







Early ontogeny of the commercially valuable fish red-bellied pacu *Piaractus brachypomus* (Characiformes, Serrasalminidae) from the Amazon, Brazil

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Abstract

The initial development of the red-bellied pacu *Piaractus brachypomus* is described using morphological, meristic and morphometric characteristics. A total of 127 individuals were analysed (47 in the yolk-sac, 35 in pre-flexion, five in flexion, 20 in post-flexion and 20 in juvenile) with standard length varying between 2.92 and 48.61 mm. The larvae are born poorly developed and have a discoidal yolk at ~6.33 mm standard length. During early ontogeny, the mouth passes from terminal to subterminal and the anal opening reaches the vertical line over the midline region of the body. There are changes in body shape from long and moderate to deep, head length from small to large, and eye diameter from moderate to large. Dendritic chromatophores were present in the ventral, dorsal and upper part of the swim bladder in the early larval stages. Rounded spots are evident all over the body in juveniles. The total number of myomeres ranges from 39 to 41 (20–23 pre-anal, 17–20 post-anal). Through the morphometric relationships, it was evidenced that the greatest changes during the initial ontogeny of *P. brachypomus* occur in the transition from the post-flexion stage to the juvenile period, indicating changes in behaviour, foraging and physiology.

KEYWORDS

Amazon basin, isometric growth, larval fish, neotropical fish, pirapitinga

1 | INTRODUCTION

Piaractus brachypomus (Cuvier, 1818), commonly known as the red-bellied pacu or pirapitinga, is a species of neotropical frugivore fish that inhabits the Amazon river basin, with distribution along the Caquetá-Japurá, Putumayo-Iça, Branco, Napo, Ucayali, Solimões, Juruá, Purus, Madeira, Tapajós, Madre de Dios, Beni, Mamoré, Iténez, Guaporé, Tocantins-Araguaia and Amazon rivers in Bolivia, Brazil, Colombia, Ecuador and Peru (Escobar *et al.*, 2019; Kolmann *et al.*, 2021). This large-sized species may reach up to 88 cm in length and 25 kg in weight. It performs trophic and reproductive migrations, and is important for commercial fishing and aquaculture (Froese & Pauly, 2022; Nico *et al.*, 2018; Santos *et al.*, 2009).

In aquaculture, certain aspects of *P. brachypomus*, such as rapid growth, reduced head size, excellent fillet yield, resistance to disease and different environmental conditions, and ease of handling (rusticity) (Guimarães & Martins, 2015; Valladão *et al.*, 2018), make this species an economically valuable resource for large-scale production. *Piaractus brachypomus* has been the focus of many studies because it has become an exotic species in the hydrographic basins of Poland, Papua New Guinea, Iran and India (Correa *et al.*, 2014; Esmaeili *et al.*, 2017; Roshni *et al.*, 2014; Zarei & Rajabi-Maham, 2017).

Although various aspects of *P. brachypomus* have been studied (Escobar *et al.*, 2015; Guimarães & Martins, 2015; Seshagiri *et al.*, 2022; Vásquez-Torres & Arias-Castellanos, 2013), our understanding of the ecology and early morphology of this species is

limited. *Piaractus brachypomus* juveniles are abundant in the marginal stretches of the rivers, lakes and flooded areas of the Amazon region and use these environments for foraging and growth (Araújo-Lima & Gomes, 2005; Santos *et al.*, 2009).

The absence of taxonomic information on the early life stages of a fish species negatively influences the specific recognition of new populations in a natural environment and limits studies on ichthyoplankton (Cajado *et al.*, 2021; Oliveira *et al.*, 2021; Reynalte-Tataje *et al.*, 2020; Silva *et al.*, 2021; Zacardi *et al.*, 2020). Therefore, to maximise knowledge about the early ontogeny of fish species in the Amazon basin, mainly those of great importance for the fishing and aquaculture sector, we described the larval and juvenile development of *P. brachypomus* using morphological, morphometric and meristic characteristics. Additionally, we estimated the growth patterns of morphometric variables through early development.

2 | MATERIALS AND METHODS

2.1 | Source of biological material

Piaractus brachypomus larvae and juveniles were obtained through induced reproduction and captive breeding performed at the Aquaculture Laboratory of the Unidade Agropecuária de Santa Rosa (UAGRO/SAGRI) in the municipality of Santarém, State of Pará, Brazil (2°40'06"S, 54°33'05"W) in June 2012. This study was approved by the Ethical Committee of Universidade Estadual do Pará (UEPA), Brazil, under the registration number 042-2012. Four specimens (two males and two females) of ~1.5 kg were used for hypophysation. For spawning, the females received the stimulus through two doses of commercial carp pituitary extract (0.5 and 5.0 mg/kg) during a 12 h interval, whereas the males received a single dose of 2.5 mg/kg when the females received their last dose.

Fertilization occurred after blending and homogenizing semen and oocytes using water to activate the process and moisturize the eggs. Subsequently, fertilized eggs were washed and distributed (300 ml) into three 200 l Zoug incubators (Silva *et al.*, 2009). The larvae were kept in the incubators for ~3 days, during which time the mouth was fully formed. Subsequently, they were transferred to an earthen fingerling pond and compacted for growth (1000 m²), where they remained for ~30 days.

2.2 | Analysis of biological material

We analysed *P. brachypomus* specimens collected at intervals of 0, 6, 12, 18, 30, 40, 48, 72, 77, 96, 98, 122, 150, 168, 336 and 504 h post-hatching (hph) for the larval period and 672 hph for the juvenile period. The individuals were anaesthetized and euthanized in 0.1% benzocaine diluted 1/10 in alcohol solution, fixed in Karnovisk solution for 24 h and packed in properly labelled, 20 ml glass vials containing 0.5% glutaraldehyde for subsequent morphological evaluation (Silva, 2006).

