BOLETIM DO INSTITUTO DE PESCA
Scientific Article

The influence of the individual variation, sex and spatial factor in somatic growth of *Serrasalmus rhombeus*, an Amazon predator fish species

Regiane Mônica dos Reis[1], Luzia da Silva Lourenço[2], Izaias Médice Fernandes[2]*

[1]Universidade Federal de Rondônia – Programa de Pós-Graduação em Ciências Ambientais – Rolim de Moura (RO), Brazil.
[2]Universidade Federal de Rondônia – Laboratório de Biodiversidade e Conservação – Rolim de Moura (RO), Brazil.
*Corresponding author: izaias.fernandes@unir.br

ABSTRACT

The Amazon is one of the regions with the greatest fish diversity on the planet. In this vast biodiversity, there is *Serrasalmus rhombeus*, a predatory species that plays a vital ecological role in aquatic ecosystems. In order to generate biological data and valuable information to management efforts, we characterized the somatic growth pattern of *S. rhombeus* and identified its sources of variation. To achieve this, individuals of *S. rhombeus* were collected from two dams between October 2018 and November 2019. Analyzing the marginal increment based on data from 158 individuals revealed the formation of a single annual growth ring at the onset of the rainy season. Individual ages ranged from 1 to 6 years old. Among the considered models, the one that provided the best explanation for the variation in somatic growth of *S. rhombeus* integrated individual variation, sex, and sites. This highlights that the rate of an individual's growth and the size it can attain are influenced by individual resource utilization, which is mediated by interindividual genetic diversity. Furthermore, this variation is associated with sex and the specific site where the individual is located.

Keywords: Amazon River Basin; Interindividual variation; Otolith; Piranha; Small hydroelectric plants.

A influência da variação individual, sexo e espaço no crescimento somático de *Serrasalmus rhombeus*, uma espécie de peixe predador da Amazônia

RESUMO

A Amazônia é uma das regiões com a maior diversidade de peixes do planeta. Nessa vasta biodiversidade, encontra-se *Serrasalmus rhombeus*, uma espécie predadora que desempenha um papel ecológico vital nos ecossistemas aquáticos. Com o objetivo de gerar dados biológicos e informações valiosas para os esforços de manejo, caracterizamos o padrão de crescimento somático de *S. rhombeus* e identificamos suas fontes de variação. Para isso, indivíduos de *S. rhombeus* foram coletados em duas represas entre outubro de 2018 e novembro de 2019. A análise do incremento marginal, baseada em dados de 158 indivíduos, revelou a formação de um único anel de crescimento anual no início da estação chuvosa. As idades individuais variaram de 1 a 6 anos. Entre os modelos considerados, aquele que melhor explicou a variação no crescimento somático de *S. rhombeus* integrou a variação individual, o sexo e os locais de coleta. Isso destaca que a taxa de crescimento de um indivíduo e o tamanho que ele pode atingir são influenciados pelo uso individual de recursos, que é mediado pela diversidade genética entre os indivíduos. Além disso, essa variação está associada ao sexo e ao local específico onde o indivíduo se encontra.

Palavras-chave: Bacia do Rio Amazonas; Otólito; Pequenas centrais hidrelétricas; Piranha; Variação interindividual.

Received: August 23, 2023 | **Approved:** February 10, 2025
Section editor: Raniere Garcez Costa Sousa

INTRODUCTION

Somatic growth is one of the most important biological processes for fisheries management and management of commercially exploited species (McDougall et al., 2018). Somatic growth is defined as the quantitative expression of development that implies an increase in body size, in the form of physical dimensions or chemical constituents, as a function of the individual's lifespan (Goldman, 2005).

Body size has striking effects on the survival, reproduction and movement of fish, shaping individual fitness, making growth a fundamental process in ecological and evolutionary dynamics (Vincenzi et al., 2014; Nater et al., 2018). Variations in somatic growth occur due to intrinsic and extrinsic differences of each individual. Thus, genetic and environmental factors (temperature, latitude, geographical distribution) and ecological interactions (competition, predation) act as determinants in growth rate (Winemiller, 1989; Shelton et al., 2013; Vincenzi et al., 2014; McDougall et al., 2018; Hansen et al., 2023).

Given this, studies on the growth of fishes have attempted to understand the factors that affect the growth of a species, as well as the importance of incorporating this information in studies on the population dynamics of those species (Shelton et al., 2013; Estlander et al., 2016; De Santana & Minte-Vera, 2017; Lourenço et al., 2017; Vastano et al., 2017; Nater et al., 2018; Tondato et al., 2018; Albuquerque et al., 2019; Maciel et al., 2019; Correa et al., 2020; Hernández et al., 2020; Tesfaye et al., 2023), since ignoring the variations that can occur in somatic growth throughout the life cycle of the organism can lead to incorrect estimates.

