



**UNIVERSIDADE FEDERAL DO OESTE DO PARÁ
ICTA - INSTITUTO DE CIÊNCIAS E TECNOLOGIA DAS ÁGUAS
CURSO DE BACHARELADO EM CIÊNCIAS BIOLÓGICAS**

ZAQUEU DOS SANTOS

**EARLY ONTOGENY OF THE COMMERCIALLY VALUABLE FISH *Piaractus
brachypomus* (CHARACIFORMES, SERRASALMIDAE) FROM THE AMAZON,
BRAZIL**

**SANTARÉM – PARÁ
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BRAZIL**

Trabalho de Conclusão apresentado ao Curso de Bacharelado em Ciências Biológicas, da Universidade Federal do Oeste do Pará, para obtenção do grau de Bacharel em Ciências Biológicas.

Orientador: Prof. Dr. Diego Maia Zacardi

**SANTARÉM – PARÁ
2022**

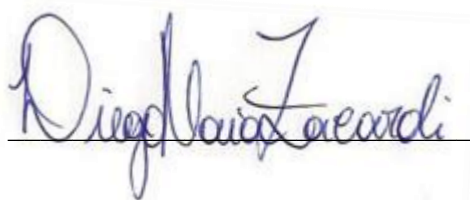
UNIVERSIDADE FEDERAL DO OESTE DO PARÁ
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ATA DE DEFESA DO TRABALHO DE CONCLUSÃO DE CURSO

Aos vinte (20) dias do mês de janeiro do ano de dois mil e vinte e três, às 14 horas e 30 minutos, realizou-se na sala 105, bloco C, prédio NSA, a sessão pública de defesa do Trabalho de Conclusão de Curso do discente Zaqueu dos Santos, intitulado Early ontogeny of the commercially valuable fish red-bellied pacu *Piaractus brachypomus* (Characiformes, Serrasalminidae) from the Amazon, Brazil, como requisito parcial para obtenção do título de Bacharel em Ciências Biológicas. Os trabalhos foram conduzidos pelo professor Dr. Diego Maia Zacardi, orientador do discente e presidente da Banca Examinadora. O discente foi dispensado de banca avaliadora, uma vez que apresentou um artigo científico, sob o mesmo título, publicado na revista Journal of Fish Biology, volume 102(1), páginas 214 a 224, ano de 2022. Após apresentação pública do Trabalho de Conclusão e Curso, o presidente da banca encerrou as atividades dando o parecer final, considerando-o APROVADO. Proclamados os resultados, foram encerrados os trabalhos e, para constar, eu Diego Maia Zacardi, na qualidade de professor orientador do Trabalho de Conclusão de Curso, lavrei a presente ata que assino juntamente com ao discente Zaqueu Dos Santos.

Santarém/PA, 20 de Janeiro de 2023.

Presidente/orientador:



Discente/concluente:



A minha mãe, a maior inspiração para realização dos
meus sonhos.

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“A alegria está na luta, na tentativa, no sofrimento envolvido e não na vitória propriamente dita.”

(Mahatma Gandhi)

RESUMO

O desenvolvimento inicial do pacu-de-barriga-vermelha *Piaractus brachypomus* é descrito usando características morfológicas, merísticas e morfométricas. Foram analisados 127 indivíduos (47 no saco vitelino, 35 em pré-flexão, cinco em flexão, 20 em pós-flexão e 20 em juvenil) com comprimento padrão variando entre 2,92 e 48,61 mm. As larvas nascem pouco desenvolvidas e têm uma gema discoidal de ~6,33 mm de comprimento padrão. Durante a ontogenia inicial, a boca passa do terminal para o subterminal e a abertura anal atinge a linha vertical sobre a região da linha média do corpo. Há mudanças na forma do corpo de longo e moderado a profundo, comprimento da cabeça de pequeno a grande e diâmetro do olho de moderado a grande. Cromatóforos dendríticos estavam presentes na parte ventral, dorsal e superior da bexiga natatória nos estágios larvais iniciais. Manchas arredondadas são evidentes em todo o corpo em juvenis. O número total de miômeros varia de 39 a 41 (20–23 pré-anal, 17–20 pós-anal). Por meio das relações morfométricas, evidenciou-se que as maiores mudanças durante a ontogenia inicial de *P. brachypomus* ocorre na transição do estágio pós-flexão para o período juvenil, indicando mudanças no comportamento, forrageamento e fisiologia.

Palavras-chave: Bacia Amazônica, crescimento isométrico, larvas de peixes, peixes neotropicais, pirapitinga.

