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Using growth rates and otolith shape to identify the population structure of *Umbrina canosai* (Sciaenidae) from the Southwestern Atlantic

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ABSTRACT

Identifying populations and establishing the connectivity between neighbouring stocks are central issues for the assessment and management of coastal marine fish species. In this paper, we analysed the population structure of the demersal sciaenid argentine croaker *Umbrina canosai,* endemic in the warm, temperate southwestern Atantic between southeastern Brazil (SE) and Argentina, by combining two phenotypic techniques: otolith shape analysis and fish growth rate. Three otolith morphotypes were consistently identified, one in the northern latitudinal range in SE, and two in the southern range of the species from southern Brazil to Argentina. Two stocks with differences in growth rate were identified, one with a significantly smaller asymptotic length in the northern range ($L_\infty =$ 340.08; $k = 0.267$; $t_0 = -2.177$) and the second in the southern range ($L_\infty = 425.08$; $k = 0.236$; $t_0 = -2.46$), where no growth differences were observed between fishes with the two otolith morphotypes. Although genetically *U. canosai* can be considered to form a single panmictic population, growth and otolith shape indicate that there are two different stocks, one in southeastern Brazil and another in the southern distribution, confirming previous parasitological studies. The difference in otolith morphotypes in the southern range suggests that two subpopulations share the same reproductive grounds, although probably feed in different locations.

Introduction

Failure to recognize the population structure of fish species exploited commercially can lead to overfishing and depletion of less productive stocks, as well as to dramatic changes in their biological attributes, productivity rates, and genetic diversity (Begg et al. 1999). Successful management of commercial fisheries requires assessing the population units of management ('stocks') and the degree of connectivity among neighbouring stocks (Siskey et al. 2020). Therefore, accurate stock identification is a central issue in fisheries and conservation sciences (Begg et al. 1999; Cadrin et al. 2014). At present, many genotypic and phenotypic methods for stock identification are available (e.g. Cadrin et al. 2014). Phenotypic methods are based on observable characteristics of individuals resulting from the interaction of their genotype with the environment. Methods based on otolith shape and growth are considered robust in determining

newly formed populations or subpopulations that may still not show genetic divergence (Waldman 2005).

Marine fish populations exhibit a range of life-history parameters in response to particular sets of ecological conditions. Thus, species inhabiting wide latitudinal ranges frequently show different biological features (Boehlert and Kappenman 1980). Therefore, the plasticity of individual life-history traits in response to environmental variation has been used as a basis for differentiating stocks (Cadrin et al. 2014). Otolith shape is a phenotypic character widely used as a marker to identify fish stocks and populations (Campana and Casselman 1993; Schulz-Mirbach et al. 2018). Due to otoliths being made up of inert acellular concretions of calcium carbonate, which remains unmodified once formed and continue growing throughout the fish's lifetime, their shape is believed to be a good representation of a fish's life (Green et al. 2009). Since otolith shapes are both genetically and

environmentally determined, they have been regarded as good indicators of immediate environmental conditions (Cardinale et al. 2004; Vignon and Morat 2010), where a fish population persists (Campana and Casselman 1993; Hüssy 2008). Therefore, it is not surprising that both otolith shape and body growth rates are considered reliable parameters to distinguish individual fish stocks from different environments (Begg et al. 1999; Cadrin et al. 2014).

In the Southwestern Atlantic Ocean, otoliths shape has been helpful for stock identification of some coastal fish species, such as *Urophycis brasiliensis* (Biolé et al. 2019), *Chaetodipterus faber* (Soeth et al. 2019), and *Pagrus pagrus* (Kikuchi et al. 2020), while growth rate comparisons have been used to characterize stocks of *P. pagrus* (Cotrina and Raimondo 1997; García and Déspos 2015); *Merluccius hubbsi* (Lorenzo et al. 2011) and *Micropogonias furnieri* (Haimovici et al. 2016). However, as far as we know, no studies have combined both otolith shape and growth rates for stock identification purposes within the Southwestern Atlantic.

The Argentine croaker *Umbrina canosai* (Berg, 1895) is a demersal sciaenid fish, endemic in the Southwestern Atlantic Ocean, between Rio de Janeiro State in southeastern Brazil (22oS) and Buenos Aires Province in Argentina (41oS) (Cousseau and Perrotta 1998; Figueiredo et al. 2002). It is fished along all its distribution, with total landings peaking at ca 25000 t in the 1970s, but decreasing to ca 7000 t in recent years (Figure 1). Since the late 1970s, it has been mostly exploited in southern Brazil, representing an important component of the trawl and gillnet shelf fisheries (Haimovici 1998; Haimovici et al. 2006; Haimovici and Cardoso 2017).

Due to its importance for the local fisheries, the population dynamics of *U. canosai* have been mainly studied in southern Brazil, where Haimovici et al. (1996) recognized this region as an important nursery ground. Haimovici and Cousin (1989) suggested a partial spawning behaviour, occurring from winter to early spring, with most specimens attaining sexual maturity at the age of two years. Regarding age and growth, Haimovici and Reis (1984) found that in this stock, individuals reach over 26 years of age and over 400 mm in total length.

A fundamental component to understand the fish stock structure often involves knowing the dynamics of the species dispersal (Cadrin and Secor 2009). Presumptive dispersal information of *U. canosai* in the region is only indirectly available, based on data from fisheries-dependent seasonal catch rate across different fishing grounds. Indeed, Gonzalez Alberdi and Nani (1967) suggested that adult *U. canosai* move into Argentinean waters in summer, returning in winter to its spawning grounds in southern Brazil. More recently, the findings of reproductively active fish within the Argentine-Uruguayan Common Fishing Zone (AU) during spring (Militelli et al. 2013) suggest that some individuals may remain resident within these waters and not return to southern Brazil to spawn. In addition, statistics of monthly landings from southern Brazil and AU show that fishing, although more intense in southern Brazil in the cold season, occurs in the entire region year-round (Figures 1 and 2). Therefore, the clear-cut hypothesis of Gonzalez Alberdi and Nani (1967) may represent an oversimplification of the migratory movements of the species in its southern range.