Throughout their lives, fish periodically deposit growth marks on calcified structures such as scales, vertebrae, and otoliths. Among these structures, otoliths are considered the most suitable for analysis of growth marks due to their lack of resorption, since, once the absorbed minerals are deposited in the otoliths, the organism will not use them again, even in conditions of extreme hunger (Campana & Thorrold, 2001; Green et al., 2009). Otolith development occurs by incremental increase, that is, through the production of alternating concentric bands of mineral-deficient zones (less dense/translucent) and mineral-rich zones (denser/opaque), forming a permanent record of fish life history events such as hatching, growth, spawning period, and migration (Campana, 2004; Panfili et al., 2009).

Biological, physiological, biochemical, genetic, environmental, geographical, and historical information is recorded through of deposition of increments into otoliths (Green et al., 2009). They are closely correlated with somatic growth (Vincenzi et al., 2014). Therefore, ontogenetic factors, genetic variability, sexual dimorphism, seasonal and spatial variation in environmental conditions, population density and resource availability (Dieterman et al., 2012; Siangas et al., 2012; DeAngelis & Grimm, 2014; Vincenzi et al., 2014; Cunha-Neto et al., 2022; Avigliano et al., 2023; Santana et al., 2023; Tesfaye et al., 2023) influence the rate of somatic growth and, in turn, the deposition of increments into otoliths.

Knowledge of the age structures and somatic growth parameters of a population are necessary information for ecological studies of population dynamics, fisheries management, and stock assessment (De Santana & Minte-Vera, 2017). Amazonian fish species exhibit a diversity of life stories that need greater understanding so that conservation strategies can be developed. Attentive to these demands, researchers have used growth rings in calcified structures to build biological and ecological knowledge about fish in the Amazon region (Arantes et al., 2010; Pouilly et al., 2014; Campos et al., 2015; Garcez et al., 2015; Duponchelle et al., 2016; Hermann et al., 2016; Sousa et al., 2016; Hauser et al., 2018; 2019a; 2019b; Waddell et al., 2019; Mereles et al., 2020; Hermann et al., 2021; Reis-Santos, et al., 2023).

Currently, studies addressing somatic growth in fish have used growth models based on individuals (Nater et al., 2018; Filipe & Kyriazakis, 2019; Morat et al., 2020; Vincenzi et al., 2020). This modeling considers the growth trajectory of everyone in the population and shows growth patterns at the population level originating in processes at the individual level (Grimm & Railsback, 2005; DeAngelis & Grimm, 2014; Lourenço et al., 2017). By doing so, individual growth perspectives provide adequate data for future implementation of population dynamics models and effective actions for planning and management of fish stocks, even for species with limited available data (Vigliola & Meekan, 2009; Alós et al., 2010).

In recent years, the rivers of the Amazon Basin have suffered major anthropogenic impacts. Amongst the main threats to aquatic biodiversity, there are hydroelectric projects due to the interruption of their longitudinal connectivity of water bodies (Castello & Macedo, 2016; Lees et al., 2016; Winemiller et al., 2016; Castello, 2021). Although the Amazon Basin rivers host 2,406 species of fish, making that one of the most diverse ichthyofaunas in the world (Jézéquel et al., 2020), the amount of biological and population data on the fishes of this ecosystem is still small compared to its diversity. Amongst the Amazon species, *Serrasalmus rhombeus* (Linnaeus, 1766) can be found in the main Amazon basins (Reis et al., 2003). *S. rhombeus* (black piranha) is a medium-sized species, reaching up to

50 cm in length, sedentary, omnivorous (Oliveira et al., 2023) and performs parental care.

Because of its predatory behavior, *S. rhombeus* plays a crucial ecological role for the equilibrium of Amazonian aquatic ecosystems by regulating the abundance of other species of fish (Goulding, 1981). In addition, this species has been one of the most successful in dams in the Amazon (Santos et al., 2006; Reis et al., 2020). In this context, this work aimed to characterize the pattern of somatic growth, build individual growth trajectories and evaluate the sources of variation in somatic growth for *S. rhombeus* in dams.

MATERIAL AND METHODS

Sample collection

Serrasalmus rhombeus individuals were collected in two dams located in the Branco River, one of the main tributaries on the right bank of the Guaporé River, Madeira River Basin, Amazonas, Brazil (Fig. 1). Approximately 390 km long, its hydrological regime is typical of the Amazon region, with periods of high and low water according to the rainfall regime (Fernandes et al., 2021). The climate of the region is monsoon (Am), with annual precipitation ranging from 1,800 to 2,300 mm, and annual average temperature between 22 and 26°C (Alvares et al., 2014), with the dry season between May and October and the rainy season from November to April (Butt et al., 2011). Due to the existence of waterfalls and rapids, the Branco River is highly targeted by hydroelectric projects, which resulted in the construction of seven small hydroelectric plants (SHPs) in its drainage basin. Among them, there are the SHP Ângelo Cassol (11°56'6,73"S, 62°04'40,35"W) with a reservoir of 2,73 km^2 and water residence time of 4.3 days, in operation since 2011 (nine years), and SHP Cachimbo Alto (11°55'0.78"S, 62°07'11.17"W), in operation since 2017 (three years), with a reservoir with 2.85 km^2 of flooded area and water residence time of five days (Reis et al., 2020) (Fig. 1).