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.

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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, Ucayalí, 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. *P. 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. *P. 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 MATERIAL AND METHODS

2.1 Source of biological material

We obtained *P. 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 and 54°33'05"W) in June 2012. This study was approved by the Ethical Committee of Pará State University, Brazil, under the registration number 042-2012. Four specimens (two males and two females) of approximately 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.

Fertilisation occurred after blending and homogenising semen and oocytes using water to activate the process and moisturise the eggs. Subsequently, fertilised eggs were washed and distributed (300 mL) into three 200-litre Zoug incubators (Silva *et al.*, 2009). The larvae were kept in the incubators for approximately 3 d, during which the mouth was fully formed. Subsequently, they were transferred to an earthen fingerling pond and compacted for growth (1000 m²), where they remained for approximately 30 d.

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 hours post-hatching (hph) for the larval period and 672 hph for the juvenile period. The individuals were anaesthetised and euthanised 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 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°C to 29.2°C, pH 6.8–7.3, dissolved oxygen 6.6–7.7 mg/L, and total ammonia 0–0.5 mg/L. However, in the excavated pond nursery, water temperature ranged from 28°C to 31.3°C, pH 5.1–7.2, dissolved oxygen 5.2–7.6 mg/L, and total ammonia 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 stages). The juvenile period was characterised 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 characterisation, 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 preanal (PAM), postanal (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) (Catalog number: LEIPAI 00128).

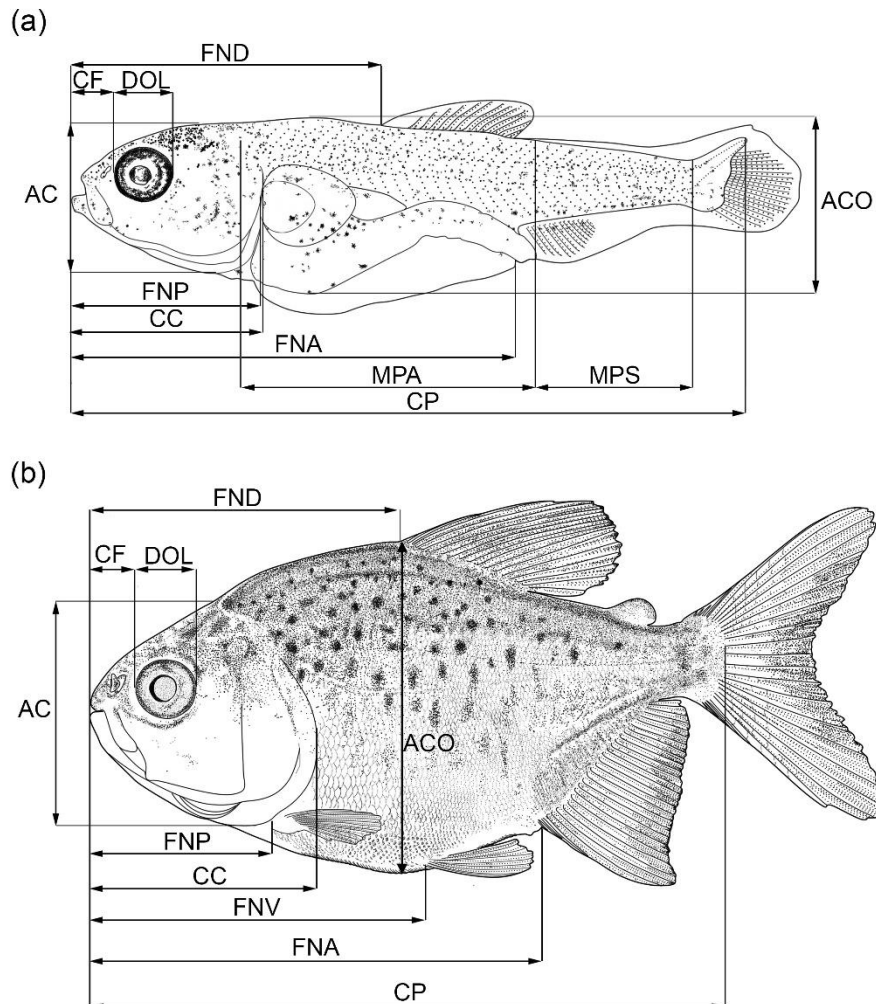


Figure 1 - Figure 1. Morphometric measurements from *Piaractus brachypomus* (Characiformes, Serrasalminidae) during the larval (a) and juvenile (b) periods.

