Full length article

Contribution of the nursery areas to the major fishing grounds of the Brazilian sardine (*Sardinella brasiliensis*) in Southeastern Brazilian Bight inferred from otolith fingerprints

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ABSTRACT

In the late seventies, studies on the population structure of *Sardinella brasiliensis* suggested the existence of two stocks (23–25°S and 26°S–28°S) based on distinct regional somatic growth rates and spawning areas. This scenario was recently confirmed by using geochemical signatures of whole otoliths combined with basic biological data from two-year-old individuals collected in southeast-south Brazil. However, information about sardine movements and connectivity between their main juvenile recruitment areas and the adult fishing grounds is currently limited. In this work, otolith natal elemental fingerprints (core section) of recruits (age 0+) and adults (age 2+), collected respectively in the main spawning areas (2019) and fishing grounds (2021) were evaluate. Otolith geochemical signatures (element/Ca) of recruits were compared with those of adult fish from the same cohort to estimate connectivity between juvenile recruitment areas (Rio de Janeiro RJ: 22°S, São Paulo SP: 23°S and Santa Catarina SC: 26°S) and regional adult populations captured in the major fishing grounds (22–23°S, 24–25°S and 26–27°S). Uni and multi-elemental signatures showed significant differences for recruits and adult's individuals. This variability was mainly driven by Ba/Ca, Cu/Ca and Mg/Ca ratios. Pairwise comparisons associated recruits and adults from the northern distribution area (RJ+SP), but differentiated them from those individual from south (SC). The leave-one-out matrix combining otolith fingerprints reassigned the individuals to their original areas with moderate to high accuracy, for both recruits (RJ: 79%, SP: 73% and SC: 67%) and adults (RJ: 75%, SP: 60% and SC: 69%). A multinomial logistic regression suggested that for the 2019 cohort the replenishment of adult populations of *S. brasiliensis* along the Southeastern Brazilian Bight was mostly derived from the northern recruitment area (RJ+SP=89%). Nonetheless, minor contribution from the southern counterparts to the northern stock was detected (11%), supporting the hypothesis of meta-population structure for this species.

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1. Introduction

The Brazilian sardine (*Sardinella brasiliensis*) is a small pelagic clupeid fish concentrated between 22ºS [Rio de Janeiro - São Tomé Cape] and 29ºS [Santa Catarina - Santa Marta Grande Cape] in depths up to 150 m, with sporadic occurrence records until 33°S (Saccardo and Rossi-Wongtschowski, 1991; Castello, 2007; Schroeder et al., 2022a). This species sustains the most important pelagic fishery in the South-eastern Brazilian Bight (SBB) (Matsuura, 1998), being targeted by purse seine vessels in two major fishing grounds, namely in Santa Catarina and Rio de Janeiro (Schroeder et al., 2022a). New onboard scientific data associated to basic biological data, distribution of juveniles and adults, body morphometrics, and shape and chemistry of otoliths, recently suggested the existence of two population-units of *S. brasiliensis* in the boundaries of such fishing area (Schroeder et al., 2022a,b,c). However, information about fish movements and connectivity between their main juvenile recruitment areas in shoreline waters and the adult fishing grounds is currently limited for this species.

At present, in terms of fisheries assessment for management purposes, a single stock of *S. brasiliensis* is considered (Cergole and Dias-Neto, 2011). The spawning of the species occurs in two main areas (23°S-25°S and 26°S-28°S) during the spring and summer (Matsuura, 1998; Rossi-Wongtschowski, 1977; Vazzoler and Vazzoler, 1965). It closely depends on the seasonal advection of the South Atlantic Central Water (SACW), which modifies the structure of the environment, increasing the availability of food for the larvae and juveniles under the Shelf Water (SW) and Tropical Water (TW) (Matsuura, 1986; Matsuura et al., 1992; Matsuura, 1996). This oceanographic phenomenon typically occurs between January and March (summer months), driven by northeasterly winds, which replace the Coastal Water (CW) by deeper and richer coastal waters from SACW due to the Ekman's transport (Matsuura, 1998; Valentin, 2001; Campos et al., 2013). Such advection is not homogenous throughout the entire species distribution area (Matsuura, 1998; Gigliotti et al., 2010). It shows a remarked occurrence in the northern area (23°S) (Rodrigues and Lorenzzetti, 2001; Valentin, 2001; Dias et al., 2014), being less intense in the southern region (28°S) (Matsuura, 1998; Acha et al., 2004; Campos et al., 2013). The spatio-temporal heterogeneity of the oceanographic features in the SBB, plays a key role for the dispersion of planktonic larvae (Dias et al., 2014; Moraes et al., 2012), making marine fish populations, such as sardines, dependent on complex patterns of dispersion (Burke et al., 2008; Brochier et al., 2018; Mosegaard and Madsen, 1996). However, during the growing juvenile phase, sardines from the different spawning areas join together and share a common feeding ground (25°S), although they apparently return later to their original places after reaching the sexual maturity (Rossi-Wongtschowski, 1977).

Studies involving distribution of eggs and larvae of *S. brasiliensis* (Matsuura, 1977, 1996, 1998; Matsuura et al., 1992), traditional body morphometry (Braga, 1987), life history traits and recruitment dynamics (Rossi-Wongtschowski, 1977; Matsuura, 1998), suggest the existence of more than one population-unit in the Brazilian southeastern-south coast (Schroeder et al., 2022a,b,c). Furthermore, a preliminary mitochondrial DNA study failed to show any genetic spatial structure for *S. brasiliensis* (Stern et al., 2018). However, in high gene flow systems where environmental heterogeneity exists (Bradbury et al., 2008; Smith and Campana, 2010; Correia et al., 2012), otolith chemistry has proven to be useful in resolving fish stock structure, migration patterns and connectivity between spawning/nursery sources and fishing grounds, because it does not require genetic diversity among populations (Correia et al., 2012; Avigliano et al., 2017; Artetxe-Arrate et al., 2019). Minor and trace elements deposited in the aragonite matrix of otoliths represent a permanent environmental record and serve as a natural tag, allowing the reconstruction of lifetime movement patterns and past environmental conditions experienced by an individual at a particular time (Campana et al., 2000; Elsdon et al., 2008; Dias et al., 2019). In metapopulation structures and using the correct spatial and temporal sampling design it is possible to understand how much the spawning, nursery or recruitment areas contribute to the replenishment of adult fish populations subject to fisheries exploitation (Hamer at al, 2011; Reis-Santos et al., 2013; Correia et al., 2014).