The physical and chemical parameters of the water used were the usual ones for fish farming in the western region of Pará, where the

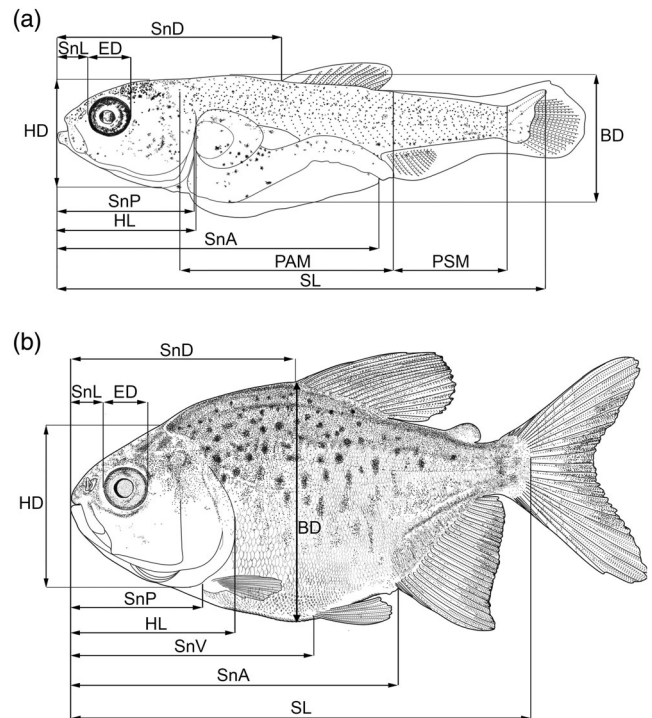


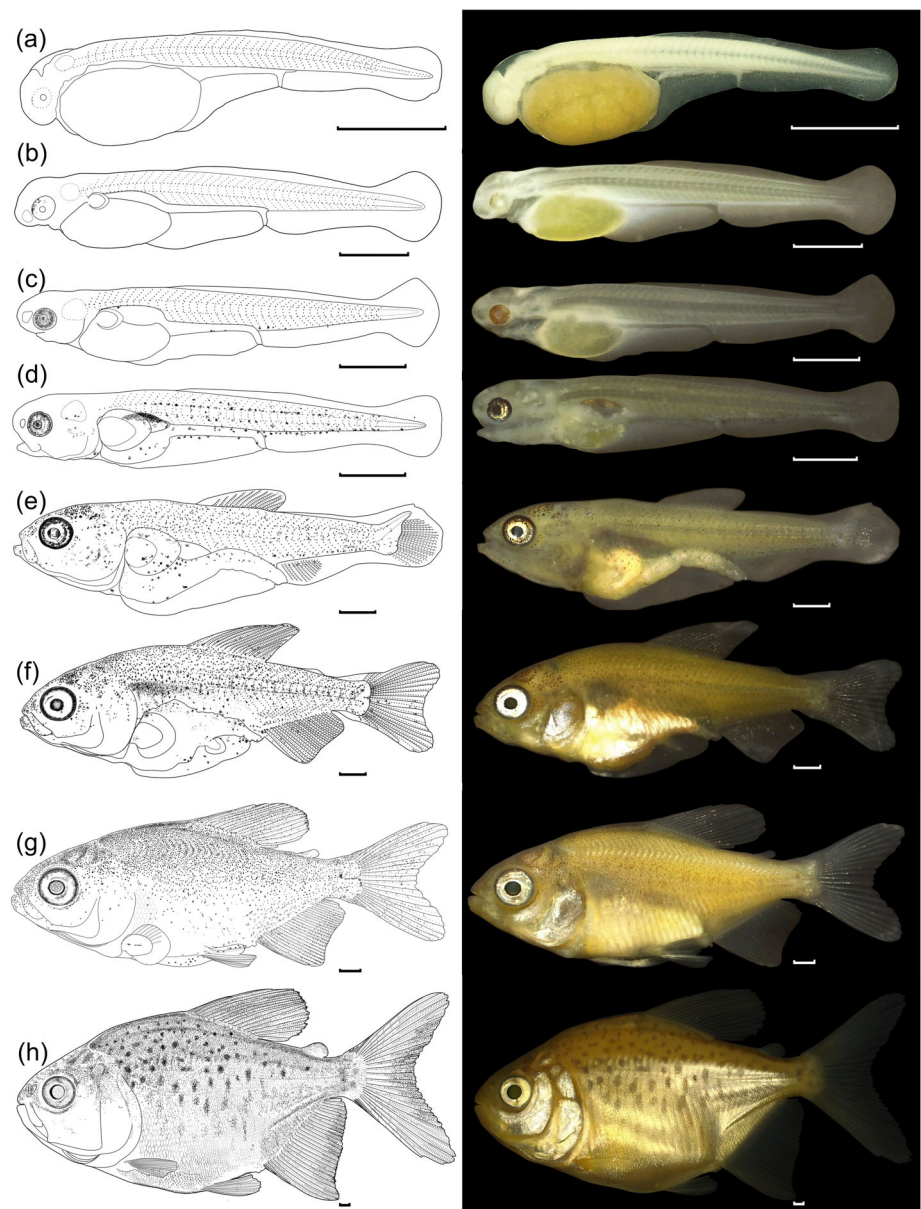
FIGURE 1 Morphometric measurements from *Piaractus brachypomus* (Characiformes, Serrasalminidae) during the (a) larval and (b) juvenile periods. BD, body depth; ED, eye diameter; HD, head depth; HL, head length; SL, standard length; SnA, snout-anal fin distance; SnD, snout-dorsal fin distance; SnL, snout length; SnP, snout-pectoral fin distance; SnV, snout-pelvic fin distance

water supply was derived from a dammed stream, with the transfer of water to a reservoir (excavated pond nursery). The average water temperature during the incubation period ranged from 28 to 29.2°C, pH 6.8–7.3, dissolved oxygen content was 6.6–7.7 mg/l and total ammonia content was 0–0.5 mg/l. However, in the excavated pond nursery, water temperature ranged from 28 to 31.3°C, pH 5.1–7.2, dissolved oxygen content was 5.2–7.6 mg/l and total ammonia content was 0–0.5 mg/l.

The individuals were classified according to their degree of development according to the method proposed by Ahlstrom *et al.* (1976) and modified by Nakatani *et al.* (2001) in the larval period, and grouped into four stages of development (yolk-sac, pre-flexion, flexion and post-flexion). The juvenile period was characterized by the absence of an embryonic fin, complete formation of the rays of all fins and the presence of scales.