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 & 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 variables) 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, 35 in preflexion, 5 in flexion, 20 in postflexion and 20 in 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.



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

Table 1. Minimum (Min), Maximum (Max), Mean, standard deviation (SD) and morphometric (%) and meristic proportions obtained from larvae and juveniles of *Piaractus brachypomus*. SL: standard length; HL: head length; SnL: snout length; ED: eye diameter; HD: head depth; BD: body depth; SnD: snout-dorsal fin distance; SnA: snout-anal fin distance; SnP: snout-pectoral fin distance; SnV: snout-pelvic fin distance; NV: not visible.

<i>Piaractus brachyomus</i>										
Variables (mm)	Larval period								Juvenile period (n= 20)	
	Yolk sac (n= 47)		Preflexion (n= 36)		Flexion (n= 5)		Postflexion (n= 20)		Min-Max	Mean±SD
	Min-Max	Mean±SD	Min-Max	Mean±SD	Min-Max	Mean±SD	Min-Max	Mean±SD		
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	Min-Max	Mode	Min-Max	Mode	Min-Max	Mode	Min-Max	Mode	Min-Max	Mode
Preanal	20-23	22 (n= 23)	20-22	22 (n= 24)	21-23	22 (n= 3)	NV	NV	NV	NV
Postanal	17-20	18 (n= 32)	17-20	18 (n= 20)	17-18	17 (n= 3)	NV	NV	NV	NV
Total	39-41	40 (n= 27)	39-41	40 (n= 23)	39-40	39 (n= 3)	NV	NV	NV	NV
Rays	Min-Max	Mode	Min-Max	Mode	Min-Max	Mode	Min-Max	Mode	Min-Max	Mode
Dorsal (D)	NV	NV	NV	NV	11-14	13 (n= 2)	14-17	II,16 (n= 9)	14-16	II,15 (n= 9)
Anal (A)	NV	NV	NV	NV	10-21	17 (n= 2)	20-26	II,25 (n= 8)	23-26	II,25 (n= 10)
Pectoral (P)	NV	NV	NV	NV	NV	NV	6-13	12 (n= 5)	13-15	I,14 (n= 11)
Pelvic (V)	NV	NV	NV	NV	NV	NV	5-8	8 (n= 11)	7-8	8 (n= 18)

3.1 Characterisation 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 ± standard deviation = 4.49 mm ± 0.94). The notochord is rectilinear and visible by transparency. The yolk-sac is relatively large and has 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 embryonic fin 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 and 17–20 in the postanal regions.

Preflexion (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 embryonic fin remains as in the anterior stage and there is no indication yet of the differentiation of the pectoral fin rays. The number of total myomeres ranges from 39 to 41 (mode = 40, n = 22), 20–23 preanal and 17–20 postanal 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 embryonic fin 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 visualise the rays of the caudal, dorsal and anal fins. Total myomeres range from 39 to 41 (mode = 40, n = 5), with 21–22 preanal and 17–18 postanal segments.

Postflexion (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; however, throughout development, the thickness of muscle tissue does not allow the visualisation 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 approximately 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 embryonic fin 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 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 preanal and 17–18 postanal segments.

3.2 Characterisation 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 visualise 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 dorsolateral part, which makes this region darker than the ventral portion of the body. Pigmentation is also evident around the eyes, on the snout, 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 embryonic fin. 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, 15–16), anal (II, 23–27), pelvic (7–8), and pectoral (I, 6–15). 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%), preflexion stage (20.06%–14.49%), and flexion stage (25.28%–29.68%) and highly varies in the postflexion 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 preflexion stage (14.95%–19.14%) to moderate in flexion

(28.90%–31.19%) and large in postflexion (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 preflexion stage they remained the same. In the flexion stage, all variables increased, except SnP, which decreased. In the postflexion stage, all variables tended to increase, except SnV, which remained the same. In the juvenile phase, 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 postflexion stage. The other variables showed allometric growth with positive values for the SnL and SnP, and negative for the SnD (Figures 3, 4; Table 2).

