Fisheries Research 193 (2017) 184–194

Contents lists available at ScienceDirect

Fisheries Research

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

Fluvio-marine travelers from South America: Cyclic amphidromy and freshwater residency, typical behaviors in *Genidens barbus* inferred by otolith chemistry

Esteban Avigliano[a,*], Mathieu Leisen[b], Rurik Romero[b], Barbara Carvalho[c], Gonzalo Velasco[d], Marcelo Vianna[e], Fernando Barra[b], Alejandra Vanina Volpedo[a,f]

[a] *Instituto de Investigaciones en Producción Animal (INPA-CONICET-UBA), Facultad de Ciencias Veterinarias, Universidad de Buenos Aires (UBA), Av. Chorroarín 280, C1427CWO, Ciudad Autónoma de Buenos Aires, Argentina*
[b] *Departamento de Geología y Centro de Excelencia en Geotermia de Los Andes (CEGA), Universidad de Chile, Plaza Ercilla 803, 8370450, Santiago, Chile*
[c] *Programa de Pós Graduação em Zoologia, Departamento de Zoologia – UFPR, Centro Politécnico (19.020), Bairro Jardim das Américas, Curitiba, Paraná, Brazil*
[d] *Instituto de Oceanografia, Universidade Federal do Rio Grande (FURG), Av. Italia, Km 8 96203-900, Rio Grande, RS, Brazil*
[e] *Laboratório de Biologia e Tecnologia Pesqueira, Instituto de Biologia, Universidade do Rio de Janeiro (UFRJ), Av. Carlos Chagas Filho 373 B1, 21941-599, RJ, Brazil*
[f] *Centro de Estudios Transdisciplinarios del Agua (CETA-UBA), Facultad de Ciencias Veterinarias, Universidad de Buenos Aires (UBA), Av. Chorroarín 280, C1427CWO, Ciudad Autónoma de Buenos Aires, Argentina*

ARTICLE INFO

Handled by Prof. George A. Rose

Keywords:
Anadromy
Diadromy
Microchemistry
Migration
Lapilli otoliths

ABSTRACT

Catfish *Genidens barbus* is a commercially fished species from the south-western Atlantic Ocean. Overfishing of this species during the last few years has caused a collapse of fisheries and in turn has led to a ban of its exploitation. In order to identify the migratory patterns of this species in four migration corridors from South America, we determined the Sr:Ca and Ba:Ca ratios in otoliths, by Laser Ablation Inductively Coupled Plasma Mass Spectrometry (LA-ICPMS). Sr:Ca and Ba:Ca ratios range between 0.90 and 9.83 mmol/mol (mean ± standard deviation: 3.86 ± 1.05 mmol/mol) and between 0.00013 and 0.10 mmol/mol (mean ± SD: 0.0094 ± 0.0160 mmol/mol), respectively. Three types of amphidromous and cyclical (annual) patterns that include the use of freshwater, estuarine and marine environments are detected. Resident freshwater fish (6.5%) are found only in Patos Lagoon. Depending on the study site, between 18 and 45% of the analyzed fish population were spawned in freshwater, while the rest were spawned in estuarine waters. The change-point analysis shows a positive correlation between changes in the transects of Sr:Ca and Ba:Ca ratios ($r = 0.63$, $p = 0.0001$), whereas the Kruskal-Wallis test shows no significant differences in the number of changes in transects of the Sr:Ca ratio between sampling sites ($H = 2.1$, $p = 0.53$). Only for Patos Lagoon the analyses show a significantly higher number of changes for the Ba:Ca ratio ($H = 9.1$, $p = 0.03$). The data indicate that the average number of movements among environments is similar between the four corridors. The number of changes of the Ba:Ca ratio appears to be higher and more variable in relation to the Sr:Ca ratio, indicating that the former could be more sensitive to environmental changes. In conclusion, this work describes for the first time, annual amphidromous migrations and dependence on freshwater for different fluvial-marine systems. The understanding of the habitat use will help design species and estuarine-specific management actions with the ultimate goal of recovering fisheries.

1. Introduction

Catfish *Genidens barbus* (Lacépède 1803) is distributed between latitudes 17°′S–40°′S, from Bahia, Brazil to San Blás, Argentina (Avigliano and Volpedo, 2015; López and Bellisio, 1965) and it is one of the most economically important species in estuaries from the southwestern Atlantic Ocean (MINAGRO, 2016; Reis, 1986a; Tavares and Luque, 2004; Velasco et al., 2007). While regional fishery statistics are often incomplete and not very regular, they show a drastic reduction in catch volume in recent decades (DINARA, 2016; IBAMA, 2009; Velasco et al., 2007). For example, in Patos Lagoon (Brazil), the main site of exploitation of this resource, the fishery declined steeply during the late 1990s, where capture dropped from 9000 tons (t) per year during the period 1972–1973 to less than 200 tons per year since

---

[*] Corresponding author.
E-mail address: estebanavigliano@conicet.gov.ar (E. Avigliano).

http://dx.doi.org/10.1016/j.fishres.2017.04.011
Received 14 October 2016; Received in revised form 10 April 2017; Accepted 18 April 2017

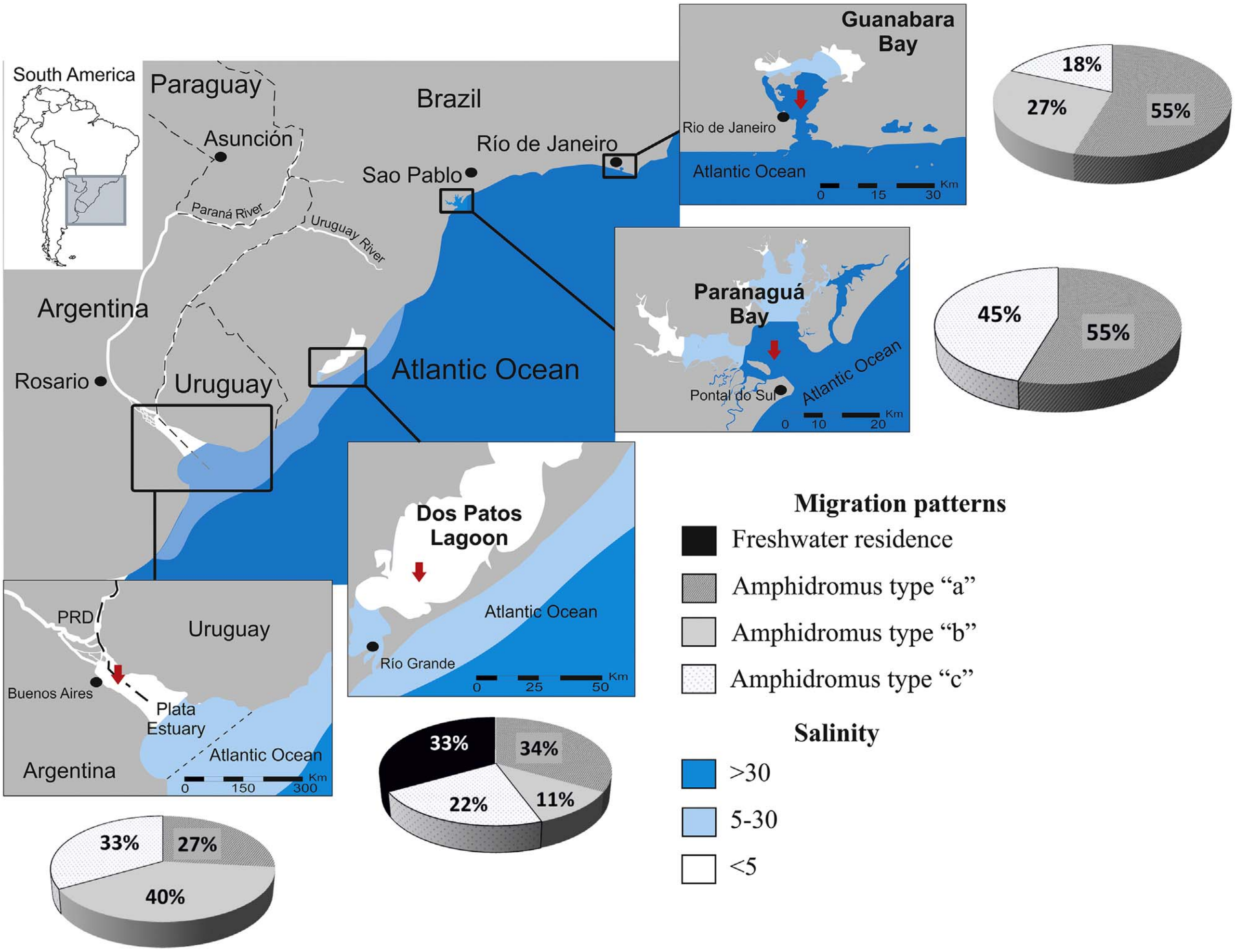

Fig. 1. Sampling sites of the catfish *Genidens barbus* (red arrows). The pie charts show the proportion of each migratory pattern for each collection site. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

1996 (IBAMA, 2009; Velasco et al., 2007).

Due to the decline of stocks supporting fisheries and the limited knowledge about its biology, this species has been included in the Red List of endangered species in Brazil. Thus, its capture, transport and marketing have been prohibited since 2015 (Di Dario et al., 2015; MMA, 2014). In Argentina, the situation is similar and Baigún et al. (2012) classified the species as vulnerable, although its capture is still allowed.

Some aspects about the life history for this species are known (Avigliano et al., 2015a, 2015b; Denadai et al., 2012; Reis, 1986b); adults (age > 7) perform reproductive migrations in spring to regions of relatively low salinity (rivers, coastal lagoons or estuaries) (Avigliano et al., 2015b; Reis, 1986b; Velasco et al., 2007; Velasco and Reis, 2004). After females spawn in estuarine or freshwater environments, males return to estuarine waters with the eggs inside their oropharyngeal cavity (Reis, 1986a; Velasco and Reis, 2004) and the juveniles are released into the lower estuary waters (Reis, 1986a; Velasco and Reis, 2004).

Despite such recent works and increased interest in relation to the vulnerability of this species, its life history is not well understood. Improved understanding such as the proportion of individuals with different migratory patterns, and age at which changes in habitat and frequency of migration take place is essential to generate policies and management actions with the ultimate goal of recovering the resource, sustaining both biodiversity and commercial exploitation in the future.

In the last decade, analysis of the Sr:Ca and Ba:Ca ratios of otolith has contributed to understanding the life history of several species that move between environments with different salinity (Daros et al., 2016; Fowler et al., 2016; Freshwater et al., 2015; Morales-Nin et al., 2012). Fish otoliths are apposition structures composed of calcium carbonate (~96%) deposited mainly as aragonite crystals in a protein matrix, and small quantities of other elements (Campana et al., 1997). As the trace elements acquired by an individual fish are preserved within the otolith microstructure formed during the corresponding ontogenetic period, their concentrations may reflect the passage of the fish through environments with differing chemical signatures (Mai et al., 2014; Phung et al., 2015; Schuchert et al., 2010; Zlokovitz et al., 2003).