The main objectives of this work were: (*i*) to assess the variation in the otolith core fingerprints (natal origin) of recruit and adult sardines from different areas in the SBB, thereby indicating separation during the recruitment; (*ii*) to evaluate the spatial heterogeneity of the otolith core fingerprints within a cohort by comparing recruits from different regions born in the same season; and finally (*iii*) to compare the otolith core fingerprints of recruits with those of adult fish of the same year-class to estimate the connectivity between the juvenile recruitment areas and the regional adult fishery grounds. The ultimate goal was to assess from which recruitment area, the replenishment of the adult populations of sardine along the Brazilian SE-S coast was mostly derived.

2. Material and methods

2.1. Biological sampling

Recruits (age 0^+) were collected in the main spawning grounds of *S. brasiliensis* in the SBB [Rio de Janeiro (RJ) - 22°S, São Paulo (SP) - 23°S and Santa Catarina (SC) - 26°S (Matsuura, 1977; Matsuura et al., 1992; Matsuura, 1996)] between January and June 2019 using beach seine nets (Fig. 1, Table 1). Fish of adult regional populations (age 2^+) from the same cohort were acquired from the industrial purse seine fleet between May and July 2021 in the major fishing grounds (RJ: 22–23°S, SP-PR: 24–25°S and SC: 26–27°S) of the Brazilian coast (Saccardo and Wongstchowski, 1991; Schroeder et al., 2022a) (Fig. 1, Table 1). Total length (TL, nearest 0.1 cm) and body weight (BW, in grams) were measured in all individuals, and sagittal otoliths carefully extracted.

2.2. Age readings

Sagittal right otoliths were embedded in epoxy resin (Buehler, Epo-Thin 2) and cut in thin transversal cross-Section (1 mm) using a precision diamond saw (Buehler, Isomet Low-speed Saw) for age estimate and further microchemistry analyses. The thin slides were grounded with silicon carbide papers (600, 1200, 2400, and 4000 grit - Struers) until the core became visible, and further polished with diamond pastes (6, 3 and 1 μm) (Buehler, Metadi II) and mounted on a conventional glass slide with one drop of epoxy resin (Buehler, Epothin 2) (Correia et al., 2012). Thereafter, annual growth increments (Saccardo et al., 1988) were counted following an existing protocol for the species (Rossi-Wongtschowski et al., 1982), but modified for transverse sections (Table 1). Annuli were blindly counted twice by an experienced reader with one-month interval, using a microscope (Olympus, CX41) with a $40 \times$ magnification under transmitted light. Only otoliths with 100% of age readings agreement were used for subsequent analyses (Correia et al., 2014; Schroeder et al., 2022b, 2022c). Two-year-old adult fish from the 2019 cohort captured in the major fishing grounds were then selected (Table 1) to evaluate connective patterns between recruits sampled in the main spawning grounds, using otolith core fingerprints.

2.3. Otolith microchemistry

Following the age reading, the sagittal otolith polished sections (~0.5 mm) were then sonicated for 3 min in ultrapure water (18.2 MΩ cm at 25oC) and dried in a laminar flow cabinet before being analyzed (Correia et al., 2012). The otolith core region was analyzed by laser ablation connected to an Inductively Coupled Plasma Mass Spectrometry (ICP-MS-LA) for both recruit and adult individuals. Elemental concentrations of the prepared otolith sections were measured using a 193-nm ArF Excimer Laser Ablation System (Photon Machines Analyte G2) coupled to an ICP-MS Agilent 7700 (Agilent Technologies). After a preliminary investigation (Schroeder et al., 2022c), seven isotopes were
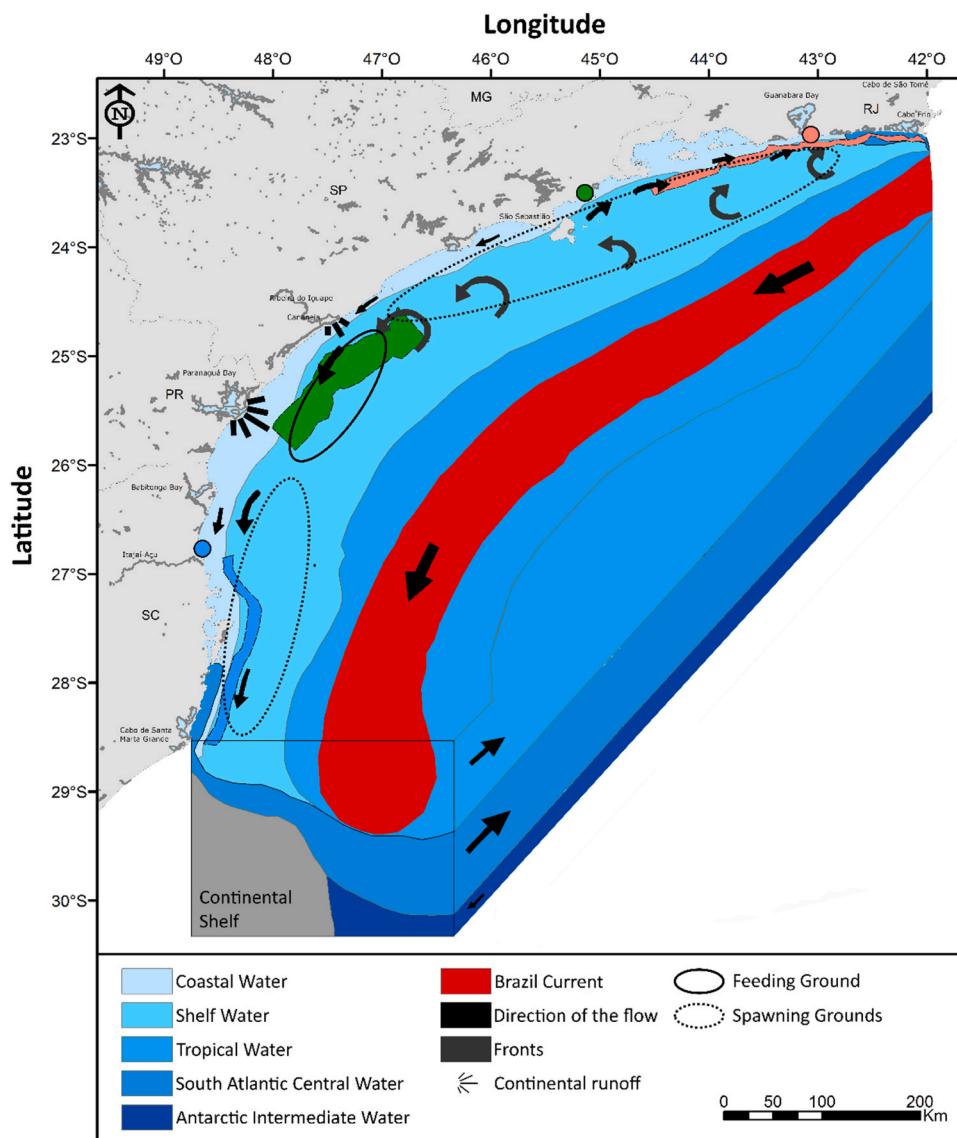
Fig. 1. Map showing the three sampling locations of *Sardinella brasiliensis* off southeast-southern Brazil. The colored solid circles represent the sampling sites for the young-of-the-year (Age-0 fish) collected in the main spawning areas (2019) and the colored dashed area adult individuals (Age- 2 fish) captured in the fishing grounds (2021) [Rio de Janeiro (RJ, red), São Paulo (SP, green), and Santa Catarina (SC, blue)]. PR represents Paraná State. Black dotted and continuous ellipses represent respectively the two spawning areas and the feeding ground for *S. brasiliensis* (according to Rossi-Wongtschowski, 1977). Continuous grey lines subdivided the study area according to the latitudinal distribution of the oceanographic characteristics: Continental runoff, Coastal Water, Shelf Water, Tropical Water, Brazilian Current, South Atlantic Central Water, and Antarctic Intermediate Water. Water mass fronts and the direction of the flow are represented by sets (according to Ribeiro, 1996).