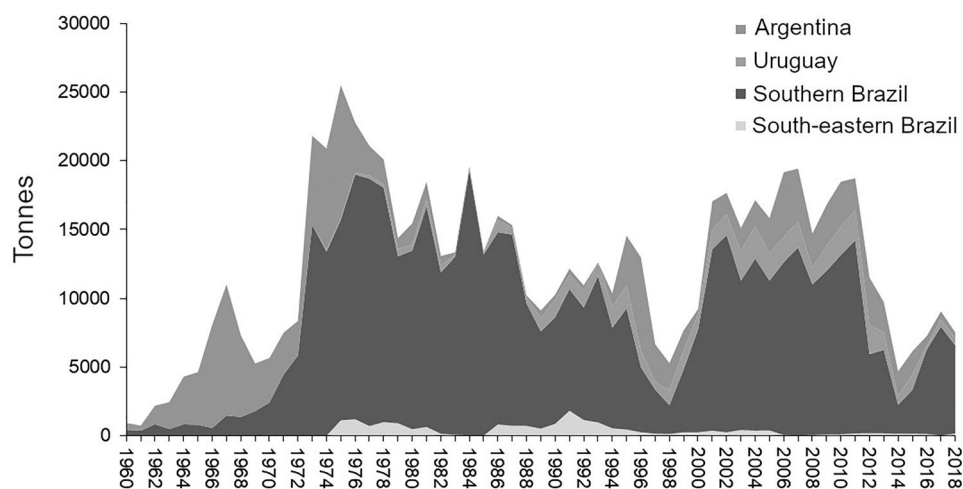
Figure 1. Recorded landings of *Umbrina canosai* in southern and southeastern Brazil, Uruguay and Argentina between 1960 and 2018. Sources: CEPERG; CTMFM; FIPERJ; IBAMA; IP; SAGyP; Sanchez et al. (2012); UNIVALI; Valentini and Pezzuto (2006).
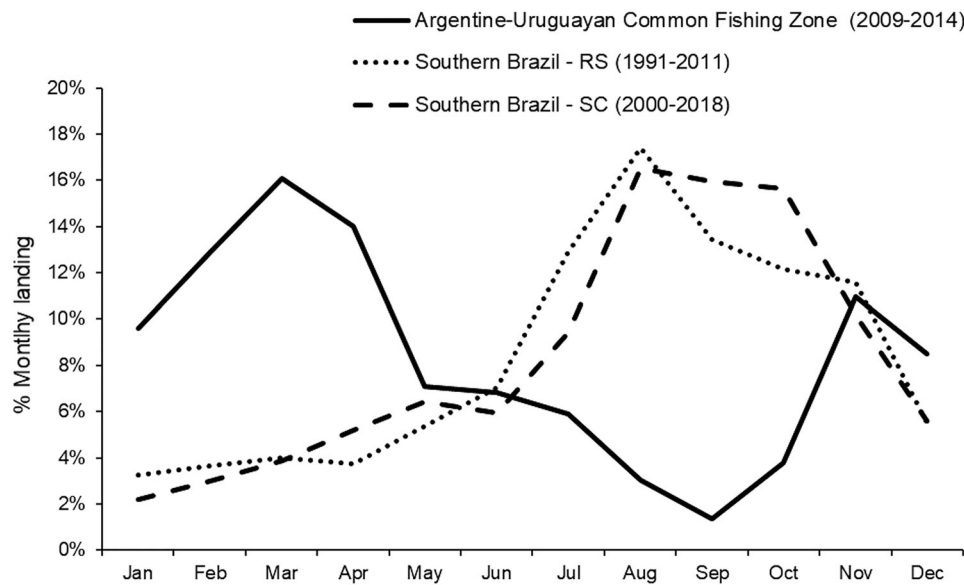
Figure 2. Mean monthly landings of *Umbrina canosai* in southern Brazil (Santa Catarina State-SC and Rio Grande do Sul State-RS) and in Argentine-Uruguayan Common Fishing Zone. Sources: CEPERG; CTMFM; UNIVALI.

Table I. Region, latitude range, data collection and number of *Umbrina canosai* otolith samples used in the analysis.

Region	Latitude range	Sample Acronym	Data collection	Total sampled specimens	Specimens in the TL 290–330 mm	Specimens in the age 4–6
Southeastern Brazil	22°S – 23°S	SE1	25/02/2019	108	82	18
		SE2	15/09/2019	122	25	69
		Total		**230**	**107**	**87**
Southern Brazil	32°S – 34°S	S1	10/02/2012	38	24	5
		S2	14/08/2012	29	5	6
		S3	19/09/2012	36	16	1
		S4	25/09/2012	28	0	5
		S5	04/09/2013	94	57	53
		S6	29/09/2016	78	28	34
		S7	05/09/2017	41	5	18
		S8	21/08/2018	16	6	4
		S9	23/08/2018	21	8	8
		S10	10/09/2018	4	2	3
		S11	19/09/2018	19	0	12
		Total		**396**	**151**	**149**
Argentine-Uruguayan Common Fishing Zone	36°-38°30´S	AU1	03/12/2015	46	2	21
		AU2	04/04/2017	47	12	4
		AU3	10/08/2016	26	14	1
		AU4	17/11/2017	8	1	1
		AU5	15/01/2019	37	16	25
		Total		**164**	**45**	**52**

Sustainable exploitation of *U. canosai* requires the identification of adequate management units (stocks). Canel et al. (2019) suggested the existence of two distinct stocks, one in southeastern Brazil and another along the southern range, including southern Brazil, Uruguay, and Argentina, based on the differentiation between metazoan parasite communities. Similarly, Haimovici et al. (2006) suggested presumptive stock delineation based on the large distance between southeastern and southern Brazil. However, Machado (2021) found a small bi-directional gene flow along the entire distribution, but still sufficient to maintain the panmixity. In this study, two phenotypical approaches were used to assist the discrimination of possible stocks of *U. canosai* along its distribution. We first analysed otolith shapes followed by a comparison of growth rates among potential stocks indicated by the analysis of otolith shapes The integrative effect of these two approaches can provide insights on the population structure of *U. canosai*, maximizing the likelihood of correctly defining the stocks throughout its distribution.

Material and methods

Data collection

Sagittal otoliths of 790 specimens of *U. canosai* were collected from commercial fishing between 2012 and 2019 in three regions, covering most of the distribution range of this species: along Rio de Janeiro and São Paulo states in southeastern Brazil (22° S – 23°S), along Rio Grande do Sul State in southern Brazil (32°S – 34°S), and from the Argentine-Uruguayan Common Fishing Zone (36°-38°30'S) (Table I and Figure 3).

Otolith shape analyses

For each specimen, the left sagittal otolith was removed, and its inner surface was photographed with the aid of an AmScope MD500 camera magnified 10x times under a Nikon SMZ800 stereo microscope. The *ShapeR* package (Libungan and Pálsson 2015) was used to analyse each image, recording the outlines as a matrix of *x* and *y* coordinates. In order to remove size-induced biases, otolith sizes were standardized so that the otolith area would be equal in all otoliths by dividing the co-ordinates of each otolith by the square root of the otolith area (Libungan et al. 2015; Libungan and Pálsson 2015). The shape patterns of each potential stock were expressed as the Wavelet coefficient, obtained with the *wavethresh* package (Nason 2012). The deviation of the reconstructed otolith outlines from the original value was evaluated with the *ShapeR* package (Libungan and Pálsson 2015) to determine the number of Wavelet coefficients needed for the analysis.