Sr:Ca and Ba:Ca ratios represent useful indicators of habitat in environments with salinity gradients, because the Sr:Ca ratio of the otolith shows a positive correspondence with salinity (Bath et al., 2000; Martin et al., 2004; Secor and Rooker, 2000; Sturrock et al., 2012), whereas the Ba:Ca has an inverse relationship with salinity (Martin and Thorrold, 2005; Miller, 2011, 2009; Walther and Thorrold, 2006). In Latin America, several diadromous species (Avigliano and Volpedo, 2016; Daros et al., 2016) have been studied, and the relationship between water element:Ca ratios and salinity in large estuaries has been reported (Albuquerque et al., 2012; Avigliano and Volpedo, 2013). Particularly in *G. barbus*, otolith element:Ca ratios have been useful to discriminate fish stocks and nursery areas among different South American estuaries (Avigliano et al., 2016, 2015b), as well as to describe some migratory aspects (Avigliano et al., 2015a). Moreover, the presence of homing behavior has been suggested in some estuaries from the southwestern Atlantic Ocean using otolith chemistry (Avigliano et al., 2016, 2015b).

Several techniques have been used to determine ontogenetic changes of the Sr:Ca and Ba:Ca ratios in otoliths, such as electron probe micro-analysis (EPMA), micro-proton-induced X-ray emission (micro-PIXE) (Daros et al., 2016; Hedger et al., 2008; Lin et al., 2007), and more recently laser ablation-inductively coupled plasma-mass spectrometry (LA-ICPMS) (Fowler et al., 2016; Kissinger et al., 2016; Morales-Nin et al., 2014; Tabouret et al., 2010). Spot and/or line scans have been performed to determine the element:Ca ratio in otoliths by LA-ICPMS.

Our specific objectives are to describe in detail the life history of specimens and estimate the proportion of different migratory patterns. We determined the Sr:Ca and Ba:Ca ratios in *G. barbus* otoliths using LA-ICPMS. We then analyzed the element:Ca profiles obtained for fishes caught in the 4 main migratory corridors of the species (Plata estuary, Argentina and Patos Lagoon, Paranaguá Bay and Guanabara Bay in Brazil). This type of information is valuable to inform resource management actions and thus contribute to their recovery.

2. Materials and methods

2.1. Study area

Sampling were conducted in the Guanabara Bay (GB), Paranaguá Bay (PB), Patos Lagoon (PL), and Plata estuary (PE) from north to south (Fig. 1, Table 1). Guanabara Bay is an estuary situated in Río de Janeiro state (Brazil). It covers an area of 338 km^2 (Fig. 1). The bay is 28 km from west to east and 30 km from south to north, but the narrow entrance to Guanabara Bay is only 1.6 km wide (Kjerfve et al., 1997). The Paranaguá Bay estuary is in the Paraná state, Brazil and has an area of 601 km^2 (Fig. 1). It is partially mixed with stratification of the water column (Kjerfve et al., 1997) (Table 1). The PL, one of the most important and larger coastal ecosystems in Brazil is a large coastal lagoon, located on the coast of Rio Grande do Sul state with a total land area of 10,360 km^2. The southern part of the system is an estuary whose total area accounts for 10% of the lagoon. The system is connected to the Atlantic Ocean by a narrow channel that is 4 km long and 740 m wide (Fig. 1). The Plata estuary represents the brackish environment of the Plata Basin (Argentina and Uruguay), with a total area of 35,000 km^2 and an average discharge of 23,000 m^3/s into the Atlantic Ocean (Guerrero et al., 1997). The outer section is 300 km wide (Guerrero et al., 2010) (Fig. 1). In relation to relative low water flow and the slope of the bottom, Guanabara and Paranaguá estuaries have a strong salinity range of 18–36 and 12–34 PSU, respectively (Table 1). The salinity range of PL and PE varies between 0 and 32 PSU (Acha et al., 2008; Seeliger et al., 1997) due to the high discharge flow of their tributaries. Patos Lagoon and Plata estuaries generate a large plume of relatively low salinity (~ 20–30 PSU) up to 1000 km long on the marine shelf (latitude: 26°–38°S) (Piola et al., 2008; Piola and Romero, 2004). The area of low salinity is larger in winter and connects both estuaries systems (Piola et al., 2008; Piola and Romero, 2004).

2.2. Sample collection

Adult catfish were caught in four estuaries (Fig. 1) with hooks, longlines and gillnets, at depths ranging from 8 to 33 m between November 2010 and May 2015. The total fish length (in cm) was recorded (Table 2) and both *lapilli* otoliths were removed, rinsed with ultrapure water (18.2 mΩ/cm) (Millipore, São Paulo, Brazil) and later cleaned of any remaining tissue with a plastic toothbrush.

We used *lapilli* otoliths rather than *sagitta* or *asteriscus* otoliths because they are larger and easier to manipulate in the Ariidae catfishes (Avigliano et al., 2015b).

2.3. Age determination, sample selection and otolith preparation

Otoliths (N = 120) were weighed using a Sartorius AG ED 2242

Table 1
Characteristics of sampling areas for *Genidens barbus*. Latitude (Lat) and Longitude (Long).

	Area (km^2)	Water surface temperature	Salinity (PSU)	Depth	Climate type/ Ecoregion	Lat. Long.
Guanabara Bay	338	18–28 °C in winter and 16–28 °C in summer (Fernandes et al., 2002; Kjerfve et al., 1997)	29.7–35.8 in winter and 18.8–36.1 in summer (da Silva et al., 2016). The maximum salinity varied from 32.5 in winter to 36 in summer (Fernandes et al., 2002)	Maximum depth is 58 m (Fernandes et al., 2002; Kjerfve et al., 1997)	Mountain tropical rainforest	22°50′58.15”S–43°10′15.74”W
Paranaguá Bay	601	18–25 °C in winter and 23–30 °C in summer (Lana et al., 2001).	12–29 in winter to 20–34 in summer (Dias et al., 2016; Lana et al., 2001).	The main channel has a depth of more than 10 m (max. 33m) (Lana et al., 2001).	Mountain subtropical rainforest	25°28′53.21”S–48°24′41.06”W
Patos Lagoon	10,360	12 °C in winter and 27.5 °C in summer (Muxagata et al., 2012).	Salinity (0–32) follows a seasonal pattern (dry summer and wet winter) influenced primarily by rainfall and wind direction (Seeliger et al., 1997).	Maximum depth is 6 m in the estuary and 18 m in the navigation channel (Guerrero et al., 2010).	Subtropical plain	31°29′59.31”S–51°40′46.24”W
Plata Estuary	35,000	Temperature varied from 8 °C to 24 °C (Guerrero et al., 1997).	Highly variable salinity (0–32) and stratification during the year influenced primarily by rainfall and wind direction (Acha et al., 2008).	Maximum depth ranges between 5 and 35 m.	Template pampan plain	34° 0′12.66”S– 58°29′24.15”W/ 35°48′6.07”S–6°14′52.92”W

Table 2
Descriptive statistics of individuals from each sampling site. N: sample size; SD: standard deviation.

	Age (year)		Total length (cm)		
	mean ± SD	range	mean ± SD	Range	N
Plata Estuary	10.5 ± 1.60	8–13	64.4 ± 7.62	52.0–78.1	14
Patos Lagoon	10.1 ± 1.69	8–13	60.7 ± 6.02	54.7–71.2	10
Paranaguá Bay	9.09 ± 1.31	8–12	64.6 ± 5.85	58.0–81.0	13
Guanabara Bay	8.73 ± 1.27	8–12	59.2 ± 9.16	45.9–75.4	11
	Long-lived fish				
Patos Lagoon	27		83.7		1
Paranaguá Bay	21		75.5		1
Total					

(Göttingen, Germany) analytical balance, washed with Milli-Q water and dried. The left otolith of each pair was embedded in epoxy resin and sectioned transversely through the core to a thickness of 700 μm using a Buehler Isomet low speed saw (Hong Kong, China) equipped with twin diamond edge blades and spacers. The number of rings in the otolith section was counted with the piece immersed in ultrapure water, using a stereomicroscope (Leica EZ4-HD, Singapore) at 40X magnification. Annual periodicity of ring formation was validated by Reis (1986a).

To avoid the effect that the fish age could have on the interpretation of the results, only individuals between 8 and 12 years were selected for analysis, except for two individuals of 21 and 27 years old captured in PB and PL, respectively (total N = 49) (Table 2). The analysis of elderly specimens (> 20 years) is of great interest because catches are currently extremely rare and movement patterns are unknown.

Otolith sections were fixed to glass slides using clear epoxy resin, followed by rinsing 3 times in Milli-Q water and drying in a laminar flow hood.

2.4. Determination of Sr:Ca and Ba:Ca ratio by LA-ICP-MS analysis

Elemental concentrations were measured using LA-ICPMS located at the Andean Geothermal Center of Excellence (CEGA), Department of Geology, Universidad de Chile, using a 193 nm ArF laser ablation system (Photon Machines Analyte G2) coupled to an ICP-MS iCapQ ThermoFisher (analytical conditions are summarized in Table 3).

Fifty μm line-scans were carried out from core to edge of each otolith to determine the abundances of isotopes ^{43}Ca, ^{88}Sr and ^{138}Ba. NIST SRM 612 silicate glass reference material was used as an external standard (Jochum et al., 2011; Pearce et al., 1997), whereas the USGS synthetic calcium carbonate MACS-3 (Jochum et al., 2012) and silicate glass NIST SRM 610 were analyzed as secondary standards. The analytical sequence comprised ablation of standards (NIST 612, NIST 610, MACS-3), ablation of two otoliths and ablation of standards.

Table 3
LA-ICPMS operating conditions.

Instrument	Parameter	Value
ArF 193 nm laser ablation		
	Laser fluence	5 mJ/cm^2
	Repetition rate	10 Hz
	Pit size	Pre ablation: 85 μm. Ablation: 50 μm
	Ablation Cell	Helex-2
	Cell He gas Flow	between 0.5 and 0.7 l/min
	Scan Speed	Pre ablation: 30 μm/s. Ablation: 10 μm/s
ICP-MS		
	Acquisition mode	Time resolved
	Nebulizer gas flow	around 0.9 l/min
	Isotopes measured	^{43}Ca, ^{88}Sr and ^{138}Ba

Prior to recording transect measurements, the otolith surface was pre-ablated using the following conditions: a spot size of 85 μm, scan speed of 30 μm/s, energy density of 5 mJ/cm^2, and a repetition rate of 10 Hz. For element abundance determination, two ablation transects were carried out on the pre-ablation line in order to eliminate noise peaks. The ablation scans were performed using a 50 μm spot size, a scan speed of 10 μm/s, an energy density of 5 mJ/cm^2, and a repetition rate of 10 Hz. All transects started at the core and ended at the edge of the otolith.

