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Age and growth of *Prochilodus lineatus* in a spatially structured population: is there concordance between otoliths and scales?

H. S. de Santana · C. V. Minte-Vera

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Abstract To better understand the ecology and biology of the curimba in the Paraná River and to provide basic information for fisheries stock assessment, this study address the following questions: Do age estimates derived from otoliths and scale agree for *Prochilodus lineatus*? What is the growth trajectory for curimba in the upper Paraná River? What is the age structure of the population in the upper Paraná River? Is there any evidence of spatial stratification in population age structure or growth? Fish were sampled in the Paraná, Ivinhema and Baia Rivers and in the Itaipu reservoir from 2012 to 2013. The otoliths showed one to eight annuli and the scales had one to six circuli. The agreement between the otoliths was higher (about 80%) than between the scales (about 70%). The agreement between otolith and scale readings was significantly low (about 40%). Using a von Bertallanfy growth function, the asymptotic standard length (L_{∞}) for the whole population was estimated to be 68.84 cm, the growth coefficient (K) was estimated to be 0.15 year^{-1} and t_0 was assumed to be 0 year. There was substantial variation in length-at-age in most but the youngest ages, in the intermediate ages there was a mix of individuals from various locations with markedly different growth rates. Our data also suggest a recruitment failure in 2012 and 2013, due to the lack to flooding, which also caused lack of habitat connectivity.

Keywords Age precision · von Bertalanffy · Migratory fish · Variability in growth · Lapillus

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Introduction

Determining the age of fish is a challenge for scientists. The main methods used are the analysis of length frequencies (Pauly and David 1981; Megalofonou 2006; Morgan et al. 2007) and the examination of marks formed periodically in calcified structures (Wright et al. 2002; Farley et al. 2013). In temperate climates the main factor regulating the formation of annual age rings in calcified structures is temperature (Santos and Barbieri 1993). However, in Neotropical regions, where the temperature variations are smaller, the growth rings are also formed with a consistent periodicity, thus other factors may be responsible for driving their formation (Barbieri et al. 2001; Ambrósio et al. 2003; Cutrim and Batista 2005).

Age and growth studies are key to modern stock assessments (e.g., Methot and Wetzel 2013). Ecological studies of population dynamics, fishery management and stock assessment depend on knowing the age structure of the population. The criteria used by the International Union for the Conservation of Nature (generation time, longevity and natural mortality rates) to categorize a species according to its conservation state also depend directly on age estimates (IUCN 2003). These criteria have been used by the Brazilian government to assess fish species and ultimately to guide decisions related to the conservation of the species. The trade-off between practicality and usefulness of otoliths and scales for age and growth studies has immediate and direct implications. The choice of an inappropriate structure can result in bias in the biological, ecological and fishery inferences and subsequent erroneous decisions when managing fisheries resources or taking conservation actions.

Several authors confirm the usefulness of otoliths as tools for ecological studies due to their continuous growth over time and lack of resorption as well as the periodicity of the annuli formation (Fitch and Brownell 1968; Gillanders and Kingsford 1996; Campana and Thorrold 2001; Pontual et al. 2003; Reichenbacher et al. 2007; Sponaugle 2010). Otoliths, however, require costly sample schemes and equipment and often involve extensive preparation (e.g., dissecting, mounting, grinding, and cutting) by a trained technician.

In South America, most freshwater fish age-and-growth studies are performed using scales (Dei Tos et al. 2010) because of their low sampling cost, relative ease of preparation, lack of requirement for expensive equipment, and no need for sacrificing the fish (Megalofonou et al. 2003; Silva and Stewart 2006). The reliability of the interpretation of circuli in scales as annuli, however, is questionable because of frequent formation of "false" circuli, regeneration, deformities, and resorption (Martins et al. 2009; Chang and Maunder 2012; Liao et al. 2013).

The curimba (or sábalo) *Prochilodus lineatus* (Valenciennes, 1836) is a characteristic South American species that undergoes long migrations to reach the reproductive areas in the floodplains (Sivasundar et al. 2001; Antonio et al. 2007). Despite their ecological and economic importance (Melo et al. 2016), populations of this species experience fishing mortality and habitat losses due to construction of reservoir dams, which lead to modifications in water quality, disruption of migratory routes and blocking of access to spawning and nursery grounds (Agostinho et al. 2007; Barletta et al. 2010).

The age structure and growth of this species were previously examined for populations in Argentina (Carozza and Cordiviola de Yuan 1991; Araya and Sverlij 1999; Baigún et al. 2013) and in the Paraná River, in Brazil (Lizama 2000; Angelini and Agostinho 2005). Most of these studies used scales or length-frequency data (but see Espinach Ros et al. 2012) despite the evidence that using the otolith for growth studies is advantageous (Campana 2001; Campana and Thorrold 2001). In order to better understand the ecology and biology of the curimba in the Paraná River and to provide basic information for fisheries stock assessment, this study addresses the following questions: Do age estimates derived from otoliths and scales agree for a tropical freshwater species, *Prochilodus lineatus*? What is the growth trajectory for for curimba in the upper Paraná River? What is the age structure of the population in the upper Paraná River? Is there any evidence of spatial stratification in population age structure or growth?

