Journal of Sea Research 199 (2024) 102500

Contents lists available at ScienceDirect

Journal of Sea Research

journal homepage: www.elsevier.com/locate/seares

Population structure and habitat connectivity of *Pogonias courbina* (Perciformes, Sciaenidae) in two Brazilian lagoon systems on south-east coast of Rio de Janeiro, Brazil, inferred from otolith shape and elemental signatures

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ARTICLE INFO

Keywords:
Sciaenidae
Natural tags
Fourier descriptors
Chemical analysis

ABSTRACT

The delimitation of fish stocks and how species use habitats are essential keys to develop and to implement fishery resources management and rational sustainable programs. Otolith shape and microchemistry analyses can provide helpful information for defining population units and solving ecological connectivity issues. The black drum, *Pogonias courbina*, is an important fishery resource in the southeastern Brazil lagoon systems, and is considered a vulnerable fish according to the IUCN Red List of Threatened Species. Thus, the present study aimed to understand the population structure and habitat connectivity of *P. courbina* in two lagoon systems in the south-east coast of Rio de Janeiro, Brazil. A total of 60 individuals were collected from the lagoons of Saquarema (SQ) and Araruama (AR), between November 2019 and April 2020. Thirty individuals from each location, all estimated to be two years old based on the counting of the annual growth increments, were used. The composition (multi-elemental signatures – MES) and shape (elliptic Fourier descriptors – EFD) of the sagittal otoliths were integrated to evaluate the population structure and the habitat connectivity of the fish inside these lagoon systems. EFD showed differences between lagoon systems, with an overall reclassification rate of 97%. The MES exhibited distinct patterns between lagoon systems, mainly driven by differences in Ba/Ca, Co/Ca, Li/Ca, Mg/Ca, Ni/Ca, Sr/Ca, and Zn/Ca ratios. The overall reclassification rate for MES was also 97% (93% and 100% for SQ and ARA, respectively). The overall reclassification rate obtained using both EFD and MES was 98%. The results suggest a clear spatial discrimination and low connectivity between these groups of two years old *P. coubina* individuals living in the studied lagoon systems. These findings imply that small-scale artisanal fisheries in the lagoon systems require more attention, aiming to maximize local management strategies for commercially exploited species.

1. Introduction

The black drum, *Pogonias courbina* (Lacepède, 1803), is a demersal marine estuarine-dependent species, distributed along the southwestern Atlantic Ocean, being found from the State of Rio de Janeiro (Brazil) to the southern Golfo of San Matias in Argentina (Azpelicueta et al., 2019). It is considered the largest fish of the Sciaenidae family in the southern hemisphere, reaching a maximum of 170 cm in total length and 66 kg in

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https://doi.org/10.1016/j.seares.2024.102500
Received 6 December 2023; Received in revised form 17 March 2024; Accepted 12 April 2024

total weight (Haimovici et al., 2006; Froese and Pauly, 2023).

Like all marine estuarine-dependent fishes, the black drum exhibits a remarkable tolerance to a wide range of salinities and temperatures. It primarily inhabits coastal marine areas, including bays and coastal lagoons, throughout the Western Atlantic Ocean (Santos and Velasco, 2021; Almeida et al., 2021). Both juveniles and adults can be found in the estuarine zones all year round, with a predominance of adults in the reproductive period (from late October to March, in southern Brazil) (Santos et al., 2016). This spatial segregation by sex during spawning was already reported in Río de la Plata estuary, Argentina (Macchi et al., 2002). This indicates that the estuarine areas can serve as spawning and nursery areas, from which juveniles migrate to the marine coastal areas after reaching sexual maturity (Haimovici et al., 2006; Haimovici and Cardoso, 2017).

The black drum is the most threatened sciaenid species in the Southwestern Atlantic, classified as endangered in Brazil (Haimovici et al., 2020; MMA, 2014). Unfortunately, regular datasets about annual fish landings in Brazil are limited. Nevertheless, in the southern Brazil (Rio Grande do Sul, Santa Catarina and São Paulo states) fishing for black drum has led to overfishing in the last years, resulting in a significant reduction in the catches from a maximum of 1450 tons in 1977 to a minimum of 2 tons in 2011 (Chao et al., 2015). Historically, captures were more abundant in the states of Rio Grande do Sul (particularly in the Patos Lagoon estuary) and Santa Catarina, but the Brazil southeast region, specifically Rio de Janeiro, also contributes significantly to the species landings. Between 2013 and 2014, landings of 10.6 tons were recorded in the Patos Lagoon estuary (São Paulo State), with some catches of small and medium-sized individuals (ranging from 27.6 to 62.4 cm) (Santos et al., 2016). In Rio de Janeiro state, the highest landings were recorded in 2011–2012 (11,143 tons) and 2017 (10,986 tons) (FIPERJ, 2013, 2022). A recent monitoring program in the lagoon systems of eastern Rio de Janeiro reported catches of approximately 1,4 tons in the Saquarema lagoon between May and August 2020, while in the lagoon system of Araruama, it was the dominant species with 389 tons captured between May 2019 and December 2020 (Tubino et al., 2021). In the lagoon systems of Saquarema (SQ) and Araruama (AR), the observed size structure showed a range from 12.5 cm to 60 cm of total length (TL) (Almeida et al., 2021). Inappropriate use of fishing gears (e.g., mesh sizes not allowed) and non-compliance with closed fishing seasons are the main factors that have led to overexploitation of the species, collapse of the stock, and have been preventing the recovery of fish stocks (Velasco et al., 2007; Haimovici and Cardoso, 2017).

Many fish species, including freshwater, brackish, and marine species such as *P. courbina*, are valuable fisheries resources that are captured and traded within coastal lagoon systems. These systems support a wide range of fishing activities, including recreational, artisanal, and, in some cases, semi-industrial fisheries (Santos et al., 2016; Olsen et al., 2018; Tubino et al., 2021). The lagoon systems in the eastern part of the state of Rio de Janeiro serve as significant repositories of aquatic diversity (Mansur et al., 2012; Franco et al., 2019b). These systems play a crucial role in the maintenance of coastal biological processes as they serve as aggregators and regulators of biodiversity and biomass (Camacho-Valdez et al., 2014). Moreover, they are recognized as highly productive aquatic ecosystems (Knoppers et al., 1999; Rosa and Batista, 2020), serving as nurseries areas and adult habitats for numerous economically valuable species (Prestrelo and Monteiro-Neto, 2016). Moreover, the artisanal fishing activity conducted in these environments constitutes a vital socioeconomic activity characterized by small-scale fisheries that utilize minimal navigation technology and employ active and passive fishing methods to capture target species (Barroso et al., 2000; Tubino et al., 2021).

The sustainable and rational management of fisheries needs a comprehensive understanding of the distribution, abundance, population structure and habitat use of the exploited fish species (Fonteles-Filho, 2011). Various factors contribute to alterations in the fish species spatial pattern within their distribution areas, often driven by environmental conditions that elicit phenotypic responses (Rooker et al., 2004; Crispo et al., 2010; Kerr and Campana, 2014). These phenotypic responses encompass a range of behavioral, morphological, and life history traits (Avigliano et al., 2014; Maciel et al., 2020; Vaz-dos-Santos et al., 2023). Furthermore, anthropogenic impacts can also exert an influence on species, leading to modifications in key life history characteristics such as size at maturity, fecundity, maximum age, and growth rate, among others (Pauly and Cheung, 2018; Olsen et al., 2018; Pauly and Dimarchopoulou, 2022).