Data reduction was done using the *Iolite* (Paton et al., 2011) software and concentration abundances were calculated based on the equation developed by Longerich et al. (Longerich et al., 1996). ^{88}Sr and ^{138}Ba raw intensities were background corrected (Fowler et al., 2016). Then, the external standard (NIST SRM 612) was used to determine the sensitivity factor of the mass spectrometer. Finally, the concentrations of Sr and Ba were calculated and normalized to the internal standard (^{43}Ca). The Ca concentration of the otolith matrix is 38.8 wt.% (Hamer et al., 2015; Yoshinaga et al., 2000). Concentrations were determined for each element every 10 μm along the continuous transects.

Accuracy and precision were determined using secondary standards. The average concentration of Sr in NIST SRM 610 measured during the analytical session was 509 ± 40 ppm, which is in acceptable agreement with the reported value of 507 ± 43 ppm (Jochum et al., 2011). The maximum deviation observed during one analytical session was 3%. For Ba, the average concentration measured is 453 ± 35 ppm, which overlaps within error with the published value of 451 ± 22 ppm (Jochum et al., 2011). The maximum deviation observed during any one analytical session was 4%. The uncertainty was determined by replicate analysis of NIST SRM 610 and NIST SRM 612. A 9% uncertainty was calculated for Sr and Ba. The limits of detection (LOD) are calculated from the standard deviation of the blank. The LOD, normalized to Ca, were 0.00235 mmol/mol for Sr:Ca and 0.00075 mmol/mol for Ba:Ca.

Concentration of Sr and Ba were expressed as molar ratios (element:Ca = mmol/mol) to account for fluctuations in the amount of material analyzed and the loss of material during the preparation process (Bailey et al., 2015; Sinclair et al., 1998).

2.5. Pattern classification and data analysis

To evaluate the consistency of the data, we used Pearson correlation between Sr:Ca and Ba:Ca ratios (Fowler et al., 2016) and bootstrap 95% confidence intervals.

Following the methods described in previous studies (Rohtla et al., 2014; Smith and Kwak, 2014; Wynne et al., 2015), we use the Sr:Ca ratio for pattern classification, because the Ba:Ca ratio could be influenced by changes in the flow of freshwater that enters the studied systems. Transition thresholds between habitats were estimated to facilitate the interpretation of transects. The transition threshold between freshwater and estuary was calculated as the mean of the Sr:Ca ratio of the edge of the otolith from sampling in freshwater habitats (Patos Lagoon, N = 10) plus twice the standard deviation (mean + 2 * SD) as suggested by Tabouret et al. (2010) and Lin et al. (2014). According to the methodology of Tabouret et al. (2010) to estimate the threshold limiting migration between estuary and sea, we used the Sr:Ca ratio of the edge of otoliths of fish caught in the outer portion of an estuary. In this work, 11 otoliths from GB (salinity ~27 PSU) were used, and the threshold was estimated as the mean of the Sr:Ca ratio + 2 * SD (Lin et al., 2014; Tabouret et al., 2010).

Several algorithms have been used to facilitate the interpretation of fish movement patterns and to infer the number of habitat changes during their life history (Hedger et al., 2008; Hegg et al., 2015; Walther et al., 2011; Wynne et al., 2015). In this work we used Change-Point analysis (CPA) to facilitate the classification of individuals and quantify the number of changes in otolith elemental ratios (Hegg et al., 2015; Shrimpton et al., 2014). CPA determined whether there had been a change in the underlying process that generated the sequence of events and identified where the change occurred. The procedure used to perform a CPA comprises a combination of cumulative sum charts (CUSUM) and bootstrapping to detect changes. The analysis provides both confidence levels and confidence intervals for each change (95% confidence is used for all confidence intervals) and it is robust to issues of non-normality (Shrimpton et al., 2014). The Change-Point Analyzer 2.3 software package (Taylor, 2000) was used for CPA.

After plotting the transects, thresholds and changes of CPA, habitat use patterns and transitions were visually classified by changes in the Sr:Ca ratio along the otolith transect (Wynne et al., 2015). The percentage that each migratory behavior is represented as a percentage in pie charts for each estuary (Fig. 1).

In this work, the patterns were defined based on habitat use, assuming similar approaches as Hedger et al. (2008) and Thibault et al. (2007), and considering the environment where the fish were spawned. These classifications only take into account habitat use with no necessary association with reproductive movements. According to Elliott et al. (2007) and McDowall (2007), amphidromy was reserved for species that migrate between freshwater and the sea, or vice versa, that is not related to breeding migrations.

We evaluate whether there is a relation between the number of changes obtained from the CPA for the Sr:Ca and Ba:Ca ratios and the fish age using ANCOVA (number of changes as a variable and age as covariate) and Pearson correlation. The existence of a co-variation with the age could affect the interpretation of the variable number of changes of the Sr:Ca and Ba:Ca ratios. Then, a Pearson Correlation Coefficient was calculated with the number of changes between patterns of Sr:Ca and Ba:Ca ratios in order to determine whether there is consistency between the two variables and if both are plausible as indicators of movements.

Finally, following Walther et al. (2011) and Shrimpton et al. (2014), the variable "number of changes" was compared. The Kruskal Wallis test was used to compare the number of changes (Sr:Ca and Ba:Ca ratios) between locations, while the Wilcoxon test was used to assess differences between transects of the Sr:Ca and Ba:Ca ratios for each site separately. Non-parametric tests were used because the variables did not fit the normal distribution and homogeneity of variance (Shapiro-Wilk, $p < 0.05$; Levene, $p < 0.05$) even after transformation $\log(x + 1)$.

3. Results

3.1. Relation between Sr:Ca and Ba:Ca ratios and threshold estimations

Otolith Sr:Ca ratio ranged between 0.90 and 9.83 mmol/mol (mean ± SD: 3.86 ± 1.05 mmol/mol), while the Ba:Ca ratio varied between 0.00013 and 0.10 mmol/mol (mean ± SD: 0.0094 ± 0.016 mmol/mol).

The reference value for movements between environments was 3.75 mmol/mol ($N = 10$) and 5.98 mmol/mol ($N = 15$) for freshwater-brackish and brackish-marine water, respectively. Then, Sr:Ca values above 5.98 were considered as corresponding to seawater, whereas values below 3.75 to freshwater. Values between the thresholds (3.75–5.98) were taken as estuarine. A weakly significant and negative correlation was found ($r = -0.3$; $p < 0.001$; $N = 23{,}925$) between the Sr:Ca and Ba:Ca ratios among all specimens analyzed. Bootstrap 95% confidence intervals were 3.85–3.89 (mean = 3.86) for Sr:Ca and 0.0092–0.0096 (mean = 0.0094) for Ba:Ca.

3.2. Life history and migration patterns allocation

Sixty-seven, 78, 55 and 82% of the fish caught in PE, PL, PB and GB, respectively, showed values below the Sr:Ca reference value of 3.75 mmol/mol (1.90–3.72 mmol/mol), suggesting that these were spawned in freshwater environments. The remaining individuals, representing 33, 22, 45 and 18% of the fish caught respectively in PE, PL, PB and GB were spawned in an estuarine environment (3.90–5.21 mmol/mol).

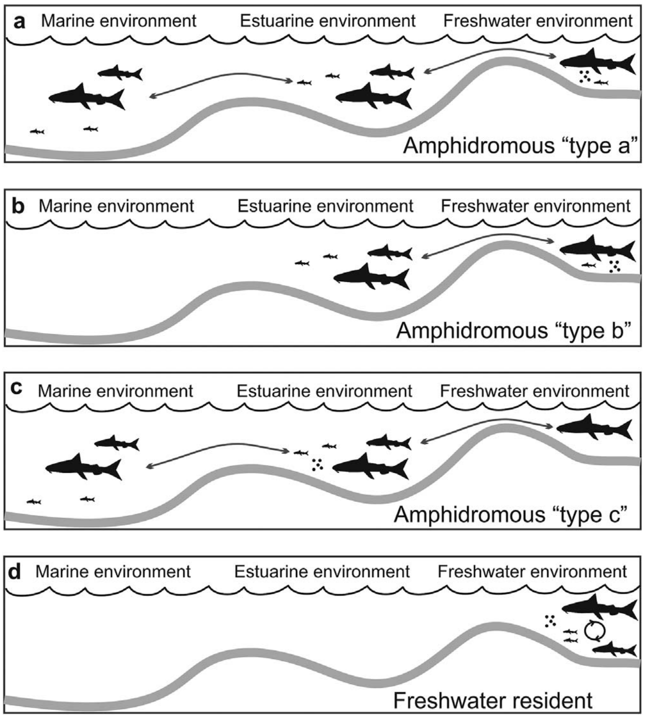

Fig. 2. Patterns obtained for *Genidens barbus*. Note the co-occurrence (cyclic) of several size-classes in different environments. a) amphidromous "type a": defined as fish spawned in freshwater and moved at least once to a marine environment (freshwater-brackish-marine water), b) amphidromous "type b": defined as individuals spawned in freshwater that migrate to brackish water (freshwater-brackish); c) amphidromous "type c": defined as individuals spawned in estuarine water that migrate to freshwater, marine or both (brackish-variable), and d) freshwater resident; defined as permanence in freshwater throughout life. The schemes do not represent gastric incubation. The definition of amphidromy was taken from McDowall (2007). Scheme modified from Potter et al. (2015a,b).

Based on our data, the patterns were defined as follows (Fig. 2): 1) amphidromous "type a": this pattern was defined as fish spawned in freshwater and moved at least once to a marine environment (freshwater-brackish-marine water), 2) amphidromous "type b": defined as individuals spawned in freshwater that migrate to brackish water (freshwater-brackish); 3) amphidromous "type c": defined as individuals spawned in estuarine water that migrate to freshwater, marine or both (brackish-variable), and 4) freshwater resident; defined as permanence in freshwater throughout life.

Two migratory patterns are common among sampling sites; amphidromous "type a" and "type c" (Figs. 1 and 3). The amphidromous pattern "type a" was observed in 55% of PB and GB populations, and 27 and 34% in PE and PL, respectively.

On the other hand, the amphidromous pattern "type c" was present in 33, 22, 45, and 18% of the fish caught in PE, PL, PB, and GB, respectively (Fig. 1). In PE, the amphidromous specimens "type b" represented the largest proportion between the patterns found (40%) with smaller proportions for PL and GB (11 and 27%, respectively) (Fig. 1). Freshwater resident pattern was present only in PL, representing 33% of individuals (Fig. 1).