Table 1

Area of capture (RJ - Rio de Janeiro, SP - São Paulo, and SC - Santa Catarina), fishing method, date of sampling, total length (TL), age group (0 +: recruits and 2 +: adults) and sample size (N) of *Sardinella brasiliensis* captured in the major spawning grounds and fishing area in the southeast-south of Brazil in 2019 and 2021.

Area	Fishing method	Date	TL (cm)		Age group (years)	N
			Range	Mean		
RJ	Beach seine nets	Jan-Fev 2019	3.57–4.75	4.07	0 +	20
	Industrial purse seine	May 2021	19.50–22.20	20.86	2 +	20
SP	Beach seine nets	Fev 2019	5.10–7.50	6.15	0 +	20
	Industrial purse seine	Jul 2021	17.56–21.99	20.96	2 +	20
SC	Beach seine nets	Jun 2019	3.00–4.60	3.45	0 +	20
	Industrial purse seine	Jun 2021	22.75–24.81	23.44	2 +	20

selected, namely ^{137}Ba, ^{65}Cu, ^{57}Fe, ^{7}Li, ^{24}Mg, ^{55}Mn, and ^{88}Sr, along with ^{43}Ca as the internal standard. Data for ^{59}Co and ^{66}Zn were also collected, but these elements were consistently below the detection limits. Laser spots diameter of 15 μm were used, with a repetition rate of 50 Hz and output energy of ~3.5 J/cm^2. Ablation were made in triplicates on each sagittal section over the otolith core region to ensure statistical robustness. The average value of the three ablations was used.

According to the relationship between sardine age (in days) and total length for the 2019 cohort (Vaz-dos-Santos and Schwingel, 2019), the core area analyzed in this study, corresponding to a 15 μm laser ablation spot, represents approximately the first two months of life for the sardines. Based on the area of collection, sardine larvae appear to live mainly on the coastal continental shelf very close to the coastline. The 'natal' otolith fingerprints extract from the core region, were assumed to represent the early life history stage of sardine, rather than the place of birth.

Precision of the analytical process was determined using the relative standard deviation (RSD) of three readings for each element, standard,

and samples (RSD < 5%). Reference material (MACS3, NIST 610, NIST 612) analysis showed acceptable recoveries rates (RR), showing median values varying between 93.35% and 100.59%. Average detection limits (LOD, ppm) based on three times the standard deviation of the estimated baseline intensity during bracketing gas blank is shown between parentheses for: ^{137}Ba, 0.16, ^{43}Ca, 663, ^{59}Co, 0.22, ^{65}Cu, 0.36, ^{57}Fe, 21.80, ^{7}Li, 0.44, ^{25}Mg, 0.18, ^{55}Mn, 0.79, ^{88}Sr, 0.05, and ^{66}Zn, 2.59. Concentrations were expressed as molar ratios in relation to Ca (element/Ca, μmol/mol).

2.4. Statistical analysis

Elemental signatures were first standardized using box-cox transformation (Rigby et al., 2019; Schroeder et al., 2022c). Homogeneity of variances prior to statistical analysis were met after box-cox transformation in all cases, as indicated by Levene test (Supplementary file). However, the Shapiro-Wilk test showed that element/Ca ratios did not achieve normality in most of cases (p < 0.05) (Supplementary file). Single-elemental signatures found in otolith's core were analyzed by permutational univariate analysis of variance (PERANOVA), and a permutational multivariate analysis of variance (PERMANOVA), after box-cox transformation, to compare multi-elemental signatures. When significant differences were found, pairwise PERMANOVA were applied, respectively to perform multiple comparisons (Avigliano et al., 2017; Soeth et al., 2019; Schroeder et al., 2022c). The reclassification of individuals to the original location was evaluated after multivariate analyses applied for microchemistry through the percentage of correctly reclassified individuals using leave-one-out cross-validation after a flexible discriminant analysis (FDA) (Schroeder et al., 2022c).

Additionally, stock composition of *S. brasiliensis* was conducted through Multinomial Logistic Regression (MLR) using the multi-elemental otolith core signature from the recruits (age 0$^+$) as baseline to determine the contributions of the three major recruitment areas to the samples of adult sardine (age 2$^+$) from the same cohort. The MLR is a classification method that has been used to estimate the contribution rates in mixed-population of *Thunnus thynnus* (Rooker et al., 2019). This model allows to estimate the probability of occurrence of each category (i.e., subpopulation-unit) as a function of explanatory variables (multi-elemental core signature) using a maximum likelihood estimator. Different from the previous studies on stock composition analysis (Millar et al., 1990; Correia et al., 2014; Hamer et al., 2011; Reis-Santos et al., 2013), MLR predicts the probability of randomly sampled individuals from the mixed sample and then assigns individuals to a category and estimates the proportions of each population. The response variable of each population follows a multinomial distribution and the probability of each category of the dependent variable is predicted from explanatory variables included in MLR (Rooker et al., 2019). According to the authors, predictions of MLR were derived for five probability thresholds: 0.5, 0.6, 0.7, 0.8 and 0.9, in which the probability of 0.5 indicates that when an individual's predicted probability for the baseline sample (i.e. RJ) is above 0.5, it will be classified to its respective population (i.e. RJ). MLR assumes that (*i*) the choice of one category is not related to the choice of the dependent variable, (*ii*) the dependent variable cannot be perfectly predicted from the independent variables, and (*iii*) multi-collinearity is relatively low for the independent variables. Predicted probabilities were estimated using by bootstrapping 1500 simulations of the baseline. All statistical analyses were performed using R (R Core Team, 2022).