Material and methods

Study area

The Paraná River is among the ten largest rivers in the world in water discharge and ranks fourth in drainage area. It plays a key role in the drainage of the entire south-central South America (Agostinho et al. 2000). The Paraná River floodplain (Fig. 1) is currently the only free stretch of the Paraná River in Brazil, its length is 230 km and its maximum width is 20 km. The river in the floodplain stretch anastomoses on multiple channels, lagoons and smaller rivers, such as the Baia and Ivinhema (Agostinho and Zalewski 1996). The floodplain is bounded downstream by the 1350 km^2 Itaipu Reservoir (24 ° 05 ′–25 ° 33′S; 54 ° 00 ′–54 ° 37′W), which was closed in 1982 on the border between Brazil and Paraguay (Agostinho et al. 1999).

Sampling

To compare otolith and scales, fish were sampled during four periods and at nine sampling sites (September and December 2012; March and June 2013) in the High Paraná River floodplain, including its main tributaries (Baia and Ivinhema Rivers), using experimental fishing with 11 different gillnet mesh sizes (24, 34, 40, 50, 60, 70, 80, 100, 120, 140 and 160 mm between opposite knots). Each gillnet remained in the water for 24 h at each sample site and was revisited every eight hours. Additionally, in the lakes associated with each subsystem, trawls were conducted.

Specimens were also sampled for otoliths from landing of the artisanal fisheries in the Itaipu reservoir. This

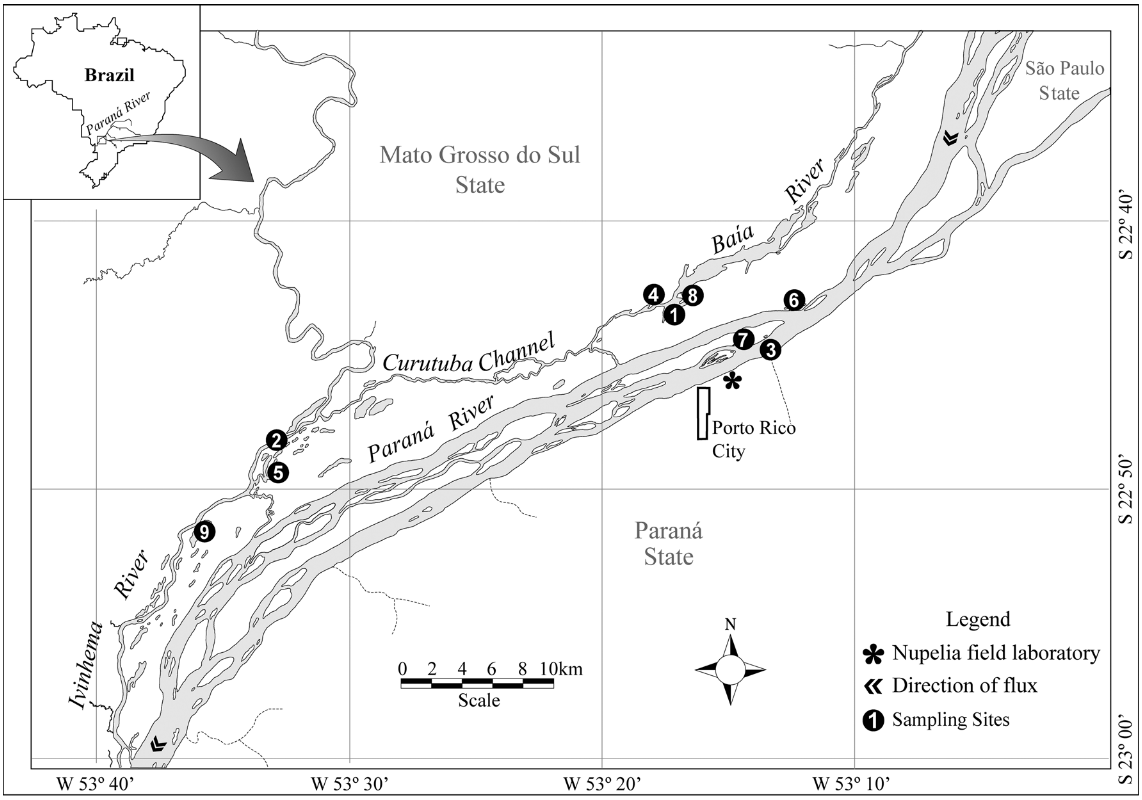


Fig. 1 Study area and location of sampling sites in the floodplain of the Upper Paraná River. (Baía River—1; Ivinhema River—2; Paraná River—3; Guaraná Lagoon—4; Patos Lagoon—5; Garças Lagoon—6; Ressaco do Pau Veio Lagoon—7; Fechada Lagoon—8; Ventura Lagoon—9

sampling was done to capture larger (and possibly older) individuals (Agostinho et al. 1993) and better represent the size distribution and age of the population. Since scales were not taken on samples from the Itaipu Reservoir, growth was assessed using otolith readings only.