The shape variation among the potential stocks was compared by a canonical analysis of principal coordinates (CAP) (Anderson and Willis 2003), applied on the Wavelet coefficient using the *capscale* function in the *vegan* package (Oksanen et al. 2013). Ordination of the stock averages along the first two canonical axes was evaluated graphically with shape descriptors. An ANOVA-like permutation test for CAP was used to assess the significance of constraints using 1000 permutations, also in the *vegan* package (Oksanen et al. 2013). A minimum of 1% was adopted as the level of significance. A Linear Discriminant Analysis (LDA) (Klecka 1980), which discriminates predefined groups based on sample observations from each group, was applied to the Wavelet coefficients to analyse the accuracy of the otolith shape classification into their sampling

origin (Libungan and Pálsson 2015). It was calculated here with 'leave-one-out' cross-validation using the *errorest* function in the *ipred* package (Peters and Hothorn 2013), which returns the posterior probabilities for the groups.

Since it was hypothesized that there might be more than one otolith morphotype in the southern distribution of the species between southern Brazil and the Argentine-Uruguayan Common Fishing Zone, a preliminary shape analysis was carried out for 560 otoliths from 16 commercial landings in the region (Table I).

Numerous studies have documented that otolith shape varies with size and age throughout the life cycle of fishes (e.g. Castonguay et al. 1991; Campana and Casselman 1993; Begg et al. 2000; Simoneau et al. 2000; Mapp et al. 2017). Therefore, the ontogenetic changes in the shape of the inner surface of the otoliths of *U. canosai* were evaluated to select a size range in which most otoliths with similar morphometric characteristics were available from all the sampled regions. For this, Ward's hierarchical clustering analysis, based on Euclidean distances, was performed considering the area, perimeter, width, and length of 240 otoliths of randomly selected fishes in the observed length range of the specimens sampled (123–462 mm). As a result, otoliths of fishes with a total length (TL) range from 290 to 330 mm, which included 303 individuals, had the best overlap among the sample groups and were chosen for shape comparisons (Figure 4 and Table I). Also, to avoid the potential influence of age-related variability in otolith shape, fish from age classes 4–6, which provided the largest sample size among available fish, were used in a second shape analysis (Table I).

Age and growth

Thin transverse sections (0.20–0.3 mm) of the sagittal otoliths were cut through the nucleus and embedded in polyester resin using a low-speed rotary saw (Buehler–Isomet). All sections were fixed on glass slides with xylol (dimethylbenzene) base mounting media (ENTELAN Merck®). Sections were examined with transmitted light under a stereoscopic microscope (×10). Alternate opaque and translucent bands were counted independently by two readers. Those that differed in on opaque band were re-examined and discarded for further analyses if differences persisted (Figure 5).

Growth in length was described for the potential stocks with the von Bertalanffy growth model from
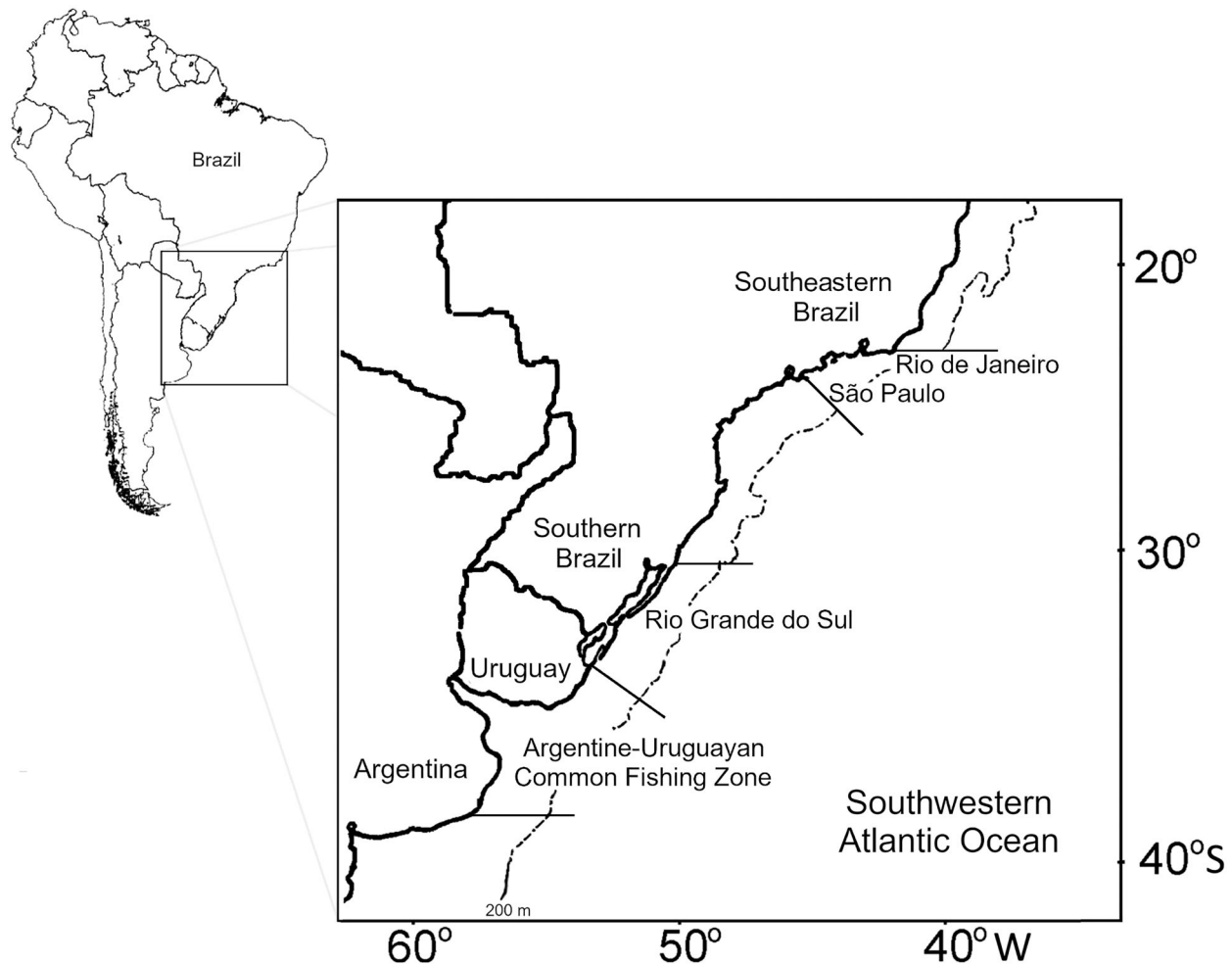
Figure 3. *Umbrina canosai* principal commercially fishing areas in Southwestern Atlantic Ocean. Lines indicate the approximate limits of the different catch areas.