3. Results

3.1. Otolith core analyses of the 1-year-old sardines (recruits, cohort 2019)

Single elemental composition of cores showed significant differences among the three recruitment area groups for Ba/Ca ratios (PERANOVA,

F = 5.627, P = 0.003) and Mg/Ca ratios (PERANOVA, F = 4.387, P = 0.036) (Fig. 2). Pairwise comparisons showed that Ba/Ca ratios of individuals sampled off RJ were significant different from those of SP (DUNN.TEST, z = 2.297, p = 0.021) and SC (DUNN.TEST, z = 2.332, p = 0.019). But no statistical differences exist between the individuals sampled in SC and SP (DUNN.TEST, z = 0.119, p = 0.904). Mg/Ca ratios were different between individuals sampled off RJ and SC (DUNN.TEST, z = 2.483, p = 0.039), but SP was not different from the individuals sampled off RJ (DUNN.TEST, z = 0.302, p = 1.000) and SC (DUNN.TEST, z = 2.131, p = 0.099) (Fig. 2).

The permutational multivariate analysis of variance indicated the existence of significant regional differences in the multi-elemental signatures (PERMANOVA, F = 2.9261, p = 0.012). Pairwise comparisons showed that multi-elemental otolith fingerprints showed that individuals sampled in SC were different from those of RJ (PAIRWISE.PERMANOVA, F = 3.384, p = 0.017), and SP (PAIRWISE.PERMANOVA, F = 2.570, p = 0.047). The FDA showed that the natal geochemical signatures of the recruitment areas partially overlap (Fig. 3). Jackknifed reclassification accuracy was relatively high showing an overall mean of 83% (Table 2). This pattern was mainly explained by Ba/Ca, Cu/Ca and Mg/Ca ratios (Fig. 3).

3.2. Otolith core analyses of the 2-year-old sardines (adults, cohort 2019)

In the case of adult individual's, single elemental composition of cores showed significant differences among regions for Cu/Ca ratios (PERANOVA, F = 5.627, p = 0.005). Pairwise comparisons showed that Cu/Ca ratios were different between SC and the other two regions between (RJ and SP) (DUNN.TEST, z = 0.871, p = 1), that did not show any differences between them (DUNN.TEST, z = −2.567, p = 0.031) (Fig. 2).

The permutational multivariate analysis of variance indicated the existence of significant differences in the multi-elemental signatures of the otolith cores (PERMANOVA, F = 3.114, p = 0.027), and pairwise comparisons gave significant differences for RJ and SC (PAIRWISE.PERMANOVA, F = 1.418, p = 0.039). Pairwise comparisons did not show differences between multi-elemental core fingerprints of adult sardine captured between RJ and SP (PAIRWISE.PERMANOVA, F = 0.819, p = 0.786), and SP and SC (PAIRWISE.PERMANOVA, F = 0.587, p = 0.587). The FDA showed three distinct groups partially overlapped among areas (Fig. 3). Jackknifed classification accuracy was medium for adults showing an overall mean of 68% (Table 2). This pattern was mainly explained by Cu/Ca ratios (Fig. 3).

3.3. Contribution of the young-of-the-year individuals to the adult exploited population

The MLR indicated that 89% of adult sardines captured in the SBB originated from recruits collected in the northern area (RJ+SP) (Table 3). The large contribution was provided by RJ recruits (70%), followed by SP's (19%) and SC's (11%) (Fig. 4). Self-recruitment was higher for RJ (95%), followed by SP (42%), and SC (21%) (Fig. 4, Table 3).