The larval and juvenile development series were evaluated using a light camera coupled to a binocular stereomicroscope (Leica S9i) and the Leica Application Suite version 4.13 (Heerbrugg, Switzerland). For morphometric characterization, 10 variables were measured: standard length (SL), snout length (SnL), eye diameter (ED), head depth (HD), body depth (BD), head length (HL) and distance from the snout to the origin of the anal (SnA), dorsal (SnD), pectoral (SnP) and pelvic (SnV) fins. Count data were obtained for the number of spines and rays of dorsal (D), anal (A), pectoral (P) and pelvic (V) fins and the number of

FIGURE 2 Early development of *Piaractus brachypomus* (Characiformes, Serrasalminidae). (a) Yolk-sac, 6 hph, 3.85 mm; (b) yolk-sac, 40 hph, 5.80 mm; (c) yolk-sac, 53 hph, 6.43 mm; (d) pre-flexion, 98 hph, 6.33 mm; (e) flexion, 168 hph, 10.14 mm; (f) post-flexion, 168 hph, 13.14 mm; (g) post-flexion, 336 hph, 17.53 mm; (h) juvenile, 672 hph, 44.76 mm. Scale bars = 1 mm



pre-anal (PAM), post-anal (PSM) and total (TM) myomeres (Figure 1a,b). All specimens analysed are deposited at the Coleção de Ovos e Larvas de Peixes (CROLP-LEIPAI), Universidade Federal do Oeste do Pará (UFOPA) (catalogue number: LEIPAI 00128).

2.3 | Statistical analysis

For the analysis of morphometric proportions, the obtained variables were expressed in percentages, and SnL, ED and HD were related to HL. By contrast, the other variables (BD, HL, SnA, SnD, SnP and SnV) were related to SL. Body relationships between ED (ED/SL), HL (HL/SL) and BD (BD/SL) were established as proposed by Leis and Trnski (1989) and modified by Nakatani *et al.* (2001).

To verify the possible ontogenetic changes of the species, morphometric variables BD, HL, SnA, SnD, SnP and SnV (response

variables) were plotted against SL (explanatory variables), whereas variables SnL, ED and HD (response variables) were plotted in relation to HL (explanatory variable) and their relationships were described by different regression models (Kováč *et al.*, 1999). The hypothesis that body growth was continuous isometric was tested using simple linear regression. Moreover, alternative hypotheses of gradual allometric growth (quadratic regression) and discontinuous isometric growth (part regression-piecewise) were verified. The best regression model selected for each morphometric variable was performed using *F* tests (Sokal & Rohlf, 1989). The significance level was $P < 0.05$.

3 | RESULTS

A total of 127 specimens were analysed, 47 in the yolk-sac, and 35 in the pre-flexion, five in the flexion, 20 in the post-flexion and 20 in the

TABLE 1 Minimum (Min), maximum (Max), mean, standard deviation (s.d.) and morphometric (%) and meristic proportions obtained from larvae and juveniles of *Piaractus brachyomus*

Variables (mm)	Larval period			Flexion (n = 5)			Post-flexion (n = 20)			Juvenile period (n = 20)					
	Yolk sac (n = 47)			Pre-flexion (n = 36)			Flexion (n = 5)			Post-flexion (n = 20)			Juvenile period (n = 20)		
	Min-Max	Mean ± s.d.		Min-Max	Mean ± s.d.		Min-Max	Mean ± s.d.		Min-Max	Mean ± s.d.		Min-Max	Mean ± s.d.	
SL	2.92-5.88	4.49 ± 0.94		5.06-6.66	5.80 ± 0.47		10.14-11.13	10.67 ± 0.37		9.18-26.35	17.86 ± 5.59		28.77-48.61	37.65 ± 6.20	
HL	0.26-1.02	0.76 ± 0.17		0.81-1.25	1.01 ± 0.14		2.98-3.47	3.22 ± 0.19		3.04-9.30	6.08 ± 2.01		9.75-15.41	12.78 ± 1.96	
SnL	0.06-0.98	0.17 ± 0.13		0.15-1.19	0.24 ± 0.17		0.42-0.57	0.52 ± 0.06		0.43-1.97	1.16 ± 0.49		1.34-3.35	2.62 ± 0.47	
ED	0.11-0.34	0.22 ± 0.06		0.27-0.43	0.37 ± 0.04		0.97-1.08	1.00 ± 0.05		1.02-2.63	1.92 ± 0.56		2.97-4.64	3.75 ± 0.57	
HD	0.18-0.77	0.44 ± 0.18		0.62-1.06	0.85 ± 0.13		2.25-2.70	2.53 ± 0.18		2.00-8.44	5.43 ± 2.05		9.60-17.44	9.60 ± 2.25	
BD	0.71-1.12	0.94 ± 0.09		0.78-1.26	1.00 ± 0.15		2.56-3.21	3.01 ± 0.28		2.76-11.70	7.16 ± 3.00		14.24-26.67	19.64 ± 4.02	
SnD	NV	NV		NV	NV		4.90-5.18	5.06 ± 0.14		4.76-13.34	9.03 ± 2.77		14.35-23.96	18.71 ± 3.08	
SnA	NV	NV		NV	NV		6.76-7.45	7.18 ± 0.28		6.68-18.73	12.35 ± 3.78		20.26-36.18	26.75 ± 4.77	
SnP	NV	NV		0.94-1.53	1.22-0.17		2.87-3.26	3.05 ± 0.14		2.87-8.31	5.54 ± 1.78		8.44-13.79	11.26 ± 1.75	
SnV	NV	NV		NV	NV		NV	NV		11.00-13.93	12.48 ± 0.99		14.97-26.17	20.03 ± 3.60	
Morphometric proportions (%)															
SnL/HL	10.69-26.87	19.06 ± 3.82		15.82-125.21	24.40 ± 17.70		14.08-17.75	15.43 ± 1.59		14.29-21.62	18.54 ± 2.14		13.76-23.34	20.43 ± 2.01	
ED/HL	17.41-35.54	29.31 ± 4.14		29.65-46.80	36.70 ± 3.85		29.87-33.64	31.41 ± 1.09		28.12-34.54	32.09 ± 2.14		27.44-31.87	29.36 ± 1.34	
HD/HL	27.73-98.50	59.87 ± 15.00		72.14-101.54	84.34 ± 3.85		75.59-77.82	74.70 ± 4.00		65.90-95.24	87.50 ± 7.49		94.39-122.65	100.26 ± 6.12	
BD/SL	14.30-33.63	21.66 ± 4.71		14.49-20.06	17.28 ± 1.48		25.28-29.68	28.19 ± 1.80		26.68-46.62	38.41 ± 6.36		47.23-55.32	51.84 ± 2.57	
HL/SL	9.36-23.10	17.19 ± 2.34		14.95-19.14	17.39 ± 1.16		28.90-31.19	30.58 ± 0.97		29.53-36.47	33.61 ± 1.96		29.26-35.62	34.03 ± 1.28	
SnD/SL	NV	NV		NV	NV		46.42-48.62	47.53 ± 0.97		47.93-52.48	50.32 ± 1.45		45.81-53.04	49.71 ± 1.63	
SnA/SL	NV	NV		NV	NV		65.66-69.27	67.23 ± 1.39		67.36-71.57	71.57 ± 1.36		69.49-74.43	70.91 ± 1.36	
SnP/SL	NV	NV		17.97 ± 24.43	21.05 ± 1.57		27.87-29.32	28.85 ± 0.54		27.85-33.13	30.76 ± 1.42		28.19-32.01	30.08 ± 1.04	
SnV/SL	NV	NV		NV	NV		NV	NV		52.18-55.77	15.91 ± 24.94		48.35-70.40	53.21 ± 4.36	
Myomeres															
Pre-anal	20-23	22 (n = 23)		20-23	22 (n = 24)		21-22	22 (n = 3)		22-23	23 (n = 5)		NV	NV	
Post-anal	17-20	18 (n = 32)		17-20	18 (n = 20)		17-18	17 (n = 3)		17-18	17 (n = 5)		NV	NV	
Total	39-41	40 (n = 30)		39-41	40 (n = 23)		39-41	40 (n = 3)		39-41	40 (n = 5)		NV	NV	
Rays															
Dorsal	NV	NV		NV	NV		11-14	13 (n = 2)		14-17	11, 16 (n = 9)		14-16	11, 15 (n = 9)	
Anal	NV	NV		NV	NV		10-21	17 (n = 2)		20-28	11, 25 (n = 8)		23-26	11, 25 (n = 10)	
Pectoral	NV	NV		NV	NV		NV	NV		6-15	12 (n = 5)		13-15	1, 14 (n = 11)	
Pelvic	NV	NV		NV	NV		NV	NV		5-8	8 (n = 11)		7-8	8 (n = 18)	