observed mean lengths at age as follows:

$$TL = (L_\infty 1 - e^{-k(t-t_o)})$$

where *TL* is the total length of the fish from the tip of the snout to the end of the upper limb of the tail in a normal position; $L\infty$ is the asymptotic length; *k* is the growth coefficient, which represents the rate at which the fish length approaches $L\infty$; and t_0 is the theoretical age at which the fish would have a length of zero. The fit of the model to the data was performed with a Bayesian approach (Kinas and Andrade 2010). The age-length data were assumed to follow a log-normal distribution: $y_i = \log N (\mu_i, \sigma^2)$, where y_i is the length distribution, .. is the mean length for each age class *i* and variance σ^2. A logarithmic version of the VBGM was used for computational convenience as follows:

$$\mu_i = \log (L_\infty) + \log (1^{-k(i-t_o)})$$

The seed values for each parameter were constructed from a non-informative prior with wide distribution intervals. The probability of *log k* was considered to follow a

normal distribution with a mean of zero and variance equal to 0.001 and was restricted to the interval of −5 and 5. The probability of *log L*❓ was considered to follow a normal distribution with a mean equal to the logarithm of the observed maximum *TL* and a variance of 0.001. The probability of t_0 was considered to follow a uniform distribution with a minimum equal to −3 and a maximum equal to zero. The probability of σ was considered to follow a uniform distribution with a minimum equal to zero and a maximum equal to five.

The posterior distributions of the parameters were obtained through the stochastic process of the Monte Carlo Markov chains (MCMC), which provides an easy and clear way to compare the resulting parameters by analysing the overlap between the posterior probability distributions. In a single chain, 31,000 iterations were generated, with a burn-in of the first 10,000 values and removal one of the two remaining values, resulting in a final sample with 10,500 values in the posterior distribution of each parameter (Kinas and Andrade 2010). These analyses were
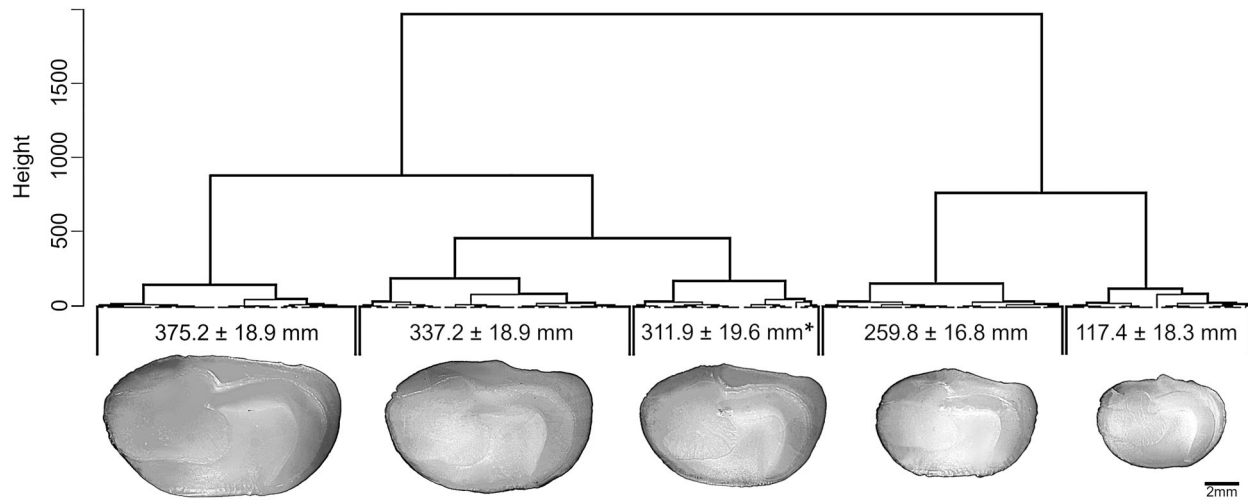
Figure 4. Dendrogram of ontogenetic relationships among otolith area, perimeter, width and length parameters from *Umbrina canosai* ranging from 123 to 462 mm TL using Ward's method of hierarchical clustering analysis based on Euclidean distances. *Mean and standard error of the selected TL range for the shape analysis.
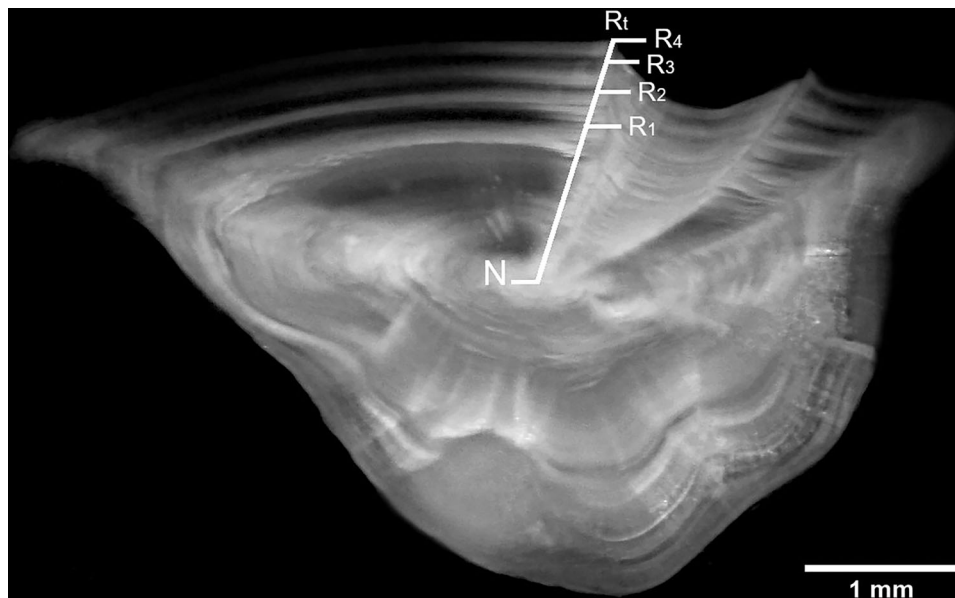

Figure 5. Thin section examined with reflected light of a four-year-old (TL = 320 mm) *Umbrina canosai* from southeastern Brazil. White letters indicate the nucleus (N), the end of each opaque band (Ri) and the border (Rt).

performed using the *OpenBUGS* package and the libraries *R2 WinBUGS* (Sturtz et al. 2005) and *BRugs* (Thomas et al. 2006).