4. Discussion

Elements per calcium ratios of the Brazilian sardine otoliths (e.g. Sr/Ca, Mg/Ca, Mn/Ca and Ba/Ca) fell into the ranges found for other marine fishes in the same study area (e.g. Daros et al., 2016; Soeth et al., 2019; Hoff et al., 2022), including a previous study using the whole chemical life-history of *S. brasiliensis* (Schroeder et al., 2022c). Significant differences were detected in the otolith chemistry during the larval/early juvenile stage of the individuals of the same cohort caught in the main spawning areas approximately 5 months after hatching. Spatial variability in otolith cores fingerprints of the recruits (age 0 +) was
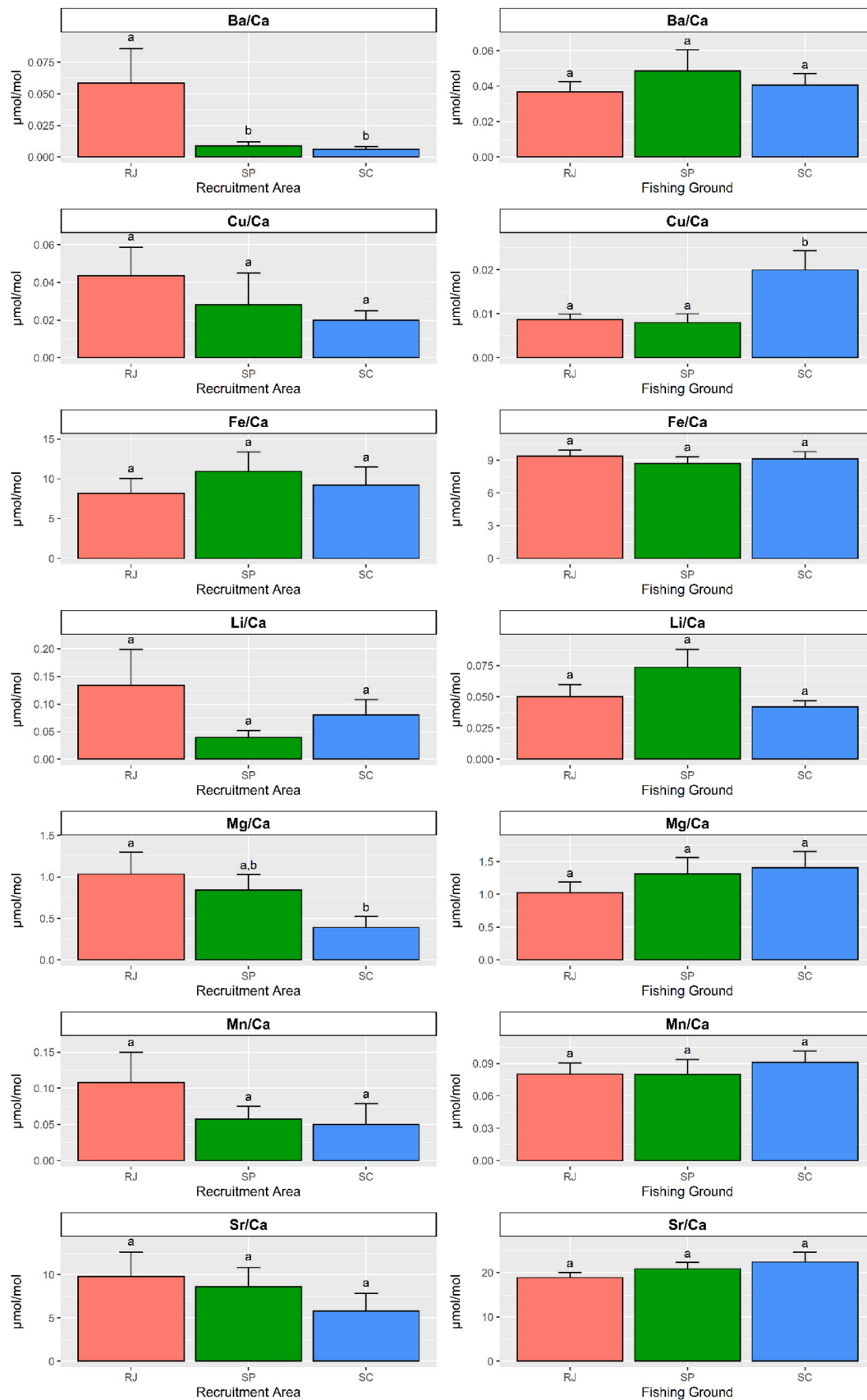
Fig. 2. Regional comparison of element/Ca ratios (expressed in μmol/mol) from the otolith's core of *Sardinella brasiliensis* of the young-of-the-year (0-age individuals, first column, Recruitment Area) sampled between January 2019 and June 2019 and adults (2-age individuals, second column, Fishing Ground) captured between May 2021 and July 2021 in coastal areas of Rio de Janeiro (RJ), São Paulo (SP), and Santa Catarina (SC). Different letters above the boxes indicate significant differences (pseudo-*t*-test, $p < 0.05$) observed by permutational univariate pair-wise analysis among regions. Data is presented as mean values ± standard errors.
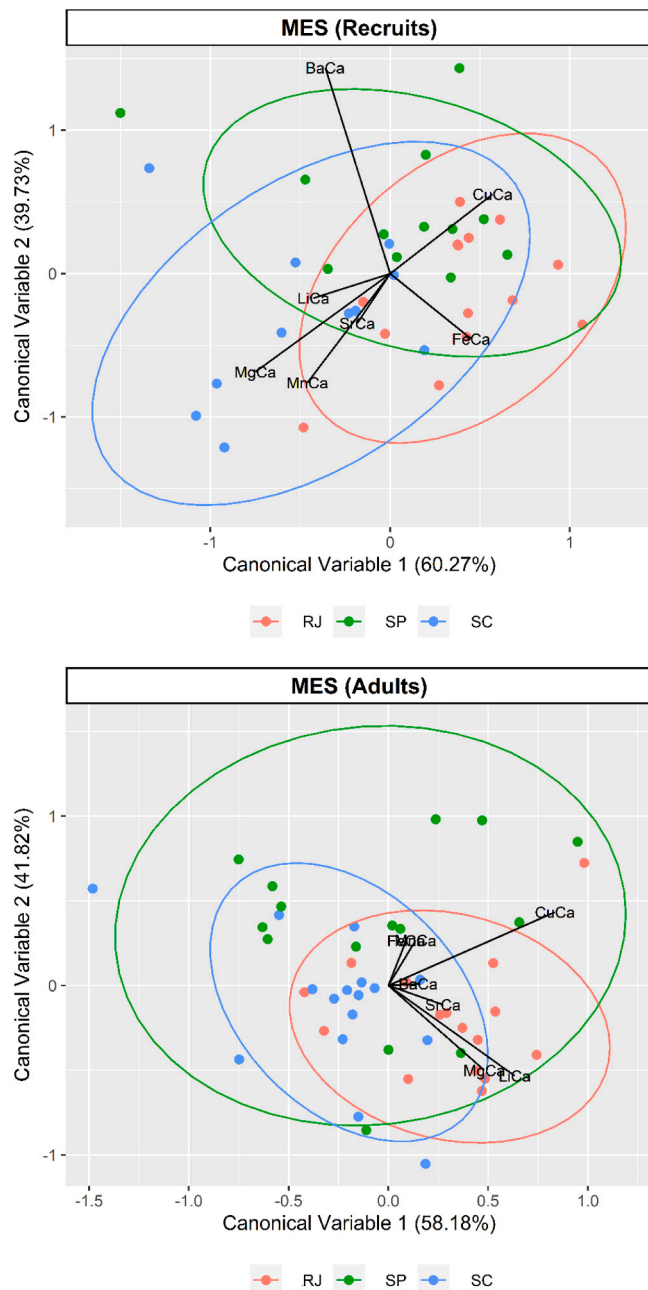
Fig. 3. Flexible discriminant analysis (FDA) obtained from the multi-elemental otolith's core signatures (MES) of *Sardinella brasiliensis* represented for the recruits (0-age individuals) sampled between January 2019 and June 2019 and adults (2-age individuals) captured between May 2021 and July 2021 in the major recruitment areas and fishing grounds. [Rio de Janeiro (RJ), São Paulo (SP), and Santa Catarina (SC)].

Table 2
The leave-one-out re-classification matrix of *Sardinella brasiliensis* based in the multi-elemental signatures (MES). Re-classification is presented for training set of FDA represented for the recruits (0-age individuals) sampled between January 2019 and June 2019 and adults (2-age individuals) captured between May 2021 and July 2021 in the major recruitment areas and fishing grounds. [Rio de Janeiro (RJ), São Paulo (SP), and Santa Catarina (SC)].

Age Group	Original Group	Predicted fishing area			Re-classification			
		Training set			% of correct re-allocation			% of overall re-allocation
		RJ	SP	SC	RJ	SP	SC	
Recruits	RJ	11	2	1	79	14	7	
	SP	2	8	1	18	73	9	83
	SC	3	1	8	25	8	67	
Adults	RJ	12	2	3	75	13	19	
	SP	1	9	2	6	60	13	68
	SC	3	4	11	19	27	69	

Table 3
Contributions (%) of the recruitment areas (recruits, 0-aged individuals) to the adult stocks (adults, 2-aged individuals) obtained through a Multinomial Logistic Regression. Abbreviations: Rio de Janeiro (RJ), São Paulo (SP), Santa Catarina (SC) and Southeastern Brazilian Bight (SBB). For more details, see M&M section. Bold values represent the self-replenishment.