Abbreviations: BD, body depth; ED, eye diameter; HD, head depth; HL, head length; NV, not visible; SL, standard length; SnA, snout-anal fin distance; SnD, snout-dorsal fin distance; SnL, snout length; SnP, snout-pectoral fin distance; SnV, snout-pelvic fin distance.

juvenile stages. The morphological description of each stage is presented in detail in Figure 2. The results referring to morphometric and meristic variables are presented in Table 1.

3.1 | Characterization of the larval period

Yolk-sac (Figure 2a-c): The larvae remain for up to 53 hph at this stage and present SL ranging from 2.92 to 5.80 mm (mean \pm standard deviation = 4.49 mm \pm 0.94). The notochord is rectilinear and visible by transparency. The yolk-sac is relatively large and has a discoidal shape. The snout is rounded. The mouth does not present apparent formation and the appearance of the nostrils has occurred. The eyes are spherical and from 3.82 mm SL have little conspicuous pigmentation on the anterior edge. The length of the intestine reaches the vertical that goes beyond the median region of the body, and the anus is not yet functional. At 5.58 mm SL (30 hph), the buds of the pectoral fin appear. No indication of the formation of the rays. Initially, the larvae are transparent, but at the end of the stage with 5.80 mm SL (40–48 hph), scarce dendritic pigments appear distributed in the upper region of the yolk, under the intestine and in the ventral region. The opercular cavity is formed at the end of the stage, in which the first gill arches with lamellar protrusions appear, partially covered by the opercula. The hyaline finfold surrounds the body from before the

dorsal median region to the distal portion of the yolk-sac. The total number of myomeres ranges from 39 to 41 (mode = 40, $n = 30$), with 20–23 segments in the pre-anal and 17–20 in the post-anal regions.

Pre-flexion (Figure 2d): This stage started at 72 hph and lasted up to 152 hph. SL ranged from 5.06 to 6.64 mm (mean \pm standard deviation = 5.80 mm \pm 0.48). The notochord, visible by transparency, remains unflexed. The body is elongated and fusiform in shape. The eyes are spherical, developed and are intensely pigmented from 6.27 mm SL (77 hph). The yolk-sac is partially absorbed and from 6.33 mm SL (98 hph) is already absent. The snout remains rounded, the mouth is open and in a subterminal position, the maxillary bones are formed and surpass the vertical that reaches the median region of the eyes. The nostrils are simple and the otoliths are visible by transparency. The eyes are spherical, developed and intensely pigmented. The operculum is in formation. The intestine is long (greater than 50% of the SL); the anal opening is situated after the vertical that exceeds the median region of the body and both are already functional. At 6.64 mm SL (98 hph), the swim bladder is inflated and visible by transparency, located in the anterior part of the body, over the stomach. At this stage, body pigmentation intensifies and dendritic chromatophores are sparsely distributed along the ventral and lateral regions of the body and concentrated in the upper part of the swim bladder. The position of the finfold remains as in the anterior stage and there is no indication yet of the differentiation of the pectoral fin rays. The