All statistical analyses were performed in the software R (R Core Team 2013), version 3.3.1.

Results

Otolith shape analysis

A preliminary shape analysis was carried out for each sample, from southern Brazil to Argentina, resulting in two potential morphotypes visually identified along the first two canonical axes (Figure 6). When the ANOVA-like permutation test compared the proposed otolith morphotypes, significant differences were observed ($F_{1,559} = 12.792$, $p = 0.001$). While one of the morphotypes (M2) was composed only of specimens from southern Brazil (Sample acronyms: S1, S2, S3, S4, S5, S6, and S11), the other one (M1) consisted of specimens from both southern Brazil and Argentine-Uruguayan Common Fishing Zone (Sample acronyms: S7, S8, S9, S10, AU1, AU2, AU3, AU4, and AU5). Consequently, southern Brazil samples were divided into two groups (SB1 and SB2) for further analyses.
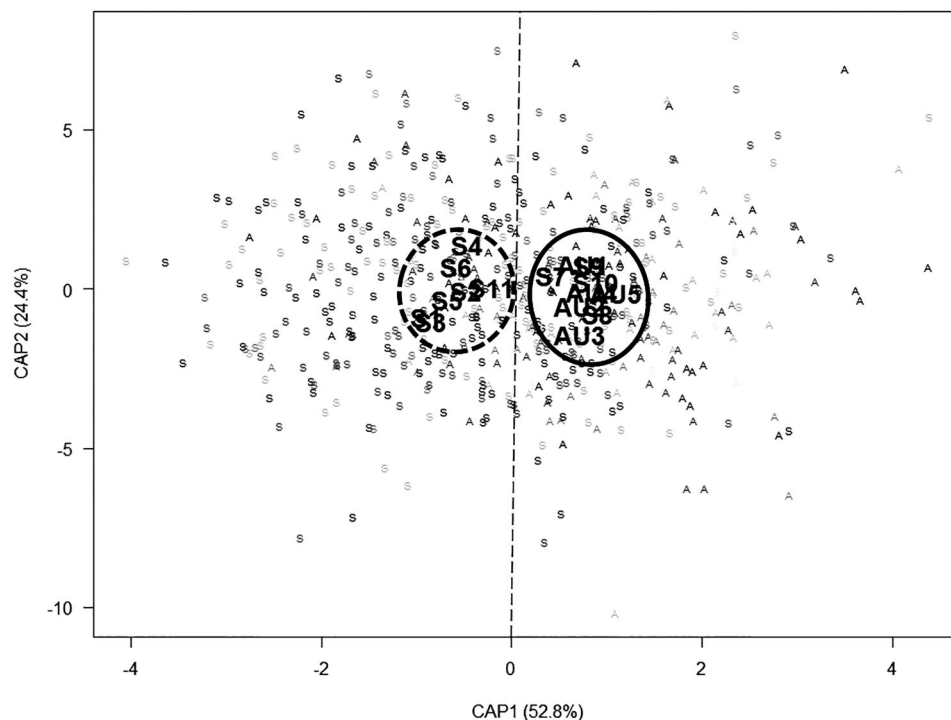
Figure 6. Otolith shape of *Umbrina canosai* from eleven commercial landings (S1 to S11) from southern Brazil and five landings from Argentine-Uruguayan Common Fishing Zone (AU1 to AU5) using Canonical analysis for Wavelet coefficient (see Table I). The black capital letters represent the mean canonical coordinates for each landing. The solid line circle indicates samples with the proposed morphotype 1 (M1) and the dashed line circle the morphotype 2 (M2).

As a next step, the otolith shape variation was analysed considering four sample groups: southeastern Brazil (SEB); southern Brazil morphotype 1 (SB1) and morphotype 2 (SB2); and Argentine-Uruguayan Common Fishing Zone (AU). The length and age composition of the samples from these potential stocks are shown in Figure 7.

The canonical analysis of the principal coordinates showed that otolith shape was not homogeneous among the groups for Wavelet coefficient (ANOVA-like. $p < 0.01$). In this analysis, 98.4% of the variation was explained by the first two axes for the whole sample; 95.7% for the 290–330 mm total length interval; and 97.6% for ages 4–6 interval (Figure 8). For the three canonical analyses, only SB1 and AU were overlapped, with SB2 and SEB appeared in different panels in which there was no overlap along any of the axes. The ANOVA-like permutation test for the Wavelet coefficient showed significant differences among all paired sampled groups ($p < 0.01$) except between SB1 and AU (Table II).

The comparison of fish of similar size, age, or otolith morphometry minimizes the effect of the confounding variables. Results showed that otolith shape analysis, including all samples, performed

well, but the classification potential increased after restricting the size and age of fish. Among the potential stocks that showed a significant difference in the ANOVA-like test, the pairwise classification success of the linear discriminant analysis (LDA) was higher, between 79% and 91%, when only the samples at age 4–6 were considered. The lowest values of classification success, between 73% and 79%, were observed when all sampled specimens were considered. Samples at 290–330 mm size range showed intermediate values, between 79% and 83%. Classification success between the SB1 and AU, for which the ANOVA-like test was not significant, always showed the lowest percentages of correct allocations, ranging between 49% and 56% (Table II).

Growth comparisons

Growth was compared among the specimens in the four sample groups. The mean total length at age showed that for ages over 3, the 95% confidence intervals among the SB1, SB2, and AU, overlapped but did not with those of SEB (Table III).