Different natural tags, such as otoliths, can be used to identify various life history patterns of fish at different spatial and temporal scales (Volpedo and Vaz-dos-Santos, 2015; Almeida et al., 2020; Schroeder et al., 2022a). Otoliths, which are metabolic inert structures composed of calcium carbonate and exhibit continuous growth, can incorporate minor and trace elements that reflect the fish's surrounding environment (Panfili et al., 2002). Besides chemical composition, the shape of otoliths has proven to be a powerful tool in studying fish population structure and habitat use (Vignon, 2012; Schroeder et al., 2022b; Muniz et al., 2020). Otolith shape is highly species-specific but also exhibits geographic variation within species, influenced by environmental factors and by the ontogenetic development of fish (Santos et al., 2017; Moreira et al., 2019; Andrade et al. 2023). The shape of otoliths has been successfully employed to unravel the fish population structure in areas characterized by high gene flow and/or environmental heterogeneity (Hoff et al., 2020; Muniz et al., 2020; Moreira et al., 2022). Chemical analysis of otoliths provides valuable insights into the environmental conditions and life history traits of fish throughout their entire lifespan, including movement patterns, migration, and habitat use (Avigliano et al., 2017; Soeth et al., 2019; Correia et al., 2021).

In the last years, the integration of the chemistry with the shape of otoliths has improved the understanding of the population structure for several groups of fish (Ferreira et al., 2019; Corrêa et al., 2022; Nzioka et al., 2023). Thus, the present study aimed (1) to study the otolith shape variations in both lagoon systems, (2) to verify possible differences in the multi-elemental otolith signatures between lagoons, and (3) to use both tools to reveal the population structure and habitat connectivity of *P. courbina* in order to guide fisheries management and governance strategies in these coastal lagoon systems.

2. Material and methods

2.1. Study area characterization

This work took place in two marine lagoon systems located in the Brazilian south-east coast (Rio de Janeiro): 1) Saquarema and 2) Araruama (Fig. 1; Table 1). This region presents a humid to semi-arid climate (Barbieri and Coe-Neto, 1999). The continental equatorial air mass prevails in the summer and the tropical Atlantic air mass in the other seasons, with incidence of cold fronts namely during the spring (Alvares et al., 2013). The hydrodynamic regime of this area is determined by the geomorphological features, the tidal channels nature, the continental runoff and the prevailing winds (Dias et al., 2021). These lagoon systems are connected to the coastal adjacent waters by single narrow channels, classified as suffocated type, allowing a semi-restricted connectivity (Miranda, 2002). Fluctuations in water level and salinity occur due to the weather events, the river runoff and the hydraulic gradient (Nichols et al., 1985; Mansur et al., 2012).

The Saquarema lagoon system, located in Saquarema city, with a population of approximately 91,938 inhabitants, is an estuarine system consisting of four interconnected coastal lagoons, one of which is connected to the sea through a short artificial channel (Fig. 1). This region includes extensive rural areas as well as urban centers in the vicinity, as documented by Barroso et al. (2000) and Silva and Molisani (2019) (Table 1).

The Araruama lagoon system, located in the cities of Cabo Frio, Araruama, São Pedro da Aldeia, Arraial do Cabo, and Iguaba Grande

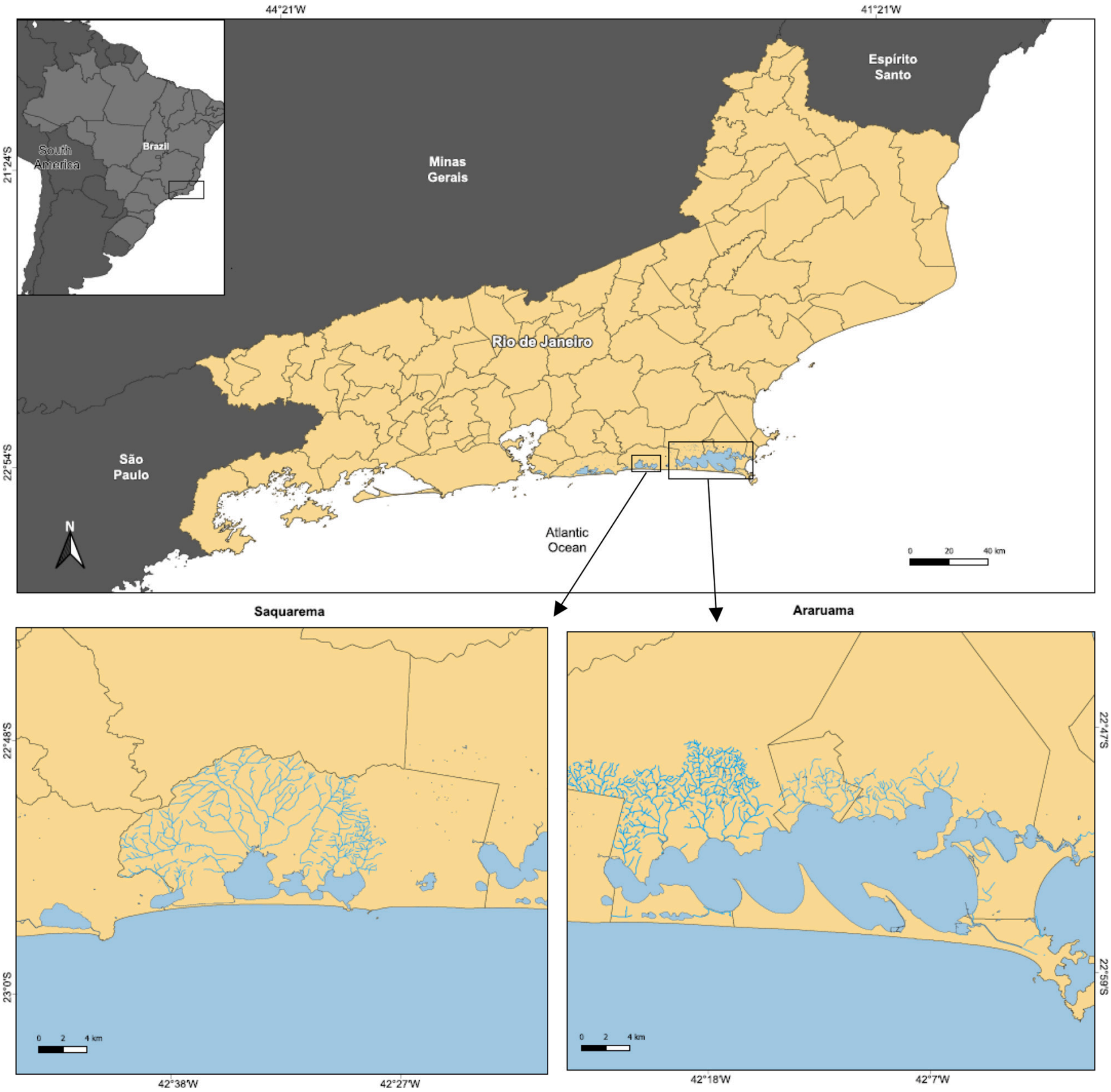

Fig. 1. A map showing the Brazilian sampling sites (Saquarema Lagoon System and Araruama Lagoon System) from which *Pogonias courbina* were collected from November 2019 to April 2020.

Table 1
Geographic coordinates, hydrological parameters, trophic state and anthropogenic profile of the two lagoon systems of eastern Rio de Janeiro, Brazil.