The individuals were collected in the months of April, October, November and December of 2018, and February, March, April, June, October and November of 2019 through experimental fishing, using fishing tackle such as spinning reel baited with ox heart, lures, trawls and throw nets. All individuals were measured for standard length (LS in cm) and weight (W in grams), and their sex was identified.

Otolith analysis

The *Lapillus* otoliths were extracted, washed in water, dried, and identified. Subsequently, the right otolith of each specimen was cast in epoxy 2001 acrylic resin in a ratio of 1:0.5. The blocks were cut crosswise in Isomet saw, sanded and polished with waterproof sandpaper (600 grit) and aluminum oxide powder until the core and increments were visible. Subsequently, each otolith was fixed on slide for microscopic examination.

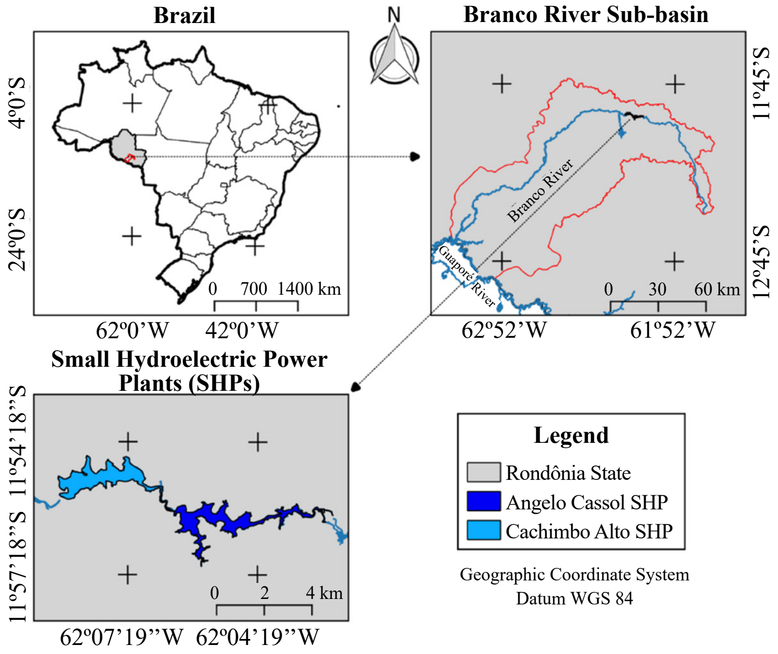

Figure 1. Study area where *Serrasalmus rhombeus* individuals were sampled, in the Branco River Basin, Rondônia, Brazil.

The slides containing the otoliths were soaked in 70% alcohol (to better highlight the opaque and translucent zones) and photographed in stereoscope with a Carl Zeiss-Axioncam IC-Zen Lite Blue 2012/SP2 camera using 1.0 × lens and 2.5 × magnification under inverted light in order to make the opaque areas appear dark and the translucent areas bright (Secor et al., 1992; Green et al., 2009).

Two independent readings were performed by the same reader. For each otolith, the distance between the nucleus to the end (edge) of the otolith and the distance between the nucleus to the end of each opaque zone, which represents the radius of each growth ring, were measured using the AxioVision 4.8.2.0 software. The coefficient of variation (CV) was used to estimate accuracy between the two readings of each otolith through Eq. 1:

$$CV_j = 100\%\text{x}\, \frac{\sqrt{\sum_{i=0}^{R} \frac{(X_{ij} - X_j)2}{R-1}}}{X_j} \qquad (1)$$

Where: *CVj*: accuracy of the age estimate for the j-th fish; *Xij*: determination of the age of the j-th fish; *Xj*: estimate of the average age of the j-th fish; *R*: number of age readings of each fish (Campana, 2001).

Periodicity of deposition of increments

The validation of the increment deposition periodicity was performed using data from the 3-year-old individuals collected between November 2018 and October 2019. To evaluate the periodicity of deposition of the increment, the absolute marginal increment analysis (MIA) was obtained by Eq. 2:

$$MIA = \frac{Rn}{Rn - 1} \qquad (2)$$

Where: *Rn*: distance between otolith nucleus and penultimate band; *Rn* -1: distance between the nucleus of the otolith and the last band (Campana, 2001).

To verify whether there was a relationship between the periodicity of the deposition of the increments and rainfall, information on the monthly rainfall in the region and the monthly averages of marginal increment of the 3-year-old individuals was used to build a graph. In this graph, the lowest marginal increment averages indicate the moment when a growth ring is formed.

