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Chemical and morphometric analyses of otoliths to differentiate snook species (*Centropomus* spp.) and assess habitat use on the southeastern Brazilian coast

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ABSTRACT

Understanding fish distribution and critical habitats during early life stages is essential for the conservation and sustainable management of coastal systems. This study used chemical and morphometric otolith analyses to discriminate snook species and track *Centropomus undecimalis* across semi-enclosed systems on Brazil's southeastern coast: Sepetiba Bay (SB), Ilha Grande Bay (IGB), Araruama Lagoon (AL), and Maricá Lagoon (ML). We hypothesized that (H1) otolith morphology and chemical composition differ between species due to distinct ecological and physiological processes and (H2) environmental conditions across habitats influence otolith characteristics of *C. undecimalis*. SB is a semi-enclosed system, receives more freshwater input, and is more altered, whereas IGB is more open, better connected to the sea, and less disturbed. AL is hypersaline with homogeneous habitats, whereas ML is mesohaline with a more heterogeneous environment. In IGB, sagittal otoliths of *Centropomus parallelus* were larger in area, length, and width, while *C. undecimalis* showed greater ellipticity and aspect ratio. *Centropomus parallelus* also had higher concentrations of Cu, Ga, Li, Mn, Pd, and Tl, supporting H1. Within *C. undecimalis*, otoliths from IGB displayed greater length, area, perimeter, and aspect ratio, while those from SB showed higher circularity and solidity. ML otoliths exhibited the highest circularity but the lowest solidity and rectangularity. Chemical analyses achieved 100% reclassification accuracy using Linear Discriminant Analysis, surpassing morphometric methods (95.4%). These findings support H2, demonstrating how environmental and chemical conditions are reflected in otoliths, enabling accurate species and habitat discrimination. Although morphometric analyses may overlook subtle differences, their integration with chemical methods provides a robust framework for understanding habitat use and support effective conservation and management of coastal fish populations.

1. Introduction

Coastal areas are highly heterogeneous habitats, shaped by variations in salinity, temperature, and the degree of human disturbance (Selleslagh and Amara, 2008; Brown et al., 2018). Many fish species rely on coastal habitats such as estuaries, bays, and lagoons during their early life stages for feeding, protection, and favorable developmental conditions (Whitfield et al., 2018; Guerreiro et al., 2021). Understanding species distribution in semi-enclosed coastal systems is key to conserving these renewable resources. Protecting critical habitats supports sustainable fisheries management and addresses challenges from environmental pressures and climate change.

Bays and coastal lagoons are vital nurseries for fish during the early life stages, offering abundant food, diverse habitats, and reduced predation risk (Seitz et al., 2020; Guerreiro et al., 2021). These semi-enclosed environments, influenced by freshwater drainage and tidal actions, exhibit variable salinity and temperature due to their shallow depth (Pritchard, 1967; Andrade-Tubino et al., 2020). Such

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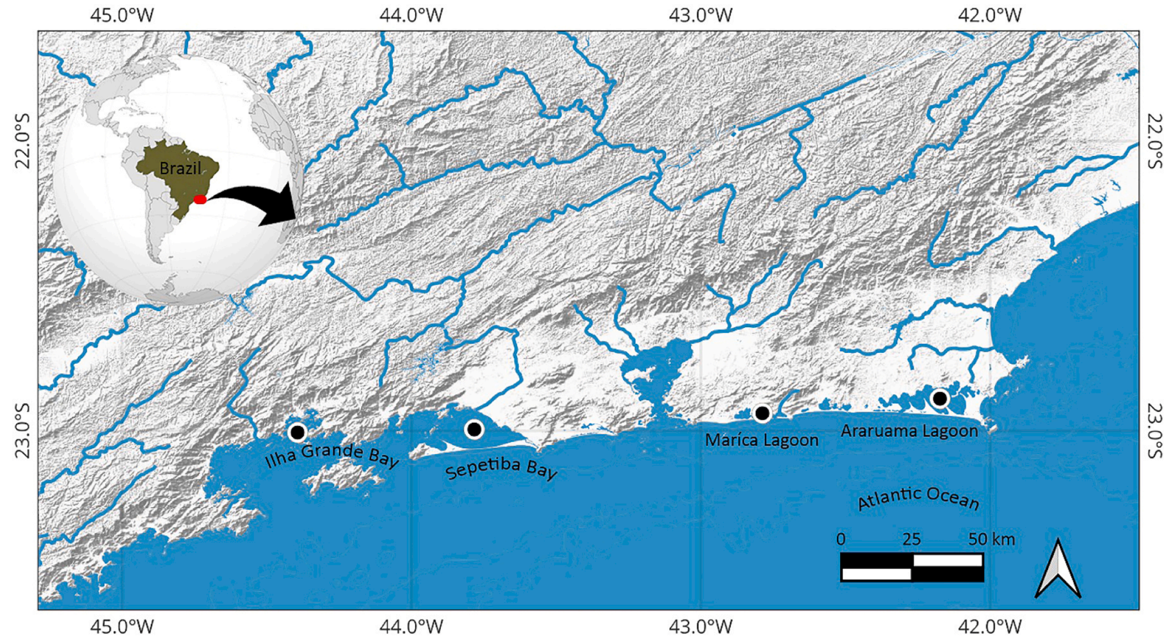

Fig. 1. Map of the state of Rio de Janeiro highlighting Ilha Grande Bay, Sepetiba Bay, Maricá Lagoon, and Araruama Lagoon.

habitats support fish species of high commercial importance (Whitfield et al., 2018; Chaves, 2020). However, anthropogenic activities threaten fish stocks, risking ecological and societal collapse (Brown et al., 2018; Ulman et al., 2020). Identifying population structures and ecosystem connectivity is essential for targeted conservation efforts, such as establishing reserves and no-take zones in critical nursery areas (Arthington et al., 2016, Franco et al., 2023).

Various approaches, including morphometric analysis (Mojekwu, 2015; Traverso et al., 2024) and otolith chemistry and morphometry (Avigliano et al., 2020; Franco et al., 2023), have been widely applied to investigate fish population distribution in semi-enclosed systems. Otoliths, calcified inner-ear structures responsible for hearing and balance, are influenced by genetic, ecological and environmental factors, allowing discrimination among species and habitat use assessment (Campana, 1999; Santos and Vaz-dos-Santos., 2023). Their growth increments, formed by calcium carbonate and trace element deposition, provide insights into environmental and physiological conditions experienced by fish throughout their life (Campana, 1999; Grønkjær, 2016). Additionally, variations in otolith shape reflect growth patterns and environmental influences, making otoliths valuable tools for studying species identification, migration, and stock differentiation (Walther and Limburg, 2012; Mahé et al., 2019).

Otolith element concentrations can reveal fish movements and habitat use across freshwater, estuarine, and marine systems (Fortunato et al., 2017; Catalán et al., 2018). Otoliths form growth rings through concentric deposition processes, with deposition rates influenced by various factors, including environmental conditions, diet, physiology, ontogeny (Campana, 1999; Grønkjær, 2016; Prichard et al., 2018). Their microchemistry serves as natural tags, offering insights into migration, connectivity, and environmental history (Tanner et al., 2013; Avigliano et al., 2018; Almeida et al., 2024).