Large cyclical oscillations in transects with amplitudes that exceed 1 mmol/mol for the Sr:Ca ratio and highly variable Ba:Ca ratios were observed in all individuals except those classified as residents (6.5%). These large oscillations are generally annual, corresponding to the growth rings of otoliths, although this annual frequency is less evident

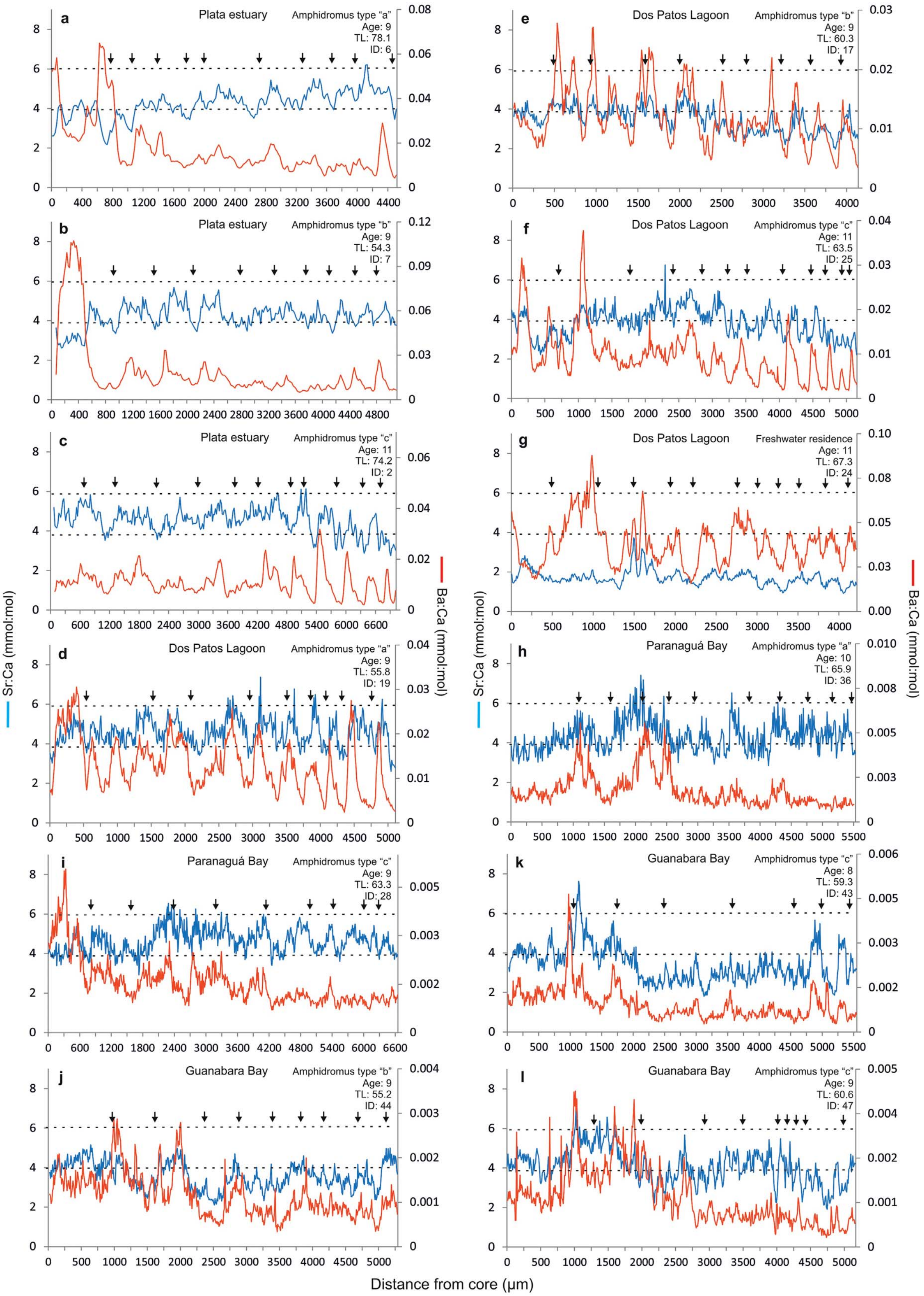

Fig. 3. Otolith microchemical profiles of *Genidens barbus* from core to edge (age: 8–12). Vertical arrows indicate otolith *annuli* (age) and black dashed lines indicate upper (marine) and lower (freshwater) thresholds for Sr:Ca. TL = total length. The data were averaged with a 10-μm interval.

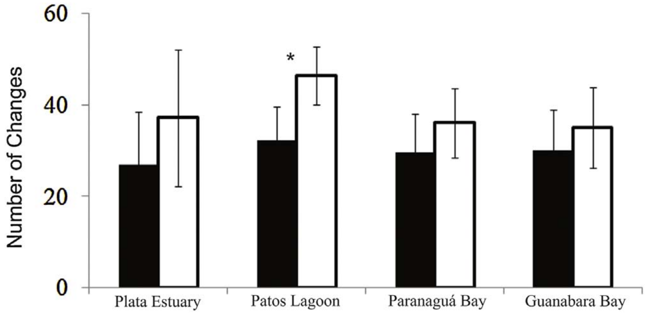

Fig. 4. Distribution of number of changes from Change-Point analysis. Mean ± SD number of change (habitats or stable chemical signature) in profiles from otoliths grouped by capture location. Results are shown for both the Sr:Ca (black bars) and Ba:Ca ratios (open bars). Asterisks indicate a statistically significant ($p < 0.05$) difference between element:Ca ratios.

in fish from GB (Fig. 3). In all amphidromous fish "type a" and "type b," the first migration to the estuarine environment occurred during the first year of life (Fig. 3). In all amphidromous fish 'type a', the age of the first entering into seawater (salinity over 27 PSU) was highly variable among individuals caught in PE, PL, and PB with a range of 1–12 years, however, the first entering occurred between the first and second year of life for all fishes from GB. A tendency to perform cyclic movements between environments of lower salinity, on the threshold limiting freshwater and estuarine was observed in all amphidromous specimens "type a" from PB, after entering the marine environment (Fig. 3).

In amphidromous specimens "type b" and "type c" no obvious changes were observed in migratory patterns throughout ontogeny (Fig. 3).

3.3. Quantification of changes in the life history

The average number of changes (moving indicators) in transects of the Sr:Ca ratio is 19.6 ± 9.3 (range: 11–46), while for the Ba:Ca ratio is 38.7 ± 11.0 (range: 20–66) (Fig. 4).

ANCOVA shows that there is no co-variation between age and number of changes ($p > 0.05$), whereas no correlation was found between age and number of changes of the Sr:Ca ($r = 0.11$, $p = 0.4$) and Ba:Ca ($r = 0.22$, $p = 0.1$) ratios. For this reason, it was not necessary to make age corrections in variables. A positive correlation was observed between the number of changes in transects of Sr:Ca and Ba:Ca ($r = 0.63$, $p = 0.0001$) ratios, which indicates that both variables are equally useful in the quantification of microenvironments.

Additionally, the Wilcoxon test shows significant differences in the number of changes between the Sr:Ca and Ba:Ca profiles only for PL ($W = 152$, $p = 0.0004$), but no difference between the two variables for the rest of the sites ($150 < W < 166$, $0.06 < p < 0.1$) (Fig. 4). The Kruskal-Wallis test shows no significant differences in the number of changes in transects of Sr:Ca between sampling sites ($H = 2.1$, $p = 0.53$), while the number of changes for Ba:Ca is significantly higher in PL ($H = 9.1$, $p = 0.03$) (Fig. 4).

3.4. Long-lived fish

The 27 year old specimen captured in the freshwater portion of PL showed Sr:Ca values in the core lower than the threshold between freshwater and estuarine. However, the threshold was exceeded several times before the first year of life (Fig. 5m). Then it showed an amphidromous migratory behavior "type c" until the age of 10. From age 9 and up, changes continued with an annual trend, maintaining Sr:Ca levels between both thresholds (freshwater-brackish and brackish-marine water, respectively). After the age of 22, the values of Sr:Ca are below the freshwater-brackish threshold. These displacements were represented by 19 and 46 changes detected by the CPA, for transects of the Sr:Ca and Ba:Ca ratios, respectively.

The 21 year old specimen captured in PB showed Sr:Ca values in the core between both thresholds. In addition, the threshold was briefly overcome only before the first year of life, suggesting an amphidromous pattern "type c" (Fig. 5n). The Sr:Ca transect shows oscillations in a markedly cyclical and annual pattern between environments and freshwater threshold with a tendency not to exceed the reference value. In this case 45 and 35 changes were detected by CPA, for transects of the Sr:Ca and Ba:Ca ratios, respectively.

4. Discussion

This work describes for the first time the cyclical amphidromous behavior pattern in *G. barbus* (in its variant types "a", "b", and "c") and confirmed a high plasticity in migratory patterns (Fig. 2) inferred by otolith Sr:Ca and Ba:Ca rarios.

The incorporation of Sr and Ba in the otolith is related to the presence of these elements in water (Macdonald and Crook, 2010; Walther and Thorrold, 2006). The oceans are particularly rich in Sr due to the presence of Sr salts (Brass and Turekian, 1974), while freshwater systems are considered as Ba sources due to the presence of this element in the sediments (Coffey et al., 1997; Li and Chan, 1979). In addition, in marine environments, upwelling could also be source of Sr and Ba (Begg et al., 2005; Ferguson et al., 2011; Lea et al., 1989).

However, the incorporation of Sr and Ba in the otolith could also be influenced by environmental (salinity, temperature) (Brown and Severin, 2009; Elsdon and Gillanders, 2003; Martin et al., 2004), genetic (Barnes and Gillanders, 2013) and physiological factors (growth rates, metabolic changes) (Kalish, 1991; Radtke and Shafer, 1992; Sturrock et al., 2014). According to Brown and Severin review (2009), the relation between Sr concentration of otolith and salinity would seem to be universal for diadromous species, although the Sr incorporation ratio and the magnitude may differ between species. Even relations between salinity and otolith/water chemistry may change especially at low salinities (< 5 PSU) (Macdonald and Crook, 2010). It has been reported that the incorporation of Sr in otoliths in certain species such as *A. japonicus* is genetically influenced, although the relation between Sr:Ca and salinity remains positive (Barnes and Gillanders, 2013). The Ba incorporation ratio in the otolith is also species-dependent and may be influenced (Miller, 2011) or not (Bouchard et al., 2015; Martin and Thorrold, 2005; Martin and Wuenschel, 2006) by other factors such as temperature. In this sense, the relation between the elements and salinity should not be deliberately assumed and it is necessary to know what factors influence the incorporation of these ones in the otolith, in order not to perform incorrect interpretations.

In the case of *G. barbus*, previous studies have shown an opposite relation between Sr:Ca and Ba:Ca levels in otolith, being consistent with the salinity reported for different environments (Avigliano et al., 2015b). Avigliano et al. (2015b) have used transects of Sr:Ca and Ba:Ca to infer the history and have obtained consistent results in relation to the previous knowledge on the biology of the species. In this paper, we found a weak negative relationship between the Sr:Ca and Ba:Ca ratios and a positive correlation between the number of changes, showing consistency between relations (Fowler et al., 2016). In this sense, we assume that significant changes in the transect correspond to changes of habitat characterized by different chemical signatures of the water (Freshwater et al., 2015; Hegg et al., 2015; Wynne et al., 2015). However, we recognize the importance of studying factors that affect the incorporation of different elements in the otoliths in order to make more accurate inferences. In this work, some minor issues remain unresolved, especially some brief increases, apparently simultaneous, in Sr:Ca and Ba:Ca ratios (Fig. 5). As mentioned above, the relation between the two elements might be weak at low salinities.