Individual growth trajectories

The individual growth trajectories were built using the back-calculation method, which aims to recalculate the body length of the fishes at ages prior to capture, as it is assumed that there is a relationship between otolith growth (increment width) and somatic growth (body length) of fish (Vigliola & Meekan, 2009). The analysis of the relationship between body length and otolith radius showed a linear relationship, so the linear biological interception back-calculation model was used in Eq. 3:

$$L_i = \frac{L_{cpt} + (R_i - R_{cpt})x(L_{cpt} - L_{op})}{R_{cpt} - Rop} \qquad (3)$$

Where: *Ri* and *Li*: radius and body size at agei; *Rcpt* and *Lcpt*: body radius and length when collected; *Rop* and *Lop*: otolith radius and initial body length (usually at age 0) (Campana, 1990; Lourenço et al., 2017).

This model is applied when the relationship between body length and otolith radius of fish is linear. As no information was found in the literature about the average value of the otolith radius of *S. rhombeus* larvae, we assumed that the Lop was 20 mm and Rop was 0.008 mm, because these were the values that best estimated lengths prior to capture close to the values of lengths observed upon capture.

Somatic growth model

The somatic growth parameters of *S. rhombeus* were estimated using the von Bertalanffy nonlinear equation. This equation determines the relation of the individual's body size, obtained through the absorption of nutrients, as a function of time (age) (Eq. 4):

$$L_t = L_\infty \left[1 - e^{k(t - t_0)}\right] \qquad (4)$$

Where: Lt: length of individuals aged t; L∞: average of the maximum asymptotic or theoretical maximum length that the fish can reach (mm); *k* (year^{-1}): constant of the individual growth rate that determines the curvature of the growth function and represents processes related to energy costs (catabolism, metabolic rates, and associated behavioral characteristics); t (year): age of individuals; t_0 (year): nominal age of the fish in which its length is 0, the point that shifts the curve to the right or left of the age axis (Lai et al., 1996; Sparre & Venema, 1997).

Based on the growth parameters obtained by the von Bertalanffy adjustment, longevity was calculated ($A_{0,95}$) (Taylor, 1960), representing the time needed for an organism to reach 95% of its growth capacity in length. The Eq. 5 was used:

$$A_{0.95} = \frac{2.996}{K + t_0} \qquad (5)$$

Where: t_0: nominal age of the fish at which its length is 0; *k*: constant of the individual growth rate.

These parameters were estimated using the von Bertalanffy model.

Estimates of growth parameters and comparison of models

The growth parameters of *S. rhombeus* were estimated using the maximum likelihood method. Four models were built using the general Eq. 6:

$$Yi(X) = Y(X) + \varepsilon_i \tag{6}$$

Where: *Yi*: recalculated length of the individual at age *X*; ε*i*: the measurement level error or residual error that demonstrates the deviations of the back-calculated length *Yi* length at age determined through the estimated growth curve *Y (X)* of each individual.

To assess the effect of individual, site, and sex on somatic growth of *S. rhombeus*, three models were built using nonlinear models mixed with the "nlme" function of the nlme package (Pinheiro & Bates, 2000).

The model 1 used random effect of the individual as a variance component, showed in Eq. 7:

$$Model\ 1 = l_{kp} = l_{k0} + i_{kp} + \varepsilon_i \tag{7}$$

Where: l_{kp}: parameter value *lk* for individual *p*; l_{k0}: base value common to all individuals; i_{kp}: random effect at individual level; ε_i: residual error.

The Model 2 used random effect of the individual and fixed effect of the site, expressed in Eq. 8:

$$Model\ 2 = l_{kp} = l_{k0} + i_{kp} + l_{kp} + \varepsilon_i \tag{8}$$

Where: l_{kp}: parameter value l_k for individual *p*; l_{k0}: base value common to all individuals; *ikp*: random effect at individual level; l_{kp}: fixed effect based on site; ε*i*: residual error.

The Model 3 used random effect of individual and fixed effect of sex, expressed in Eq. 9:

$$Model\ 3 = l_{kp} = l_{k0} + i_{kp} + s_{kp} + \varepsilon_i \tag{9}$$

Where: l_{kp}: parameter value *lk* for individual *p*; l_{k0}: base value common to all individuals; i_{kp}: random effect at individual level; s_{kp}: fixed effect based on sex; ε_i: residual error.

The Model 4 used random effect of individual and fixed effect of site and sex, as expressed in Eq. 10:

$$Model\ 4 = l_{kp} = l_{k0} + i_{kp} + l_{kp} + s_{kp} + \varepsilon_i \tag{10}$$

Where: l_{kp}: parameter value l_k for individual *p*; l_{k0}: base value common to all individuals; i_{kp}: random effect at individual level; l_{kp}: fixed effect based on site; s_{kp}: fixed effect based on sex; ε_i: residual error.