Snook species, such as *Centropomus undecimalis* (Block, 1762) and *Centropomus parallelus* Poey, 1860) (Centropomidae), are valuable fishery resources along the southwestern Atlantic coast, supporting both commercial and recreational fisheries (Fonseca et al., 2020). These amphidromous fish inhabit marine, estuarine, and freshwater environments, with *C. parallelus* more common in rivers and lagoons, while *C. undecimalis* prefers habitats like mangroves and complex substrates (Dantas and Barletta, 2016). Both species are protandrous hermaphrodites, transitioning from male to female, with females typically larger (Perera-García et al., 2011; Assis et al., 2019).

Juvenile snook typically occupy hypoxic freshwater nurseries, such as shallow streams and drainage channels, before transitioning to estuaries and deeper waters as they mature (Tucker and Campbell, 1988; Nascimento et al., 2022). Spawning occurs in brackish waters during late spring and summer, with adults moving to rivers and lagoons with lower salinity post-spawning (Perera-García et al., 2011; Lowerre-Barbieri et al., 2014; Nascimento et al., 2022). Otolith microchemistry highlights their migrations across marine, brackish, and freshwater habitats, demonstrating their adaptability to varying salinities (Dantas, and Barletta, 2016). Nevertheless, habitat destruction remains a significant threat, contributing to population declines (Chaves, 2020).

Identifying juvenile snooks solely based on external morphology is often challenging due to their frequent co-occurrence in the same habitats and the subtle nature of diagnostic traits during early life stages. Although some morphological differences between *Centropomus* species have been described, such as variation in body size and anal fin characteristics (Figueiredo-Filho et al., 2021), these features are often size-dependent and difficult to apply in sympatric populations. These limitations highlight the importance of otolith-based approaches as more reliable tools for species discrimination and population assessment. Previous studies have successfully distinguished species within the same genus using otolith characteristics (Lord et al., 2012; Zischke et al., 2016). Carvalho et al. (2024) also used otolith morphometry to differentiate juvenile *Centropomus undecimalis* and *Centropomus ensiferus* in Brazil.

In this context, this study was conducted across different semi-enclosed coastal systems along the southeastern coast of Brazil. The selection of the study areas was based on their contrasting environmental characteristics, hydrological connectivity, and degrees of marine and freshwater influence (Knoppers and Kjerfve, 1999; Copeland et al., 2003; Teixeira et al., 2009), which are key drivers of otolith chemical and morphological signatures (Catalán et al., 2018; Zischke et al., 2016). These semi-enclosed coastal systems represent a gradient of salinity, productivity, and habitat complexity, enabling the evaluation of how local environmental conditions are incorporated into otolith structure and elemental composition. By integrating sites with distinct physicochemical and ecological attributes, this study provides an opportunity to test whether otolith-based markers reflect spatial environmental heterogeneity and population structuring in snook species. This approach directly addresses gaps in the literature regarding the role of semi-enclosed coastal systems in shaping otolith signatures and population connectivity in amphidromous fishes along the Brazilian coast, where comparative multi-system analyses remain scarce.

This study aimed to investigate how different semi-enclosed coastal systems along the southeastern Brazilian coast influence the morphometry and chemistry of snook otoliths. We hypothesized (H1) that these analyses would allow discrimination between coexisting *C. undecimalis* and *C. parallelus*, revealing potential differences in their ecological or metabolic strategies. Furthermore, we hypothesized (H2) that *C. undecimalis* would show distinct contingents within each estuarine system, reflecting the unique chemical profiles of each location. By integrating otolith morphometry and microchemistry across contrasting coastal systems, this research contributes to a better understanding of habitat use, population connectivity and the ecological processes shaping amphidromous fish population, providing valuable insights for conservation and management strategies.

2. Material and methods

2.1. Study area

Four semi-enclosed coastal systems along the southeastern coast of Brazil were selected for this study: Araruama Lagoon (AL), Maricá Lagoon (ML), Sepetiba Bay (SB), and Ilha Grande Bay (IGB) (Fig. 1). The Araruama (210 km^2) and Maricá (34 km^2) lagoons are classified as "choked" lagoons due to their narrow connections to the sea (Knoppers and Kjerfve, 1999; Silvestre et al., 2017).

Maricá Lagoon features interconnected compartments and provides a sheltered, heterogeneous environment, with shallow areas, muddy bottoms in its inner sections, and sandy bottoms near the sea connection. Araruama Lagoon has an average depth of 3 m, while Maricá Lagoon averages 2 m (Carvalho et al., 2024). Araruama Lagoon is hypersaline, with an average salinity of 52, whereas Maricá Lagoon is mesohaline, with a salinity of 18 (Kjerfve et al., 1996; Franco et al., 2019; Carvalho et al., 2024).

Sepetiba Bay (450 km^2) and Ilha Grande Bay (600 km^2) differ in salinity and geomorphological characteristics. Sepetiba Bay, a semi-enclosed system, has a salinity gradient ranging from 28 in its inner zone to 33 in the outer zone (Andrade-Tubino et al., 2020). It receives inflows from rivers and streams and includes a mangrove area in its innermost part, located within the Guaratiba State Biological Reserve. The southern boundary features Restinga da Marambaia, a restricted-access area managed by the Brazilian Navy, Army, and Air Force (INEA, 2021a). Additionally, Sepetiba Bay is part of the Boto-Cinza Environmental Protection Area (APA), which extends into the outer region of Ilha Grande Bay, as established by Municipal Law No. 962 of April 10, 2015 (Cordeiro, 2024).

Ilha Grande Bay has a salinity range of 30–36 (Teixeira et al., 2009) and features small mangrove areas and minor rivers on both the mainland and the central island. It is surrounded by several protected areas, including the Tamoios Ecological Station, Cairuçu Environmental Protection Area, and Juatinga State Ecological Reserve, located in the municipalities of Angra dos Reis and Parati (ICMBIO, 2021; INEA, 2021b; INEA, 2021c). On the island itself, protected areas include Ilha Grande State Park, Praia do Sul State Biological Reserve, and Aventureiro Park, established by State Decree No. 15,273 of June 26, 1971 (Rio de Janeiro, 1971), State Decree No. 4972 of December 2, 1981 (Rio de Janeiro, 1981), and State Law No. 6793 of May 28, 2013 (Rio de Janeiro, 2013).

Sepetiba Bay, by contrast, is heavily affected by anthropogenic activities such as port operations, industrial development, fishing, and submarine construction (Copeland et al., 2003). Ilha Grande Bay experiences relatively fewer human impacts, although it hosts significant facilities, including a nuclear power station, an oil terminal, and a shipyard (Teixeira et al., 2009).

2.2. Fish collection

A total of 129 pairs of otoliths were extracted, including 115 from *C. undecimalis* and 14 from *C. parallelus*. The *C. undecimalis* samples were collected from three estuarine systems: 17 from SB (TL = 4.1–10.6 cm), 52 from ML (TL = 3.6–12.1 cm), and 46 from IGB (TL = 9.7–17.9 cm). The 14 *C. parallelus* samples (TL = 9.5–16.8 cm) were collected from IGB. For otolith chemistry analysis of *C. undecimalis*, otoliths from ten individuals from AL, located further north in the state of Rio de Janeiro, were included and compared with 13 otoliths from ML and 11 from IGB.