Comparisons of the von Bertalanffy's growth parameters showed that the credibility intervals for SB1,
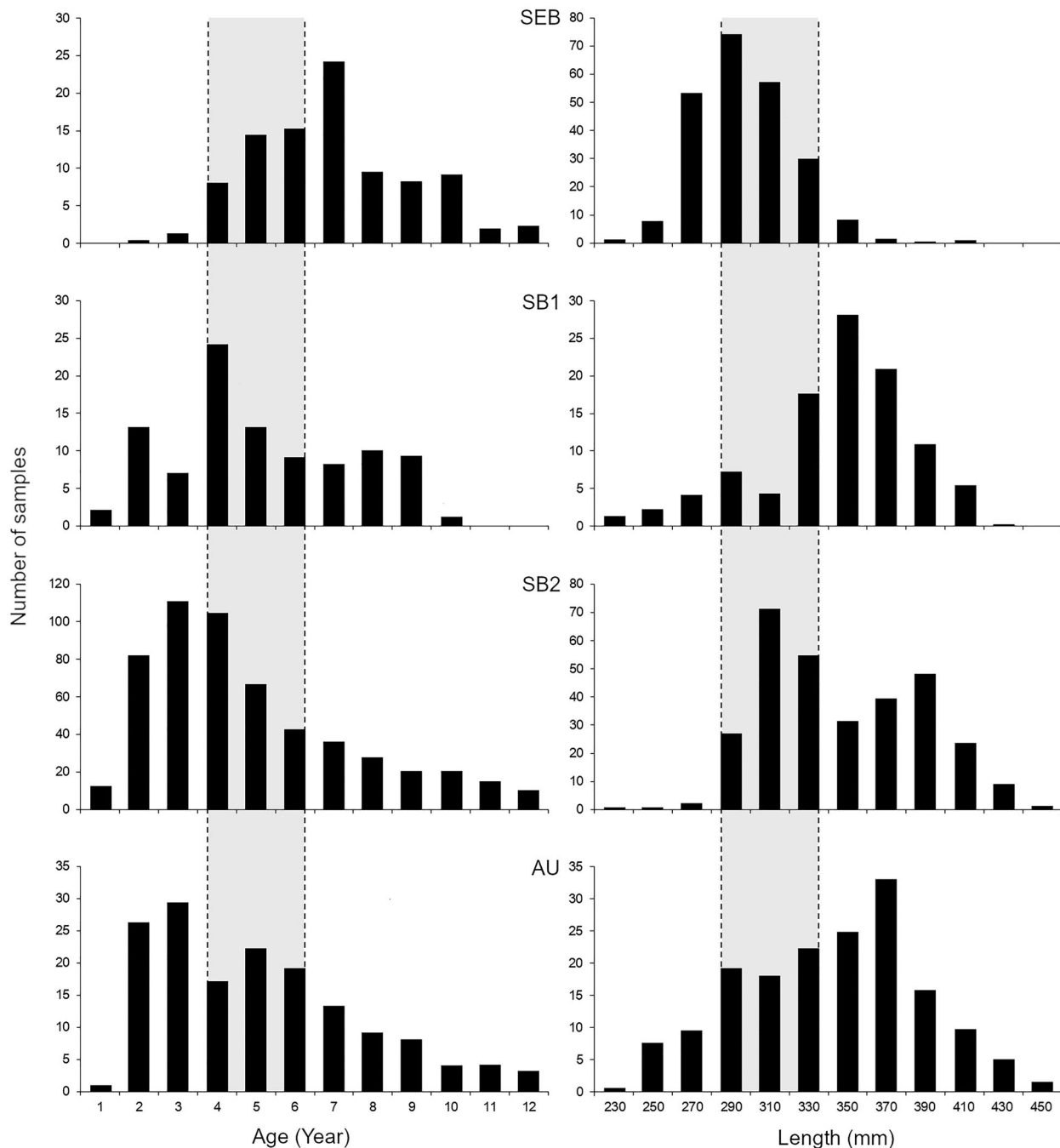
Figure 7. The length and age composition of the four sample groups of *Umbrina canosai* used for otolith shape analysis and fish growth comparisons: southeastern Brazil (SEB); southern Brazil with otolith morphotype 1 (SB1) and otolith morphotype 2 (SB2); and Argentine-Uruguayan Common Fishing Zone (AU). Gray segments indicate the age (left) and length (right) ranges selected for the otolith shape analysis.

SB2 and AU overlapped, indicating no significant differences among these growth curves; however, a significant difference was observed between the curves of SEB and the pooled samples of SB1, SB2, and AU (Figure 9). When von Bertalanffy's parameters were considered individually, only L_∞ was significantly lower for the SEB (Table IV). Therefore, two patterns were observed in terms of growth, one with bigger fishes in the southern distribution (SB1, SB2, and AU) and a second with smaller fishes in southeastern Brazil (SEB).

Discussion

Otolith shape analysis and growth parameters provided insights into the stock structure of *U. canosai* throughout its distribution, supporting the existence
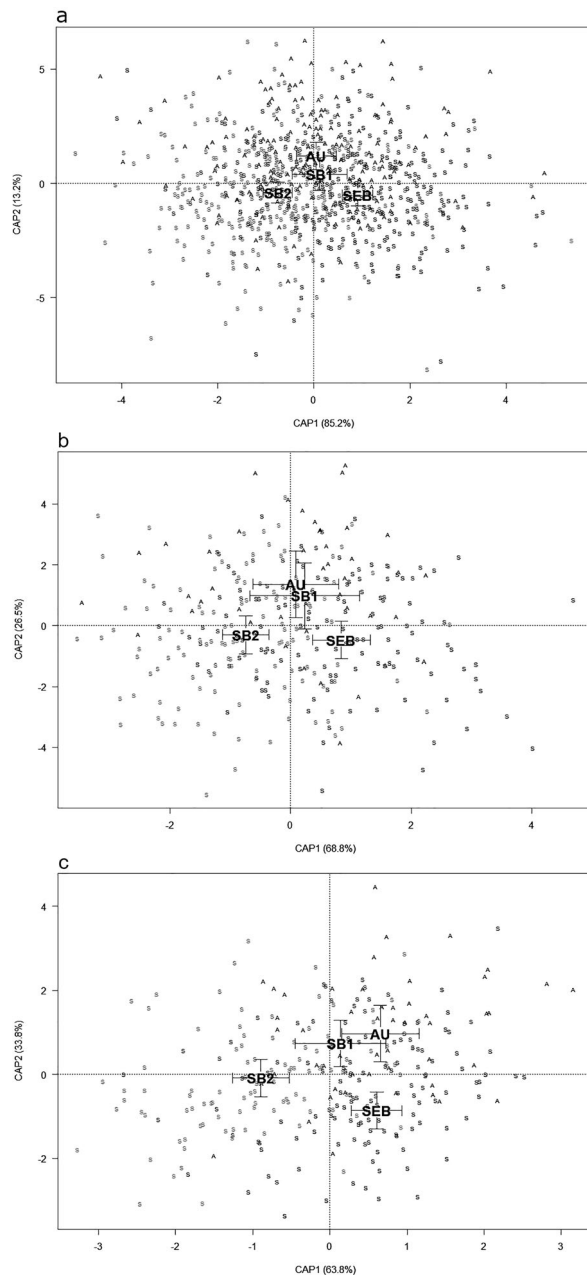
Figure 8. Otolith shape variation among *Umbrina canosai* from the four sampled groups in the Southwestern Atlantic using Canonical analysis with the Wavelet coefficients for all sampled specimens (a); samples of 290–330 mm TL interval (b) and samples in the 4–6 age classes interval (c). Black letters represent the mean canonical coordinates surrounded by standard error for the potential stocks: southeastern Brazil (SEB); southern Brazil with otolith morphotype 1 (SB1) and morphotype 2 (SB2); and Argentine-Uruguayan Common Fishing Zone (AU).