Lagoon System	Coordinates	Area (km^2)****	Dranaige basin area (km^2)****	Depth range (m)****	Water residence time (days)****	Water temperature range (°C)**	Salinity range****	Average rainfall (mm/year)**	Trophic state***	Predominant anthropogenic contribution*
Saquarema	22°93′S 42°49′W	21.2	215	0.6–2.4	27	18–33	9–34	1.3	supereutrophic	Domestic sewage/ agricultural waste
Araruama	22°88′S 42°01′W	225	285	0.5–18	84	21–29	12–60	0.9	supereutrophic	Cultural eutrophication/ intense tourism/ mineral extraction: salt and shell limestone

Source of data: Barroso et al. (2000)*, Knoppers et al. (2009)**, Bertucci et al., (2016)*, Silva and Molisani (2019)*** and Dias et al. (2021)****.

inhabited by respectively 234,077, 136,109, 107,556, 30,827 and 29,344 people, is an estuarine system comprising three interconnected lagoons and a long artificial channel that connects to the adjacent sea (Fig. 1). Traditional salt mining, shell extraction (limestone), and fishing activities have been replaced by tourism and real estate speculation in the region. Consequently, the area has undergone a gradual transformation. The disorganized demographic growth along its banks has intensified the human pressure, revealing a continuous process of eutrophication in this environment over the years (Bertucci et al., 2016) (Table 1).

2.2. *Fish sampling and age estimates*

Fish were caught monthly by the artisanal fishermen in Saquarema and Araruama lagoon systems, during one full year, from July 2019 to June 2020. Fish were preserved in ice and transported to the laboratory, where they were measured (total length: TL, cm), weighed (total mass: TM, g) and aged (age group: years). A total of 402 individuals ranging from 12.4 to 52.0 cm in TL were collected (Saquarema: $n = 145$, TL = 31.7 ± 6.7 cm, and Araruama: $n = 257$, TL = 31.3 ± 5.5 cm). The sagittal otoliths were removed with plastic tweezers, cleaned with distilled water and stored dry in decontaminated microtubes. The left and right sagittal otoliths (sagittae) were identified according to the position of the *rostrum* and *sulcus acusticus*, and then used for the analyses (Secor et al., 1992).

For age readings, the left sagittal otoliths were embedded in transparent epoxy resin (Buehler, Epothin), and a transverse cross-section (0.6 mm) was taken out preserving the core region using a precision diamond saw (Bueler, Isomet Low-speed Saw) (Vaz-dos-Santos, 2015). Slices were ground with silicon carbon papers of 800, 1200 and 2400 grit (Buehler, Ø 200 mm SiC Paper) to expose the primordium, and further polished with 6, 3 and 1 μm diamond pastes (Buehler, Metadi II) (Correia et al., 2012). All readings were performed with the otolith's slices immersed in a clearing agent (ethanol:glycerol) using a stereoscopic microscope (Leica, S9i) under transmitted light with 6× magnification. Counts of the annual growth rings were carried out by two independent and experienced readers; only otoliths with 100% agreement were used (Moura et al., 2020). The overall fish age ranged from 0 to 6 years old.

For bulk otolith analyses it is an important pre-requisite to use fish from the same year group, ideally adults, and collected in a relatively narrow time window, to avoid ontogenetic and environmental confounding effects (Moreira et al., 2019; Correia et al., 2021; Almeida et al., 2023). Subsequently, sixty pre-selected individuals of *P. courbina* (30 from each location) of the same age group (2 years old, the most abundant collected age group) were used in this study for further otolith shape and chemical analyses. All used fish (TL = 30.8 ± 0.5 cm) were considered adults [Age > Age at first maturation (A_{50}) (2 years) (Santos and Velasco, 2021; Olsen et al., 2018)] and have been caught between November 2019 and April 2020 (Table 2).

2.3. *Otolith shape analysis*

The right otoliths were placed with sulcus acusticus up and the rostrum pointing to the left, and thereafter photographed by a stereoscopic microscope (Leica, S9i) using reflected light against a black background with 6× magnification. The obtained high-resolution images were binarized (threshold pixel value of 0.2) using ShapeR (Libungan and Pálsson, 2015). Otolith's contours were described with elliptical Fourier descriptors (EFD) generated using the ShapeR package version 0.1–5 (Libungan and Pálsson, 2015) of the R programming environment (R Development Core Team, 2023). The software generated 35 harmonics for each otolith, each one consisting of four coefficients (a, b, c and d), resulting in 140 EFD per otolith. The EFD were considered invariant in relation to the starting point of reading, scale, rotation and otolith size, therefore, the first three descriptors (a1, b1 and c1) were excluded (Libungan and Pálsson, 2015; Ben Labidi et al., 2020; Khedher et al., 2021). The first 12 harmonics reached 98.5% of the mean cumulative power. Therefore, 45 [=(12 × 4)-3] normalized EFDs were used for subsequent otolith shape analyses.

Table 2
Sample size (N), total length (TL) and otolith mass (OM) of *Pogonias courbina* individuals collected in the two lagoon systems of eastern Rio de Janeiro, Brazil. Values are presented as means and standard errors (SE).

Lagoon System	N	TL (cm)	OM (mg)
		Mean ± SE	Mean ± SE
Saquarema	30	31.2 ± 0.9	227.62 ± 14.71
Araruama	30	30.4 ± 0.5	230.17 ± 7.48

2.4. *Otolith elemental analysis*

Following the shape analysis, the same right otoliths were prepared for chemical elemental analyses following pre-existent protocols (Patterson et al., 1999; Rooker et al., 2001; Correia et al., 2011). Otoliths were cleaned with ultrapure water (H_2O, Milli-QR System, Milli-Q-Water) in an ultrasonic bath for 5 min, immersed in 3% (*v*/v) ultrapure hydrogen peroxide (H_2O_2, Fluka, TraceSelect) for 15 min to remove adherent organic tissues, and decontaminated in 1% (v/v) ultrapure nitric acid (HNO_3, Honeywell Fluka, TraceSELECT™, ≥69.0%) for 10 s to remove surface contamination, followed by a triple immersion in ultrapure water (Rooker et al., 2001). Otoliths were allowed to dry overnight in a laminar flow hood and stored in decontaminated Falcon tubes. Finally, the otoliths were weighed on an analytical balance (0.01 mg), dissolved for 15 min in 65% ultrapure HNO_3 (v/v), and diluted with ultrapure water (> 18.2 MΩ.cm at 25 °C) to a final volume of 15 mL (i.e., 2% HNO3 v/v and 0.2% TDS m/v, Soeth et al., 2019). Some pre-selected minor and trace elements (^{137}Ba, ^{59}Co, ^{65}Cu, ^{7}Li, ^{26}Mg, ^{55}Mn, ^{60}Ni, ^{88}Sr and ^{66}Zn), including the calcium (^{44}Ca), that were usually above the limits of detection (LOD) in fish otoliths (Correia et al., 2021), were assessed by solution-based inductively coupled plasma mass spectrometry (SB-ICP-MS). An iCAP™ Q (Thermo Fisher Scientific, Bremen, Germany) equipped with a concentric glass nebulizer, a Peltier-cooled deflector baffled cyclonic spray chamber, a standard quartz torch, and a two-cone interface design (sample and skimmer cones) was used. A nebulizer and plasma gas, high purity argon (99.9997%) (Gasin II, Leça da Palmeira, Portugal) was used. Equipment control and data acquisition were performed using Qtegra™ software (Thermo Fisher Scientific, Bremen, Germany). The conditions of instrument operation were: RF power, 1550 W; argon flow rate, 14 L/min; auxiliary argon flow rate, 0.8 L/min; nebulizer flow rate, 0.98 L/min. To minimize the effect of plasma fluctuations or different nebulizer aspiration rates among the samples, the Indium (^{115}In), Scandium (^{45}Sc), Terbium (^{159}Tb) and Yttrium (^{89}Y) were monitored as internal standards (Moura et al., 2020). To avoid possible sequence influences, the otolith samples were analyzed randomized in an analytical triplicate. The LOD were calculated from the individual calibration of the curves using the three sigma criteria and were (in μg/L): ^{137}Ba (0.064), ^{43}Ca (3943), ^{59}Co (0.005), ^{65}Cu (0.048), ^{7}Li (0.012), ^{24}Mg (0.410), ^{55}Mn (0.031), ^{60}Ni (0.100), ^{88}Sr (13.8) e ^{66}Zn (0.410). A certified multi-element reference material for otoliths (NIES 22) was used to determine the analytical accuracy (recovery rate, RR), which varied between 88% and 118%. The relative standard deviation (RSD), used to evaluate the precision, ranged between 1.21% and 4.10%. Both values (RSD and RR) are within the analytical accepted values (Dove et al., 1996: RSD: <20% and RR: 75%–125%). The concentration of the minor and trace elements, initially in μg element/L solution, was transformed into μg element/g otolith and finally into μg element/g Ca (Higgins et al., 2013).