The lapilli were removed from 467 individuals collected, and scales were collected from 317 specimens. The extraction of the otoliths and scales was performed in the field after the fish were identified, measured and weighed. The standard length (SL) was measured to the nearest 0.1 mm, and the total weight (TW) was measured to the nearest 0.1 g. To extract the otolith, a transverse cross section was made on the dorsal surface of the fish's head. In the laboratory, the right otolith of each individual was embedded in epoxy resin and cut using a low speed saw with a diamond Buehler® disc. About three cross sections of 0.27 mm thickness were made in each otolith, subsequently the sections were polished and fixed to microscope slides. The otoliths were later read under a microscope stereoscope at a 40× increase (Fig. 2). The scales were prepared according to Vazzoler (1982). The scales were collected in the axial region of the pectoral fin (location with good quality scales for being protected by the fin; also the probability of loss and replacement of scales located in this region is low.). All scales collected for each specimen were inspected for signs of regeneration, scratches, deformities or any changes that made it difficult to view the circuli. Three to five scales were selected to be prepared as follows: each scale was immersed for 5 min in a Potassium Hydroxide 4% (KOH) solution for removal of dirt and mucus, then it was immersed in water to remove excess KOH and finally it was bathed in 10% phenol to prevent the proliferation of fungi and microorganisms. The scales were subsequently dried and mounted on microscope slides for later reading stereoscope microscope at magnification 10× (Fig. 2). Two independent readings were performed for each structure by the same reader (HSS). The readings were done "blindly", i.e. with no access to any information about the location and date of the sampling, or weight and length of the fish.

Data analysis

The age estimates were plotted to assess age bias between readings of the same structure and between otoliths and scales (e.g., Campana et al. 1995). Also, tests for symmetry and precision were performed (Hoenig et al. 1995). Random ageing errors are expected to produce a symmetrical matrix, with the main diagonal indicating the number of specimens for which there was perfect agreement between readings and the off diagonal showing the disagreements, which are likely to fall into either side. The significance values for tests of symmetry were obtained by means of Bowker's symmetry test (Bowker 1948). How far the counts will spread will depend on the precisions of the readings. The precision of the readings was assessed using Average Percentage Error (APE) calculated as follows:

$$APE = \frac{1}{n}\sum_{j=1}^{n}\left[\frac{1}{r}\sum_{i=1}^{r}\left[\frac{|X_{i,j}-X_j|}{X_j}\right]\right] \quad (1)$$

where n = number of otoliths or scales, r = number of readings, X_{ij} = number of rings in the otolith or scale *j* in the reading *i* and X_j = average number of rings for the otolith or scale *j* in the *r* readings.

The periodicity of annuli/circuli formation for both otoliths and scales was evaluated using marginal increment analysis, which is an indirect method that compares the last fully formed annuli and the last developing annuli as follows:

$$IM = (R_t - R_i)/(R_i - R_j) \quad (2)$$

where R_t = total radius, R_i = radius of the last ring and R_j = radius of the penultimate ring. The period of ring formation is indicated by the marginal increment values and occurs in periods when these values are close to zero.

In order to investigate possible differences in growth rates among locations (Baia, Ivinhema, Paraná and Itaipu), the length-at-age was back-calculated for all specimens using Campana's (1990) method. This is a biological intercept method that uses two values: L_o, fish length when body growth is proportional to otolith growth, and O_o, otolith length when otolith growth is proportional to the fish growth. The back-calculated length is estimated using Eq. 3:

$$BCL_i = L_c + (L_c - L_o)(O_i - O_c)/(O_c - L_o) \quad (3)$$

where BCL_i = back-calculated length at age *i*, L_c = length of the fish, L_o = length of the fish when their growth is proportional to the otolith growth, O_i = otolith radius at age (ring) *i*, O_c = otolith radius and O_o = otolith length when their growth is proportional to the fish growth. The value used for L_o was 0 cm (because the otolith is formed in the early development of fish) and the value of O_o was 0.2 mm (Ogle and College 2013). The average length-at-age by location was computed from the back-calculated lengths. Sites with larger average size may offer better conditions for growth and development.

The growth parameters were estimated by fitting the von Bertalanffy growth curve using the least squares method:

$$L_t = L_\infty\left[1 - exp^{(-K*(t-t_0))}\right] \quad (4)$$

where L_t = length at age *t*, L_∞ = asymptotic length, K = growth coefficient, t = age and t_0 = theoretical age when length is equal to zero.

All analyses were performed using the R platform (R Core Team 2014) with the following packages: FSA, lattice and ggplot2. The significance level was $\alpha = 5\%$.

Results

The standard length of the 467 individuals in the sample ranged from 11 to 54 cm (Table 1, Fig. 3). The larger individual was sampled in the Itaipu reservoir (53.6 cm), while the smallest was sampled in the main channel of the Paraná River (11.1 cm). The readings of each structure were precise with low average percentage (APE) values. However, the otolith errors were systematically smaller than those of the scales (Table 2).

The proportions of each length class collected from 2009 to 2013 in the Upper Paraná River floodplain demonstrate that it is possible to follow the modal progression of lengths (Fig. 4). However, it is noted that from 2012 the predominant length class becomes almost static, indicating that the fish grow little from 2012 to 2013. This is also reflected in the similarity of the observed lengths of the fish three and 4 years of age estimated by both the otoliths, and through the scales. There was no recruitment in 2010–2013, and fish hatched in 2009 (only year with individuals under 10 cm) are represented in 2012 and 2013 as three and 4 year olds (Fig. 4), thus confirming estimated otolith age.