Movement patterns were inferred using transition thresholds estimated at 3.75 and 5.98 mmol/mol (freshwater-brackish and brackish-marine water, respectively). While transition thresholds between environments seem to vary among teleost fish, our estimates are

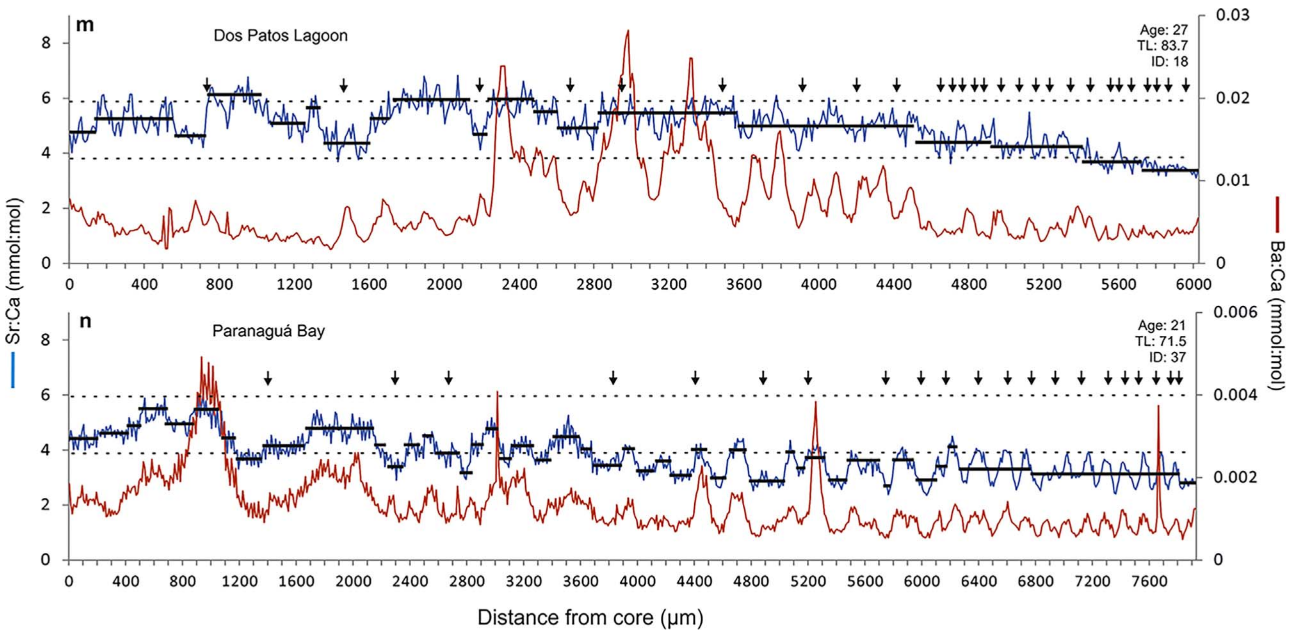

Fig. 5. Otolith microchemical profiles of long-lived *Genidens barbus* (age: 27–21) from the core to the otolith edge. Black dashed lines indicate upper (marine) and lower (fresh water) thresholds for the Sr:Ca ratio, and vertical arrows indicate otolith *annuli* (age). The data were averaged with a 10-µm interval. Horizontal lines illustrate stable signatures identified using change-point analysis for the Sr:Ca ratio. TL = total length.

consistent with those reported for other diadromous species. For example, Fowler et al. (2016) has reported values between 3.3–6.4 mmol/mol for *Mugil cephalus* while Kanai et al. (2014) reported values between 4.2 and 6.4 mmol/mol for *Zenarchopterus dunckeri*. However, other species were associated with significantly lower values of reference, as *Osmerus mordax* (~2.3–4.2 mmol/mol) (Bradbury et al., 2008) or *Gobiomorus dormitor* (~3 mmol/mol for freshwater-brackish) (Smith and Kwak, 2014).

The number of changes for transects Sr:Ca and Ba:Ca ratios were similar among sites (except for Ba:Ca in PL), suggesting that on average, the number of fish movements is similar between capture sites. It is interesting to note that the number of changes tended to be higher for the Ba:Ca compared to Sr:Ca ratio, being this difference significant only for PL (Fig. 4). Peaks in Ba levels in water may be associated with inflow of freshwater to the estuaries, with the Ba:Ca ratio in the otolith more susceptible to this variation (Hamer et al., 2006; Rohtla et al., 2014; Tabouret et al., 2011, 2010). In this respect, PL represents a shallow depth lagoon system (Table 1) and it is plausible that the pulses of flooding of the tributaries have an effect on the water Ba levels, which could be recorded as changes in the Ba:Ca ratio in otoliths.

Regarding the life history of *G. barbus*, after fertilization, males incubate the eggs in the oropharingeal cavity up to 3 months from the site of mating to the exterior portion of the estuary (high salinity), where juveniles are released (Reis, 1986b). Using stable carbon isotopes in muscle and size structures, Pereyra et al. (2016) and Araújo (1988) have suggested that births occurred in estuarine waters. Based on the structure of sizes and ages, Velasco and Reis (2004) suggested that the juveniles remained in the estuary during the first 3 years of life, and then moved to the sea to feed, where they remained until about the age of first sex maturity (> 7 years). Then, adults enter estuarine waters for reproductive purposes.

According to the Sr:Ca and Ba:Ca ratios obtained here, we conclude that fishes are spawned in the estuary, as suggested by Reis (1986b), Araújo (1988) and Pereyra et al. (2016), but also in freshwater (Figs. 3 and 4). This paper is the first to report spawning and hatching of this species in freshwater because previous studies were performed using "free" juveniles already incubated. Our results do not support the current model of estuarine residence during the first 3 years of life, followed by a marine residence between years 3–7 (Velasco and Reis, 2004) as a common behavior for the species. On the contrary, we observed considerable variability in migratory patterns during the juvenile and pre-adult period, including residence and cyclical migration between freshwater, estuarine and marine environments.

In the long-lived specimens, particularly in the 27 year old specimen, changes in patterns throughout their ontogenetic development were observed, with amphidromous "type c" during its first years of life, and freshwater residency in the last 4 years (Fig. 5). Freshwater resident pattern for PL was first reported by Avigliano et al. (2015a) for specimens between 9 and 14 years old. These authors have also reported the presence of freshwater residence in a specimen caught in the PE, during the first 7 years of life. In this paper, the absence of freshwater residence in PB and GB could be because the freshwater environments represent a very small surface in these fluvio-marine systems. However, this could also be related to the capture effort in freshwater. In this regard, the presence of residence patterns in PG and GB remains unknown.

Cyclical migration in the non-reproductive juvenile and pre-adult stages, but juvenile or pre-adult (age < 7) is an interesting behavior, and it remains unknown if it is linked to trophic habits, evolutionary history, or either seasonal environmental changes (temperature, salinity). Regular cyclical or annual migration has been previously reported for other species such as *M. curema* (Fowler et al., 2016), *Anguilla mossambica* (Lin et al., 2014), and *A. anguilla* (Panfili et al., 2012), but it is the first time that this pattern is reported for *G. barbus*. Annual co-occurrence (cyclic) of several size-classes of *G. barbus* has been previously suggested in different regions of estuaries as PL, Chuí, Tramandaí, Mampituba (Brazil) (Mendoza-Carranza and Vieira, 2008; Velasco et al., 2007; Vieira, 2006). This supports our conclusions, mainly that cyclical migration is common not only in the adult stages but throughout life.

Marine incursions in diadromous fish provides them with the opportunity to grow more quickly and have higher fecundity through the exploitation of rich food resources, whereas returning to continental waters fosters adaptation of stocks to favorable local spawning conditions (Elliott et al., 2007; Lucas et al., 2001; McDowall, 2001). Furthermore, marine incursions in migratory fish could also facilitate connectivity between estuaries, as observed in different salmonids (Cury, 1994; McDowall, 2001). According to McDowall (2001), a low percentage of straying in species may have long-term evolutionary advantages. This way the fish could move into new environments, and perhaps more beneficial ones in terms of food and reproduction, especially if the natal site had changed.

It has been reported that there is a relative connectivity among populations of the estuary of PE and PL, although it would predominate segregation (Avigliano et al., 2016). This corridor of inter-estuarine connectivity is affected by plumes of relative low salinity (20–30 PSU) up to 1000 km long on the platform (Braga et al., 2008; Möller et al., 2008; Piola and Romero, 2004) (Fig. 1). Our movement threshold between the outer edge of estuaries and the ocean (Sr:Ca: 5.98 mmol/mol) was calculated for a salinity of ~27 PSU. However, it is possible that specimens can move on the plume of moderate salinity, movement that is not recorded in the otolith Sr:Ca levels exceeding the threshold, thus underestimating the percentage of individuals amphidromous "type a" in PE and PL. The hypothesis of displacement between PE and PL on the plumes could explain the relative low percentages of individuals entering the sea in relation to those observed for PB and GB (27 and 34% for RDP and LDP, and 55% for PB and GB, respectively), and the reported connectivity between both locations (Avigliano et al., 2016, 2015b).

Other authors have proposed classifications such as semi-anadromy, catadromy, semi-catadromy, freshwater, estuarine, and marine migrant, based on the reproductive life cycle of fish (Elliott et al., 2007; Potter et al., 2015a). However, these classifications only consider "simple" life cycles (only few displacements) and they do not consider cyclic movements, or "stable" patterns along fish life. In our case, these classifications do not apply, due to non-reproductive cyclic migration of pre-adult stages, as well as to variability in ontogenetic patterns of fish. If we try to use Elliott et al. (2007) and Potter et al. (2015b) classifications in our results, the amphidromous pattern "type a" could be associated with anadromy, assuming a reproductive migration of adults. A few authors have deepened into amphidromy, considering the great variability of this migratory pattern (McDowall, 2007, 2001, 1988; Miles et al., 2014). Even, variants of freshwater and seawater have been mentioned. (McDowall, 2001, 1988; Miles et al., 2014). Even, variants of freshwater and seawater have been mentioned (McDowall, 1988). In this paper, considering pre-adult stages, this amphidromous pattern "type a" could be related to a strict amphidromy (non-reproductive migration among three environments) (McDowall, 1988). Nevertheless, a new term could be introduced to describe "type b or c" patterns: semi-amphidromy, implying a non-reproductive migration among two environments (freshwater-brackish or brackish-variable, respectively).

Finally, in this work it has been highlighted that the distance between rings (Fig. 5) is relatively variable, suggesting differences in growth rates among different habitats. Then, considering that different growth rates can affect the shape of the otolith, it would be interesting to investigate habitat use through otolith shape and otolith microstructure analysis for stocks identification (Ferguson et al., 2011).