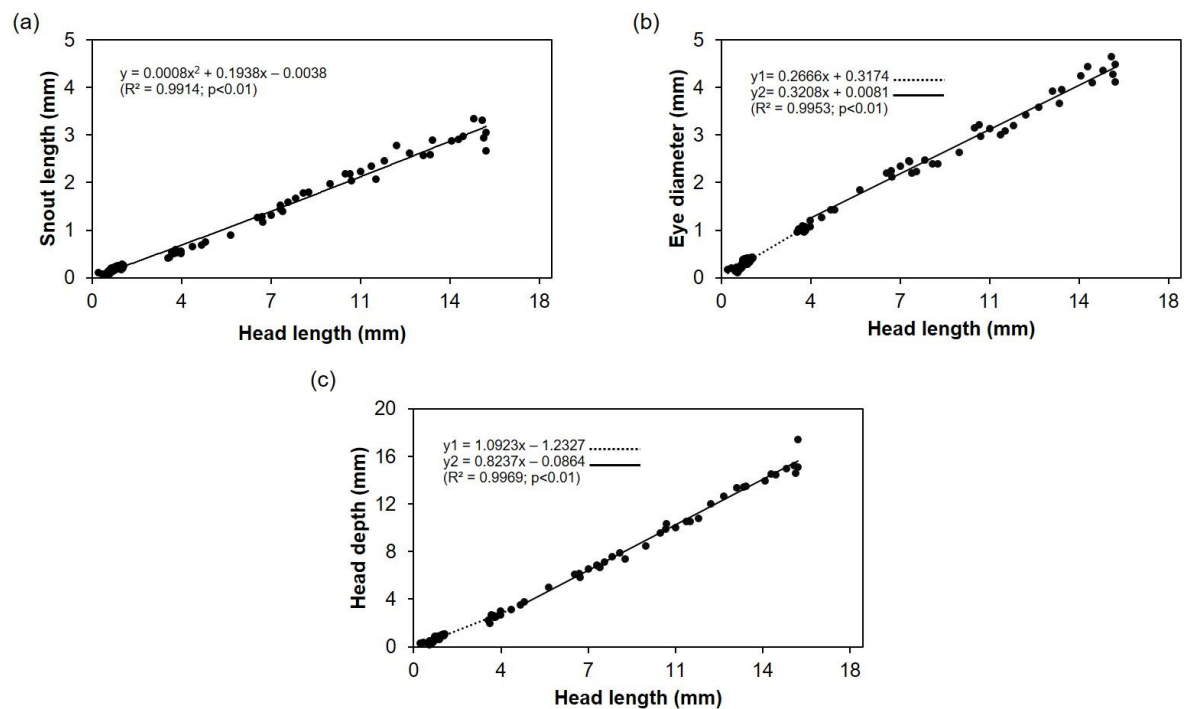


Figure 3. Morphometric relationships (mm) between head length and snout length (a), eye diameter (b) and head depth (c) during development of *Piaractus brachypomus* (Characiformes, Serrasalminidae).