Juvenile fish were collected using beach seines with a net measuring 12 m by 2.5 m, featuring a mesh size of 7.5 mm and 30 m ropes at each end. The fish were preserved on ice and transported to the laboratory, where their total length (cm), weight (g), and sex were recorded. The heads were then removed with scissors on the ventral side, and the otoliths were extracted using tweezers. After removing the membranes, the otoliths were washed in distilled water and stored dry in Eppendorf tubes.

To compare the chemical composition between *C. undecimalis* (TL = 12.7–15.7 cm) and *C. parallelus* (TL = 10.3–15.8 cm), ten individuals from each species were analyzed. For the morphometric comparison, the study included 46 *C. undecimalis* individuals (TL = 9.7–17.9 cm) and 14 *C. parallelus* individuals (TL = 9.5–16.8 cm). Individuals selected for otolith chemical analyses were chosen to maximize size overlap among systems and minimize ontogenetic bias. Although some variation in body size among systems was unavoidable due to natural differences in environmental conditions and population structure, individuals within comparable total length ranges were prioritized. Comparisons among systems were conducted using *C. undecimalis* individuals with overlapping total length ranges (TL = 12.7–15.7 cm), while interspecific comparisons between *C. undecimalis* and *C. parallelus* were performed using individuals with comparable body sizes (TL = 10.3–15.8 cm). This approach allowed differences in otolith elemental composition to be interpreted primarily as responses to environmental variability among coastal systems rather than ontogenetic effects.

2.3. Otolith morphometry

Sagittae otoliths were photographed with the sulcus facing upwards using a Leica 250 M microscope equipped with a Leica MC 170 HD camera. The photographs included a scale and otolith numbering, generated with Leica LAS 4.13.0 software. The images were then analyzed with ImageJ software to obtain shape data, including length, width, area, perimeter, roundness, aspect ratio, solidity, circularity, ellipticity, and rectangularity. These images were converted to 24-bit bitmap format and imported into Shape v. 1.3 software (Iwata and Ukai, 2002).

Statistical analyses were performed to compare species and identify distinct groups of *C. undecimalis* within the three estuarine systems. Otolith morphology was characterized by measuring area, perimeter, roundness, aspect ratio (AR), solidity, length, width, circularity, ellipticity, and rectangularity, as described by INMETRO (2017). The first nine measurements were obtained using ImageJ software, and the last two were calculated using the formulas from Tuset et al. (2003):

$$(OL - OW) / (OL + OW) \text{ and } OA / (OL + OW)$$

where OA = Otolith area, OL = Otolith length, and OW = Otolith width.

The Shapiro-Wilk test was used to assess data normality, and non-parametric analyses were applied since the data did not meet normality assumptions. To account for potential size effects on otolith shape, Spearman’s correlation was used to examine the influence of standard length (SL) on all shape indices. The individual size effect was removed from each sample using an allometric estimation model with

Table 1

Number of individuals (N), average total length (TL, mm), and mean ± standard deviation of otolith morphometric measurements for *C. undecimalis* and *C. parallelus* in the studied estuarine systems. All morphometric measurements are in mm, except for Aspect Ratio (dimensionless) and Area (mm^2).

System	N	TL ±SD	Area	Perimeter	Circularity	Ellipticity	Rectangularity	Length	Width	Solidity	Roundness	Aspect Ratio
Centropomus undecimalis												
SB	17	72.35 ± 19.17	4.99 ± 1.84	9.01 ± 1.82	0.75 ± 0.03	0.26 ± 0.02	0.70 ± 0.02	3.44 ± 0.68	2.00 ± 0.36	0.96 ± 0.01	0.57 ± 0.02	1.76 ± 0.07
IGB	46	133.87 ± 16.57	14.06 ± 3.74	16.02 ± 1.96	0.68 ± 0.04	0.30 ± 0.02	0.72 ± 0.01	5.96 ± 0.76	3.24 ± 0.41	0.96 ± 0.01	0.53 ± 0.02	1.90 ± 0.06
ML	52	87.36 ± 17.78	5.92 ± 1.74	10.83 ± 2.00	0.63 ± 0.05	0.27 ± 0.02	0.70 ± 0.01	3.80 ± 0.64	2.18 ± 0.33	0.95 ± 0.01	0.56 ± 0.02	1.80 ± 0.06
Centropomus parallelus												
IGB	14	134.71 ± 20.41	19.33 ± 5.42	17.82 ± 2.45	0.75 ± 0.05	0.24 ± 0.02	0.71 ± 0.01	6.56 ± 0.98	4.05 ± 0.57	0.97 ± 0.01	0.60 ± 0.03	68. ± 0.09

Lombarte and Lleonart's (1993) normalization, based on the equation $y' = y (x_0 / x)^b$, where y' is the normalized variable, y is the raw data value, x_0 is the smallest length (3.6 cm), and b (2.91) is the allometric coefficient relating length (cm) to weight (g). The mean and standard deviation of each shape index, along with fish total length (cm), were then calculated for each coastal system. The Kruskal-Wallis test and linear discriminant analysis (LDA) were applied to compare shape indices among locations for each species. A Student's t-test was used to identify differences in shape indices between the two snook species in IGB. The mean otolith contour was computed using the ShapeR package, based on the reconstruction of 64 Wavelet coefficients (Libungan and Pálsson, 2015), along with LDA. Statistical analyses were conducted using Shape 1.3 and R 4.0.2.

To compare the two species, a Student's *t*-test was used for normally distributed data, while the Wilcoxon Rank Sum Test (Mann-Whitney test) was applied to non-normally distributed data. For the *C. undecimalis* group in IGB, ANOVA and the Tukey test were performed to identify site differences in normally distributed data. For non-normally distributed data, the Kruskal-Wallis and Wilcoxon Rank Sum Tests were used to assess site differences.

2.4. Otolith Chemistry

The chemical composition of the entire otolith was determined using the nitric acid dissolution technique, following prior decontamination. The sagittal otoliths were decontaminated by soaking in 3% hydrogen peroxide (H_2O_2, Fluka TraceSelect) for 15 min, followed by three washes with 1% ultrapure nitric acid (HNO_3, Fluka TraceSelect) for 30 s each. They were then rinsed twice with ultrapure water (Milli-Q) for 5 min and dried in a laminar flow hood (Patterson et al., 1999; Rooker et al., 2001). The otoliths were weighed on an analytical balance (0.0001 g) and subjected to hot dissolution overnight in 10% ultrapure HNO_3 to a final volume of 10 ML. The same procedure was applied to blanks and certified standards (FEBS-1 and $CaCO_3$). Otoliths were randomly analyzed to avoid sequence effects. Elemental quantification was performed using inductively coupled plasma-mass spectrometry (ICP-MS) with a NexIon 300X spectrometer (PerkinElmer, USA). Instrumental conditions were as follows: plasma flow rate: 17 L min^{-1} ; carrier gas flow rate: 0.98 L min^{-1} ; auxiliary gas flow rate: 0.92 L min^{-1} ; radiofrequency power: 1100 W; replicates: 5.