2.5. *Data analysis*

Element/Ca concentrations were checked for normality, homogeneity of variance and presence of outliers (Grubb's test) (Correia et al., 2021). However, since almost all elemental ratios did not fulfill the parametric assumptions, even after being log10(x + 1) transformed, non-parametric statistics were used. In order to ensure that spatial variations in the otolith mass (OM) (as proxy of the fish size) cannot influence the MES differences among locations, the relationship between the OM and the element/Ca ratios was tested by an analysis of covariance (ANCOVA) using the OM as a covariate (Daros et al., 2016; Campana et al., 2000; Schroeder et al., 2022a). A positive relationship was observed for Zn/Ca (ANCOVA, $p < 0.05$), and a negative relationship for Li/Ca, Ba/Ca, Mg/Ca and Mn/Ca (ANCOVA, $p < 0.05$). The effect of the OM on otolith chemistry was removed by subtracting the common within-group linear slope multiplied by the OM from the original element/Ca ratios (Campana et al., 2000). Spatial differences in individual fingerprints were explored among sites by permutational univariate analysis of variance (PERANOVA). Pairwise PERANOVAs were used, if needed, to test differences between locations ($p < 0.05$). Permutational multivariate analysis of variance (PERMANOVA), based on the Euclidean distance (9999 permutations), was employed to test multi-elemental differences in otolith MES among sites. Pairwise PERMANOVAs were used to verify differences in otolith MES between sites. A flexible discriminant analysis (FDA) was applied to the EFD, MES and both combined to examine the accuracy of the reclassification. The FDA uses nonlinear combination of predictors, being useful for modelling non-normal multivariate data (Kassambara, 2017; Schroeder et al., 2022a). Ward's hierarchical clustering analysis without prior classification were used to evaluate differences between locations for EFD, MES and both combined data (Vaz-dos-Santos et al., 2023). A Principal Component Analysis (PCA) was applied to EFD, MES (covariance matrix) and both combined (correlation matrix) to evaluate the variability between groups (Almeida et al., 2020). All univariate and multivariate statistics were performed using the vegan (Oksanen et al., 2021) and exchange packages in the R programming environment (R Development Core Team, 2023). Results are presented as mean ± standard errors. A confidence level of $\alpha = 0.95$ was adopted.

3. Results

3.1. *Otolith shape analysis*

The otolith contour outlines obtained from the EFD means presented visual differences between the lagoon systems, especially in the dorsal and ventral edges, and also in the post-rostrum (Fig. 2). EFD between the lagoon systems showed significant differences (PERMANOVA, pseudo-F = 5.819; df = 1; $p < 0.001$). The cluster using EFD allowed to identify three groups: the first representing a mix from the two locations, the second composed mostly of Araruama lagoon system individuals and the third group only of Saquarema individuals (Fig. 3A). The PCA presented a complete overlap between Saquarema and Araruama lagoon systems, with the samples mainly concentrated in the lower central portion of the graph (Fig. 4A). Samples from Saquarema showed greater dispersion due to the influence of the descriptors a2, b2, d1 and d2, reflecting greater morphological variability (Fig. 4A). The samples from Araruama remained more concentrated closer to each other, due to the less morphological heterogeneity (Fig. 4A). The dataset showed an overall reclassification of the individuals to their original locations of 97% (97% Saquarema and 97% Araruama) (Table 3).

3.2. *Otolith elemental analysis*

3.2.1. *Uni-elemental analysis*

The Ba/Ca, Co/Ca, Li/Ca, Mg/Ca, Ni/Ca, Sr/Ca and Zn/Ca showed diferences between lagoon systems (PERANOVA; $p < 0.05$) (Table 4).

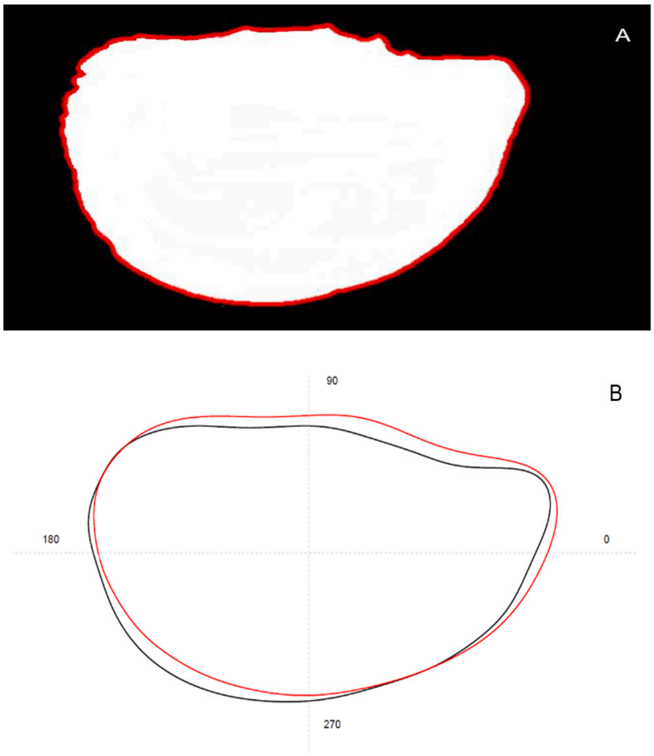

Fig. 2. Digital binarized image of a *Pogonias courbina* otolith showing the outer contour (A). Mean otolith contours by lagoon system (B). Saquarema: red; Araruama: black. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

However, the Cu/Ca (overall range: 1.20–2.10 μg/g) (Fig. 5) and Mn/Ca (overall range: 8.20–23 μg/g) (Fig. 5) ratios did not show any significant diferences between lagoon systems (PERANOVA; $p > 0.05$). The Ba/Ca (overall range: 11–38 μg/g) (Figura 5), Co/Ca (overall range: 1.14–1.69 μg/g) (Fig. 5), Mg/Ca (overall range: 68–124 μg/g) (Fig. 5), Ni/Ca (overall range: 13–21 μg/g) (Fig. 5) and Zn/Ca (overall range: 0.80–1.60 μg/g) (Fig. 5) ratios were higher in Saquarema lagoon system (PERANOVA; $p < 0.05$). The Li/Ca (overall range: 0.32–0.57 μg/g) (Fig. 5) and Sr/Ca (overall range: 4463–6416 μg/g) (Fig. 5) ratios were higher in Araruama lagoon system (PERANOVA; $p < 0.0001$).