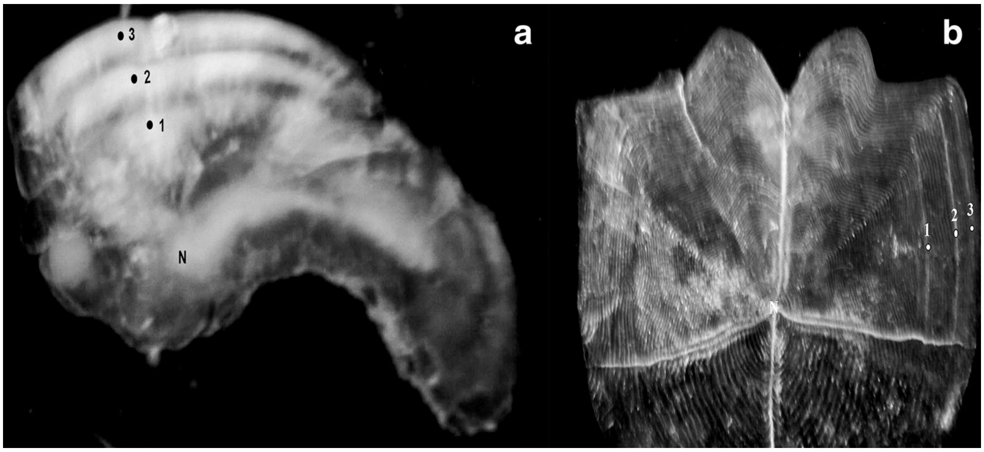


Fig. 2 Otolith (**a**) and scale (**b**) of the same individual of *Prochilodus lineatus*. The photos were taken under reflected light with the aid of a Scientific Digital Microscope Camera (model OPT5000 Power) and a stereoscopic microscope with magnification of 40× for the otolith and 10× for the scale

The otoliths showed one to eight annuli and the scales had one to six circuli (Table 1). The Paraná River had the widest age range (1 to 7 years), while Baia River had the narrower age range (three to five). There was high level of agreement between the two readings on each otoliths (Fig. 5) and precision between the two readings was inversely proportional to age. The two readings on the scales showed lower agreement but, like otoliths there were no significant differences between readings (attested by Bowker's Test) (Fig. 6). Low precision of age estimates derived from scales occurred in all ages classes.

The mean agreement between otoliths and scale readings for the same fish was only 41.28% (mean coefficient of variation = 10.81) (Table 2), this analysis was made using the mean between the two readings. This value includes both the variability due to reading (with is expected to be low) and the variability due to the type of structure. Most of the fish for which both otoliths and scales were readable showed three to four annuli in the otolith. Most of the three-annuli otoliths corresponded to three-circuli scales, but most of the four-annuli otoliths corresponded to three-circuli scales, indicating a bias (Fig. 7).

The frequency and period of formation of growth rings on the scales and otoliths were verified by marginal increment analysis. The smaller marginal increment values were in March and June for scales and otoliths, respectively, while the largest were in December (Fig. 8). This indicates that only one growth ring is formed every year, probably in the middle of the year, coinciding with winter, which is the coldest season.

The back-calculated lengths indicated that there were differences in the average length-at-age (and possibly in the growth rates) among locations. The oldest fish (8 years) was captured in Itaipu reservoir Age-1 fish, for example, were on average larger in Itaipu reservoir (25.10 cm ± 2.09 SD) than in the three locations within the floodplain (Baia River: mean = 21.66 cm; SD = 1.03, Ivinhema River: 22.16 ± 1.77 SD and Paraná River:

Table 1 Variation of standard length, number of otoliths and scales sampled, and range of ages for otoliths and scales for sampling location (Baia, Ivinhema, Paraná and Itaipu)

Location	Standard length range (cm)	Number of otoliths	Number of scales	Age range (Otoliths annuli)	Age range (Scales circuli)
Baia	13.2–29.5	142	138	3–5	1–5
Ivinhema	17.5–45.0	133	100	2–7	1–6
Paraná	11.1–40.0	80	79	1–7	1–5
Itaipu	28.8–53.6	112	0	3–8	[a]
Total	11.1–53.6	466	317	1–8	1–6

