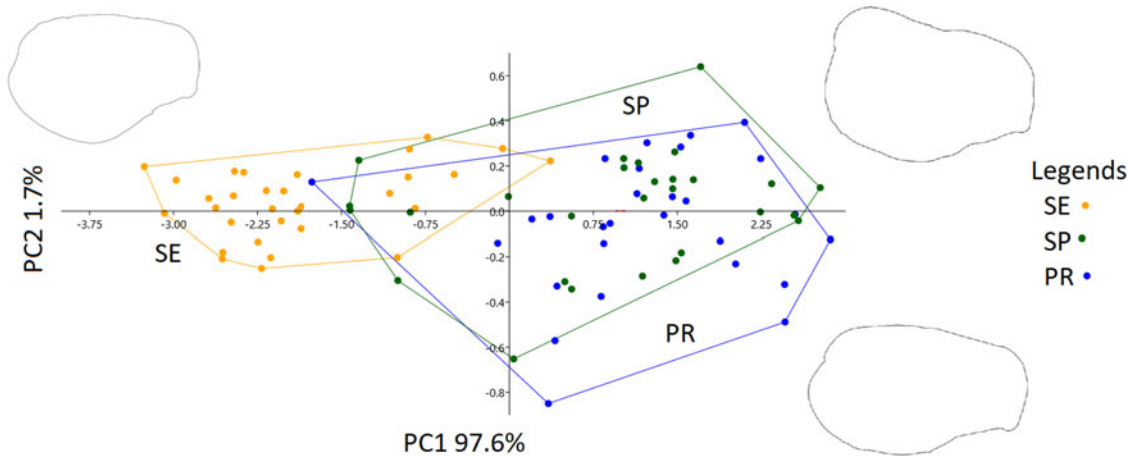
Figure 4. PCA scatterplot for the sagitta otolith contour of *L. breviceps* from Sergipe (SE; yellow dots), northeastern Brazil, São Paulo (SP; green dots), southeastern Brazil, and Paraná (PR; blue dots), southern Brazil.

Table 2. Reclassification of sagittae otolith of *L. breviceps* between those collected in the northeastern (Sergipe, SE), southeastern (São Paulo, SP), and southern Brazil (Paraná, PR) by the LDA

Sites	SE	SP	PR	Total
SE	20 (62.5%)	6 (18.7%)	6 (18.7%)	32
SP	7 (25%)	17 (60.7%)	4 (14%)	28
PR	6 (21.4%)	6 (57.1%)	16 (57.4%)	28
Total	33	29	26	88

percentage (62.50%), followed by PR (60.71%) and SP (57.14%) (Table 2). The MANOVA evidenced a significant difference in otolith shape among sites ($F = 2.3$; $P < 0.05$). The otolith shape from specimens originating from SE was significantly different from those originating from SP ($P < 0.05$).

Discussion

The sagitta otoliths of *L. breviceps* presented a bullet shape, characteristic of many sciaenids (Volpedo and Echevarria, 1999; Waessle *et al.*, 2003; Tuset *et al.*, 2008; Siliprandi *et al.*, 2014). Two morphotypes were identified, the most elongated in northeastern Brazil (SE) and one with prominence and excisura in southeastern–southern Brazil (SP–PR). The presence of two morphotypes may indicate environmental influences and connectivity (or not) between populations.

Northeastern Brazil is characterized by a bottom water temperature varying between 25.5 and 29.6°C (Cardoso and Haimovici, 2011), and it is considered an oligotrophic environment (Heileman, 2009). Conversely, southeastern–southern Brazil presents lower temperature and higher productivity, influenced by constant input of nutrients from estuaries (Rossi-Wongtschowski and Madureira, 2006; Lessa *et al.*, 2018). These environmental differences may have influenced the presence of two morphotypes in the otoliths of *L. breviceps*. Other sciaenids also showed distinct morphotypes influenced by habitat and environmental parameters. *Paralonchurus brasiliensis* (Steindachner, 1875) e.g. presented elongated morphotype otoliths as a result of a river nutrient input, differing from the rounded morphotype found in populations living far from the mouth of the Paraíba do Sul River (Oliveira *et al.*, 2009). *Argyrosomus japonicus* (Temminck & Schlegel, 1843) also presented two morphotypes, associated with the presence of a river input and, hence, higher productivity influencing the growth

rate (Ferguson *et al.*, 2011). *M. furnieri* (Desmarest, 1823) presented three otolith morphotypes along southeastern–southern Brazil, related to oceanographic processes occurring far from the coast (Santos *et al.*, 2017). Thus, more productive areas provide greater food availability influencing the growth rate of otoliths and their morphology (Verocai *et al.*, 2023).

The continental shelf of southeastern–southern Brazil represents a transitional region between tropical and subtropical climates and has 13 large estuaries increasing the input of nutrients to the continental shelf (Spalding *et al.*, 2007; Lessa *et al.*, 2018). This environmental similarity between southeastern and southern Brazil (SP and PR) is probably the reason behind the similar shapes of *L. breviceps* otoliths sampled at those areas. Along with the similarity of environmental parameters, the otolith shape may indicate connectivity between populations of *L. breviceps* from São Paulo and Paraná. *L. breviceps* inhabits the shallow inner shelf (<50 m deep) in all ontogenetic phases (Bessa *et al.*, 2014; Porcaro *et al.*, 2014), allowing gene flow between populations of *L. breviceps*, resulting in a similar otolith shape between these two populations. However, the morphotype of otoliths is influenced by several parameters, such as temperature and salinity (Popper and Fay, 2011). In addition to environmental parameters, genetics and reproductive behaviours can influence shape otoliths. Recent studies demonstrate the importance of genetics and otolith shape in populational studies of marine fishes. Results of Ibanez *et al.* (2022), e.g. demonstrated that genetics studies for *Mugil curema* indicated variations on a macro-scale and otoliths on smaller scales. A similar otolith shape between populations having gene flow has been observed in other species, such as the Batrachoididae *Opsanus beta* (Goode & Bean, 1880) (Carvalho *et al.*, 2022), and the Sciaenidae *Umbrina canosai* Berg, 1895 (Kikuchi *et al.*, 2021).

The analysis of the contour of otolith shape is an important tool which suggested the existence of connected and separated populations of *L. breviceps* along the Brazilian coast. We further recommend studies involving the otolith chemistry and genetics to assess possible migration between the populations of the northeastern and southeastern–southern Brazil.

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