The elemental concentration data obtained through total dissolution were log-transformed ($\log(x + 1)$) to better meet the assumptions of normality and homoscedasticity. A Student's *t*-test was used to compare elemental concentrations between the two species, while Kruskal-Wallis variance analysis was applied for comparisons among the three locations. Additionally, LDA was performed on the elemental concentrations to assess identification accuracy, measured as the percentage of correctly classified cases among the sites.

The total length and elemental composition of otoliths from ten specimens of each species, all captured at IGB, were compared. The following isotopes were evaluated: ^{107}Ag, ^{27}Al, ^{75}As, ^{197}Au, ^{11}B, ^{137}Ba, ^{9}Be, ^{209}Bi, ^{79}Br, ^{44}Ca, ^{114}Cd, ^{140}Ce, ^{59}Co, ^{53}Cr, ^{133}Cs, ^{65}Cu, ^{163}Dy, ^{166}Er, ^{153}Eu, ^{57}Fe, ^{69}Ga, ^{157}Gd, ^{74}Ge, ^{202}Hg, ^{165}Ho, ^{127}I, ^{115}In, ^{39}K, ^{139}La, ^{7}Li, ^{175}Lu, ^{24}Mg, ^{55}Mn, ^{98}Mo, ^{23}Na, ^{93}Nb, ^{143}Nd, ^{60}Ni, ^{31}P, ^{208}Pb, ^{105}Pd, ^{141}Pr, ^{194}Pt, ^{85}Rb, ^{185}Re, ^{103}Rh, ^{132}Ru, ^{34}S, ^{121}Sb, ^{45}Sc, ^{82}Se, ^{28}Si, ^{147}Sm, ^{118}Sn, ^{88}Sr, ^{181}Ta, ^{159}Tb, ^{47}Ti, ^{232}Th, ^{205}Tl, ^{169}Tm, ^{238}U, ^{51}V, ^{182}W, ^{89}Y, ^{172}Yb, ^{66}Zn and ^{90}Zr. The Shapiro-Wilk test was used to assess the distribution of otolith length samples and elemental concentrations (mg/L). For non-parametric distributions, a logarithmic transformation (base 10) was applied with one added to avoid negative values. A Student's *t*-test was used for parametric distributions, while the Wilcoxon test was applied for non-parametric distributions, including those that did not meet the assumptions of normality even after transformation.

3. Results

On average, *C. undecimalis* individuals from IGB had the largest total length (133.87 ± 16.57 mm) and otolith area (14.06 ± 3.74 mm^2) among the studied sites. *Centropomus parallelus* individuals from IGB displayed a similar total length (134.71 ± 20.41 mm), but had a larger otolith area (19.33 ± 5.42 mm^2) compared to *C. undecimalis* (Table 1). Although the otolith morphometrics of *C. undecimalis* from AL were not measured, the average total length of individuals from this site was 103.8 ± 16.68 mm.

3.1. Comparisons between species

The measurements of otolith area ($t = 3.403$; $p = 3.4 \times 10^{-3}$), perimeter ($t = 2.526$; $p = 2.1 \times 10^{-2}$), circularity ($t = 4.821$; $p = 1.1 \times 10^{-4}$), aspect ratio ($t = 8.211$; $p = 2.34 \times 10^{-4}$), roundness ($t = 7.907$; $p = 6.74 \times 10^{-4}$), solidity ($t = 3.876$; $p = 1.1 \times 10^{-3}$), length ($t = 2.124$; $p = 4.8 \times 10^{-2}$), width ($t = 4.928$; $p = 1.2 \times 10^{-4}$), and ellipticity ($t = 8.896$; $p = 7.02 \times 10^{-5}$) showed significant differences between the two species in IGB. However, rectangularity did not differ significantly ($t = 1.302$; $p = 0.20$). *Centropomus parallelus* had greater otolith area, circularity, length, perimeter, roundness, solidity and compared to *C. undecimalis*, whereas *C. undecimalis* exhibited greater ellipticity and aspect ratio (Fig. 2).

The shape indices achieved a reclassification accuracy of 96.43% in distinguishing between the otoliths of the two species, with one specimen of *C. parallelus* misclassified as *C. undecimalis*. In contrast, the otolith contour and chemistry achieved a total reclassification accuracy of 100% (LDA, $p < 0.05$) (Table 2). *Centropomus parallelus* exhibited significantly higher average concentrations of the elements Li, Mn, Cu, Ga, Pd, and Tl compared to *C. undecimalis* (Table 3).

3.2. Comparisons between locations

All shape indices exhibited significant differences among locations (Fig. 3). Specifically, area ($p = 2.2 \times 10^{-16}$), aspect ratio