of discrete populations in southeastern Brazil and the southern range of the species distribution. This discreteness can be attributed to the differences in environmental conditions between these two regions. The southeastern Brazilian coast (22oS to 28oS) is a

transition area between tropical and warm temperate coasts with a relatively strong eddy activity of the oligotrophic Brazil Current (Campos et al. 2000). In contrast, the continental shelf of southern Brazil, Uruguay, and northern Argentina (32oS to 39oS), in the western boundary of the Subtropical Convergence, is characterized by the confluence between the northward-flowing cold-nutrient rich waters from the Malvinas Current and the southward flowing oligotrophic tropical waters of the Brazil Current (Ciotti et al. 1995). Similarly, isolated stocks between these regions have been documented using a variety of methods for several species of coastal fishes such as *Urophycis brasiliensis* (Pereira et al. 2014; Biolé et al. 2019), *Pagrus pagrus* (Soares et al. 2018; Kikuchi et al. 2020), *Micropogonias furnieri* (Luque et al. 2010; Vasconcellos et al. 2015; Haimovici et al. 2016), *Trachurus lathami* (Braicovich et al. 2012), *Macrodon ancylodon* (Yamaguti 1979; Rodrigues et al. 2013), *Chaetodipterus faber* (Soeth et al. 2019), *Paralichthys isosceles* (Alarcos et al. 2016) and *Pinguipes brasilianus* (Timi et al. 2010). The latitudinal isolation of these species has been attributed to the lack of conspicuous migration patterns, geographical distance, and differences in oceanographic features, explaining also the pattern observed for *U. canosai*.

In addition to these environmental causes, the differences in growing rates recorded for *U. canosai* can be attributed to the differential structure of the food web between regions and, consequently, to the availability of its main preys, benthic invertebrates (Haimovici et al. 1989). Indeed, higher abundance and faster growth of *U. canosai* in its southern range can be related to the influence of cold productive waters of sub-Antarctic origin and the Rio de la Plata runoff that reaches southern Brazil in the cold season (Capítoli and Bemvenuti 2006). In contrast, the slower growth of the species in the southeastern Brazilian Bight can be explained by the influence of the warm Brazil Current and the seasonal upwelling of the South Atlantic Central Water (SACW), which favours high pelagic productivity in summer but results in low benthic productivity (Gaeta and Brandini 2006). The same pattern of lower growth along southeastern relative to southern Brazil was also observed for the whitemouth croaker *M. furnieri*, another abundant benthic feeder on soft-bottom communities along the whole region (Haimovici et al. 2016).

Umbrina canosai is considered to be an indicator species of the winter, coastal, demersal bony fish assemblage along southern Brazil (Martins and Haimovici 2017). In this region, the species spawns in multiple batches between late winter and late spring. Larger

Table II. Analysis of variance (ANOVA-like) permutation test of the otolith shape among *Umbrina canosai* morphotypes in *a priori* comparisons, and the percentage of classification success (C.s.) of Linear Discriminant Analysis (LDA) of southeastern Brazil (SEB); southern Brazil otolith morphotype 1 (SB1) and 2 (SB2); and Argentine-Uruguayan Common Fishing Zone (AU). Statistically significant *p*-values are in bold.

	All samples					Samples at TL 290–330 mm					Samples at age 4–6				
Comparisons	d.f.	MS	F	P	C.s.	d.f.	MS	F	p	C.s.	d.f.	MS	F	p	C.s.
All	3	5.786	9.609	0.001		3	3.34	5.397	0.001		3	3.04	5.367	**0.001**	
SB1 vs. SB2	1	0.946	4.374	**0.004**	77%	1	0.70	3.200	**0.008**	82%	1	1.167	4.972	**0.001**	79%
SB 1 vs. SEB	1	0.793	4.213	**0.002**	79%	1	0.53	2.565	**0.010**	83%	1	1.192	5.901	**0.010**	85%
SB1 vs. AU	1	0.173	0.835	0.513	55%	1	0.15	0.779	0.567	49%	1	0.290	1.368	0.17	56%
SB2 vs. SEB	1	4.897	24.765	**0.001**	76%	1	2.33	10.923	**0.001**	80%	1	2.987	13.73	**0.001**	91%
SB2 vs. AU	1	1.511	7.206	**0.001**	73%	1	0.99	4.677	**0.001**	79%	1	1.44	7.366	**0.001**	80%
SEB vs. AU	1	1.549	8.390	**0.001**	73%	1	0.89	4.460	**0.001**	79%	1	0.616	3.041	**0.010**	80%
Residual	783	158.97				300	63.19				284	53.61	61.27		

females are the first to start spawning and then, move southward, followed by males and smaller females which remain in spawning areas for a longer period of time (Haimovici and Cousin 1989). However, in more recent years, small numbers of spawning females were reported in research surveys along Uruguay and Argentina during late spring (Militelli et al. 2013). Furthermore, although far more abundant in the cold seasons, it occurs and is fished year-round in southern Brazil (Figure 2), suggesting that not all *U. canosai* have the same migratory behaviour. Therefore, some degree of mixture and segregation, that cannot be easily quantified, seems to exist between fishes spawning in Argentine, Uruguayan, and southern Brazilian waters. Nevertheless, identifying any migratory behavioural diversity based on solely capture data must be interpreted with caution since catchability of a fish may be seasonally influenced by factors other than migration, and further evidence is required (Potts et al. 2018).