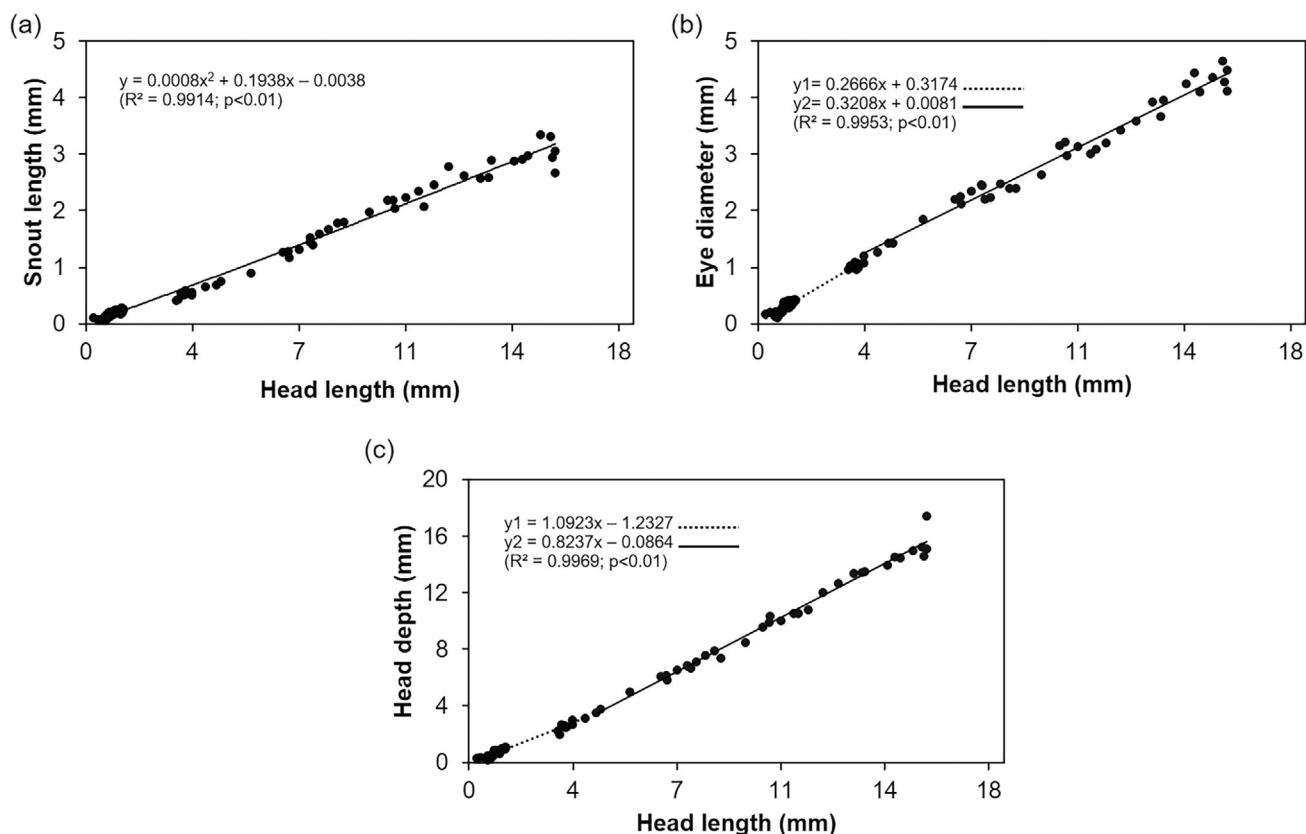


FIGURE 3 Morphometric relationships (mm) between head length and snout length (a), eye diameter (b) and head depth (c) during development of *Piaractus brachypomus* (Characiformes, Serrasalminidae)

number of total myomeres ranges from 39 to 41 (mode = 40, $n = 22$), 20–23 pre-anal and 17–20 post-anal segments.

Flexion (Figure 2e): The specimens at this stage were observed only at 168 hph and presented SL ranging from 10.14 to 11.13 mm (mean \pm standard deviation = 10.70 mm \pm 0.33). The notochord, visible by transparency, is already flexed. The mouth becomes terminal, the nostrils double and the otoliths are no longer visible. The snout, eyes, operculum, intestine and swim bladder, despite being more developed, remain morphologically similar to the previous stage. The pigmentation pattern intensifies, with dendritic and punctiform chromatophores distributed irregularly over the entire body and concentrated in the dorsal region of the head. The finfold involves only the posterior part of the dorsal fin to the base of the pectoral fin in the ventral region of the body. At 10.54 mm (168 hph), it is possible to visualize the rays of the caudal, dorsal (11–14) and anal fins (10–21). Total myomeres range from 39 to 41 (mode = 40, $n = 3$), with 21–22 pre-anal and 17–18 post-anal segments.

Post-flexion (Figure 2f–g): This stage started from 168 hph, lasting up to 336 hph. The SL of the larvae ranged from 9.84 to 26.35 mm (mean \pm standard deviation = 17.87 mm \pm 5.10). Initially, the notochord is visible by transparency, but throughout development, the thickness of muscle tissue does not allow the visualization of this structure, neither the muscle segments (myomeres) nor the swim bladder. The head presents the dorsal region, with convex shape and a rhomboid body. Pelvic fin buds appear in 9.84 mm SL larvae (168 hph); the adipose fin is visible and the first rays of the pelvic fins begin to appear at 16.13 mm SL (168 hph). These rays are already fully formed at 18.99 mm SL (336 hph). At \sim 17.50 mm SL (336 hph), the unpaired fins are in the final stages of formation with flexible ray segmentation. It is possible to observe the remnants of the finfold located in the ventral region between the isthmus and the anus. The pigmentation pattern remains similar to the previous stage, although it is more intense at the top of the head and under the flanks. Pigmentation is visible between the rays of the pelvic, anal, caudal and dorsal