In conclusion, *G. barbus* uses freshwater, estuarine and marine environments, presenting different migratory patterns that may vary depending on the ontogenetic stage of development. While the dominance of each pattern varies among the studied sites, the most important are 3 migrant forms and freshwater resident. This work needs to be linked to specific management objectives and, based on these results, the implementation of fishery management actions throughout the migratory fluvio-marine corridor is suggested. Special attention should be directed towards places where specimens are residents, such as the freshwater section of PL.

Acknowledgments

The analytical work was supported by CONICYT-Fondequip instrumentation grant EQM120098. Authors are indebted to CONICET (PIP 112-20120100543CO), ANPCyT (PICT 2015-1823), Universidad de Buenos Aires (UBACYT 20020150100052BA), Instituto de Oceanografia from Universidade Federal do Rio Grande (FURG), Centros Asociados para el Fortalecimiento de Posgrados Program (CAFP BA 43/13 Brazil/Argentina), Long Term Ecological Program-CNPq (PELD403809/2012-6) and FAPERJ (E26/110.114/2013 and E26/112.636/2012) for financial support for the sampling. We thank the Editor and anonymous reviewers for their constructive comments, which helped us to improve the manuscript.

References

Acha, M.E., Mianzan, H., Guerrero, R., Carreto, J., Giberto, D., Montoya, N., Carignan, M., 2008. An overview of physical and ecological processes in the Rio de la Plata Estuary. Cont. Shelf Res. 28, 1579–1588. http://dx.doi.org/10.1016/j.csr.2007.01.031.

Albuquerque, C.Q., Miekeley, N., Muelbert, J.H., Walther, B.D., Jaureguizar, A.J., 2012. Estuarine dependency in a marine fish evaluated with otolith chemistry. Mar. Biol. 159, 2229–2239. http://dx.doi.org/10.1007/s00227-012-2007-5.

Araújo, F.G., 1988. Distribuição, abundância relativa e movimentos sazonais de bagres marinhos (Siluriformes, Ariidae) no estuário da Lagoa dos Patos (RS), Brasil. Rev. Bras. Zool. 5, 509–543. http://dx.doi.org/10.1590/S0101-81751988000400002.

Avigliano, E., Volpedo, A.V., 2013. Use of otolith strontium:calcium ratio as an indicator of seasonal displacements of the silverside (*Odontesthes bonariensis*) in a freshwater-marine environment. Mar. Freshwater Res. 64, 746. http://dx.doi.org/10.1071/MF12165.

Avigliano, E., Volpedo, A.V., 2015. New records of anadromous catfish *Genidens barbus* (Lacépède, 1803) in the Paraná Delta (South America): evidence of extension in the migration corridor? Mar. Biodivers. Rec. 8, 1–3. http://dx.doi.org/10.1017/S175526721400147X.

Avigliano, E., Volpedo, A.V., 2016. A review of the application of otolith microchemistry toward the study of Latin American fishes. Rev. Fish. Sci. Aquacult. 24, 369–384. http://dx.doi.org/10.1080/23308249.2016.1202189.

Avigliano, E., Velasco, G., Volpedo, A.V., 2015a. Assessing the use of two southwestern Atlantic estuaries by different life cycle stages of the anadromous catfish *Genidens barbus* (Lacépède, 1803) as revealed by Sr:Ca and Ba:Ca ratios in otoliths. J. Appl. Ichthyol. 31, 740–743. http://dx.doi.org/10.1111/jai.12766.

Avigliano, E., Velasco, G., Volpedo, A.V., 2015b. Use of lapillus otolith microchemistry as an indicator of the habitat of *Genidens barbus* from different estuarine environments in the southwestern Atlantic Ocean. Environ. Biol. Fish. 98, 1623–1632. http://dx.doi.org/10.1007/s10641-015-0387-3.

Avigliano, E., Carvalho, B., Velasco, G., Tripodi, P., Vianna, M., Volpedo, A.V., 2016. Nursery areas and connectivity of the adults anadromous catfish (*Genidens barbus*) revealed by otolith core microchemistry in the southwestern Atlantic Ocean. Mar. Freshwater Res. http://dx.doi.org/10.1071/MF16058.

Baigún, C.R.M., Nestler, J.M., Minotti, P., Oldani, N., 2012. Fish passage system in an irrigation dam (Pilcomayo River basin): When engineering designs do not match ecohydraulic criteria. Neotrop. Ichthyol. 10, 741–750. http://dx.doi.org/10.1590/S1679-62252012000400007.

Bailey, D.S., Fairchild, E., Kalnejais, L.H., 2015. Microchemical signatures in juvenile winter flounder otoliths provide identification of natal nurseries. Trans. Am. Fish. Soc. 144, 173–183. http://dx.doi.org/10.1080/00028487.2014.982259.

Barnes, T.C., Gillanders, B.M., 2013. Combined effects of extrinsic and intrinsic factors on otolith chemistry: implications for environmental reconstructions. Can. J. Fish. Aquat. Sci. 70, 1159–1166. http://dx.doi.org/10.1139/cjfas-2012-0442.

Bath, G.E., Thorrold, S.R., Jones, C.M., Campana, S.E., McLaren, J.W., Lam, J.W.H., 2000. Strontium and barium uptake in aragonitic otoliths of marine fish. Geochim. Cosmochim. Acta 64, 1705–1714. http://dx.doi.org/10.1016/S0016-7037(99)00419-6.

Begg, G.A., Campana, S.E., Fowler, A.J., Suthers, I.M., 2005. Otolith research and application: current directions in innovation and implementation. Mar. Freshwater Res. 477–483. http://dx.doi.org/10.1071/mf05111.

Bouchard, C., Thorrold, S.R., Fortier, L., 2015. Spatial segregation, dispersion and migration in early stages of polar cod *Boreogadus saida* revealed by otolith chemistry. Mar. Biol. 162, 855–868. http://dx.doi.org/10.1007/s00227-015-2629-5.

Bradbury, I.R., Campana, S.E., Bentzen, P., 2008. Otolith elemental composition and adult tagging reveal spawning site fidelity and estuarine dependency in rainbow smelt. Mar. Ecol. Prog. Ser. 368, 255–268. http://dx.doi.org/10.3354/meps07583.

Braga, E.S., Chiozzini, V.C., Berbel, G.B.B., Maluf, J.C.C., Aguiar, V.M.C., Charo, M., Molina, D., Romero, S.I., Eichler, B.B., 2008. Nutrient distributions over the Southwestern South Atlantic continental shelf from Mar del Plata (Argentina) to Itajaí (Brazil): winter-summer aspects. Cont. Shelf Res. 28, 1649–1661. http://dx.doi.org/10.1016/j.csr.2007.06.018.

Brass, G.W., Turekian, K.K., 1974. Strontium distribution in Geosecs oceanic profiles. Earth Planet. Sci. Lett. 23, 141–148. http://dx.doi.org/10.1016/0012-821X(74)90041-7.

Brown, R.J., Severin, K.P., 2009. Otolith chemistry analyses indicate that water Sr:Ca is the primary factor influencing otolith Sr:Ca for freshwater and diadromous fish but not for marine fish. Can. J. Fish. Aquat. Sci. 66, 1790–1808. http://dx.doi.org/10.1139/F09-112.

Campana, S.E., Thorrold, S.R., Jones, C.M., Gunther, D., Tubrett, M., Longerich, H., Jackson, S., Halden, N.M., Kalish, J.M., Piccoli, P., de Pontual, H., Troadec, H., Panfili, J., Secor, D.H., Severin, K.P., Sie, S.H., Thresher, R., Teesdale, W.J., Campbell, J.L., 1997. Comparison of accuracy, precision, and sensitivity in elemental assays of fish otoliths using the electron microprobe, proton-induced X-ray emission, and laser ablation inductively coupled plasma mass spectrometry. Can. J. Fish. Aquat. Sci. 54, 2068–2079. http://dx.doi.org/10.1139/cjfas-54-9-2068.

Coffey, M., Dehairs, F., Collette, O., Luther, G., Church, T., Jickells, T., 1997. The behaviour of dissolved barium in estuaries. Estuar. Coast. Shelf Sci. 45, 113–121. http://dx.doi.org/10.1006/ecss.1996.0157.

Cury, P., 1994. Obstinate nature: an ecology of individuals. Thoughts on reprodudive behavior and biodiversity. Can. J. Fish. Aquat. Sci. 51, 1664–1673. http://dx.doi.org/10.1139/f94-167.

DINARA, 2016. Dirección Nacional de Recursos Acuáticos, Uruguay. http://www.dinara.gub.uy. (Accessed 20 January 2017).

Daros, F.A., Spach, H.L., Correia, A.T., 2016. Habitat residency and movement patterns of *Centropomus parallelus* juveniles in a subtropical estuarine complex. J. Fish Biol. 88, 1796–1810. http://dx.doi.org/10.1111/jfb.12944.

Denadai, M.R., Bessa, E., Santos, F.B., Fernandez, W.S., da Costa Santos, F.M., Feijo, M.M., Dias Arcuri, A.C., Turra, A., 2012. Life history of three catfish species (Siluriformes: Ariidae) from southeastern Brazil. Biota Neotrop. 12, 74–83.

Di Dario, F., Di Alves, C.B.M., Boos, H., Frédou, F.L., Lessa, R.P.T., Mincarone, M.M., Pinheiro, M.A.A., Polaz, C.N.M., Reis, R.E., Rocha, L.A., Santana, F.M., Santos, R.A., Santos, S.B., Vianna, M., Vieira, F., 2015. A better way forward for Brazil's fisheries. Science 363 (80), 1079.

Dias, T.H., de Oliveira, J., Sanders, C.J., Carvalho, F., Sanders, L.M., Machado, E.C., Sá, F., 2016. Radium isotope (223Ra, 224Ra, 226Ra and 228Ra) distribution near Brazil's largest port, Paranaguá Bay, Brazil. Mar. Pollut. Bull. 224–229. http://dx.doi.org/10.1016/j.marpolbul.2016.07.004.

Elliott, M., Whitfield, A.K., Potter, I.C., Blaber, S.J.M., Cyrus, D.P., Nordlie, F.G., Harrison, T.D., 2007. The guild approach to categorizing estuarine fish assemblages: a global review. Fish Fish. 8, 241–268.

Elsdon, T.S., Gillanders, B.M., 2003. Relationship between water and otolith elemental concentrations in juvenile black bream *Acanthopagrus butcheri*. Mar. Ecol. Prog. Ser. 260, 263–272. http://dx.doi.org/10.3354/meps260263.

Ferguson, G.J., Ward, T.M., Gillanders, B.M., 2011. Otolith shape and elemental composition: Complementary tools for stock discrimination of mulloway (*Argyrosomus japonicus*) in southern Australia. Fish. Res. 110, 75–83. http://dx.doi.org/10.1016/j.fishres.2011.03.014.

Fernandes, L.D.D., Bonecker, S.L.C., Valentin, J.L., 2002. Dynamic of decapod crustacean larvae on the entrance of Guanabara Bay. Braz. Arch. Biol. Technol. 45 (4), 491–498.