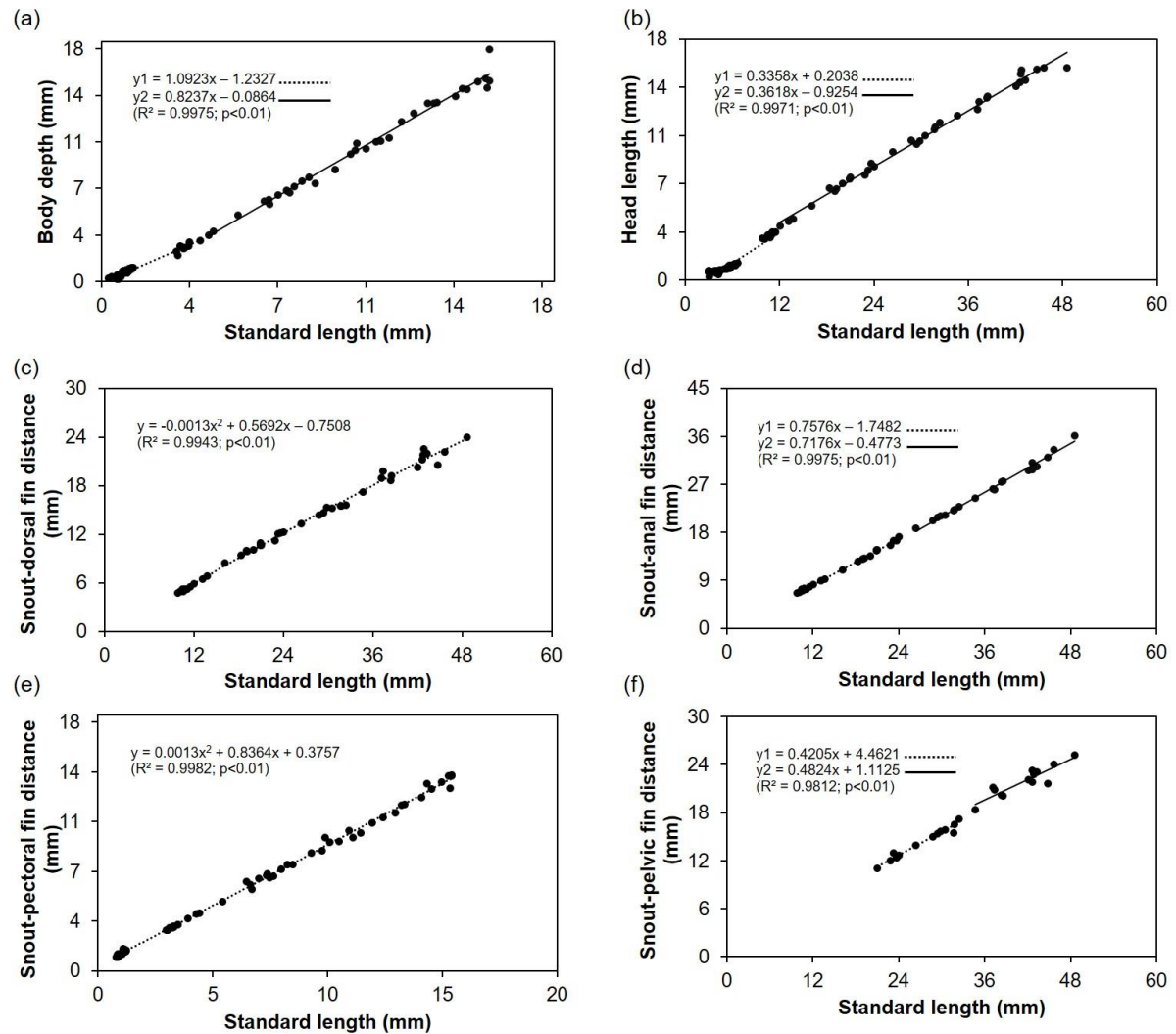


Figure 4. Morphometric relationships (mm) between the standard length and body depth (a), head length (b), snout-dorsal fin distance (c), snout-anal fin distance (d), snout-pectoral fin distance (e) and snout-pelvic fin distance (f) during the early development of *Piaraactus brachypomus* (Characiformes,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

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 *Piaraactus brachypomus*. R^2 = coefficient of determination. BM = best model, BP = breaking point (mm), n = number of analyzed individuals. Bold values represent a significant difference ($p < 0.05$).

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	0.995	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	0.981	0.9764	4.20	29.78	17.48	S	18.10	26

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 non-functional 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, maximise its chances of survival in the environment.

The larvae of *P. brachypomus*, maintain endogenous reserves until close to 98 hph (preflexion 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 preflexion stages. This is associated with the need for the formation of sensory and locomotor structures that 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 more success in capturing food. The beginning of the exotrophic phase soon after the absorption of endogenous reserves prevents starvation and maximises 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 Serrasalminidae 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 Serrasalminidae, the presence of the long intestine, extending beyond the midline of the body, together with the absence of a forward-facing predorsal 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 predorsal spines facing forward (visible from the beginning of the postflexion 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 postflexion, distinguishes *P. brachypomus* from *Metynnias* 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, Jégu & Giarrizzo, 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 presents myomeres ranging from 39 to 41 segments and postanal segments from 17 to 20 compared with 33–35 total and 12–15 postanal segments (Nakatani *et al.*, 2001). However, for other sympatric species of Serrasalminidae (e.g., *M. asterias*, *M. lobatus*, *M. albiscopum* and *M. aureum*), the variation of both total, preanal and postanal myomeres presents some overlap and is not useful for differentiate them. *P. 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 serrasalmids 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 occurs 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 maximise 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 maximising the chances of survival.

In conclusion, the larvae of *P. brachypomus* are initially altricial; however, 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 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.

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CONTRIBUTIONS

ZS: Conceptualization; Methodology; Visualization; Formal Analysis; Investigation; Writing – Original Draft. LSO: Methodology; Writing – Review and Editing. RAC: Formal Analysis; Validation, Writing – Review and Editing. FKSS and LVFS: Writing – Review and Editing. DMZ: Writing – Review and Editing; Supervision; Project administration.