3.2.2. *Multi-elemental analysis*

Significant differences were found for the MES between the lagoon systems (PERMANOVA; pseudo-F = 35.005; df = 1; $p < 0.0001$). The cluster using MES allowed to identify two groups: the first representing only individuals from Saquarema lagoon system and the second composed mostly of Araruama individuals (Fig. 3B). The PCA presented a separation between the samples of Saquarema and Araruama lagoon systems, driven mainly by the Ba/Ca, Li/Ca, Mg/Ca and Zn/Ca ratios (Fig. 4B). The Saquarema samples remained displaced towards the left portion of the graph, showing high discrimination due to higher concentrations of Ba/Ca, Mg/Ca and Zn/Ca ratios (Fig. 4B). The Araruama samples remained grouped in the right portion of the graph due to the high Li/Ca concentrations (Fig. 4B). The reclassification matrix obtained also showed an overall reclassification of the individuals to their original locations of 97% (93% Saquarema and 100% Araruama) (Table 3).

3.3. *Otolith shape and chemical analyses combined*

EFD and MES combined showed significant differences between the two lagoon systems (PERMANOVA; pseudo-F = 5.8187; df = 1; $p < 0.001$). The cluster using EFD and MES data allowed to identify three groups: with the first representing a mix from the Saquarema and

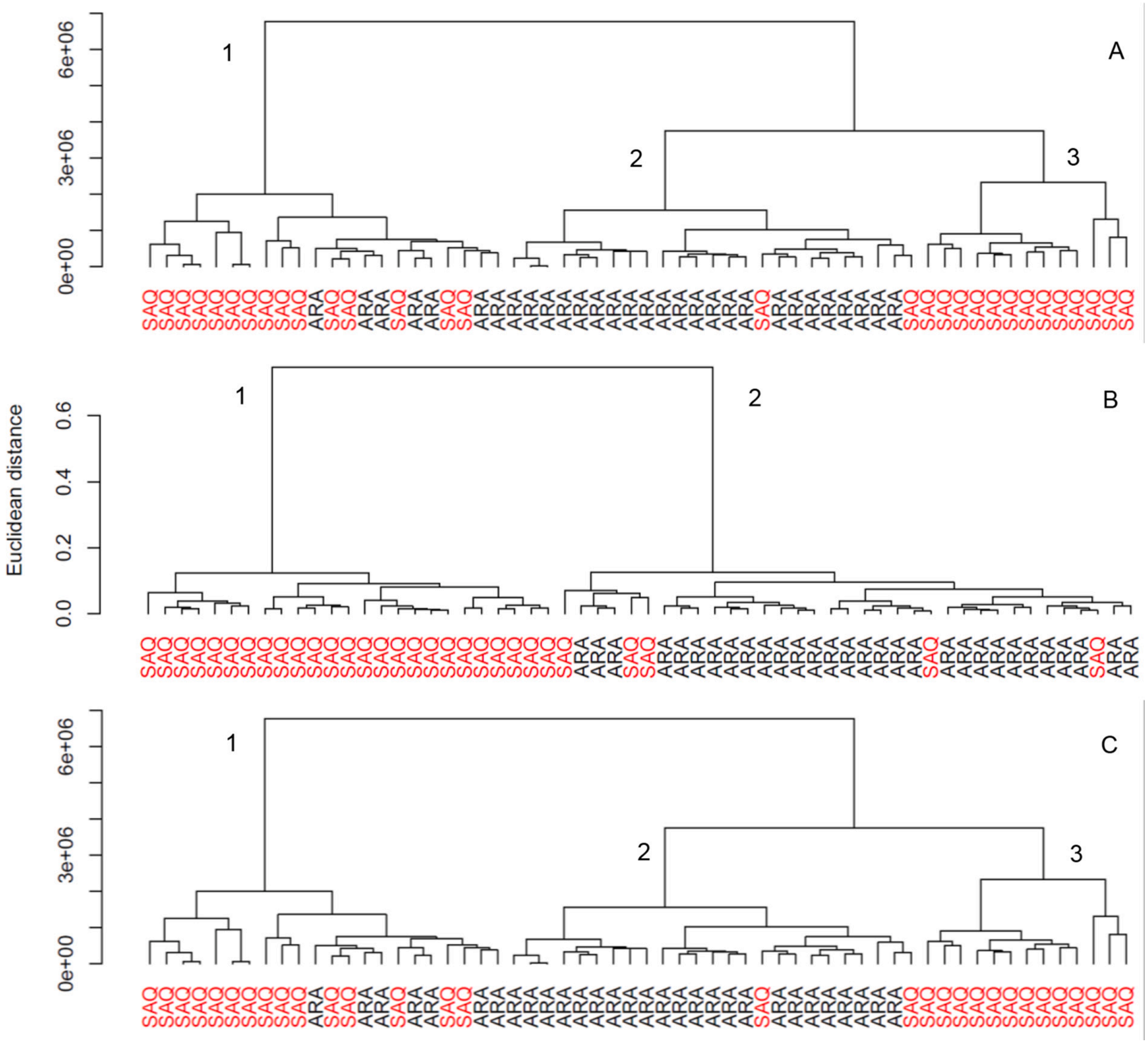

Fig. 3. Dendrograms showing groups of the *Pogonias courbina* otoliths using elliptic Fourier descriptors (A), multi-elemental signatures (B) and combining both techniques (C).

Araruama lagoon systems, the second composed mostly of Araruama individuals and the third group only of Saquarema individuals (Fig. 3C). The PCA presented a separation between the samples of Saquarema and Araruama lagoon systems, driven mainly by the Ba/Ca, Li/Ca, Mg/Ca, Sr/Ca and Zn/Ca ratios, and a2, b4, b5, b6, c10 and d2 descriptors (Fig. 4C). The Ba/Ca, Mg/Ca and Zn/Ca ratios, and a2, b5, c10 and d2 descriptors had a high influence on the discrimination of the Saquarema samples, which remained displaced to the lower portion of the graph (Fig. 4C). The Li/Ca and Sr/Ca ratios, and descriptors b4 and b6 directed the discrimination of the Araruama samples, which remained grouped in the upper central portion of the graph (Fig. 4C). The obtained reclassification matrix showed an overall reclassification of the individuals to their original locations of 98% (97% Saquarema and 100% Araruama) (Table 3).