Adults	Recruits		
	RJ	SP	SC
RJ	**95**	2	3
SP	38	**42**	20
SC	43	36	**21**
SSB	70	19	11

suggested from the whole otolith elemental composition of *S. brasiliensis* in the same area (Schroeder et al., 2022c).

Strontium and barium per calcium ratios are often used as spatial geochemical tracers (Nelson and Powers, 2020; Sturrock et al., 2015; Thomas et al., 2017), and are usually related with environmental water salinity (Elsdon and Gillanders, 2005; Izzo et al., 2018; Webb et al., 2012). The absence of regional differences in Sr/Ca ratios could be expected considering the existent cross-shelf gradient with salty ocean waters and coastal productive waters (de Macedo-Soares et al., 2014; Lopes et al., 2006). Adults of *S. brasiliensis*, which are typically found until 60 m (Gigliotti et al., 2010), exhibited more stable profiles of Sr/Ca than Ba/Ca ratios in the same study area (Schroeder et al., 2022c). A previous work supported these findings, where only small changes in salinity seem to occur in a water column between 50 and 100 m depth (de Macedo-Soares et al., 2014). Although Sr and Ba elements have been related to salinity gradients, usually varying in opposite ways, the variability in Ba/Ca ratios may not only reflect changes in water salinity (Artetxe-Arrate et al., 2019). The main sources of Ba in the marine environment are usually associated with terrestrial runoff (Hamer et al., 2006; Moreira et al., 2018; Shaw et al., 1998) and upwelling processes (Lea et al., 1989). Cabo Frio upwelling may play an important role in the incorporation of Ba in the core of recruit's otoliths from the northern sampling area (RJ) (de Macedo-Soares et al., 2014; Möller et al., 2008; Piola et al., 2008), because this region is under the influence of SACW near the coastal waters and coastal lagoons (e.g., Guanabara Bay, Itaipú Lagoon). The higher Ba value recorded in otoliths from *Trachurus trachurus* and *Scomber colias* collected at the Portuguese Atlantic coast was partially explained by the rivers outflow and/or costal upwelling (Moreira et al., 2018; Correia et al., 2021). Moreover, an increase in the Ba/Ca ratio found in *Thunnus albacares* caught in the western Indian Ocean has been suggested to reflect periods of residence near upwelling zones (Artetxe-Arrate et al., 2019). Recently a high Ba/Ca content has found in otoliths of *Micropogonias furnieri* collected in RJ and it has been
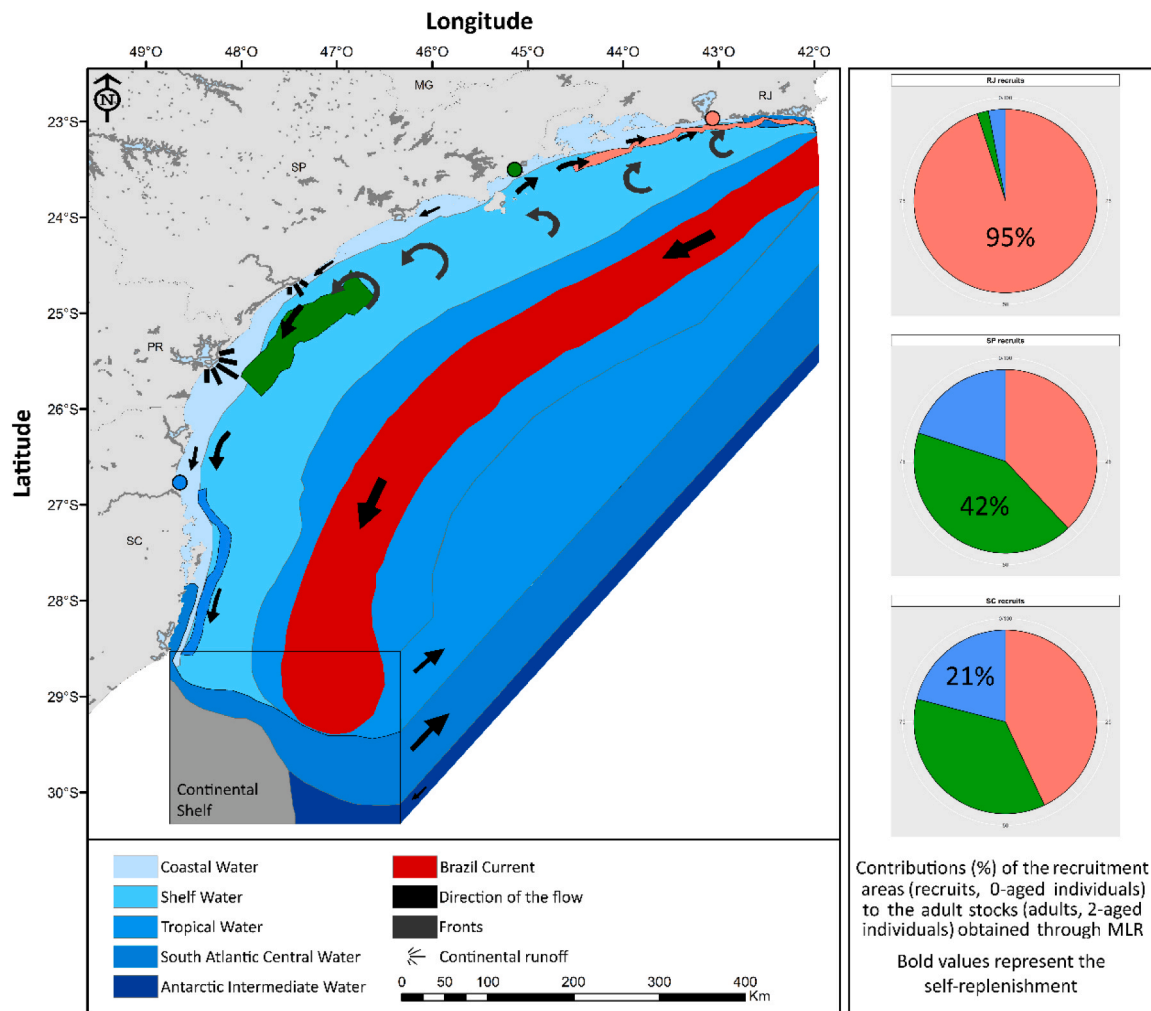
mostly driven by Ba/Ca and Mg/Ca, while in adult sardine (age 2^+) differences were observed for Cu/Ca ratios.