REFERENCES

- Ahlstrom, E. H., Butler, J. L., & Sumida, B. Y. (1976). Pelagic stromateoid fishes (Pisces, Perciformes) of the Eastern Pacific: kinds, distributions, and early life histories and observations on five of these from the Northwest Atlantic. *Bulletin of Marine Science*, 26, 285–402.
- Andrade, M. C., Jégu, M., & Giarrizzo, T. (2016). *Tometes kranponhah* and *Tometes ancylorhynchus* (Characiformes: Serrasalminidae), two new phytophagous serrasalmids, and the first *Tometes* species described from the Brazilian Shield. *Journal of Fish Biology*, 89, 467–494.
- Andrade, M. C., Fitzgerald, D. B., Winemiller, K. O., Barbosa, P. S., & Giarrizzo, T. (2019). Trophic niche segregation among herbivorous serrasalmids from rapids of the lower Xingu River, Brazilian Amazon. *Hydrobiologia*, 829, 265–280.
- Araújo-Lima, C. A. R. M., & Donald, E. (1988). Número de vértebras de Characiformes do rio Amazonas e seu uso na identificação de larvas do grupo. *Acta Amazonica*, 18, 351–358.
- Araújo-Lima, C. A. R. M., & Gomes, L. C. (2005). Criação de tambaqui. In B. Baldisserotto & L. C. Gomes (Eds.), *Espécies nativas para piscicultura no Brasil* (pp. 175–202). Santa Maria: Editora UFSM.
- Araújo-Lima, C. A. R. M., Kirovsky, A. L., & Marca, A. G. (1993). As larvas dos pacus, *Mylossoma* spp (Teleostei; Characidae), da Amazônia Central. *Revista Brasileira de Biologia*, 53, 591–600.
- Aruho, C., Walakira, J. K., Bugenyi, F., Rutaisire, J., & Reading, B. J. (2019). Morphology and functional ontogeny of the digestive tract of *Barbus altianalis* larvae. *African Zoology*, 54, 137–149.
- Assega, F. M., Birindelli, J. L. O., Bialezki, A., & Shibatta, O. A. (2016). External morphology of *Lophiosilurus alexandri* Steindachner, 1876 during early stages of development, and its implications for the evolution of Pseudopimelodidae (Siluriformes). *PloS One*, 11, e0153123.
- Blaxter, J. H. S. (1986). Development of sense organs and behaviour of teleost larvae with special reference to feeding and predator avoidance. *Transactions of the American Fisheries Society*, 115, 98–114.
- Blaxter, J. H. S. (1988). Pattern and variety in development. In W. S. Hoar & D. J. Randall (Eds.), *The physiology of developing fish: eggs and larvae* (pp. 1–58). San Diego, CA: Academic Press.
- Borges, M. E. E., Nakatani, K., Bialezki, A., & Felis, M. E. G. (2000). Diferenciação do número de vértebras de algumas espécies de Characiformes (Osteichthyes) da bacia do Rio Paraná, Brasil. *Acta Scientiarum. Biological Sciences*, 22, 539–544.
- Cajado, R. A., Oliveira, L. S., Silva, F. K. S., & Zacardi, D. M. (2021). Early development of the Neotropical fish known as long sardine *Triporthus auritus* (Valenciennes 1850) (Characiformes, Triporthidae). *Journal of Applied Ichthyology*, 37, 759–769.
- Cavicchioli, M., Nakatani, K., & Shibatta, O. A. (1997). Morphometric variation of larvae and juveniles of the piranhas *Serrasalmus spilopleura* and *S. marginatus* (Characidae: Serrasalminae) of the Paraná basin, Brazil. *Ichthyological Exploration of Freshwaters*, 8, 97–106.
- Correa, S. B., Betancur-R, R., de Mérona, B., & Armbruster, J. W. (2014). Diet shift of Red Belly Pacu *Piaractus brachypomus* (Cuvier, 1818) (characiformes: Serrasalminidae), a Neotropical fish,