4. Discussion

Otolith shape and chemical signatures revealed strong phenotypic variations in *P. courbina* individuals between the two hereby studied coastal lagoon systems (Saquarema and Araruama). These phenotypic differences can be attributed to the regional environmental conditions experienced by the fish while they lived in each lagoon, or in the adjacent coastal areas, which could act both as potential drivers. In both lagoon systems, there is a gradual increase in salinity from the inner sectors towards the ocean, a pattern previously reported by several authors (Rosa and Batista, 2020; Andrade-Tubino et al., 2020; Camara et al., 2023). However, the Araruama lagoon, characterized as a hypersaline system, displays the highest salinity values in their intermediate sectors due to the presence of salt pans used for salt extraction (Lamego, 1946; Giffoni, 2000; Moreira-Turcq, 2000). These contrasting environmental conditions may influence fish feeding, growth, and behavior, leading to variations in otolith shape and chemistry. When variations in natural tags are observed among groups of fish of the same age, it suggests distinct environmental histories, and consequently, otolith shape and chemistry can serve as valuable indicators for stock discrimination (Kerr and Campana, 2014; Volpedo and Vaz-dos-Santos, 2015; Nazir and Khan, 2021). The hereby results suggest the existence regional exogenous environmental differences, that could even influence endogenous processes, that affected the shape and incorporation of elements into the otolith calcium carbonate matrix of the black drum. Thus, the natural tags used here, suggested the presence of two *P. courbina* subpopulations with limited connectivity, highlighting the species' remarkable phenotypic variability, with implications on the local fisheries management of these coastal lagoons.

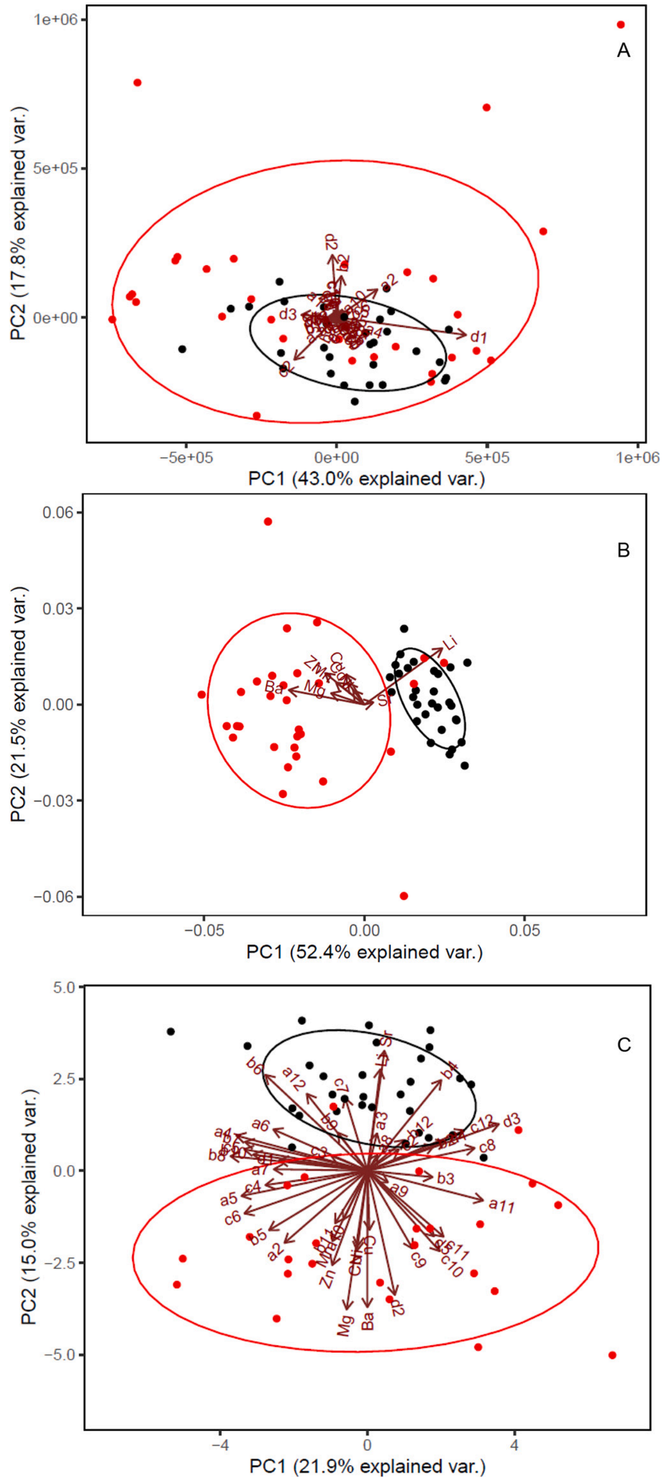

Fig. 4. Principal component analysis (PCA) presenting the distribution of groups of the *Pogonias courbina* otoliths using elliptic Fourier descriptors (A), multi-elemental signatures (B) and combining both techniques (C).

Table 3
Reclassification matrix for *Pogonias courbina* based on elliptic Fourier descriptors (A), multielemental signatures (B) and combining both techniques (C).

	Predicted locations		
Original locations	Saquarema	Araruama	% Correct
A			
Saquarema	29	1	97
Araruama	1	29	97
Total	30	30	97
	Saquarema	Araruama	
B			
Saquarema	28	2	93
Araruama	0	30	100
Total	28	32	97
	Saquarema	Araruama	
C			
Saquarema	29	1	97
Araruama	0	30	100
Total	29	31	98

Table 4
Comparison of *Pogonias courbina* element/Ca ratios between locations by PERANOVA. Significant statistical differences ($p < 0.05$) were marked in bold.

Element	Source	df	SS	Pseudo-F	p
Ba/Ca	Location	1	0.542	76.15	**0.0001**
	Residual	58	0.413		
	Total	59			
Co/Ca	Location	1	0.007	6.13	**0.0163**
	Residual	58	0.065		
	Total	59			
Cu/Ca	Location	1	0.007	2.58	0.1159
	Residual	58	0.146		
	Total	59			
Li/Ca	Location	1	0.153	60.30	**0.0001**
	Residual	58	0.147		
	Total	59			
Mg/Ca	Location	1	0.160	47.44	**0.0001**
	Residual	58	0.196		
	Total	59			
Mn/Ca	Location	1	0.013	1.93	0.1698
	Residual	58	0.391		
	Total	59			
Ni/Ca	Location	1	0.010	7.40	**0.0083**
	Residual	58	0.080		
	Total	59			
Sr/Ca	Location	1	0.040	76.60	**0.0001**
	Residual	58	0.030		
	Total	59			
Zn/Ca	Location	1	0.051	18.45	**0.0002**
	Residual	58	0.160		
	Total	59			

The EFD have been successfully applied to discriminate marine fish groups in the Southwest Atlantic, including in the Brazilian waters, using sagittal otoliths. Studies have investigated species such as *Abudefduf saxatilis* (Adelir-Alves et al., 2019), *Isopisthus parvipinnis* (Hoff et al., 2020), *Genidens genidens* (Maciel et al., 2020), *Micropogonias furnieri* (Franco et al., 2023), *Eugerres brasilianus* (Almeida et al., 2023) and *Opisthonema oglinum* (Vaz-dos-Santos et al., 2023). The shape of otoliths is one of the phenotypic characteristics widely employed to distinguish fish populations. This is due to the fact that otolith morphology varies geographically under the influence of genetics and local environmental conditions (Cardinale et al., 2004; Capoccioni et al., 2011; Bacha et al., 2014). Conversely, some authors argue that when genetic differences are absent, local environmental conditions primarily account for the variations in otolith shape (Katayama and Isshiki, 2007; Legua et al., 2013; Madureira and Monteiro-Neto, 2020). Moreover, advancements in otolith shape assessment methods have resulted in highly accurate responses, particularly when the dataset comprises otoliths from fish within the same age groups (Ferguson et al., 2011; Mapp et al., 2017; Moreira et al., 2019). It is well known that otolith morphology can vary according to different extrinsic and intrinsic attributes of the fish species, such as size, ontogeny, diet, and reproduction, as well as environmental factors, including physical-chemical water quality, habitat use, and depth (Cardinale et al., 2004; Bacha et al., 2014; Moura et al., 2020). However, the hereby findings are clear regarding the variation in otolith shape in both lagoons, resulting in specific characteristics for *P. courbina* regional populations. Thus, the combination of evaluating