[a] Scales were not collected in Itaipu Reservoir

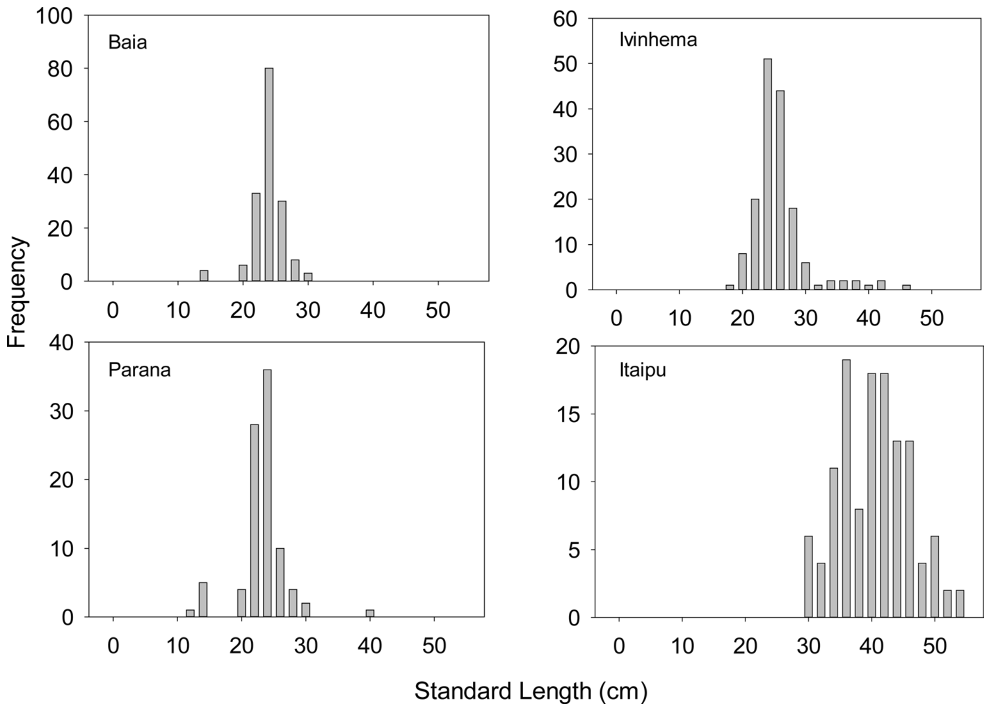


Fig. 3 Standard length frequency distributions for the *Prochilodus lineatus* collected in 2012 and 2013 in the Parana River, Ivinhema River, Baia River and Itaipu reservoir

21.35 ± 1.16 SD). In fact, the average length at age was larger in Itaipu reservoir for all age groups. Among the other locations, the Ivinhema River had the largest fish, with the exception of ages 5 and 6, which were larger in the Paraná River (Fig. 9).

The von Bertalanffy growth model was fit using the ages determined by otoliths. The asymptotic standard length (L_∞) was estimated to be 68.84 cm, the growth coefficient (K) was estimated to be 0.15 year^{-1} and t_0 was set to 0 (Fig. 9). There was substantial variation in length-at-age in most but the youngest ages, in the intermediate ages there was a mix of individuals from various locations with markedly different growth rates (Fig. 10).

Table 2 Percent agreement between the readings and average percentage error (APE) for otoliths, scales and otoliths *versus* scales

	Specimens (*n*)	Agreement (%)	APE (%)
Otoliths	467	84.15	2.20
Scales	317	72.24	4.54
Otoliths *versus* Scales[a]	281	41.28	7.64

[a] The Bowker's symmetry test showed that the contingency table is significantly asymmetric, thus there is a significant difference between otolith and scale readings

Discussion

For *Prochilodus lineatus*, we found significant differences between age estimates obtained through the scales and otoliths. Estimates of agreement and precision of the readings were higher for otolith than for scales, indicating that the growth rings are more easily distinguished in the otoliths. There was variability in age estimated by the scales due to difficulties associated with reading, especially for older fish. Our results are similar to those found by others. Kruse et al. (1997), for example, found no significant differences among readings for either otolith or scales in trout, but significant differences between the two structures as well as greater precision for otoliths readings.

Based on marginal increment analysis, we found evidence that only one ring is formed in *P. lineatus* otoliths and scales per year, and this formation occurs in the middle of the year, during the winter. Ring formation can be driven by many events, such as