Fowler, A.M., Smith, S., Booth, D.J., Stewart, J., 2016. Partial migration of grey mullet (*Mugil cephalus*) on Australia's east coast revealed by otolith chemistry. Mar. Environ. Res. 119, 238–244. http://dx.doi.org/10.1016/j.marenvres.2016.06.010.

Freshwater, C., Trudel, M., Beacham, T.D., Neville, C.E., Tucker, S., Juanes, F., 2015. Validation of daily increments and a marine-entry check in the otoliths of sockeye salmon *Oncorhynchus nerka* post-smolts. J. Fish Biol. 87, 169–178. http://dx.doi.org/10.1111/jfb.12688.

Guerrero, R.A., Acha, E.M., Framiñan, M.B., Lasta, C.A., 1997. Physical oceanography of the Río de la Plata Estuary, Argentina. Cont. Shelf Res. 17, 727–742. http://dx.doi.org/10.1016/S0278-4343(96)00061-1.

Guerrero, R., Piola, A., Molinari, G., Osiroff, A., 2010. Climatología de temperatura y salinidad en el Río de la Plata y su Frente Marítimo, Argentina-Uruguay. Mar del Plata, Argentina .

Hamer, P.a., Jenkins, G.P., Coutin, P., 2006. Barium variation in *Pagrus auratus* (Sparidae) otoliths: a potential indicator of migration between an embayment and ocean waters in south-eastern Australia. Estuar. Coast. Shelf Sci. 68, 686–702. http://dx.doi.org/10.1016/j.ecss.2006.03.017.

Hamer, P., Henderson, A., Hutchison, M., Kemp, J., Green, C., Feutry, P., 2015. Atypical correlation of otolith strontium: calcium and barium: calcium across a marine-freshwater life history transition of a diadromous fish. Mar. Freshwater Res. 66, 411–419. http://dx.doi.org/10.1071/MF14001.

Hedger, R.D., Atkinson, P.M., Thibault, I., Dodson, J.J., 2008. A quantitative approach for classifying fish otolith strontium: calcium sequences into environmental histories. Ecol. Inform. 3, 207–217. http://dx.doi.org/10.1016/j.ecoinf.2008.04.001.

Hegg, J.C., Giarrizzo, T., Kennedy, B.P., 2015. Diverse early life-history strategies in migratory Amazonian catfish: implications for conservation and management. PLoS One 10, e0129697. http://dx.doi.org/10.1371/journal.pone.0129697.

IBAMA, 2009. Desembarque de pescados no Rio Grande do Sul. Annual Report. Centro de Pesquisa do Rio Grande, RS, Brasil.

Jochum, K.P., Weis, U., Stoll, B., Kuzmin, D., Yang, Q., Raczek, I., Jacob, D.E., Stracke, A., Birbaum, K., Frick, D.A., Günther, D., Enzweiler, J., 2011. Determination of reference values for NIST SRM 610-617 glasses following ISO guidelines. Geostand. Geoanal. Res. 35, 397–429. http://dx.doi.org/10.1111/j.1751-908X.2011.00120.x.

Jochum, K.P., Scholz, D., Stoll, B., Weis, U., Wilson, S.A., Yang, Q., Schwalb, A., Börner, N., Jacob, D.E., Andreae, M.O., 2012. Accurate trace element analysis of speleothems and biogenic calcium carbonates by LA-ICP-MS. Chem. Geol. 318–319, 31–44. http://dx.doi.org/10.1016/j.chemgeo.2012.05.009.

Kalish, J.M., 1991. Determinants of otolith chemistry: seasonal variation in the composition of blood plasma, endolymph and otoliths of bearded rock cod *Pseudophycis barbatus*. Mar. Ecol. Prog. Ser. 74, 137–159. http://dx.doi.org/10.3354/meps075137.

Kanai, T., Nanjo, K., Yamane, K., Amano, Y., Kohno, H., Watanabe, Y., Sano, M., 2014. Utilization patterns of estuarine and marine habitats by the halfbeak *Zenarchopterus dunckeri* at Iriomote Island, southern Japan, evaluated from otolith microchemistry. Fish. Sci. 80, 1231–1239. http://dx.doi.org/10.1007/s12562-014-0797-8.

Kissinger, B.C., Gantner, N., Anderson, W.G., Gillis, D.M., Halden, N.M., Harwood, L.A., Reist, J.D., 2016. Brackish-water residency and semi-anadromy in Arctic lake trout (*Salvelinus namaycush*) inferred from otolith microchemistry. J. Great Lakes Res. 42, 267–275. http://dx.doi.org/10.1016/j.jglr.2015.05.016.

Kjerfve, B., Ribeiro, C.H.A., Dias, G.T.M., Filippo, A.M., Da Silva Quaresma, V., 1997. Oceanographic characteristics of an impacted coastal bay: Baía de Guanabara, Rio de Janeiro, Brazil. Cont. Shelf Res. 17, 1609–1643. http://dx.doi.org/10.1016/S0278-4343(97)00028-9.

López, R., Bellisio, N., 1965. Contribución al conocimiento del *Tachysurus barbus* (Lacepede), bagre del mar argentino (Pisces. Ariidae), in: Anais Do Segundo Congreso Latino-Americano de Zoología. Sao Paulo, Brazil, pp. 145–153.

Lana, P.C., Marone, E., Lopes, R.M., Machado, E.C., 2001. The subtropical estuarine complex of Paranaguá Bay, Brazil. Ecol. Stud. 144, 131–145. http://dx.doi.org/10.1007/978-3-662-04482-7_11.

Lea, D.W., Shen, G.T., Boyle, E.A., 1989. Coralline barium records temporal variability in equatorial Pacific upwelling. Nature 340, 373–376. http://dx.doi.org/10.1038/340373a0.

Li, Y.H., Chan, L.H., 1979. Desorption of Ba and 226Ra from river-borne sediments in the Hudson estuary. Earth Planet. Sci. Lett. 43, 343–350. http://dx.doi.org/10.1016/0012-821X(79)90089-X.

Lin, S.H., Chang, C.W., Iizuka, Y., Tzeng, W.N., 2007. Salinities, not diets, affect strontium/calcium ratios in otoliths of *Anguilla japonica*. J. Exp. Mar. Bio. Ecol. 341, 254–263. http://dx.doi.org/10.1016/j.jembe.2006.10.025.

Lin, Y.J., Jessop, B.M., Weyl, O.L.F., Iizuka, Y., Lin, S.H., Tzeng, W.N., 2014. Migratory history of African longfinned eel *Anguilla mossambica* from Maningory River, Madagascar: discovery of a unique pattern in otolith Sr:Ca ratios. Environ. Biol. Fish. 98, 457–468. http://dx.doi.org/10.1007/s10641-014-0275-2.

Longerich, H.P., Jackson, S.E., Günther, D., 1996. Laser ablation inductively coupled plasma mass spectrometric transient signal data acquisition and analyte concentration calculation. J. Anal. At. Spectrom. 11, 899–904. http://dx.doi.org/10.1039/JA9961100899.

Lucas, M.C., Baras, E., Thom, T.J., 2001. Migration of Freshwater Fishes. Blackwell Science Ltd, London, United Kingdom.

Möller, O.O., Piola, A.R., Freitas, A.C., Campos, E.J.D., 2008. The effects of river discharge and seasonal winds on the shelf off southeastern South America. Cont. Shelf Res. 28, 1607–1624. http://dx.doi.org/10.1016/j.csr.2008.03.012.

MINAGRO, 2016. Subsecretaría de Pesca y Acuicultura, Argentina.M inisterio de Agroindustria. Available from: http://www.minagri.gob.ar/site/pesca/index.php.

MMA, 2014. Ministério do Meio Ambiente do Brasil. Portarias Nos. 443, 444, 445, de 17 de Dezembro de 2014, Diário Oficial da União. Ministério do Meio Ambiente, Brasilia.

Macdonald, J.I., Crook, D.A., 2010. Variability in Sr:Ca and Ba:Ca ratios in water and fish otoliths across an estuarine salinity gradient. Mar. Ecol. Prog. Ser. 413, 147–161. http://dx.doi.org/10.3354/meps08703.

Mai, A.C.G., Condini, M.V., Albuquerque, C.Q., Loebmann, D., Saint'Pierre, T.D., Miekeley, N., Vieira, J.P., 2014. High plasticity in habitat use of *Lycengrawulis grossidens* (Clupeiformes, Engraulididae). Estuar. Coast. Shelf Sci. 141, 17–25. http://dx.doi.org/10.1016/j.ecss.2014.01.014.

Martin, G.B., Thorrold, S.R., 2005. Temperature and salinity effects on magnesium, manganese, and barium incorporation in otoliths of larval and early juvenile spot *Leiostomus xanthurus*. Mar. Ecol. Prog. Ser. 293, 223–232. http://dx.doi.org/10.3354/meps293223.

Martin, G.B., Wuenschel, M.J., 2006. Effect of temperature and salinity on otolith element incorporation in juvenile gray snapper Lutjanus griseus. Mar. Ecol. Prog. Ser. 324, 229–239. http://dx.doi.org/10.3354/meps324229.

Martin, G.B., Thorrold, S.R., Jones, C.M., 2004. Temperature and salinity effects on strontium incorporation in otoliths of larval spot (*Leiostomus xanthurus*). Can. J. Fish. Aquat. Sci. 61, 34–42. http://dx.doi.org/10.1139/F03-143.

McDowall, R.M., 1988. Diadromy in Fishes: Migrations Between Freshwater and Marine Environments. Croom Helm, London.

McDowall, R.M., 2001. Anadromy and homing: two life-history traits with adaptive synergies in salmonid fishes? Fish Fish. 2, 78–85. http://dx.doi.org/10.1046/j.1467-2979.2001.00036.x.

McDowall, R.M., 2007. On amphidromy, a distinct form of diadromy in aquatic organisms. Fish Fish. 8 (1), 1–13. http://dx.doi.org/10.1111/j.1467-2979.2007.00232.x.

Mendoza-Carranza, M., Vieira, J.P., 2008. Ontogenetic niche feeding partitioning in juvenile of white sea catfish *Genidens barbus* in estuarine environments, southern Brazil. J. Mar. Biol. Assoc. U. K. 89, 839. http://dx.doi.org/10.1017/S0025315408002403.

Miles, N.G., Walsh, C.T., Butler, G., Ueda, H., West, R.J., 2014. Australian diadromous fishes – challenges and solutions for understanding migrations in the 21st century. Mar. Freshwater Res. 65, 12–24. http://dx.doi.org/10.1071/MF12340.

Miller, J.A., 2009. The effects of temperature and water concentration on the otolith incorporation of barium and manganese in black rockfish Sebastes melanops. J. Fish Biol. 75, 39–60. http://dx.doi.org/10.1111/j.1095-8649.2009.02262.x.

Miller, J.A., 2011. Effects of water temperature and barium concentration on otolith composition along a salinity gradient: implications for migratory reconstructions. J. Exp. Mar. Bio. Ecol. 405, 42–52. http://dx.doi.org/10.1016/j.jembe.2011.05.017.