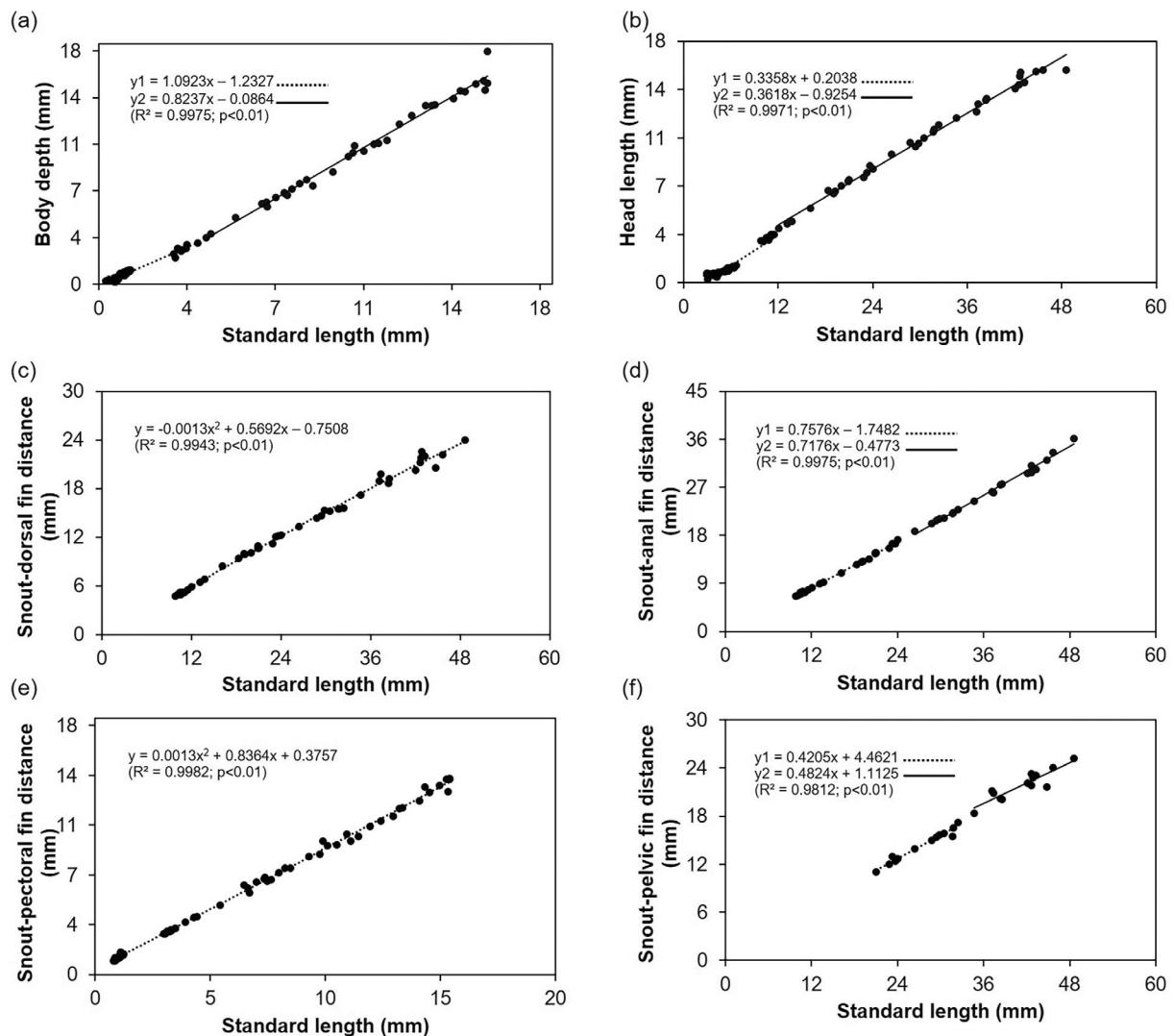


FIGURE 4 Morphometric relationships (mm) between the standard length and body depth (a), head length (b), snout-dorsal fin distance (c), snout-anal fin distance (d), snout-pectoral fin distance (e) and snout-pelvic fin distance (f) during the early development of *Piactus brachypomus* (Characiformes, Serrasalminae)

TABLE 2 Values of Simple linear regression (L), quadratic (Q) and piecewise (S) regression analyses of morphometric variables in relation to head length (HL) and standard length (SL) of larvae and juveniles of *Piaractus brachypomus*

Relations	R^2			Test F			BM	BP	n
	L	Q	S	Q/L	S/Q	S/L			
SnL/HL	0.9915	0.9898	0.9910	-20.67	16.40	-3.42	Q	0.74	127
ED/HL	0.9937	0.9950	0.9969	32.24	75.39	63.48	S	1.12	127
HD/HL	0.9951	0.9967	0.9969	60.12	7.94	35.71	S	3.39	127
BD/SL	0.9906	0.9943	0.9975	80.49	156.32	168.82	S	4.96	127
HL/SL	0.9951	0.9969	0.9971	72.00	8.48	42.41	S	3.67	127
SnD/SL	0.9935	0.9943	0.9943	17.40	0.00	8.63	Q	12.89	45
SnA/SL	0.9982	0.9985	0.9984	24.80	-7.69	7.69	S	18.18	45
SnP/SL	0.9981	0.9982	0.9982	6.89	0.00	3.42	Q	4.94	80
SnV/SL	0.9756	0.9810	0.9764	4.20	29.78	17.48	S	18.10	26

Note: Bold values represent a significant difference ($P < 0.05$).

Abbreviations: BM, best model; BP, breaking point (mm); ED, eye diameter; HD, head depth; HL, head length; L, linear regression; n = number of analysed individuals; Q, quadratic; R^2 = coefficient of determination; S, piecewise; SL, standard length; SnA, snout-anal fin distance; SnD, snout-dorsal fin distance; SnL, snout length; SnP, snout-pectoral fin distance; SnV, snout-pelvic fin distance.

fins, with emphasis on a band of pigments in the distal portion of the anal fin rays. At this stage, it is already possible to observe the appearance of scales. The count of the total number of fin elements (spines and rays) is dorsal 14–17 (mode = 16), anal 20–28 (mode = 25), pelvic 5–8 (mode = 8) and pectoral 6–15 (mode = 12). The number of total myomeres ranges from 39–41 (mode = 40, $n = 13$), with 22–23 pre-anal and 17–18 post-anal segments.

3.2 | Characterization of the juvenile period

This period started at 504 hph and the SL of the individuals ranged from 28.77 to 48.61 mm (mean \pm standard deviation = 37.65 mm \pm 6.04) (Figure 2h). The head has a convex dorsal profile, terminal mouth, double nostrils and spherical and well-pigmented eyes. The opercula are apparently formed. The anal opening is situated in the vertical that goes beyond the median region of the body. The body has a rhomboid shape, compressed laterally, and has abdominal saws that form a keel in the anteroventral region. Throughout the body, it is possible to visualize the presence of small cycloid scales. The pigmentation is composed of punctiform chromatophores that form conspicuous, rounded and variable-sized spots (always smaller than the pupil) distributed along the body, mainly above the lateral line. In addition to these evident spots, the body has numerous dendritic and punctiform pigments distributed in greater concentration in the dorso-lateral part, which makes this region darker than the ventral portion of the body. Pigmentation is also evident around the eyes, on the snout and nostrils and between the rays of the fins. The distal part of the anal and caudal fin rays has pigments forming a band at its extremities. Absence of finfold. All other fins are already formed and with segmented rays. The sequence of complete fin formation, including segmentation of the rays is caudal, dorsal (II, 14–16), anal (II, 23–26), pelvic (7–8) and pectoral (I, 13–15). Due to the development of muscle tissue, myomere counting is not possible.

3.3 | Morphometric relationships

The body is moderate to long in yolk-sac larvae (33.63%–14.30%), pre-flexion stage (20.06%–14.49%) and flexion stage (25.28%–29.68%) and highly variable in the post-flexion stage (26.68%–46.62%) and juveniles (47.23%–55.32%). The head can vary from small in yolk-sac larvae (9.36%–23.10%) and pre-flexion stage (14.95%–19.14%) to moderate in flexion (28.90%–31.19%), and large in post-flexion (29.53%–36.47%) and juvenile (29.26%–35.62%) stages. The eyes are moderate to large throughout the larval stage (17.41%–46.80%) and moderate in the juvenile period (27.44%–31.87%). In yolk-sac larvae, the HD and SnL variables increased, whereas in the pre-flexion stage they remained the same. In the flexion stage, all variables increased, except SnP, which decreased. In the post-flexion stage, all variables tended to increase, except SnV, which remained the same. In the juvenile period, most variables remained; only SnA increased (Table 1).