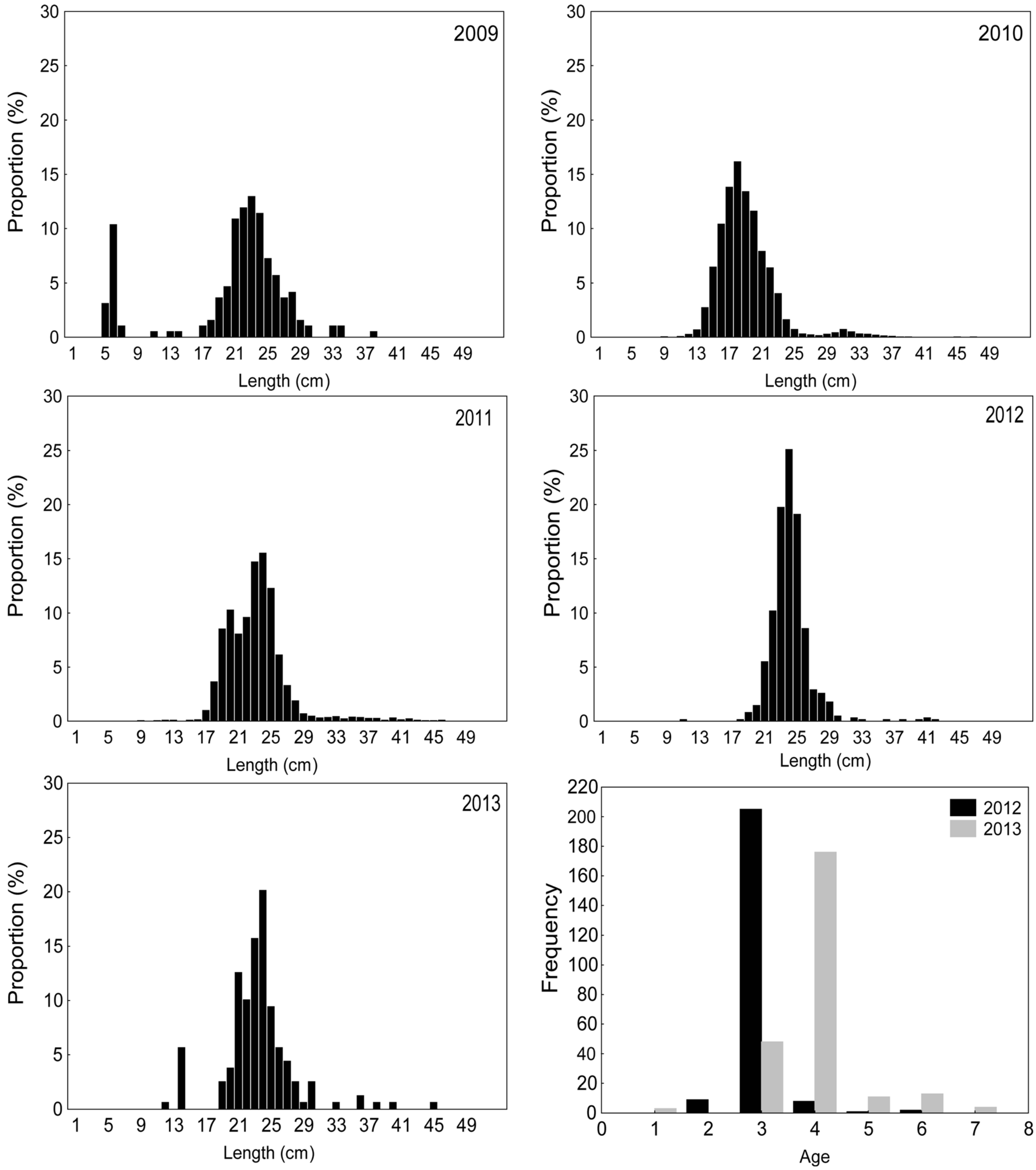


Fig. 4 Proportions of each length class collected from 2009 to 2013 in the Upper Paraná River floodplain (Parana, Baia and Ivinhema Rivers) and age distribution in 2012 and 2013 years

temperature variations, maturation, reproduction, migration, food and water level variations (Cailliet et al. 2001; Ambrósio et al. 2003). In tropical freshwater ecosystems, synergy exists between these factors, primarily water levels, reproduction and temperature (Santos and Barbieri 1993). Dei Tos et al. (2009) also found that scale circuli of the migratory fish dourado *Salminus brasiliensis* (Cuvier 1816) were formed during the winter. Although the marginal increment analysis produces reliable results regarding the period of annuli formation (Campana 2001), it is advisable that validation using direct methods such as chemical marks, mark-recapture studies or aging of known-age fishes be attempted to confirm the results (Francis et al. 2010).

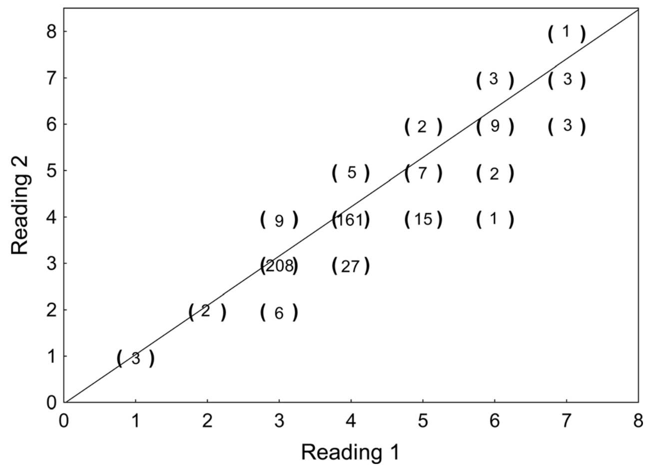


Fig. 5 Agreement between the first and second readings from the lapilli otoliths of *Prochilodus lineatus* in the High Parana River floodplain and Itaipu Reservoir. *Numbers in parentheses* indicate the number of observations on the respective ages

Otolith are known to have only mineral accretion and no reabsorption (e.g., Wright et al. 2002), while scales can show both false circuli and reabsorption (e.g., Khan and Khan 2009), so it is expected that otolith interpretation will be more accurate. Nonetheless, only direct validation can estimate the accuracy of the age estimations. A long-term study should be performed to assess the accuracy and, if possible, complete a tagging experiment where fish are measured and marked with tetracycline (e.g., Wild and Foreman 1980). Upon recapture, the fish need to be measured and otoliths and scales need to be extracted.