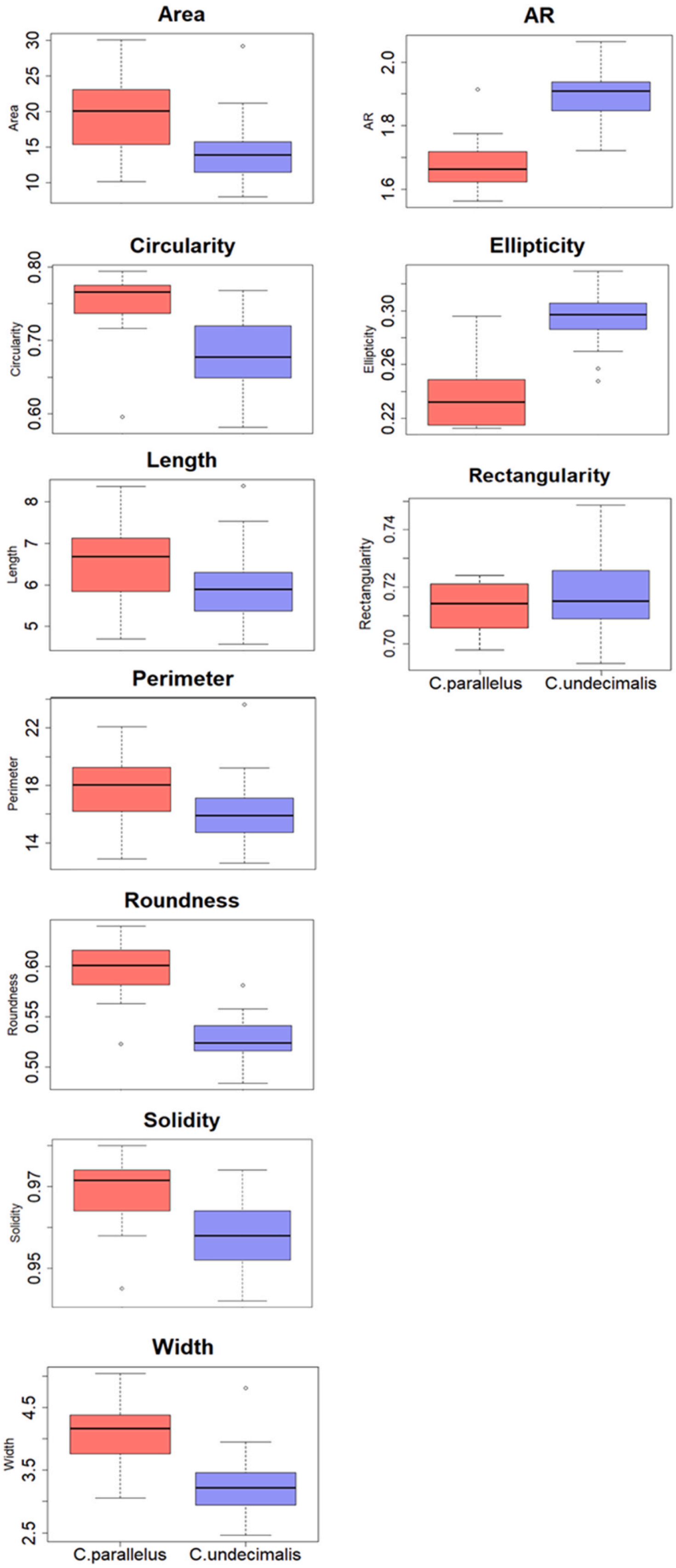

Fig. 2. Boxplot charts displaying the morphometric indices of otoliths from *Centropomus parallelus* and *Centropomus undecimalis* from Ilha Grande Bay. The left column shows indices that were higher in *C. undecimalis* (area, circularity, length, perimeter, roundness, solidity and width), while the right column shows indices that were higher in *C. parallelus* (aspect ratio (AR) and ellipticity), as well as rectangularity, which showed no significant difference.

Table 2
Results of LDA: Percentage of correct classification based on otolith shape indices, wavelets, and chemistry for *Centropomus undecimalis* and *Centropomus parallelus* from Ilha Grande Bay.

Shape Index	C. parallelus	C. undecimalis	Total	% of correct classification
C. parallelus	13	1	14	92,86
C. undecimalis	0	46	46	100
Total	13	47	60	**96,43**
Wavelets				
C. parallelus	14	0	14	100
C. undecimalis	0	46	46	100
Total	14	46	60	**100**
Chemistry				
C. parallelus	10	0	10	100
C. undecimalis	0	10	10	100
Total	10	10	20	**100**

Table 3
Mean ± standard deviation of elemental concentrations (mg L^{-1}), along with results of Student's *t*-test and Wilcoxon rank sum test, including *p*-values, for otoliths of *Centropomus undecimalis* and *Centropomus parallelus* captured in Ilha Grande Bay (IGB). All analyses were conducted with 18 ° of freedom.

Element	**C. undecimalis**	**C. parallelus**	**Test**	**Result**	***p*-value**
Cu	0.63 ± 0.35	1.10 ± 0.71	Wilcoxon	77	0.045*
Ga	0.07 ± 0.02	0.08 ± 0.08	Student's *t*-test	0.321	0.014*
Li	0.04 ± 0.03	0.07 ± 0.04	Student's *t*-test	1.637	0.040*
Mn	0.44 ± 0.14	0.84 ± 0.61	Student's *t*-test	2.021	0.005**
Pd	1.12 ± 0.33	1.84 ± 1.20	Wilcoxon	79	0.029*
Tl	O.007 ± 0.003	0.005 ± 0.002	Student's *t*-test	5.115	7.24×10^{-5}**

($p = 6.18 \times 10^{-9}$), ellipticity ($p = 6.78 \times 10^{-9}$), length ($p = 2.2 \times 10^{-16}$), perimeter ($p = 2.2 \times 10^{-16}$), width ($p = < 2.2 \times 10^{-16}$), and rectangularity ($p = 2.94 \times 10^{-10}$) were higher in IGB compared to other locations (Kruskal-Wallis, $p < 0.05$). Conversely, circularity ($p = 4.66 \times 10^{-9}$), solidity ($p = 7.90 \times 10^{-8}$), and roundness ($p = 6.21 \times 10^{-9}$) were greater in the otoliths from SB. Otoliths from ML exhibited the lowest solidity.

Reconstructing the otolith contours by location using wavelets revealed a subtle difference, with a more pronounced distinction in the average contour of *C. undecimalis* from IGB (Fig. 4).

The shape indices (area, perimeter, circularity, ellipticity, rectangularity, aspect ratio, roundness, length, and width) exhibited distinct separation by location, achieving approximately 95% reclassification accuracy using LDA. The scatter plots of the first two discriminant axes (Fig. 5) showed minimal overlap between locations. This pattern was consistent for both harmonic and chemical element concentrations, though only for elements with values above the detection limit. LDA using the harmonics of the analyzed otoliths revealed a clear distinction among the three locations, achieving 100% reclassification accuracy (Table 4).

3.3. Chemistry

A total of 24 elements analyzed in the otoliths of *C. undecimalis* showed significant differences among the IGB, ML, and AL systems. These elements are as follows: Al, Ba, Ce, Co, Cr, Cu, Eu, Ga, I, Li, Mg, Mn, Na, Nb, Ni, P, Rb, Re, Ru, S, Sc, Sn, Ti, V.

AL presented the highest concentration of Li and the lowest concentrations of I and Nb, while ML showed the highest concentrations of Ba, Ga, Mg, Mn, Rb and V and the lowest concentrations of Li and Sn (Figures S1 and S2 in the Supplementary Information). IGB did not exhibit a higher concentration of any element; however, it had the lowest concentrations of Al, Cu, Eu, Ni, P, Re, S, Sc, Ti and V. The concentrations of Ce, Co, Cr, Na and Ru showed differences only between ML and IGB, with all being higher in ML (Table 5, Figures S2 in the Supplementary Information).

The chemical analysis, which compared elemental otolith concentrations among the three studied systems (IGB, AL, and ML), achieved a total reclassification accuracy of 100% within the analyzed dataset, according to LDA ($p < 0.05$). This indicates that chemical data provided more effective discrimination among the systems compared to shape indices. (Table 6). LDA scatter plots of the first two axes (Fig. 6) also showed minimal overlap between locations.

4. Discussion

4.1. Species differentiation

We detected differences in otolith shape and chemical element concentrations between the snook species *Centropomus undecimalis* and *C. parallelus*, supporting H1. Wavelet-based shape analysis proved effective in distinguishing between these species within the studied system. *C. parallelus* had larger otoliths in terms of area, length, and width, whereas *C. undecimalis* exhibited greater ellipticity and aspect ratio, reflecting species-specific morphological differences. The higher concentrations of trace elements (e.g., copper, gallium, lithium, manganese, palladium and thallium) in *C. parallelus* otoliths suggest differences in environmental exposure or physiological processing. These findings suggest the presence of distinct ecological or metabolic strategies, possibly driven by habitat preferences, water quality differences, or species-specific mechanisms of element incorporation. Element incorporation into otoliths depends on both exogenous factors, such as element availability in the water, and endogenous factors, including growth rate and ontogeny (Miller, 2011; Sturrock et al., 2012, 2015; Turner and Limburg, 2015). Since all individuals were collected from IGB under similar environmental conditions, endogenous factors likely play a major role in the observed differences in trace element incorporation between the two species.

Prichard et al. (2018) identified differences in trace element concentrations among three *Cottus* species in the Lake Michigan basin, attributing these variations to differences in individual physiology and otolith crystallization rates. Similarly, Reis-Santos et al. (2008) observed that element concentration differences in the otoliths of five flatfish species were driven more by species-specific responses to similar environmental conditions than by habitat changes.