To compare the four models, the Akaike information criterion (AIC) was used. The lower values indicate the models which best fit the data on length at age (Wagner et al., 2007). In addition to the AIC, to evaluate the differences between the models, we also considered the values of Δi (Δi < 2: strong support in the data; Δi > = 2 and < 7: little support in the data; Δi > 10: no support in the data) which allows the acceptability of each model to be analyzed numerically, and the weight (*Wi*), which refers to the probability of a given model, in cases of data resampling (Burnham & Anderson, 2002). All the analyses were performed using the R program (R Core Team, 2020).

RESULTS

A total of 202 *S. rhombeus* was captured, of which 39 were discarded due to problems in the processing of otoliths. Individuals with up to nine growth rings were sampled, but fish aged between 7 and 9 years old were excluded from the analysis, due to the low number of specimens at these ages (five individuals), resulting in a database with 158 individuals. Standard length ranged from 121 to 255 mm in females (mean ± standard deviation – SD: 175.42 ± 29.04 mm) and from 125 to 230 mm (mean ± SD: 175.42 ± 29.04 mm) in males (Table 1).

Table 1. Individual number (N), age, range of length standard (range LS), mean of length standard (mean LS) and standard deviation (SD) for female and male of *Serrasalmus rhombeus* in Ângelo Cassol and Cachimbo Alto dams, Rondônia, Brazil.

Sites	Sex	N	Age (years old)	Range LS (mm)	Mean LS (mm)	SD
Grouped individuals	Females	76	1–6	121.0–255.0	186.06	30.73
	Males	82	1–6	125.0–230.0	175.42	29.04
Ângelo Cassol	Females	30	1–6	134.0–235.0	180.50	31.77
	Males	44	1–6	133.0–230.0	177.79	27.14
Cachimbo Alto	Females	46	1–6	121.0–255.0	189.70	29.82
	Males	38	1–6	125.0–287.0	172.68	31.24

Based on the number of rings, individuals aged from 1 to 6 years old were identified. Females showed greater variation in body length by age than males, in addition to reaching greater body length at a younger age. When the data were analyzed separately by site and sex, the mean length at age was also higher for females, regardless of the sample site (Fernandes, 2025).

Periodicity and deposition of growth increments

The lowest absolute MIA values were found between November (mean ± SD: 0.862 ± 0.02 mm) and December (mean ± SD: 0.856 ± 0.036 mm) of 2018 (Fig. 2). Thus, the marginal increment of *S. rhombeus* decreases at the end of the dry season and the start of the rainy season. Given these results, *S. rhombeus* forms one ring per year with marking at the start of the rainy season.

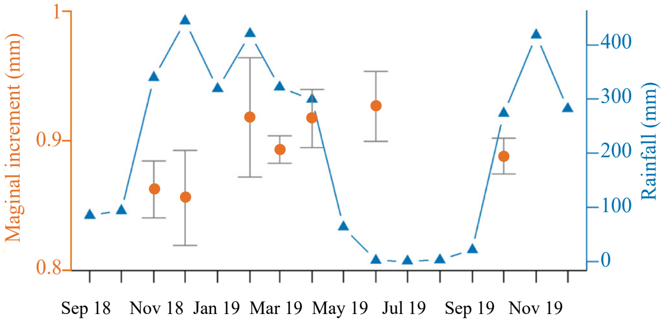

Figure 2. Mean and standard deviation of the absolute marginal increment analysis of the otolith (circles) and rainfall (triangles) of *Serrasalmus rhombeus* in the period from September 2018 to November 2019 in the Ângelo Cassol and Cachimbo Alto small hydroelectric plant dams, Rondônia, Brazil.

Individual growth trajectories

Length regression of *Lapillus* otoliths regarding the body length of *S. rhombeus* was linear and significant ($r^2 = 0.64$, $p < 0.002$) (Fig. 3). Since the relationship was linear, we applied the linear biological interception method to recalculate body length at the ages prior to collection and then compare the mean lengths at the age of collection of each sex with the back-calculated mean lengths by age group (Table 2).

Estimates of growth parameters and comparison of models

Among the four models tested, Model 4, which considers the individual effect, site and sex combined, was the best fit for the data on length at age according to the AIC and, therefore, the model that best explains the variation in growth for the species, followed by Models 3, 1 and 2 (Fernandes (2025); Table 3). Given these results, individual characteristics, site and sex are the main sources of variation for the growth of *S. rhombeus*.