The growth parameters estimated in this study ($\hat{L}_\infty =$ 68.84 cm $\hat{K} = 0.15$ year $^{-1}$ and $\hat{t}_0 = 0$ year) differ from those obtained by other authors for the same species. Araya and Sverlij (1999) estimated the asymptotic length at 60 cm and the growth coefficient to be nearly 0.3 cm, whereas Lizama (2000) working with length frequencies in the High Paraná River estimated L_∞ to be 60 and the growth coefficient K to be 0.17 year^{-1}. Espinach Ros et al. (2012) estimated the asymptotic length of 47.5 cm for *P. lineatus* in Argentina, and Silva and Stewart (2006) using otoliths and scales estimated the L_∞ at 39.8 and 45.7 cm for *P. nigricans*, respectively. Espinach Ros et al. (2012) also discuss that sábalo does not grow continuously, so that there are phases of rapid growth and slow growth phases. The growth parameter estimates may have been influenced by the variability in length-at-age. The back-calculated lengths demonstrate that fish from the same habitat have minor variations in length-at-age, while individuals from different locations tend to large differences in length-at-age. This means that the habitat where the fish spends most of life exert strong influences on its length and growth rates. The mix of fish from different areas may influence the estimate of the growth parameters.

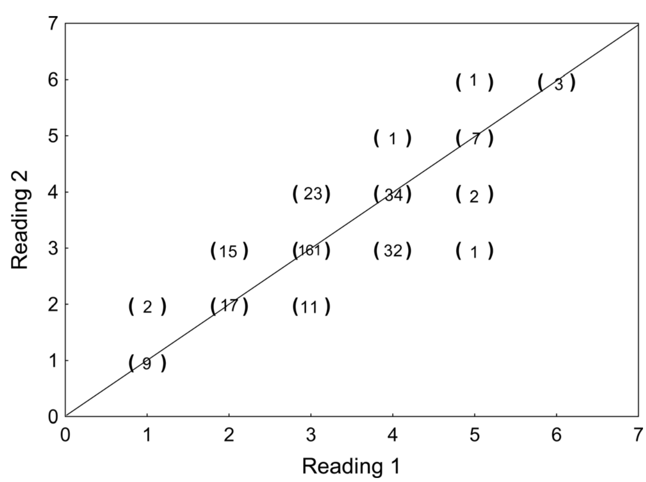


Fig. 6 Agreement between the first and second readings from the scales of *Prochilodus lineatus* in the High Parana River floodplain. *Numbers in parentheses* indicate the number of observations on the respective ages

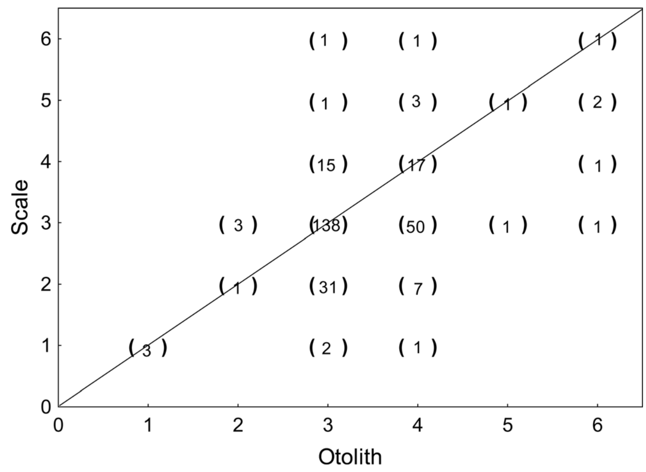


Fig. 7 Agreement between the otolith and scale readings of *Prochilodus lineatus* in the High Parana River floodplain. *Numbers in parentheses* indicate the number of observations on the respective ages

The differences in length-at-age among different locations can reflect habitat influences, as shown for other fish (Jackson et al. 2010; Lourenço et al. 2012). The habitat characteristics such as food, shelter and density of predators can influence growth patterns, especially for juveniles that are subject to higher pressures as competition and predation, as these individuals live in high densities, thus higher growth rates will occur in places that offer better conditions. Also, genetic diversity, stock separation or selectivity and fishing pressure are factors that may lead to differences in the length and age of individuals from different locations (McIlwain et al. 2005; Jackson et al. 2010).

The older fish were caught in the Ivinhema River and in the Itaipu reservoir. The Ivinhema River is protected by the Mato Grosso do Sul State as a State Park where no fishing is allowed. This area is also considered a nursery area, mainly for migratory species (Reynalte-Tataje et al. 2013), thus older animals might migrate there to spawn. The occurrence of older individuals in the Itaipu reservoir is attributed to the spatial stratification of the *P. lineatus*, it is known that the older individuals live in the main channel of the river and in the Itaipu reservoir, whereas the younger individuals live in the floodplain and associated areas (Agostinho et al. 1993). Itaipu reservoir is a feeding habitat for adult *P. lineatus* (Agostinho et al. 1993). Also, the migrations significantly influence the age structure of the population. This species migrates several hundreds of kilometers in the region, when older individuals leave their sites to reach the nursery areas and headwaters of rivers to spawn. Antonio et al. (2007) used mark and recapture data to demonstrate migrations of up to 300 km from the release site. During these migrations the fish mainly explored the tributaries, finding alternative migration routes due to the