Physiological factors may help explain the success of microchemical stock discrimination in relatively homogenous marine environments (Sturrock et al., 2015). Sturrock et al. (2014) demonstrated that physiological processes can outweigh environmental influences on otolith microchemistry, as blood plasma is often tightly regulated and minimally correlated with ambient element concentrations. Similarly, Miller (2011) highlighted the need to evaluate both abiotic and biotic factors in otolith elemental incorporation to ensure accurate interpretation of field data.

Among the elements compared between the two studied species, several have been examined for their incorporation into fish otoliths. Copper (Cu) and Lithium (Li) may be randomly trapped in the crystal lattice and are sensitive to environmental factors, though Cu can also be strongly influenced by physiological variables (Hüssy et al., 2021). Gallium (Ga) has been linked to environmental concentrations (Hanson and Zdanowicz, 1999), while thallium (Tl), a toxic element to aquatic organisms (Shotyk et al., 2019), is associated with anthropogenic activities such as coal burning, cement production, and mining (Couture et al., 2011; Karbowska, 2016). Manganese (Mn) has been connected to hypoxia in some studies (Mohan et al., 2014; Limburg et al., 2015) but is

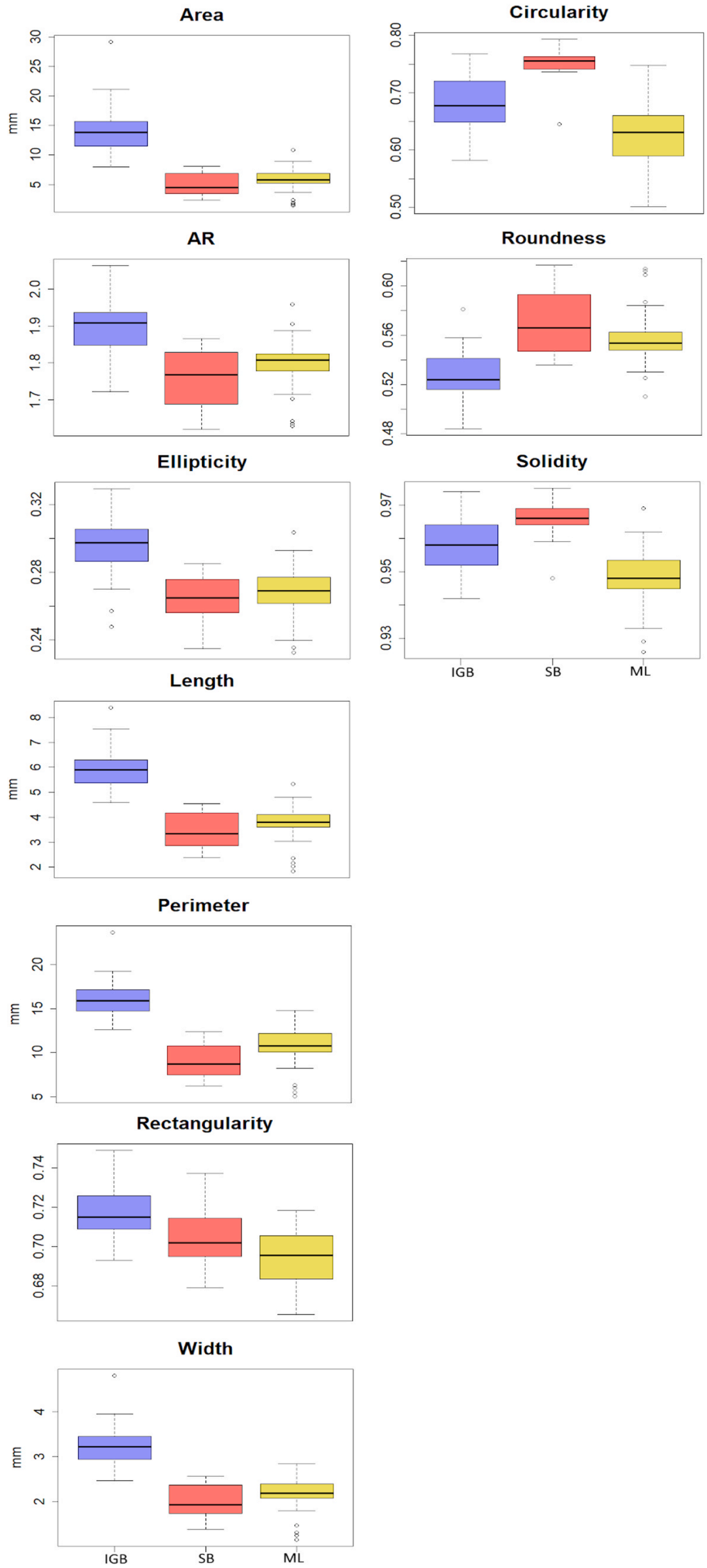

Fig. 3. Boxplot charts displaying the morphometric indices of otoliths from *Centropomus undecimalis* captured in Ilha Grande Bay (IGB), Sepetiba Bay (SB) and Maricá Lagoon (ML). The left column shows the indices that were higher in IGB (area, aspect ratio (AR), ellipticity, length, perimeter, rectangularity, and width), while the right column shows the indices that were higher in SB (circularity, roundness, and solidity).

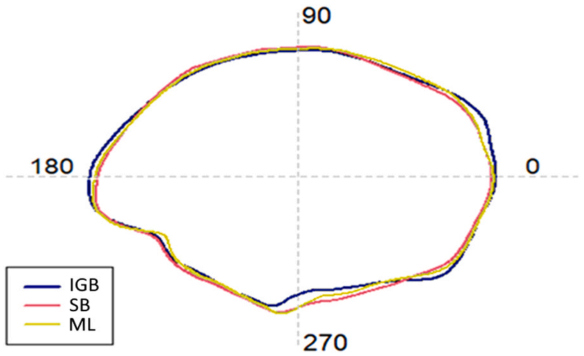

Fig. 4. Average outline of sagitta otolith morphotypes of *Centropomus undecimalis* from Ilha Grande Bay (IGB), Sepetiba Bay (SB) and Maricá Lagoon (ML).

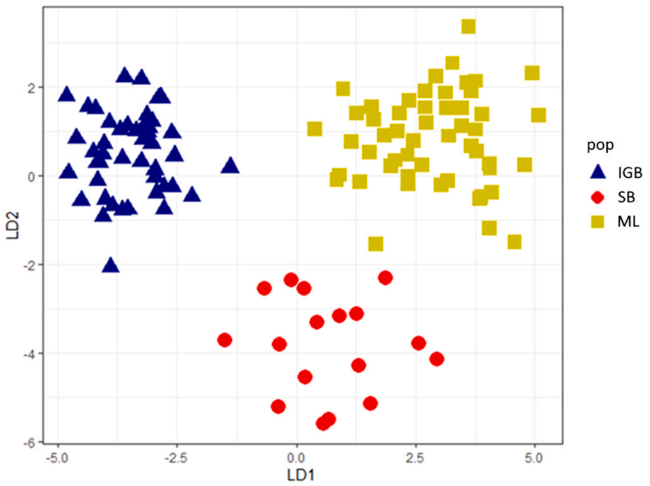

Fig. 5. LDA scatterplot based on the harmonics of *C. undecimalis* otoliths from the three analyzed systems: IGB, Ilha Grande Bay; SB, Sepetiba Bay; ML, Maricá Lagoon.