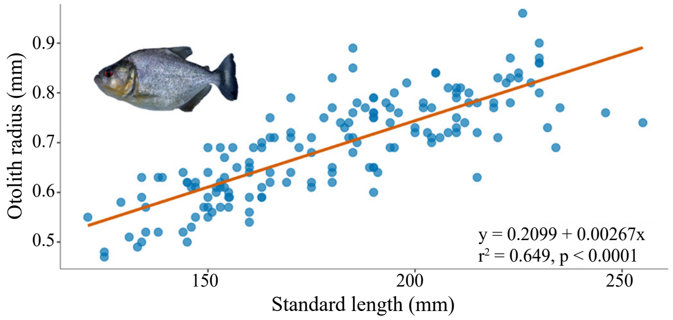

Figure 3. Relationship between body length and radius of *Serrasalmus rhombeus Lapillus* otolith sampled at the Ângelo Cassol and Cachimbo Alto small hydroelectric plant dams, Rondônia, Brazil.

Table 2. Comparison of body length at catch with body length back-calculated by age group for *Serrasalmus rhombeus* sampled at Ângelo Cassol and Cachimbo Alto small hydroelectric plant dams, Rondônia, Brazil.

Age (years old)	Catch length		Backcalculation length	
	Females	Males	Females	Males
1	143.57	138.50	135.12	132.54
2	154.92	160.25	140.49	142.17
3	186.58	176.60	164.39	156.46
4	196.94	183.11	169.30	157.98
5	210.50	209.63	178.01	176.36
6	227.25	226.00	193.55	193.78

Table 3. Results of model selection for somatic growth of *Serrasalmus rhombeus* based on a Akaike information criterion (AIC) comparison of four models.

Rank	Model	AIC	Δi	Wi	k
Model 1	Individual	3,707.0	4.9	0.065	5
Model 2	Individual + site	3,709.6	7.4	0.018	8
Model 3	Individual + sex	3,705.1	2.9	0.175	8
Model 4	Individual + sex + site	3,702.2	0.0	0.741	11

Δi: acceptability of each model; *Wi*: plausibility of each model; *k*: number of parameters of the nonlinear regression model.

Model 4, which considered the effect of individual, site and sex variation on growth parameters, presented the best fit for the data on length at age. The values of the parameters estimated by this model are presented in Table 4. In addition, growth trajectories were constructed for everyone at the Ângelo Cassol and Cachimbo Alto SHP dams (Fig. 4).

Table 4. Estimates of growth parameters (L_{∞}, k t0), confidence intervals (CI) and longevity $A_{0,95}$ (years old) for *Serrasalmus rhombeus* individual, site and sex model based on Model 4.

Parameters	**Ângelo Cassol SHP**			
	Females		**Males**	
	Estimate	**95%CI**	**Estimate**	**95%CI**
$L\infty$ (mm)	215.26	201.21–229.32	213.24	184.94–241.55
k (year^{-1})	0.32	0.24–0.39	0.28	0.16–0.39
t_0 (year^{-1})	-2.32	-2.82–-1.81	-2.84	-3.82–-1.85
$A_{0,95}$ *(years old)*	7.04		7.86	
Parameters	**Cachimbo Alto SHP**			
	Females		**Males**	
	Estimate	**95%CI**	**Estimate**	**95%CI**
$L\infty$(mm)	238.01	220.36–255.66	235.99	204.09–243.44
k (year^{-1})	0.22	0.16–0.28	0.18	0.08–0.28
t_0 (year^{-1})	-3.08	-3.70–-2.46	-3.60	-4.70–-2.50
$A_{0,95}$ *(years old)*	10.54		13.04	

SHP: small hydroelectric plant; 95%CI: 95% confidence interval.