Physical-chemical proprieties of seawater, such as chemical composition, salinity and temperature associated to physiological aspects of fish, like age, growth, metabolism, and ontogeny can influence the deposition of chemical elements into otoliths (Izzo et al., 2018; Nelson and Powers, 2020; Thomas et al., 2017). These differences may also have a genetic basis (Clarke et al., 2011). However, because a preliminary mitochondrial genetic study failed to show any spatial genetic structure of *S. brasiliensis* in Brazilian waters (Stern et al., 2018), the observed differences in otolith elemental chemistry may be related to the oceanographic mesoscale features of the SBB, as previous

Fig. 4. Contributions (%) of the recruitment areas (recruits, 0-aged individuals) to the adult stocks (adults, 2-aged individuals) obtained through a MLR is indicated by the colors in each pie chart. Continuous grey lines subdivided the study area according to the latitudinal distribution of the oceanographic characteristics: Continental runoff, Coastal Water, Shelf Water, Tropical Water, Brazilian Current, South Atlantic Central Water, and Antarctic Intermediate Water. Water mass fronts and the direction of the flow are represented by sets (according to Ribeiro, 1996). Abbreviations: Rio de Janeiro (RJ), São Paulo (SP), Santa Catarina (SC) and Southeastern Brazilian Bight (SBB). For more details, see M&M section.

suggested that it would be related to the influence of Guanabara Bay and its continental water runoff with low salinity (Franco et al., 2023).

The presence of transition metals, such as Cu in fish otoliths, is primarily due to their physiological roles, but environmental influence should be taken also into account (Halden et al., 2000; Ranaldi and Gagnon, 2008; Thomas et al., 2017). Consistent higher levels of Cu were also found in fish otolith captured in bays rather than in ocean environments (Forrester and Swearer, 2002), consistent with industrialized locations under intense port activity (Hoff et al., 2022). Such records of Cu present in otoliths allowed to separate fish from different estuaries based on its concentration found in the sediment (Forrester, 2005). Indeed, a gradient concentrations of Cu were recorded in sediment samples along the Itajaí -Açu river, ranging from 0.08 μmol/Kg in upstream stations until 0.0004 μmol/Kg in the adjacent shelf region (Pereira Filho et al., 2021). Results obtained suggest that the use of Cu concentrations in sardine otoliths can act as a reliable environmental indicator.

Magnesium per calcium ratios in otoliths was also higher in the recruits from RJ. Mg concentrations in otoliths usually did not change in response to temperature, but reflect water composition and/or diet (Martin and Thorrold, 2005; Woodcock et al., 2012). It is also an essential element for several cellular processes, indicating a high physiological response in its regulation (Barnes and Gillanders, 2013; Hamer and Jenkins, 2007; Martin and Thorrold, 2005). As a general rule, Mg/Ca it is not considered a reliable environmental indicator (Sturrock et al., 2012; Woodcock et al., 2012). Although not significantly influenced by salinity (Martin and Thorrold, 2005; Hamer et al., 2006; Miller, 2011), Mg/Ca was found to be significantly higher at warm temperatures (Stanley et al., 2015; Hausmann et al., 2019). Marine waters off RJ were found to be warmer than in SC (de Macedo-Soares et al., 2014). In addition, significant higher values of Mg/Ca were coincident to the ones found for Ba/Ca, which were also observed for other small pelagic species like *Sardina pilchardus* (Correia et al., 2014), *Trachurus picturatus* (Moreira et al., 2018) and *Scomber colias* (Correia et al., 2021) at the Portuguese coast. The spatial patterns in the incorporation of Ba and Mg in otoliths' core may reflect habitat-specific characteristics for small pelagic fish during early life, which could be associated to distinct salinity regimes presenting also different metabolic responses, as previously suggested for *S. brasiliensis* (Schroeder et al., 2022b).

The incorporation of Ba and Mg in otoliths' multi-elemental core signatures may indicate unique responses to temperature or salinity changes, depending on elements and environmental effects that sardines were exposed to during the early life (Tian et al., 2021). In recent years, one of the world's largest marine warming hotspots extending from Cabo Frio (Brazil, 22°S) to Tierra del Fuego (Argentina, 55°S) was detected, as its water temperature has increased above the global

average (Hobday and Pecl, 2014; Popova et al., 2016). Satellite-derived sea surface temperatures have shown positive anomalies of 0.5 °C between 2000 and 2016 in this region (Hobday and Pecl, 2014; Franco et al., 2020). Such anomalies have induced a poleward displacement of the wind patterns over the South Atlantic which lead to a southward expansion of the warm waters of the Brazil Current (BC) over the past decades, and a subsequent warming along its path (Lumpkin and Garzoli, 2011; Artana et al., 2019; Franco et al., 2020). Long-term observations on estuaries and sandy beaches at Sepetiba Bay (~ 23° S), which serve as rearing grounds for commercially important fishes such as *S. brasiliensis*, suggest that boundaries of fish fauna distribution may have displaced poleward (Araújo et al., 2018), presumably in response to ocean warming (Franco et al., 2020). Moreover, changes in the presence and relative abundance of *S. brasiliensis* over four decades (1980–2010), suggest that the region is facing a "tropicalization" of the marine community (Franco et al., 2020). The plausibility of the "tropicalization" process in the region is in agreement with the poleward expansion of tropical fish (Vergés et al., 2014; Franco et al., 2020; Perez and Sant'Ana, 2022).

The early studies on the population structure of *S. brasiliensis* suggested two distinct spawning grounds (23–25°S and 26–28°S), with juveniles sharing a common feeding area (25–26°S), returning later to their original spawning grounds after reaching the sexual maturation (with 16.8 cm TL) (Rossi-Wongtschowski, 1977). Thus, the spatial patterns of multi-elemental otolith core signatures in the major spawning areas and fishing grounds, can support the existence of separate environmental conditions that could produce distinct somatic and growth conditions at the extremes of the species distribution area (Saccardo and Wongstchowski, 1991, Schroeder et al., 2022b,c).

In the SBB, mesoscale ocean dynamics, like the seasonal advection of nutrient rich waters and shelf width, enhances the formation of retention areas and/or stability of the water column (Matsuura, 1986), which plays an important role in the spatial structuring of *S. brasiliensis* spawning areas (Dias et al., 2014; Gigliotti et al., 2010; Moraes et al., 2012). The occurrence of upwelling phenomena in the mid continental shelf off RJ (23°S) is favored by the coastline orientation and the narrow continental shelf (Rodrigues and Lorenzzetti, 2001; Valentin, 2001) compared to the south sector in SC (Campos et al., 2013). The spawning habitat of *S. brasiliensis* becomes larger to the south, as the continental shelf gets wider, providing a thermally stable environment (Gigliotti et al., 2010; Lopes et al., 2006; Matsuura, 1998), where two main spawning grounds are recognized, one in SC e another in Paraná (PR) (Dias et al., 2014; Gigliotti et al., 2010; Moraes et al., 2012). However, due to the coastline orientation, coastal upwelling only occurs under the influence of favorable winds (Campos et al., 2013). In contrast, the coastline of RJ shows an abrupt change in orientation that causes strong meandering of the BC (Rodrigues and Lorenzzetti, 2001), and a coastal wind-driven upwelling due to constant north-eastern winds during the summer pumping the colder SACW from the shelf slope to the coast (Campos et al., 2013).