Table 4
Results of LDA: Percentage of correct classification for otolith shape indices and wavelets of *Centropomus undecimalis* across each study system. IGB, Ilha Grande Bay; SB, Sepetiba Bay; ML, Maricá Lagoon. The total number of individuals is also indicated.

Shape Index	IGB	SB	ML	Total	% of correct classification
IGB	45	0	1	46	97.83
SB	0	16	1	17	94.12
ML	1	2	49	52	94.23
Total	46	18	51	115	**95.39**
Wavelets					
IGB	46	0	0	46	100
SB	0	17	0	17	100
ML	0	0	52	52	100
Total	46	17	52	115	**100**

also strongly influenced by physiological variables such as ontogeny (Miller, 2011; Bot Neto et al., 2020). Hamer and Jankins (2007) further suggest that differing metabolic rates in *Platycephalus bassensis* and *Pagrus auratus* could influence Mn incorporation into otoliths.

Although the *Centropomus* species studied share the same genus and inhabit similar environments (Gonzalez et al., 2019), they exhibit distinct growth rates (Medeiros et al., 2021). These differences lead to variations in ontogeny at different life stages, which, in turn, affect element deposition in otoliths (Heimbrand et al., 2020). Growth rate differences between *Centropomus* species can also vary by location. For instance, *C. undecimalis* generally grows faster than *C. parallelus* in Mexico (Meza et al., 2006), while *C. parallelus* exhibits higher growth rates than *C. undecimalis* in Brazil (Ximenes-Carvalho et al., 2007). This suggests that environmental factors influence growth rates (Aliaume et al., 2000), thereby affecting elemental deposition in otoliths. However, although the consistent differences in element concentrations between the two species studied may be another differentiating factor between the species, such differences remain unexplained.

Differences in body size among systems are expected along coastal gradients shaped by geomorphology, ocean connectivity, and physicochemical conditions (Elliott and Whitfield, 2011; Izzo et al., 2015). By selecting individuals within overlapping size ranges, we minimized ontogenetic effects on otolith chemistry. Consequently, the observed spatial patterns in otoliths shape and elemental composition are more strongly associated with environmental heterogeneity among systems than with size-related variation (Campana, 1999; Elsdon et al., 2008; Seitz et al., 2020). Previous studies have shown that otolith elemental signatures reflect habitat-specific environmental conditions and can be used to infer spatial variability and population structuring across coastal environments (Sturrock et al., 2012; Avigliano et al., 2018; Maichak de Carvalho et al., 2020). Therefore, otolith chemistry provides a robust framework for linking environmental gradients to spatial patterns in fish populations. Future studies focusing on their distribution and environmental interactions will be essential for understanding the role of environmental and physiological factors in shaping these differences.

4.2. *Distribution of Centropomus undecimalis in semi-enclosed ecosystems*

Our hypothesis (H2) that the different environmental conditions of each semi-enclosed system influence the shape and chemical composition of *C. undecimalis* otoliths was supported by this study. Individuals from IGB exhibited otoliths with higher morphometric indices (length, area, width, perimeter, aspect ratio, ellipticity, and rectangularity), while those from SB showed greater circularity, solidity, and roundness. Otoliths from ML had the lowest solidity and rectangularity. Additionally, chemical analyses effectively distinguished individuals from the semi-enclosed systems (IGB, ML, and AL).

The Rio de Janeiro coast features diverse environments, such as bays and lagoons, each with distinct characteristics like salinity, which may influence otolith shape. For example, the more elliptical shape of *C. undecimalis* otoliths may be linked to these environmental variations. Bot Neto et al. (2020) observed changes in otolith shape throughout ontogeny, correlating habitat and salinity exposure with a transition from elliptical to trapezoidal forms. The greater rectangularity observed in IGB otoliths suggests a more elongated shape, potentially associated with higher swimming activity and a more planktivorous diet (Biolé et al., 2019). Conversely, rounder otoliths from other systems may indicate lower swimming activity and a diet richer in invertebrates (Assis et al., 2020). These findings align with the general pattern that pelagic fish exhibit elongated otoliths, while demersal fish tend to have more rounded shapes (Volpedo et al., 2008).

By combining shape indices and harmonics, we successfully differentiated *C. undecimalis* otoliths from IGB, SB, and ML with high classification accuracy—95.39% using shape indices and 100% using wavelets. Contrary to our expectation that salinity differences would drive more pronounced distinctions between bays and the lagoon, morphometric indices and wavelets revealed stronger differences for IGB compared to SB and ML. This suggests that factors other than salinity, such as local ecological or physiological differences, may play a larger role in influencing otolith shape.

Otolith chemistry proved highly effective in distinguishing *C. undecimalis* across environments, avoiding biases from ecological or morphological comparisons. Fish from IGB, AL, and ML were classified with 100% reclassification accuracy. Individuals from AL exhibited higher concentrations of elements such as Al, Cu, and Li, while those from ML had elevated Ba, Mg, and Ni levels. Lombarte and Lleonart

Table 5

Comparison of the mean ± standard deviation of chemical elements concentrations (ppm) in Ilha Grande Bay (IGB), Maricá Lagoon (ML) and Araruama Lagoon (AL), along with *p*-values from tests comparing each coastal system. An asterisk (*) indicates a significant difference at the 0.05 significance level.