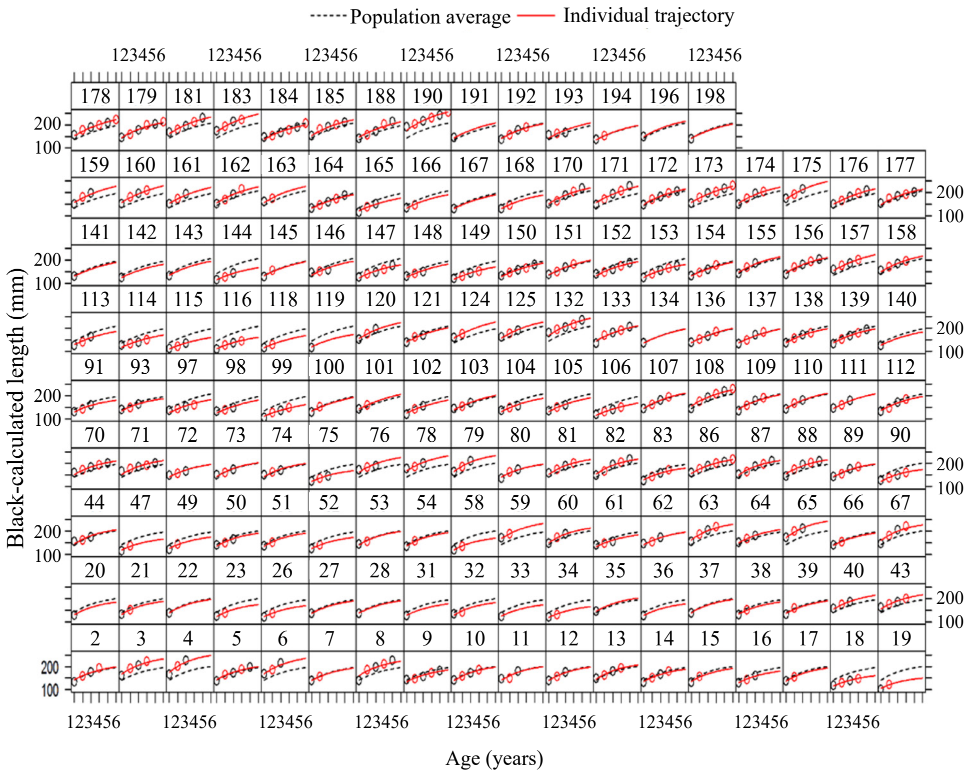

Figure 4. Individual growth trajectories of *Serrasalmus rhombeus* caught at the Ângelo Cassol and Cachimbo Alto small hydroelectric plants, Rondônia, Brazil.

DISCUSSION

The *Lapillus* otoliths of *S. rhombeus* have good visibility and periodicity of growth marks, so they can be considered suitable for ring counting and used for age estimates. We also found that, when combined, the individual, site and sex factors are sources of variation in growth for *S. rhombeus* in dams.

Determining age based on the reading of the growth rings of six years old for *S. rhombeus* was similar to what was found for the red piranha (*Pygocentrus nattereri*) (Serrasalmidae) in rivers of Bolivian Amazon (Duponchelle et al., 2007). The longevity estimate ($A_{0.95}$) varied from 7 to 13 years old for *S. rhombeus*. It was higher than estimates already recorded for other species of the same genus (Sousa et al., 2013; Sá-Oliveira et al., 2015; Vicentin et al., 2018).

MIA showed an annual pattern in the formation of growth rings for *S. rhombeus*, as it was found for other Neotropical fish species such as *Pseudoplatystoma corruscans* (Mateus & Petrere Júnior, 2004), *Pygocentrus nattereri* (Duponchelle et al., 2007, 2012), *Piaractus mesopotamicus* (Ambrosio et al., 2014; Lourenço et al., 2017), *Cichla temensis* (Campos et al., 2015), and *Prochilodus lineatus* (De Santana & Minte-Vera, 2017; Santana et al., 2018; Haimovici et al., 2022). The formation of growth marks at the end of the dry season and the start of rainy season (between November and December) was similar to that found for *Pygocentrus nattereri*, in rivers of the Bolivian Amazon (Duponchelle et al., 2007).

Seasonal markings on calcified structures are usually associated with life strategies of species, environmental changes, and availability of food resources (Nóbrega & Lessa, 2009; Tesfaye et al., 2023). Our results confirmed the relationship between the seasonal hydrological cycle, typical of tropical aquatic ecosystems, and changes in the growth rate of Amazonian fishes (Pérez & Fabré, 2009; Grønkjaer, 2016; Costa et al., 2018; Hauser et al., 2018; Haimovici et al., 2022), since the monthly averages of marginal increments were constant throughout the year, except in the transition period between the dry and rainy seasons and when the dams reached their lowest levels and water volume.

The seasonal variation of rainfall has a strong influence on the diet of Neotropical fishes, since during the rainy season and rising water levels of rivers large plain areas are flooded. These temporarily flooded environments provide a large supply of energy to the system due to their large amount of plant (leaves, fruits and seeds) and animal (insects) resources, resulting in greater availability and quality of food resources, while in the dry season the availability of resources decreases (Walker et al., 2013; Sanferla & Súarez, 2016). Thus, seasonal change in resource availability and, consequently, in fish growth results in different patterns of deposition of otolith growth increments, as these structures are formed through the absorption of nutrients from food and the environment (Campana, 2001, 2004; Dieterman et al., 2012).

Although *S. rhombeus* is a predatory species with an omnivorous diet, restriction of resources during the low water period can increase (intra and interspecific) competition, which may result in increased expenditure of energy for the acquisition of food resources. Therefore, the rainy season is likely to represent a period of more favorable trophic conditions for this species, which leads to an increase in somatic growth, while the drought period implies less favorable conditions and a lower growth rate.

Individual, site, and sex characteristics are the main sources of variation in growth for *S. rhombeus*. Individual heterogeneity may be linked to genetic factors and the phenotypic plasticity of each individual. Genetic differences between individuals are a determining factor in the heterogeneity of growth since some individuals may be genetically predisposed to grow faster than other individuals in the same population. In addition to genetic differences in growth performance, even individuals being exposed to the same biotic and abiotic factors, access to resources occurs individually. Therefore, the growth of individuals does not behave homogeneously in a population (Lourenço et al., 2017; Nater et al., 2018; Haimovici et al., 2022). In addition, individuals react differently to external stimuli because of innate differences in growth potential arising from variation in metabolic rates and behavioral traits (Nater et al., 2018; Filipe & Kyriazakis, 2019).