3.4 | Body growth

The variables ED and HD related to HL, and BD, HL, SnA and SnP related to SL were better represented by the discontinuous isometric growth model. The breakpoint of these variables was observed during the post-flexion stage. The other variables showed allometric growth with positive values for the SnL and SnP, and negative for the SnD (Figures 3 and 4, and Table 2).

4 | DISCUSSION

During early development, many Characiformes species, mainly migratory species, such as *P. brachypomus*, are poorly developed soon after hatching, with scarce pigmentation in the eyes, a nonfunctional mouth

and rapid absorption of the yolk (Lima *et al.*, 2021; Oliveira *et al.*, 2012), and are therefore considered altricial. These characteristics are associated with the reproductive aspects and strategies of each species, such as high fecundity, rapid embryonic development and absence of parental care (Fuiman, 2002; Nakatani *et al.*, 2001). Furthermore, body modifications occur over the ontogeny of *P. brachypomus* that allow the species to go through the critical phase of early development and thus maximize its chances of survival in the environment.

The larvae of *P. brachypomus* maintain endogenous reserves until close to 98 hph (pre-flexion stage); after this interval they showed total yolk absorption. This result contrasts with that found for other neotropical Characiformes species (Lima *et al.*, 2021; Santos *et al.*, 2017; Silva *et al.*, 2022). Normally, yolk-absorption time and duration of each stage vary according to the species (Godinho *et al.*, 2003; Lima *et al.*, 2013). However, despite interspecific variations, factors such as temperature and the condition of breeding matrices can influence the initial ontogenetic processes of fishes (Cruz *et al.*, 2022; Lima *et al.*, 2013; Santos *et al.*, 2017).

In fish farming, after yolk absorption, when this feeding transition occurs, the post-larval phase begins: the larvae begin to feed exogenously, mainly on plankton present in the water and a balanced diet, as observed for other Amazonian species (Lima *et al.*, 2021; Silva *et al.*, 2022). However, this phase of fish farming is not always successful for *P. brachypomus* larvae, as the post-larvae may not adequately accept the artificial diet, favouring low nutrition and poor formation of vital structures, such as the digestive tract and fins, and eye pigmentation (Portella *et al.*, 2014).

Among the main functional organs, the first to be formed in *P. brachypomus* are the eyes, nostrils, swim bladder and mouth, which appear along the yolk-sac and pre-flexion stages. This is associated with the need for the formation of sensory and locomotor structures, which occur simultaneously in the search for adequate exogenous foods (Aruho *et al.*, 2019; Oliveira *et al.*, 2020; Silva *et al.*, 2021).

Complementarily, the functional swim bladder allows the larvae to move along the water column and have greater mobility and stability (Blaxter, 1986). These conditions provide the species with more success in capturing food. The beginning of the exotrophic phase soon after the absorption of endogenous reserves prevents starvation and maximizes the growth and development of *P. brachypomus* larvae, with positive reflexes throughout the initial ontogeny (Kjørsvik *et al.*, 2011; Kojima *et al.*, 2015; Portella *et al.*, 2014).

The mouth in the terminal position, the eyes ranging from moderate to large and the intestine reaching the middle region of the body in *P. brachypomus* are common features of Serrasalminae during the early stages and are associated with the trophic guild of herbivorous or omnivorous fishes (Andrade *et al.*, 2019; Araújo-Lima *et al.*, 1993; Nakatani *et al.*, 2001; Oliveira *et al.*, 2022). Despite the general morphological similarity of the early stages of *P. brachypomus* with other Serrasalminae, the presence of the long intestine, extending beyond the midline of the body, together with the absence of a forward-facing pre-dorsal spine, distinguishes *P. brachypomus* of the species of the genus *Serrasalmus*, *Pygocentrus* and *Pristobrycon* for having a short

intestine, not exceeding half of the body and the presence of pre-dorsal spines facing forward (visible from the beginning of the post-flexion stage) (Cavicchioli *et al.*, 1997; Machado-Allison, 1987; Nakatani *et al.*, 2001). In addition, the presence of a short adipose-fin base (less than one-third of the dorsal fin), visible in post-flexion, distinguishes *P. brachypomus* from *Metynnis* species, which have an elongated adipose base (more than one-third of the base of the dorsal fin dorsal) (Ota, 2015).

The formation of fins during the initial ontogeny of fish comprises an important aspect as it is associated with locomotor capacity (Santos *et al.*, 2017, 2020). The development of these structures is linked to changes in the functional characteristics of the species, allowing the larvae to explore new habitats conducive to protection and food capture. The sequence of complete fin formation observed in *P. brachypomus* (caudal, dorsal, anal, pelvic and pectoral) is similar to that observed for other Characiformes (Nakatani *et al.*, 2001; Oliveira *et al.*, 2022; Santos *et al.*, 2017; Silva *et al.*, 2022) that have swimming and feeding associated with the pelagic region. However, this pattern contrasts with what was observed for *Triportheus auritus* (Valenciennes, 1850) and *T. paranensis* (Gunther 1874), species that have swimming and feeding associated with the subsurface of the water column (Cajado *et al.*, 2021; Oldani, 1979).

The colour pattern composed of scarce pigmentation that intensifies along ontogeny recorded in *P. brachypomus* is observed in altricial larvae of other fish species that have essentially pelagic behaviour (Cajado *et al.*, 2021; Oliveira *et al.*, 2021; Sanches *et al.*, 2001). However, when chromatophores (dendritic and punctate) and melanophores are present and widely distributed throughout the body, they constitute one of the basic and fundamental characters to differentiate *P. brachypomus* from other congeners in the Amazon basin.