- in the Sepik-Ramu River Basin, Papua New Guinea. *Neotropical Ichthyology*, 12, 827– 834.
- Cruz, S. E. C., Riesco, M. F., Martínez-Bautista, G., Calzada-Ruiz, D., Martínez-Burguete, T., Peña-Marín, E. S., ... Fernández, I. (2022). Larval development in Tropical Gar (*Atractosteus tropicus*) is dependent on the embryonic thermal regime: ecological implications under a climate change context. *Fishes*, 7, 16.
- Escobar, L., M. D., Andrade-López, J., Farias, I. P., & Hrbek, T. (2015). Delimiting evolutionarily significant units of the fish, *Piaractus brachypomus* (Characiformes: Serrasalminidae), from the Orinoco and Amazon River Basins with insight on routes of historical connectivity. *Journal of Heredity*, 106, 428– 438.
- Escobar, L., M. D., Ota, R. P., Machado-Allison, A., Andrade-López, J., Farias, I. P., & Hrbek, T. (2019). A new species of *Piaractus* (Characiformes: Serrasalminidae) from the Orinoco Basin with a redescription of *Piaractus brachypomus*. *Journal of Fish Biology*, 95, 411– 427.
- Froese, R., & Pauly, D. (2022). FishBase. World Wide Web Electronic Publication.
- Fuiman, L. A. (2002). Special considerations of fish eggs and larvae. In L. A. Fuiman & R. G. Werner (Eds.), *Fishery science. The unique contributions of early life stages* (pp. 1– 32). Oxford: OXON: Blackwell Publishing.
- Fuiman, L. A., & Higgs, D. M. (1997). Ontogeny, growth and the recruitment process. In R. C. Chambers & E. A. Trippel (Eds.), *Early Life History and Recruitment in Fish Populations* (pp. 225– 249). London: LND: Chapman & Hall.
- Gisbert, E., Merino, G., Muguet, J. B., Bush, D., Piedrahita, R. H., & Conklin, D. E. (2002). Morphological development and allometric growth patterns in hatchery-reared California halibut larvae. *Journal of Fish Biology*, 61, 1217– 1229.
- Godinho, H. P., Santos, J. E., & Sato, Y. (2003). Ontogênese larval de cinco espécies de peixes do São Francisco. In H. P. Godinho & A. L. Godinho (Eds.), *Águas, peixes e pescadores do São Francisco das Minas Gerais* (pp. 133– 148). Belo Horizonte: PUC Minas.
- Guimarães, I. G., & Martins, G. P. (2015). Nutritional requirement of two Amazonian aquacultured fish species, *Colossoma macropomum* (Cuvier, 1816) and *Piaractus brachypomus* (Cuvier, 1818): a mini review. *Journal of Applied Ichthyology*, 31, 57– 66.
- Khémis, I. B., Gisbert, E., Alcaraz, C., Zouiten, D., Besbes, R., Zouiten, A., ... Cahu, C. (2013). Allometric growth patterns and development in larvae and juveniles of thick-lipped grey mullet *Chelon labrosus* reared in mesocosm conditions. *Aquaculture Research*, 44, 1872– 1888.
- Kjørsvik, E., Galloway, T. F., Estevez, A., Sæle, Ø., & Moren, M. (2011). Effects of larval nutrition on development. In G. J. Holt (Ed.), *Larval Fish Nutrition* (pp. 219– 248). Hoboken: John Wiley & Sons, Inc..
- Kojima, J. T., Leitão, N. J., Menossi, O. C. C., Freitas, T. M., Dal-Pai Silva, M., & Portella, M. C. (2015). Short periods of food restriction do not affect growth, survival or muscle development on pacu larvae. *Aquaculture*, 436, 137– 142.
- Kolmann, M. A., Hughes, L. C., Hernandez, L. P., Arcila, D., Betancur, R., Sabaj, M. H., ... Ortí, G. (2021). Phylogenomics of Piranhas and Pacus (Serrasalminidae) uncovers how dietary convergence and parallelism obfuscate traditional morphological taxonomy. *Systematic Biology*, 70, 576– 592.
- Kováč, V., Copp, G. H., & Francis, M. P. (1999). Morphometry of the stone loach, *Barbatula barbatula*: do mensural characters reflect the species' life history thresholds? *Environmental Biology of Fishes*, 56, 105– 115.
- Leis, J. M., & Trnski, T. (1989). *The larvae of Indo-Pacific shorefishes*. Honolulu: University Hawaii Press.