Element	IGB	ML	AL	IGB x AL	AL x ML	IGB x ML
Al	9.0 ± 2.6	16.1 ± 4.8	15.4 ± 6.9	1.6×10^{-2} *	0.92	3.7×10^{-3} *
Ba	2.61 ± 2.76	5.5 ± 1.2	2.96 ± 1.44	9.9×10^{-2}	1×10^{-3} *	1.4×10^{-3} *
Ce	$8.5 \times 10^{-3} \pm 2.5 \times 10^{-3}$	$1.5 \times 10^{-2} \pm 6.1 \times 10^{-3}$	$1.3 \times 10^{-2} \pm 6.6 \times 10^{-3}$	0.12	0.64	0.01*
Co	2.5 ± 0.4	2.9 ± 0.1	2.7 ± 0.4	5.4×10^{-2}	0.98	1.8×10^{-2} *
Cr	0.4 ± 0.1	0.78 ± 0.15	0.7 ± 0.2	0.23	0.35	8.3×10^{-3} *
Cu	2.1 ± 0.3	2.6 ± 0.3	2.55 ± 0.48	1.5×10^{-2} *	0.28	8.9×10^{-4} *
Eu	$2.2 \times 10^{-3} \pm 2.7 \times 10^{-3}$	$4.9 \times 10^{-3} \pm 2.7 \times 10^{-3}$	$3.5 \times 10^{-3} \pm 2 \times 10^{-3}$	2.4×10^{-2} *	0.19	4.6×10^{-3} *
Ga	0.09 ± 0.09	0.21 ± 0.05	0.12 ± 0.06	2.9×10^{-2} *	1.4×10^{-3} *	1.8×10^{-3} *
I	0.30 ± 0.09	0.29 ± 0.07	0.17 ± 0.05	3.5×10^{-4} *	4.9×10^{-4} *	0.95
Li	0.19 ± 0.03	0.16 ± 0.01	0.23 ± 0.03	1.5×10^{-3} *	5.1×10^{-4} *	1.5×10^{-3} *
Mg	25.6 ± 4.7	36.3 ± 6.5	26.7 ± 4.7	0.88	6.5×10^{-4} *	1.1×10^{-4} *
Mn	3 ± 1.6	5.3 ± 1.7	3.5 ± 2.6	0.6	2.9×10^{-3} *	2.9×10^{-3} *
Na	2193 ± 180	2548 ± 230	2302.2 ± 425.9	0.67	0.12	1.4×10^{-2} *
Nb	$5.6 \times 10^{-3} \pm 4.6 \times 10^{-3}$	$4 \times 10^{-3} \pm 1.7 \times 10^{-3}$	$1.9 \times 10^{-3} \pm 1.4 \times 10^{-3}$	1.9×10^{-2} *	1.9×10^{-2} *	0.65
Ni	81.5 ± 12.5	93.1 ± 2.3	91.3 ± 14.2	2.3×10^{-3} *	0.15	6.5×10^{-4} *
P	510.7 ± 113.9	1061.2 ± 151.3	986.2 ± 250.9	2.4×10^{-6} *	0.58	0 *
Rb	0.09 ± 0.02	0.12 ± 0.03	0.09 ± 0.02	0.86	3.8×10^{-3} *	8.9×10^{-4} *
Re	$2.1 \times 10^{-4} \pm 5.9 \times 10^{-4}$	$2.2 \times 10^{-4} \pm 3.8 \times 10^{-4}$	$5 \times 10^{-4} \pm 7.4 \times 10^{-4}$	1.5×10^{-3} *	1	2.3×10^{-3} *
Ru	0.84 ± 0.15	0.98 ± 0.1	0.90 ± 0.17	0.23	0.56	2.7×10^{-2} *
S	10778.9 ± 2566.3	21436.6 ± 2710.7	19824.9 ± 5224.2	7×10^{-6} *	0.54	1×10^{-7} *
Sc	13.6 ± 2.7	26.2 ± 3.2	24.6 ± 6.9	1×10^{-5} *	0.69	3×10^{-7} *
Sn	0.52 ± 0.18	0.08 ± 0.03	0.50 ± 0.26	0.97	6.4×10^{-6} *	2.1×10^{-6} *
Ti	7.1 ± 1.3	13.3 ± 1.7	12.4 ± 3.4	1.8×10^{-5} *	0.63	5×10^{-7} *
V	$0.04 \pm 6.3 \times 10^{-3}$	0.08 ± 0.01	0.06 ± 0.02	3.9×10^{-4} *	2.5×10^{-2} *	1×10^{-7} *

Table 6

Results of LDA: Percentage of correct classification for otolith elemental concentrations of *Centropomus undecimalis* across each study system. IGB, Ilha Grande Bay; AL, Araruama Lagoon; ML, Maricá Lagoon. The total number of individuals is also indicated.

Chemistry	IGB	AL	ML	Total	% of correct classification
IGB	10	0	0	10	100
AL	0	11	0	11	100
ML	0	0	13	13	100
Total	10	11	13	34	**100**

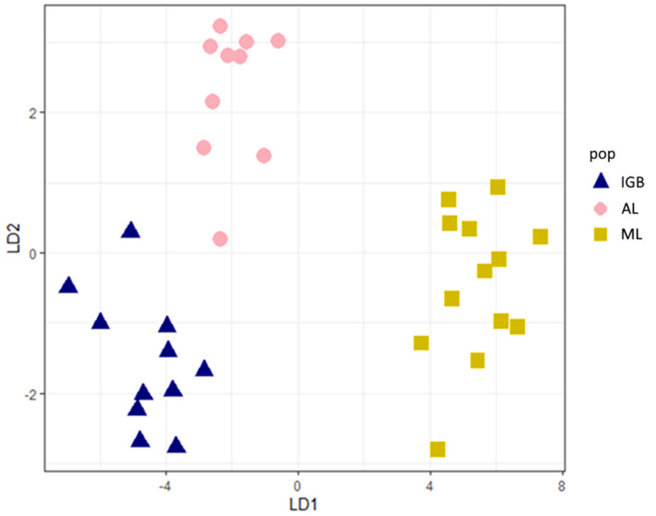

Fig. 6. LDA scatterplot based on the chemistry of *C. undecimalis* otoliths from the three analyzed systems: IGB, Ilha Grande Bay; AL, Araruama Lagoon; ML, Maricá Lagoon.

(1993) observed that decreasing temperature with habitat depth significantly influences otolith growth in carbonate-saturated conditions, with growth typically showing negative allometry. Almeida et al. (2024) used otolith microchemistry to assess *C. undecimalis* habitat use, identifying natal origins shaped by marine waters and ontogenetic shifts within lagoons.

Greater differences in element concentrations were observed between the estuarine IGB and the mesohaline ML, suggesting that salinity may influence these patterns. Salinity and temperature are known to significantly affect otolith element concentrations (Thomas and Swearer, 2019). Lower salinities can negatively impact growth rates in saltwater fish (Sampaio and Bianchini, 2002; Lisboa et al., 2015), indirectly influencing otolith size and elemental composition (Turner and Limburg, 2015). Interestingly, although Mg and Ca often correlate positively with salinity (Gillanders and Munro, 2012), we observed higher concentrations in ML, an oligohaline system. The positive association of Ba with low salinity (Dorval et al., 2007; Elsdon et al., 2008) was confirmed, as ML exhibited the highest Ba concentrations. Li concentrations were positively correlated with salinity, with the hypersaline AL having the highest values.

Pollution from anthropogenic activities may also affect otolith shape and element concentrations (Adeogun and Chukwuka, 2011; Gharred et al., 2020), as seen in other species and locations (Khan et al., 2021). Otolith microchemistry provides valuable insights into the role of semi-enclosed environments and their potential connectivity to the sea, which is critical for conserving fish that rely on these habitats (Pease et al., 2023).

The use of more than one type of analysis, such as chemical and morphometric, to study the otoliths in the present research was important and is even recommended, as it allowed us comparing the methods and obtaining more robust results, since a single method can fail for different reasons, such as the homogeneity of the fish population (Nazir and Khan, 2021).

Future research should focus on the ecological and physiological processes influencing otolith chemistry and prioritize elements sensitive to environmental and physiological factors. Such targeted approaches will enhance our understanding of habitat use and inform conservation strategies for *C. undecimalis* and similar species.

CRediT authorship contribution statement

Gustavo Videira Santos: Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Conceptualization. **Tatiana D. Saint Pierre:** Writing – review & editing, Methodology, Formal analysis. **Taynara Pontes Franco:** Writing – review & editing, Visualization, Validation, Methodology, Formal analysis, Conceptualization. **Araújo Francisco Gerson Gerson:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Funding acquisition.

Declaration of Competing Interest

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

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fishres.2026.107724.

Data availability

Data will be made available on request.

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