Morales-Nin, B., Geffen, A.J., Pérez-Mayol, S., Palmer, M., González-Quirós, R., Grau, A., 2012. Seasonal and ontogenic migrations of meagre (*Argyrosomus regius*) determined by otolith geochemical signatures. Fish. Res. 127–128, 154–165. http://dx.doi.org/10.1016/j.fishres.2012.02.012.

Morales-Nin, B., Pérez-Mayol, S., Palmer, M., Geffen, A.J., 2014. Coping with connectivity between populations of *Merluccius merluccius*: An elusive topic. J. Mar. Syst. 138, 211–219. http://dx.doi.org/10.1016/j.jmarsys.2014.04.009.

Muxagata, E., Amaral, W.J.a., Barbosa, C.N., 2012. Acartia tonsa production in the Patos Lagoon estuary, Brazil. ICES J. Mar. Sci. 69, 475–482. http://dx.doi.org/10.1093/icesjms/fsr166.

Panfili, J., Darnaude, A.M., Lin, Y.J., Chevalley, M., Iizuka, Y., Tzeng, W.N., Crivelli, A.J.,

2012. Habitat residence during continental life of the European eel *Anguilla anguilla* investigated using linear discriminant analysis applied to otolith Sr:Ca ratios. Aquat. Biol. 15, 175–185. http://dx.doi.org/10.3354/ab00414.

Paton, C., Hellstrom, J., Paul, B., Woodhead, J., Hergt, J., 2011. Iolite: freeware for the visualisation and processing of mass spectrometric data. J. Anal. At. Spectrom. 26, 2508. http://dx.doi.org/10.1039/c1ja10172b.

Pearce, N.J.G., Perkins, W.T., Westgate, J.A., Gorton, M.P., Jackson, S.E., Neal, C.R., Chenery, S.P., 1997. A compilation of new and published major and trace element data for NIST SRM 610 and NIST SRM 612 glass reference materials. Geostand. Newsl. 21, 115–144. http://dx.doi.org/10.1111/j.1751-908X.1997.tb00538.x.

Pereyra, P.E.R., Mont'Alverne, R., Garcia, A.M., 2016. Carbon primary sources and estuarine habitat use by two congeneric ariid catfishes in a subtropical coastal lagoon. Zool 33, 1–7. http://dx.doi.org/10.1590/S1984-4689zool-20150075.

Phung, A.T., Tulp, I., Baeyens, W., Elskens, M., Leermakers, M., Gao, Y., 2015. Migration of diadromous and landlocked smelt populations studied by otolith geochemistry. Fish. Res. 167, 123–131. http://dx.doi.org/10.1016/j.fishres.2015.02.004.

Piola, A.R., Romero, S.I., 2004. Analysis of space-time variability of the plata river plume. Gayana (Concepción) 68, 482–486. http://dx.doi.org/10.4067/10.4067/S0717-65382004000300030.

Piola, A.R., Romero, S.I., Zajaczkovski, U., Grande, M., 2008. Space-time variability of the Plata plume inferred from ocean color. Cont. Shelf Res. 28 (13), 1556–1567.

Potter, I.C., Tweedley, J.R., Elliott, M., Whitfield, A.K., 2015a. The ways in which fish use estuaries: a refinement and expansion of the guild approach. Fish Fish. 16, 230–239. http://dx.doi.org/10.1111/faf.12050.

Potter, I.C., Tweedley, J.R., Elliott, M., Whitfield, A.K., 2015b. The ways in which fish use estuaries a refinement and expansion of the guild approach. Fish Fish. 16, 230–239. http://dx.doi.org/10.1071/MF16058.

Radtke, R., Shafer, D., 1992. Environmental sensitivity of fish Otolith Microchemistry. Mar. Freshw. Res. 43 (5), 935–951. http://dx.doi.org/10.1071/MF9920935.

Reis, E.G., 1986a. Age and growth of the marine catfish, *Netuma barba* (Siluriformes, Ariidae), in the estuary of the Patos Lagoon (Brasil). Fish. Bull. 84, 679–686.

Reis, E.G., 1986b. Reproduction and feeding habits of the marine catfish, *Netuma barba* (Siluriformes, Ariidae), in the estuary of the Patos Lagoon (Brazil). Atlantica 8, 35–55.

Rohtla, M., Vetemaa, M., Taal, I., Svirgsden, R., Urtson, K., Saks, L., Verliin, A., Kesler, M., Saat, T., 2014. Life history of anadromous burbot (*Lota lota*, Linneaus) in the brackish Baltic Sea inferred from otolith microchemistry. Ecol. Freshwater Fish 23, 141–148. http://dx.doi.org/10.1111/eff.12057.

Schuchert, P.C., Arkhipkin, A.I., Koenig, A.E., 2010. Traveling around Cape Horn: otolith chemistry reveals a mixed stock of *Patagonian hoki* with separate Atlantic and Pacific spawning grounds. Fish. Res. 102, 80–86. http://dx.doi.org/10.1016/j.fishres.2009.10.012.

Secor, D.H., Rooker, J.R., 2000. Is otolith strontium a useful scalar of life cycles in estuarine fishes? Fish. Res. 46, 359–371. http://dx.doi.org/10.1016/S0165-7836(00)00159-4.

Seeliger, U., Odebrecht, C., Castello, J.P., 1997. Subtropical convergence environments: the coast and sea, in: The Southwestern Atlantic. p. 308.

Shrimpton, J.M., Warren, K.D., Todd, N.L., Mcrae, C.J., Glova, G.J., Telmer, K.H., Clarke, A.D., 2014. Freshwater movement patterns by juvenile Pacific salmon *Oncorhynchus* spp. before they migrate to the ocean: oh the places you'll go!. J. Fish Biol. 85, 987–1004. http://dx.doi.org/10.1111/jfb.12468.

Sinclair, D.J., Kinsley, L.P.J., McCulloch, M.T., 1998. High resolution analysis of trace elements in corals by laser ablation ICP-MS. Geochim. Cosmochim. Acta 62, 1889–1901. http://dx.doi.org/10.1016/S0016-7037(98)00112-4.

Smith, W.E., Kwak, T.J., 2014. Otolith microchemistry of tropical diadromous fishes: spatial and migratory dynamics. J. Fish Biol. 84, 913–928. http://dx.doi.org/10.1111/jfb.12317.

Sturrock, A.M., Trueman, C.N., Darnaude, A.M., Hunter, E., 2012. Can otolith elemental chemistry retrospectively track migrations in fully marine fishes? J. Fish Biol. 81, 766–795. http://dx.doi.org/10.1111/j.1095-8649.2012.03372.x.

Sturrock, A.M., Trueman, C.N., Milton, J.A., Waring, C.P., Cooper, M.J., Hunter, E., 2014. Physiological influences can outweigh environmental signals in otolith microchemistry research. Mar. Ecol. Prog. Ser. 500, 245–264. http://dx.doi.org/10.3354/meps10699.

Tabouret, H., Bareille, G., Claverie, F., Pécheyran, C., Prouzet, P., Donard, O.F.X., 2010. Simultaneous use of strontium:calcium and barium:calcium ratios in otoliths as markers of habitat: application to the European eel (*Anguilla anguilla*) in the Adour basin, South West France. Mar. Environ. Res. 70, 35–45. http://dx.doi.org/10.1016/j.marenvres.2010.02.006.

Tabouret, H., Lord, C., Bareille, G., Pécheyran, C., Monti, D., Keith, P., 2011. Otolith microchemistry in Sicydium punctatum: indices of environmental condition changes after recruitment. Aquat. Living Resour. 24, 369–378. http://dx.doi.org/10.1051/alr/2011137.

Tavares, L.E., Luque, J.L., 2004. Community ecology of the metazoan parasites of white sea catfish, Netuma barba (Osteichthyes: Ariidae), from the coastal zone of the state of Rio De Janeiro, Brazil. Braz. J. Biol. 64, 169–176. http://dx.doi.org/10.1590/s1519-69842004000100019.

Taylor, W., 2000. Change-Point Analyzer 2.0 Shareware Program. Taylor Enterprises, Libertyville, Illinois.

Thibault, I., Dodson, J.J., Caron, F., Tzeng, W.N., Iizuka, Y., Shiao, J.C., 2007. Facultative catadromy in American eels: testing the conditional strategy hypothesis. Mar. Ecol. Prog. Ser. 344, 219–229. http://dx.doi.org/10.3354/meps06944.

Velasco, G., Reis, E., 2004. Changes in growth seasonality throughout *Netuma barba* (Lacépède, 1803) (Siluriformes, ariidae) ontogeny. Braz. J. Biol. 64, 913–914.

Velasco, G., Reis, E.G., Vieira, J.P., 2007. Calculating growth parameters of *Genidens barbus* (Siluriformes, Ariidae) using length composition and age data. J. Appl. Ichthyol. 23, 64–69. http://dx.doi.org/10.1111/j.1439-0426.2006.00793.x.

Vieira, J.P., 2006. Ecological analogies between estuarine bottom trawl fish assemblages from Patos Lagoon, Rio Grande do Sul, Brazil and York River, Virginia, USA. Rev. Bras. Zool. 23, 234–247. http://dx.doi.org/10.1109/CEFC-06.2006.1633024.

Walther, B.D., Thorrold, S.R., 2006. Water, not food, contributes the majority of strontium and barium deposited in the otoliths of a marine fish. Mar. Ecol. Prog. Ser. 311, 125–130. http://dx.doi.org/10.3354/meps311125.

Walther, B.D., Dempster, T., Letnic, M., McCulloch, M.T., 2011. Movements of diadromous fish in large unregulated tropical rivers inferred from geochemical tracers. PLoS One 6, e18351. http://dx.doi.org/10.1371/journal.pone.0018351.

Wynne, L.M.P., Wilson, K.A., Limburg, K.E., 2015. Retrospective examination of habitat use by blueback herring (*Alosa aestivalis*) using otolith microchemical methods. Can. J. Fish. Aquat. Sci. 72, 1073–1086. http://dx.doi.org/10.1139/cjfas-2014-0206.

Yoshinaga, J., Nakama, A., Morita, M., Edmonds, J.S., 2000. Fish otolith reference material for quality assurance of chemical analyses. Mar. Chem. 69, 91–97. http://dx.doi.org/10.1016/S0304-4203(99)00098-5.

Zlokovitz, E.R., Secor, D.H., Piccoli, P.M., 2003. Patterns of migration in Hudson River striped bass as determined by otolith microchemistry. Fish. Res. 63, 245–259. http://dx.doi.org/10.1016/S0165-7836(03)00069-9.

da Silva, D.R., Paranhos, R., Vianna, M., 2016. Spatial patterns of distribution and the influence of seasonal and abiotic factors on demersal ichthyofauna in an estuarine tropical bay. J. Fish Biol. 89, 821–846. http://dx.doi.org/10.1111/jfb.13033.