The Cabo Frio Front (20–24°S) may explain the similarity observed in the core fingerprints of sardines between RJ and SP (Campos et al., 1996; Lopes et al., 2006; Stevenson, 1996). These fronts are caused by wind-induced upwelling, forming an elongated cyclonic loop, and are best developed during austral summer and fall, from January through June (Belkin et al., 2009; Campos et al., 1996; Stevenson, 1996). This feature seems to act as a retention cell including the south coast of RJ and the northern coast of SP under the domain of the warmest and salty SW (Campos et al., 2000). The south limit of Cabo Frio Front delimits an area characterized by a quasi-permanent cyclonic cell between São Sebastião and Paranaguá (24–26°S) and contributes to larval retention over the most part of SP and entire littoral of PR (Dias et al., 2014). This region also receives the contribution of several freshwater runoffs from the Ribeira do Iguape and Itajaí -Açu river, as well as many small and medium size estuaries (e.g., Paranaguá, Babitonga and Cananéia-Iguape) that contribute to the mixing of CW (Daros et al., 2016;

Soeth et al., 2019; Hoff et al., 2022) which may be responsible for the significant difference observed regarding the Brazilian sardines caught in RJ and SP from those of SC.

The use of natal otolith chemical fingerprints to infer the origin of adults indicated the adults of RJ from the 2019 cohort collected in the SBB (i.e. collected as age 2 + in 2021) were almost entirely supplied by the self-recruitment (RJ, 95%), while adult sardine caught off SC receive a large contribution of northern recruitment areas (RJ+SP, 89%). Such geographical expansion regarding the contribution of the northern recruitment area to the southern regions might be related to the spawning behavior of the species. Spawning of *S. brasiliensis* is found to occur between 50 and 70 m depth, with larvae reaching depths beyond 200 m in the northern fishing area (Matsuura, 1977). One possibility is that part of the larvae resulting from the spawning events are transported offshore becoming subjected to the transport of BC, to regions further south. This mechanism has already been suggested for *S. brasiliensis* (Schroeder et al., 2022c) and is well known for other commercial squid and fish species in the region (Franco et al., 2006; Schroeder and Perez, 2013; de Macedo-Soares et al., 2014). The presence of adult sardines in commercial seine fishing operations up to 150 m reinforces this theory (Schroeder et al., 2022a). Furthermore, cross-shelf migratory movement are known for other sardine species, like *Sardinops sagax* and *Sardinella aurita,* and seems to be linked with the search for feeding areas and/or spawning at shelf break where the upwelling of the SACW takes place (Brandini, 2006; Brochier et al., 2018; Schroeder et al., 2022b). The similarity of the otolith core fingerprints of adult sardines from with both north and south recruitment areas may characterize the region around 25°S as a transition area. According to early hypotheses on *S. brasiliensis* population structure, the continental shelf marine environment in this region, presents itself as an important feeding area for both stocks (Rossi-Wongtschowski, 1977). Anyway, these findings should be evaluated with caution since it is a highly mobile pelagic species, in which we are retrospectively evaluating its natal stage, although the geochemical signature was consistent within the adult individuals of the same year class.

The otolith core fingerprints reflect the environmental exposure integrated over the early fish's life; thus, could act as a natural tag, being particularly useful for tracking characteristics during early life, as such nursery grounds or mixing of individuals over short periods (Hamer at al, 2011; Reis-Santos et al., 2013; Correia et al., 2014). The MLR assumes that all possible recruitment sources have been sampled, otherwise recruitment values are overestimated (Millar, 1990; Rooker et al., 2019). Moreover, this study was based on a single cohort and may not represent the fish population dynamics in the following consecutive years under exploitation (Correia et al., 2014). Although the otolith core signature would be related to the larval and early juvenile periods, differences observed at the boundaries of species distribution from the 2019 cohort, corroborate the results obtained using eggs and larvae (Matsuura, 1977; Matsuura et al., 1992; Matsuura, 1996), juveniles and adults (Rossi-Wongtschowski, 1977; Schroeder et al., 2022a), traditional morphometrics (Braga, 1987), body geometric morphometrics, otolith shape analysis, and the bulk otolith composition of *S. brasiliensis* using specimens 2-years-old collected in 2018 (Schroeder et al., 2022b, 2022c). These suggest a robust spatial population structure and indicates that the industrial purse seine fishery is exploiting two distinct population-units, despite the major contribution from the northern juvenile recruitment area. The degree of differentiation obtained over geographically short distances evidenced that adult sardines form regionally distinct adult populations (RJ+SP, and SC).

It is important to highlight that during the study period there was evidence of spatial segregation off southeast Brazil, when the stock almost collapses. Moreover, the results support the hypothesis that sardine populations along the SBB comprise a classic meta-population structure. This has implications for local depletion as once the major recruitment area (RJ) highly depend on self-recruiting to replenish them. This result requires knowledge of the exploitation potential of

each subpopulation in order to establish individual regional management measures (i.e. catch quotas) for each stock, in a way that does not compromise the sustainability of this main pelagic resource in Brazilian waters. It is also important an evaluation of the long-term temporal stability of the population structure and spawning areas for the species.

CRediT authorship contribution statement

In the hereby manuscript, each author was responsible for the following task(s): **Rafael Schroeder**: Idea conceptualization, Fish sampling, Laboratorial work, Data analysis, Manuscript writing, Manuscript review. **Paulo R. Schwingel**: Fish sampling, Manuscript review, Funding acquisition. **Richard Schwarz**: Laboratorial work, Manuscript review. **Felippe A. Daros**: Fish sampling, Laboratorial work, Manuscript review. **Taynara P. Franco**: Fish sampling, Laboratorial work, Manuscript review. **Natasha T. Hoff**: Fish sampling, Laboratorial work, Manuscript review. **Ana Méndez Vicente**: Data analysis, Manuscript review. **Jorge P. Castro**: Manuscript review, Funding acquisition. **André M. Vaz-dos-Santos**: Manuscript review. **Alberto Teodorico Correia**: Idea conceptualization, Laboratorial work, Data analysis, Manuscript writing, Writing – review & editing, Tasks supervision, 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.

Data availability

Data will be made available on request.

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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.2023.106825.

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