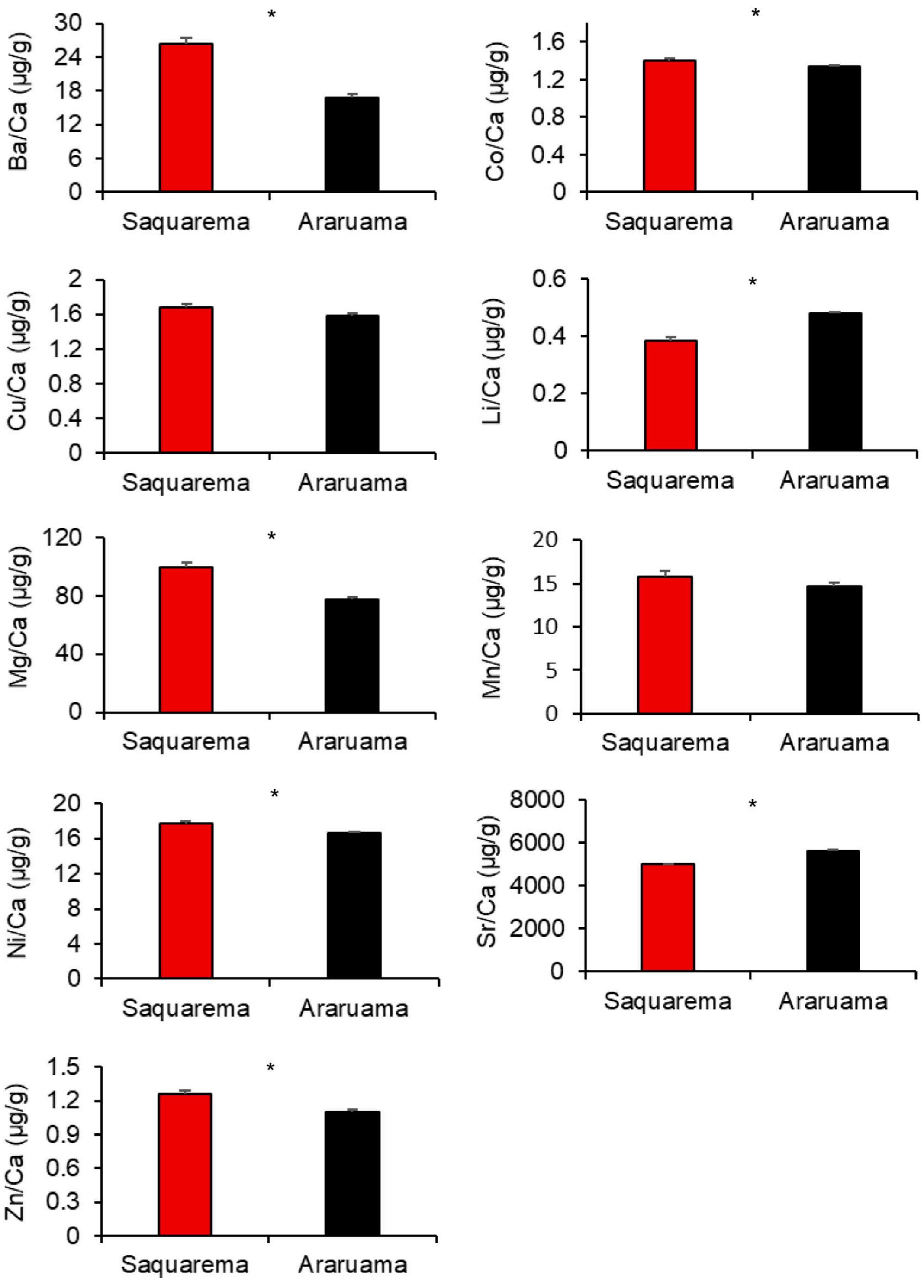

Fig. 5. Element/Ca ratios in otoliths of *Pogonias courbina* collected in the lagoons systems of eastern Rio de Janeiro, Brazil. Elemental concentrations (detrended concentrations) are showed as mean values ± standard errors. *Significant statistical differences (PERANOVA: $p < 0.05$).

fish from the same age group, associated with geometric contour analysis (EFD), that decomposes the complex curves of otoliths into a sum of harmonically related ellipses, proved to be an efficient methodology for discriminating populations of *P. courbina*.

The elemental composition of *P. courbina* otoliths was similar to other studies carried out to the Sciaenidae family (*Cynoscium nebulosus*: Comyns et al., 2008; *Isopisthus parvipinnis*: Hoff et al., 2022; *Micropogonias furnieri*: Franco et al., 2023). The most commonly used elements in microchemical studies of otoliths are the strontium (Sr), the barium (Ba), the manganese (Mn) and the magnesium (Mg), among others. The Sr/Ca and Ba/Ca ratios typically display opposing trends when characterizing the habitat salinity use, indicating the species' utilization of marine, brackish or freshwater environments (Gillanders, 2002; Franco et al., 2019a; Ferreira et al., 2023). Temperature and salinity are the primary environmental factors that influence otolith chemistry, particularly in estuaries where multiple abiotic factors can vary (Elsdon et al., 2008). Several studies have demonstrated correlations between the Ba:Ca and Sr:Ca ratios and temperature and salinity

(Stanley et al., 2015; Mazloumi et al., 2017; Nelson and Powers, 2019). The Ba/Ca ratios commonly exhibit a positive correlation with temperature and a negative correlation with salinity, whereas the Sr/Ca ratios generally show positive correlations with both variables. Moreover, these variables serve as reliable predictors of the estuarine gradient, aiding in the characterization of its compartments. Additionally, it is essential to consider the interactive influence of temperature and salinity, along with their spatial variations in estuaries (Barletta and Lima, 2019), to comprehensively understand the environmental factors that can impact fish otoliths. When comparing the lagoon systems, it becomes evident that the Saquarema lagoon exhibits characteristics of an estuarine environment in contrast to the hypersaline Araruama lagoon (See the Table 1). However, the latter system also includes typically estuarine areas in its innermost sector due to the contributions from the continental run-off. In the case of Mg, studies have shown more variability, with limited relationships reported between Mg concentrations in water and otoliths (Wells et al., 2003; Dorval et al., 2007; Hamer and Jenkins, 2007). Some authors associated the incorporation of Mg into otoliths with salinity, temperature and ontogenetic changes (Gaetani and Cohen, 2006; Avigliano et al., 2015b; Bouchard et al., 2015;). Magnesium is enriched in the blood of fish compared to the endolymph fluid that surrounds otoliths (Melancon et al., 2009), indicating a physiological fractionation of this element within the endolymph. However, Shearer and Åsgård (1992) argued that fish can regulate magnesium uptake from both water-borne and dietary sources, ensuring that their magnesium requirements are always met. When water quality is poor due to anthropogenic discharges (such as increased urbanization, domestic and/or industrial effluents, and agricultural inputs), certain heavy metals can be incorporated into the otoliths. This can indicate that individuals have been exposed to varying levels of water pollution throughout their lives (Lacerda et al., 1999). The relatively low variations observed in the Ni/Ca, Co/Ca, and Zn/Ca ratios, despite being significant among the lagoons, raise important questions. These environments serve as hotspots for biodiversity and human activities while also acting as a sink for continental runoff, leading to long-term accumulation and detrimental effects on the biota (Kjerfve, 1994; Esteves et al., 2008). The exception among these heavy metals is for the incorporation of Zn into the otoliths of some euryhaline species, which can be influenced by factors such as diet (Ranaldi and Gagnon, 2008), growth (Avigliano et al., 2015; Hüssy et al., 2021), and reproductive activity (Sturrock et al., 2015). Just like salinity, the Li/Ca and Sr/Ca ratios were higher in Araruama, which can be attributed to the abundance of these elements in seawater (Avigliano et al., 2017; Walther and Nims, 2015; Nelson and Powers, 2019) and in hypersaline coastal lagoons (Franco et al., 2019a). Strontium is primarily found in marine environments and is mainly associated with Sr salts, while Li is released into the marine environment through rock weathering processes (Bouchard et al., 2015). Additionally, Carvalho et al. (2020) also observed a positive correlation between Li and salinity. However, they suggested caution when interpreting Li/Ca ratios, as decreasing trends in this ratios may be linked to ontogenetic variations rather than to environmental changes. On the other hand, strontium exhibited a strong correlation with salinity (Izzo et al., 2018), indicating that the Sr/Ca ratio can serve as an excellent proxy for salinity.