Juveniles of *P. brachypomus* have rounded spots evident throughout the body. This characteristic allows them to be distinguished from (1) *Colossoma macropomum* (Cuvier, 1816) by the presence of dendritic pigments irregularly distributed throughout the body and the presence of a spot on the mid-flank region (Nakatani *et al.*, 2001), (2) *Piaractus orinoquensis* Escobar, Ota, Machado – Allison, Andrade-López, Farias & Hrbek, 2019, by the presence of a conspicuous eye-shaped spot located on the flanks (Machado-Allison, 2020), (3) *Pristobrycon striolatus* (Steindachner, 1908) due to the presence of dendritic pigments irregularly distributed throughout the body and a humeral spot (Machado-Allison, 2020), (4) *Myloplus asterias* (Müller & Troschel, 1844) due to the presence of punctate chromatophores, regularly distributed throughout the body with absent spots or bands (Oliveira *et al.*, 2022), (5) *Myloplus lobatus* (Valenciennes, 1850) due to the presence of brownish vertical bands and grouped pigments that form spots on the dorsal region of the head (Oliveira *et al.*, 2022), (6) *Mylossoma aureum* (Spix & Agassiz, 1829) due to its intensely pigmented anal and dorsal fins, as well as an absent posterolateral region of the body (Araújo-Lima *et al.*, 1993), (7) *Mylossoma albiscopum* (Cope, 1872) due to the presence of a spot on the side of the body, pigments on the caudal peduncle and vertical bands in the anterior region of the body, (Araújo-Lima *et al.*, 1993), (8) *Tometes kranponhah* Andrade *et al.*, 2016, by the presence of a well-defined humeral spot,

dark spot on the central part of the operculum and vertically or circularly elongated spots on the ventral part of the flanks (Andrade *et al.*, 2016), and (9) *Prosomyleus rhomboidalis* (Cuvier 1818) for not having spots along the body (individuals smaller than 35 mm SL) (Ponton & Mérigoux, 2001).

Another useful feature in the identification of fish larvae, even if they present intra- and interspecific variation, is the count of total or partial myomeres (Araújo-Lima & Donald, 1988; Cajado *et al.*, 2021; Pereira *et al.*, 2017). Myomeres generally correspond to the number of vertebrae, including those of the Weberian apparatus and urostyle, plus one more unit (Araújo-Lima & Donald, 1988; Borges *et al.*, 2000). The larvae of *P. brachypomus* can be diagnosed when compared to tambaqui *C. macropomum* because they present myomeres ranging from 39 to 41 segments and post-anal segments from 17 to 20 compared with 33–35 total and 12–15 post-anal segments (Nakatani *et al.*, 2001). However, for other sympatric species of Serrasalminae (e.g., *M. asterias*, *M. lobatus*, *M. albiscopum* and *M. aureum*), the variation of total, pre-anal and post-anal myomeres presents some overlap and is not useful for differentiating them. *Piaractus brachypomus* differs from these species by counting rays in the dorsal fin (15–16 vs. ≥ 20 rays) (Araújo-Lima *et al.*, 1993; Oliveira *et al.*, 2022). Thus, the integrative approach using morphological and meristic data is essential for identifying and differentiating between *P. brachypomus* and other sympatric serrasalminids of the Amazon basin.

The morphometric variables analysed in *P. brachypomus* larvae and juveniles were represented by different growth models. These differences are directly associated with body changes (e.g., body mass and volume), emergence of sensory structures and changes in allometric forms, including the interference of extrinsic variables, i.e., social interaction and environmental factors (Fuiman & Higgs, 1997; Silva *et al.*, 2021). In *P. brachypomus*, the allometric growth observed in the variables SnD, SnP and SnL is related to changes in body and head shape that occur over the early development with feeding habits and locomotion of the species (Cajado *et al.*, 2021; Osse & van den Boogaart, 1999).

For the other measured variables (BD, HL, SnA, SnV, HD and ED), a discontinuous isometric growth was observed, i.e., an abrupt change in growth form. For *P. brachypomus*, the greatest body metamorphosis and breakpoints occur during the transition from the post-flexion to juvenile period. According to one study (Kováč *et al.*, 1999), for the breakpoint to be significant, it is necessary that it be associated with some morphological, physiological or survival event. It is at this stage of development that significant changes occur, such as the change in the shape of the body and head and the complete formation of the fins. The occurrence of metamorphosis in the development of *P. brachypomus* can be considered essential for survival in the early life cycle of the species because *Piaractus* larvae have a coordinated development of their sensory, locomotor, digestive and skeletal structures, which allows for the rapid growth and increase in skills that aid in perception, identification and escape from predators (Leitão *et al.*, 2011; Portella *et al.*, 2014).

Morphological and morphometric changes throughout fish ontogeny are associated with specific ecological and physiological requirements and may provide clues about their phylogenetic implications

(Assega *et al.*, 2016; Cajado *et al.*, 2021; Silva *et al.*, 2021). The main changes observed in the early development of *P. brachypomus* are common to the Serrasalminae family and may be directly related to the need to change habitat from the lentic to lotic system (Araújo-Lima *et al.*, 1993; Nakatani *et al.*, 2001; Oliveira *et al.*, 2022). The differential growth in the variables ED, HD and HL reflects dietary changes in the gill apparatus and improvements in vision and the sensory system (Khemis *et al.*, 2013; Kováč *et al.*, 1999; Silva *et al.*, 2021). This enables the larvae to react to visual stimuli and maximize their motor and sensory abilities, facilitating the detection of prey (Blaxter, 1988; Gisbert *et al.*, 2002). The changes recorded in BD, SnA and SnV may reflect an improvement in swimming performance (Rodrigues-Ribeiro *et al.*, 2022), enabling a greater interaction between species and the environment, consequently maximizing the chances of survival.

In conclusion, the larvae of *P. brachypomus* are initially altricial, but in the early stages they develop the organs associated with feeding (eyes, mouth and digestive tract), breathing (gills and operculum) and balance in the water column (swim bladder). The growth patterns of body structures reflect changes in behavioural, ecological and physiological characteristics imposed on the species through development. The greatest body metamorphosis occurs during the transition from the larval to the juvenile period. A combination of characteristics, such as the position of the anus, length of the adipose fin, colour pattern and number of fin rays and myomeres, is useful when used in an integrative manner to differentiate this species from other Serrasalminae from the Amazon basin.

AUTHOR CONTRIBUTIONS

Zaqueu Santos: conceptualization, methodology, visualization, formal analysis, investigation, writing – original draft. Lucas S. Oliveira: methodology, writing – review and editing. Ruineris A. Cajado: formal analysis, validation, writing – review and editing. Fabíola K.S. Silva and Lenise V.F. Silva: writing – review and editing. Diego M. Zacardi: writing – review and editing, supervision, project administration.

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ETHICS STATEMENT

The capture, euthanasia and use of fish larvae and juvenile in this study complied with the guidelines and animal welfare laws of the Conselho Nacional de Controle e Experimentação Animal and was

approved by the Ethical Committee of Universidade do Estado do Pará – Brazil, under registration number 042-2012.

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