Migration is an important aspect of spatial population structuring, often determining the degree of connectivity or isolation across population sub-components (Frisk et al. 2014). Partial migration is defined as the existence of migrant and resident contingents within a population and occurs across a broad range of fishes (Dingle 1996; Secor 1999). It could be the case of *U. canosai,* for which it can be hypothesized that, after spawning in the cold season, a group of *U. canosai* performs 'longer migrations' between the spawning grounds in southern Brazil and northern Argentina (SB1+AU). In contrast, a second group performs shorter migrations, remaining year-round in southern Brazil or reaching most northern Uruguay (SB2). Whereas the utilization of different feeding grounds has the advantage of reducing density-dependent resource use limitations (Chapman et al. 2012), it exposes organisms to different environmental and biological conditions, driving to phenotypic variability. If so, the two

Table III. Mean observed TL (mm) at age (years) and their confidence interval (C.I., α = 0.05) for *Umbrina canosai* from: southeastern Brazil (SEB); southern Brazil otolith morphotype 1 (SB1) and morphotype 2 (SB2); Argentine-Uruguayan Common Fishing Zone (AU); and for SB1, SB2 and UA pooled.

|	SEB			SB1			SB2			AU			SB1, SB2 + UA		
Age	TL	C.I.	n	TL	C.I.	n	TL	C.I.	n	TL	C.I.	n	TL	C.I.	n
1				227.5	4.9	2	233.7	8.2	8				232.7	6.9	10
2				279.7	10.1	13	280.1	8.6	30	280	7.8	26	280.1	5.3	69
3	259.0	15.7	2	317.1	12.9	7	314.7	5.6	66	299.6	8.7	29	311.8	4.6	102
4	262.5	6.8	14	340.5	10.0	15	337.3	6.3	59	329.7	7.6	17	336.9	4.5	91
5	288.6	6.5	30	349.5	8.5	12	355.9	8.4	31	347.2	6.7	22	353.2	5.2	65
6	300.3	4.3	49	350.9	11.1	7	365.6	10.7	19	356.3	6.6	19	361.2	6.1	45
7	310.3	7.2	40	369.9	21.3	6	380	11.8	21	365.2	5.6	13	375.2	7.6	40
8	321.0	12.0	13	373.5	10.2	10	388.4	8.7	16	387.8	7.3	9	385.0	5.7	35
9	308.5	7.9	8	388.9	10.2	9	385.8	14.8	14	387.5	15.3	8	386.9	8.4	31
10	322.6	22.4	9	408		1	404.9	8.0	7	397.5	21.7	4	403.8	7.2	12
11	327.0	31.6	3				404.5	12.9	8	393.8	17.6	4	399.7	10.9	12
12	334.0	35.3	3				408.4	14.4	5	411.7	29.0	3	409.2	12.3	8
13							414.4	17.7	7				414.4	17.7	7
14							431.7	10.3	3				431.7	10.3	3
15							414.3	14.9	4				414.3	14.9	4
16							415.3	30.9	3				415.3	30.9	3
17							431.5	38.3	2				431.5	38.2	2
Total			171			82			303			154			539
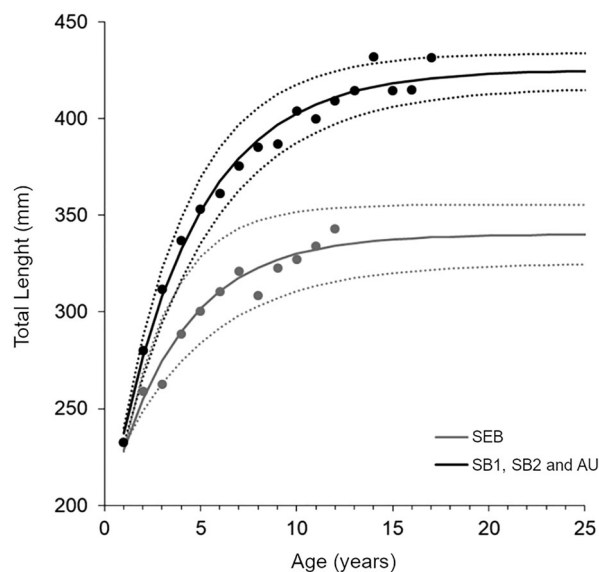
Figure 9. Von Bertalanffy's growth curves of *Umbrina canosai* fitted to the mean observed length at age for southeastern Brazil (SEB), in gray, and for the pooled data of southern Brazil with otolith morphotype 1 (BS1) and morphotype 2 (BS2), and Argentine-Uruguayan Common Fishing Zone (AU), in black. Full circle indicates the mean observed total length at age. Continuous lines indicate the growth curve and pointed lines the upper and lower parameter's credibility intervals (Cr.l., α = 0.025).

subgroups may not differ genetically; however, the different otolith phenotypes mirror two different life-history traits within the same population.

Differential intraspecific migratory patterns are not uncommon in closely related fish species from the same region. For example, a subpopulation of *M. furnieri,* the most abundant sciaenid in the study region (Acha et al. 2012), was found to be composed of at least two differential migratory groups, each displaying a different reproductive migratory behaviour in the Rio de la Plata estuary, as shown by differences in the otolith weight and growth between specimens spawning at the beginning and at the end of the reproductive season (Norbis and Verocai 2005). These

authors hypothesized that, whereas the group that spawned first moves southward along the Argentinian coast, the second moves northwards towards southern Brazil. Therefore, it is quite likely that *U. canosai* displays variations in its spawning-related migration patterns between Brazil and Argentina.

In conclusion, the existence of both northern and southern stocks was supported by our findings of differences both in otolith shape and growth parameters and conforms with the findings of a previous study in which stock structure was proposed based on differences in the structure of parasite communities (Canel et al. 2019). Therefore, we propose that the population should be split into discrete stock units for future management purposes. These differences can be related to the large geographical distance separating them and the low migration rate among both regions (Machado 2021). Regarding the southern distribution, the species should be considered as a single stock for fishery management purposes. However, the possible existence of two groups or subpopulations that overlap in their reproductive grounds, but differ in their feeding migrations, cannot be discarded. Although additional studies such as tagging experiments or otolith microchemistry analysis are necessary, our findings based on otolith shape analysis provided sufficient evidence to further investigations into the migratory patterns of *U. canosai* within the region.

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Table IV. Von Bertalanffy's growth parameters and their respective credibility interval (Cr.l., α = 0.025) for the mean observed TL at age *Umbrina canosai* from: southeastern Brazil (SE); southern Brazil with otolith morphotype 1 (SB1) and morphotype 2 (SB2); Argentine-Uruguayan Common Fishing Zone (AU); and for SB1, SB2 and UA pooled.

		SEB	SB1	SB2	UA	SB1, SB2 + UA
	Lower Cr.l	325.27	382.74	416.26	407.39	416.07
L_∞	Mean	340.08	406.57	424.72	421.88	425.08
	Upper Cr.l	355.52	432.95	433.41	435.83	433.84
	Lower Cr.l	0.207	0.211	0.212	0.198	0.207
K	Mean	0.267	0.295	0.245	0.23	0.236
	Upper Cr.l	0.389	0.425	0.286	0.287	0.275
	Lower Cr.l	−2.973	−2.876	−2.876	−2.988	−2.928
t_0	Mean	−2.177	−1.958	−2.35	−2.591	−2.46
	Upper Cr.l	−0.631	−1.015	−1.828	−1.729	−1.931

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