The salinity gradient is often used to delineate habitats, directly or indirectly, influencing the dispersal patterns and recruitment success of fish inhabiting estuarine areas and/or coastal lagoons (Kimura et al., 2000; Gelwick et al., 2001; Rooker et al., 2004). The Araruama lagoon, classified as a hypersaline system due to its negative water balance resulting from evaporation surpassing fluvial and pluvial discharges, can lead to alterations in the dynamics of the black drum population (e.g., body size, growth rate, age of sexual maturation, diet) compared to the Saquarema lagoon, which has a positive water balance influenced by tidal variations and a small channel in extension (Kjerfve et al., 1996; Miranda, 2002). Almeida et al. (2021) identified variations in the feeding regime of *P. courbina* and relative condition factor indices between the lagoon systems. Specifically, in Saquarema lagoon, gastropods were the primary food source, whereas, in Araruama, barnacles were the dominant dietary items. These findings support that diet plays a crucial role in determining the phenotypic characteristics of otoliths. Olsen et al. (2018) investigated intraspecific variation among populations of black drum, focusing specifically on a population inhabiting a hypersaline estuary. The study revealed that black drum from the Upper Laguna Madre mature at an earlier stage compared to the other populations. Additionally, the authors compared other life history traits, such as fecundity, maximum age, maximum size, and growth rate, with those of other populations. They observed significant differences in these variables, indicating deviations from the typical life history strategy observed in sciaenids (known as periodic strategists) and suggested a more opportunistic behavior. The authors attributed these variations to the specific habitat in which the species developed, namely a hypersaline lagoon. Therefore, EFD and MES proved to be high-resolution proxies for distinguishing the groups of *P. courbina* between Saquarema and Araruama lagoons, emphasizing the high local fidelity of both sub-populations and limited connectivity, at least until the two-year old.

The narrow channels connecting lagoon systems to the sea, can also serve as physical barriers, limiting the movement of individuals between estuarine environments and the coastal zone (Bilton et al., 2002). In southern Brazil *P. courbina* has been observed to migrate between the coastal zone and shallow estuarine areas, being classified it as a marine estuarine-dependent species (Vieira et al., 1998; Macchi et al., 2002; Santos et al., 2016). Moreover, genetic studies have revealed absence of population structure among *P. courbina* in southern Brazil, Uruguay, and Argentina, attributed to factors such as long lifespan and discrete migration rates, resulting in slow recolonization processes (Machado et al., 2020). However, investigations conducted on *P. cromis* in the Baffin Bay Complex in the USA have identified a subpopulation with unique characteristics, including higher recruitment rates and smaller maturation sizes compared to other areas. These traits are a result of the hyperhaline conditions within these systems and the subpopulation's fidelity to specific habitat conditions (Olsen, 2014; Ajemian et al., 2018). Therefore, our findings corroborate that *P. courbina* presents a great ability to adapt to varying ecosystem conditions, with their subpopulations demonstrating high fidelity to their respective habitats - system lagoons of Saquarema and Araruama.

Finally, our results confirm the discrimination between two-year-old individuals of *P. courbina* collected in the lagoon systems of Saquarema and Araruama, as indicated by FDA. The physiographic and physical-chemical characteristics of these lagoon systems contribute to the morphological and multi-element phenotypes differentiation found in *P. courbina* otoliths. However, the lack of in situ recorded environmental data is a limitation of this study, given that fish otolith chemistry is influenced by the exposure to multiple environmental variables, which could somewhat bias the interpretation of the results. Although the interpretation of these data should be done cautiously, the hereby distinction between the two subpopulations of black drum underscores the importance of implementing separate management measures for each lagoon system. This is especially crucial considering that the species is not only a significant fishing resource in the lagoons but is also listed in the IUCN Red List and the MMA Red List due to its vulnerability to fishing overexploitation. In the Araruama lagoon system, the species is protected by a fishing moratorium/fishing closed (law SAP/MAPA N° 1.217, 19/08/2022, 2022), while in the Saquarema lagoon system, there are only restrictions on gear and fishing areas (*Law IBAMA N°41/1996,* 1996), without any specific conservation measures targeting the species.

Future studies should focus on describing the life history parameters separately for subpopulations within the lagoon systems in eastern Rio de Janeiro. Furthermore, the identification of new stocks of *P. courbina* along the entire southwestern coast of the Atlantic is necessary for fisheries management and conservation purposes.

CRediT authorship contribution statement

Paulo Roberto Camponez de Almeida: Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization. **Marcus Rodrigues da Costa:** Writing – review & editing, Supervision, Project administration, Conceptualization. **Ana Tereza Rodrigues Ribeiro:** Investigation, Formal analysis. **Agostinho Almeida:** Writing – review & editing, Resources. **Rui Azevedo:** Writing – review & editing, Methodology, Formal analysis. **Cassiano Monteiro-Neto:** Writing – review & editing. **Alberto Teodorico Correia:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Formal analysis, Conceptualization.

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.

Data availability

Data will be made available on request.

Acknowledgements

The present study is part of the project "Pesquisa Marinha e Pesqueira," which is an offset measure established under a consent decree between the company PRIO and the Federal Public Prosecutors' Office in Rio de Janeiro. The project was funded by the Brazilian Fund for Biodiversity (FUNBIO). The authors thank the financial support provided by the Coordination for the Improvement of Higher Education Personnel (CAPES) and the Brazilian Fund for Biodiversity (FUNBIO) for the execution of the subproject titled "Sistemas Lagunares do Leste Fluminense- SLLF (short title)" within the framework of the Project "Mecanismos Reguladores da Produção Pesqueira nos Sistemas Lagunares do Leste Fluminense: estado atual e cenários futuros." Additionally, this study received support from international funds through FCT—Foundation for Science and Technology, as part of UIDB/04423/2020 and UIDP/04423/2020. We thank the scientific initiation scholarship PIBIC/UFF Leonardo Salgado for the map, and the other fellows working on this project.

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