Morphological differences between males and females are a very common feature in fish (Araujo-Lima & Goulding, 1997; Kritzer, 2004; Duponchelle et al., 2007; Rypel, 2007; Nóbrega & Lessa, 2009; Estlander et al., 2016; Lourenço et al., 2017; Hauser et al.,2018; Maciel et al., 2019). Differences in body size between males and females may be related to genetic factors, balance in energy allocation between reproductive and growth activities, vulnerability to predators, parental care (Rypel, 2007; Maciel et al., 2019) and changes in the environment due to different responses between females and males to exogenous factors (Estlander et al., 2016). Another factor that may be related to the difference in growth, which normally favors females, may be associated with reproductive activity, because gonadal maturation requires greater internal volume and energy expenditure for females in egg production and spawning than for males (Duponchelle et al., 2007; Lourenço et al., 2017).

Different environments, such as different dams, may differ in environmental conditions and resource availability, as well as ecological factors such as competition, predation, density and recruitment, and may influence the growth rates of individuals (Duponchelle et al., 2007; Estlander et al., 2016; Izzo et al., 2017; Vastano et al., 2017; Hauser et al., 2018; McDougall et al., 2018; Maciel et al., 2019; Hernández et al., 2020). The two dams analyzed in this study can be considered young. SHP Ângelo Cassol has been in operation for nine years, and SHP Cachimbo Alto for only three (Reis et al., 2020). Young dams have a large supply of organic matter, consequently high primary productivity in the first years of formation. However, such productivity tends to decrease as time passes (Mol et al., 2007; Agostinho et al., 2016). Such conditions can benefit opportunistic sedentary species adapted to lentic environments (Agostinho et al., 2008; Muniz et al., 2019; Reis et al., 2020) as *S. rhombeus*, one of the most successful species in dams in the Amazon.

Therefore, our study showed that incorporating the effect of individual variability, sex, and site into growth parameters provides more accurate data and contributes to a better understanding of the possible sources of variations in fish growth. Furthermore, individual-based models have shown that most species exhibit inter-individual variation in resource use (Araújo et al., 2011; DeAngelis & Grimm, 2014; Vincenzi et al., 2014; Lewis et al., 2021), and here we demonstrated this effect on the growth of *S. rhombeus* in dams.

CONCLUSION

Serrasalmus rhombeus forms a single annual ring, and the marking occurs between the months of November and December, at the end of the dry season and the start of the rainy season, and when the dams reach their lowest levels. Individuals up to 6 years old were recorded, and the estimated longevity ranged from 7 to 13. Among the evaluated factors, individual variation, site, and sex are important sources of variation working together in the growth of *S. rhombeus* in dams.

Therefore, the management of native species, whether they are important for fishing or species of key ecological importance, such as *S. rhombeus*, ought to consider the interindividual variation between sex and between the different environments where these species are being managed. Using the same management strategies for cosmopolitan species occurring in different drainage basins can lead to failure, since the response to local characteristics is individual and varies with sex.

Given the ecological importance that *S. rhombeus* can exercise in the balance of ecosystems, incorporating knowledge about the sources of variation in the growth of the species can contribute to this species management on the aquatic community, especially in altered environments, such as dams.

CONFLICT OF INTEREST

Nothing to declare.

DATA AVAILABILITY STATEMENT

The data are available in a data repository. https://doi.org/10.6084/m9.figshare.28448072.v1

AUTHORS' CONTRIBUTIONS

Conceptualization: Lourenço, L.S., Fernandes, I.M.; **Formal analysis:** Reis, R.M., Lourenço, L.S., Fernandes, I.M.; **Methodology:** Reis, R.M., Lourenço, L.S., Fernandes, I.M.; **Writing – original draft:** Reis, R.M.; **Supervision:** Lourenço, L.S., Fernandes, I.M.; **Writing – review & editing:** Lourenço, L.S., Fernandes, I.M.; **Project administration:** Fernandes, I.M.; **Final approval:** Fernandes, I.M.

FUNDING

Fundação Rondônia de Amparo ao Desenvolvimento das Ações Científicas e Tecnológicas e de Pesquisa do Estado de Rondônia.

Grant No.: 01.1331.00031-00.049/2017

ACKNOWLEDGEMENT

We thank the Laboratório de Ictiologia e Pesca at the Universidade Federal de Rondônia, *campus* Porto Velho. The authors would also like to thank professor Carolina Doria and professor Marilia Hauser dos Santos for their support in processing the otoliths.

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