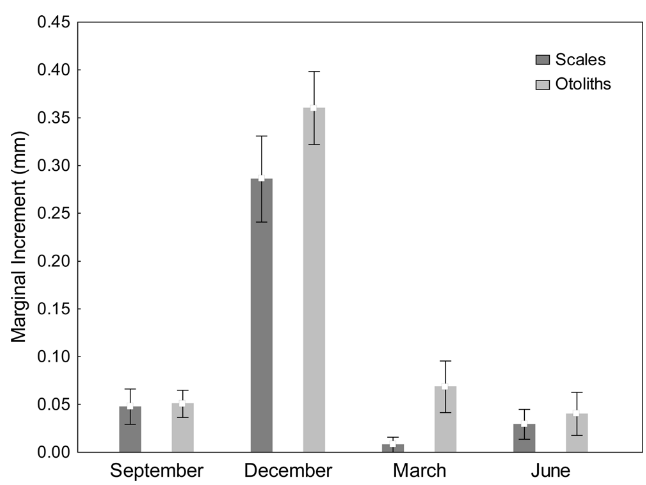
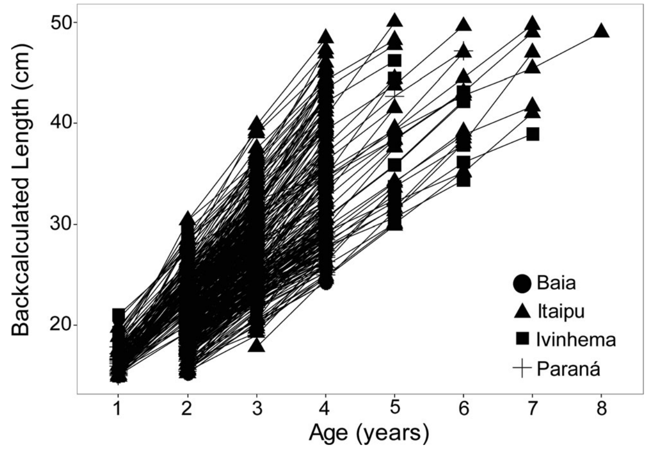


Fig. 8 Mean (± SD) of marginal increment obtained using otoliths and scales during September, December, Mach and June

Fig. 9 Back-calculated lengths-at-ages at each local (Baia, Ivinhema and Parana Rivers, and Itaipu reservoir)

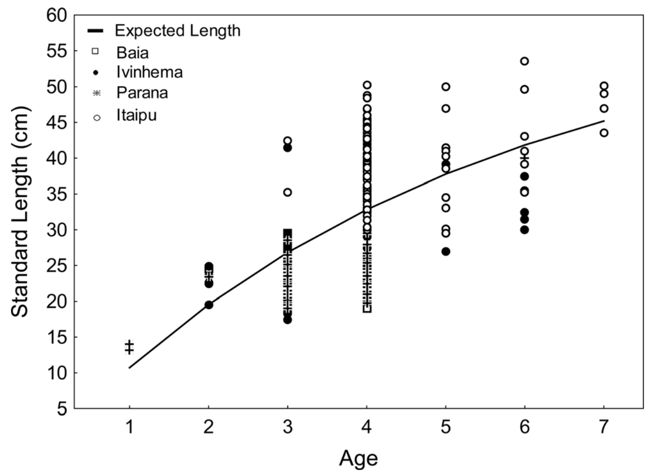


many existing dams along the Paraná River (e.g., Porto Primavera upstream).

Both migration and recruitment processes are directly influenced by water levels (Gomes and Agostinho 1997). The environmental conditions of the floodplain explain the smaller length-at-age for fish that were sampled in Baia and Ivinhema Rivers. The ecosystem functions of a floodplain depend on minimum water levels to establish connectivity with their lateral environments. The Paraná River requires a level of 3.5 m (as measured in the Porto Rico hydrological station) to overflow towards the floodplain (Thomaz et al. 2004). When the river overflows there are optimal conditions for strong recruitment and individual growth (Gomes and Agostinho 1997; Agostinho et al. 2004), but the Paraná River did not overflow in 2012 and 2013, the highest monthly water level average was 3.4 m in January. These conditions explain the absence of young fish in the samples and the slow growth of some individuals, mainly those in the Paraná and Baia Rivers.

Length and age frequencies in the years 2012 and 2013 indicate a failure in the recruitment of *P. lineatus*. Migratory species depend on water levels and suitable places for breeding and spawning. However, in years when there is no flooding, individuals in the lagoon cannot complete the migration due to the isolation of the lagoon. On the other hand, only individuals who are in the main channel of the river and in the Itaipu reservoir can migrate and complete the reproductive cycle. Mochek and Pavlov (1998) in Bolivia also found that not all individuals migrate, concluding that a portion of the population is resident and the other one portion completes the reproductive migration. This migration pattern could explain the slow growth of individuals living in the floodplain and fast growth of residing in the Itaipu reservoir.

Fig. 10 Growth curve of the *Prochilodus lineatus* estimated from the otolith readings ($\hat{L}\infty = 68.84$, $\hat{K} = 0.15$ and $\hat{t}_0 = 0$). *Solid line* represents the expected length-at-age



Our results support the importance of the tributaries and smaller rivers to the conservation of the species and the management of its fisheries because they contribute to the survival and growth of juvenile fish (up to 2 years old). Still, we highlight the importance of considering the spatial stratification of the population and the variability of length at age, since fish from different locations have different growth trajectories. More effort is needed to generate spatially explicit growth models.

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