- Leitão, N. J., Pai-Silva, M. D., Almeida, F. L. A., & Portella, M. C. (2011). The influence of initial feeding on muscle development and growth in pacu *Piaractus mesopotamicus* larvae. *Aquaculture*, 315, 78–85.
- Lima, A. F., Makrakis, M. C., Gimenes, M. F., Makrakis, S., Silva, P. S., & Assumpção, L. (2013). Mudanças morfológicas no trato digestório e composição da dieta de larvas e juvenis do linguado *Catathyridium jenynsii* no reservatório de Itaipu, rio Paraná, Brasil. *Iheringia, Série Zoologia*, 103, 214–221.
- Lima, D. L. G., Cajado, R. A., Silva, L. V. F., Maia, J. L. S., & Zacardi, D. M. (2021). Morphological description of the initial development of *Brycon amazonicus*. *Biota Amazônia*, 11, 60–67.
- Machado-Allison, A. (1987). *Los peces de los llanos de Venezuela: un ensayo sobre su historia natural* (2nd ed.). Caracas: Universidad Central de Venezuela, Consejo de Desarrollo Científico y Humanístico.
- Machado-Allison, A. (1987). *Los peces de los llanos de Venezuela: un ensayo sobre su historia natural* (2nd ed.). Caracas: Universidad Central de Venezuela, Consejo de Desarrollo Científico y Humanístico.
- Machado-Allison, A. (2020). *Los peces de los llanos de Venezuela: uno ensayo sobre su historia natural* (4th ed.). Caracas: Consejo de Desarrollo Científico y Humanístico, Academia de Ciencias Físicas, Matemáticas y Naturales.
- Nakatani, K., Agostinho, A. A., Bialezki, A., Baumgartner, G., Sanches, P. V., Makrakis, M. C., & Pavanelli, C. S. (2001). *Ovos e larvas de peixes de água doce: desenvolvimento manual de identificação*. Maringá: EDUEM.
- Nico, L. G., Jégu, M., & Andrade, M. C. (2018). Family Serrasalminidae - Piranhas and Pacus. In P. van der Sleen & J. S. Albert (Eds.), *Field guide to the fishes of the Amazon, Orinoco, and Guianas* (pp. 172–196). Princeton: Princeton University Press.
- Oldani, N. O. (1979). Identificación y morfología de larvas y juveniles de *Triportheus paranensis* (Gunther, 1874) (Pisces, Characidae). *Revista de la Asociación de Ciencias Naturales del Litoral*, 10, 61–71.
- Oliveira, C. C., Suzuki, M. A. L., Oliveira, L. S., & Zacardi, D. M. (2020). Description of the initial development and temporal distribution of *Microphilypnus tapajosensis* larvae and juveniles in a reservoir in the Eastern Amazon. *Ciência e Natura*, 42, e49.
- Oliveira, F. G., Bialezki, A., Gomes, L. C., Santin, M., & Taguti, T. L. (2012). Desenvolvimento larval de *Brycon hilarii* (Characiformes, Characidae). *Iheringia, Série Zoologia*, 102, 62–70.
- Oliveira, L. S., Cajado, R. A., Silva, F. K. S., Bialezki, A., & Zacardi, D. M. (2021). Larval development of the freshwater croaker *Pachypops fourcroyi* (La Cépède 1802) (Perciformes: Sciaenidae). *Journal of Fish Biology*, 99, 2056–2059.
- Oliveira, L. S., Cajado, R. A., Silva, F. K. S., Andrade, M. C., & Zacardi, D. M. (2022). Early development of two commercially valuable fish from the lower Amazon River, Brazil (Characiformes: Serrasalminidae). *Neotropical Ichthyology*, 20.
- Osse, J. W. M., & van den Boogaart, J. G. M. (1999). Dynamic morphology of fish larvae, structural implications of friction forces in swimming, feeding and ventilation. *Journal of Fish Biology*, 55, 156–174.
- Ota, R. P. (2015). Revisão taxonômica e Filogenia morfológica de *Metynnis* Cope, 1878 (Characiformes: Serrasalminidae) (pp. 1–478). Manaus: Instituto Nacional de Pesquisas da Amazônia.
- Pereira, L. H. A., Bialezki, A., & Bonecker, A. C. T. (2017). Larval and juvenile development of *Tatia intermedia* (Siluriformes: Auchenipteridae). *Journal of Fish Biology*, 90, 1098–1103.

- Ponton, D., & Mérigoux, S. (2001). Description and ecology of some early life stages of fishes in the River Sinnamary (French Guiana, South America). *Folia Zoologica*, 50, 1– 116.
- Portella, M. C., Jomori, R. K., Leitão, N. J., Menossi, O. C. C., Freitas, T. M., Kojima, J. T., ... Carneiro, D. J. (2014). Larval development of indigenous South American freshwater fish species, with particular reference to pacu (*Piaractus mesopotamicus*): A review. *Aquaculture*. Elsevier, 20(2014), 402– 417.
- Reynalte-Tataje, D. A., Lopes, C. A., Massaro, M. V., Hartmann, P. B., Sulzbacher, R., Santos, J. A., & Bialetzki, A. (2020). State of the art of identification of eggs and larvae of freshwater fish in Brazil. *Acta Limnologica Brasiliensia*, 2020, e6.
- Rodrigues-Ribeiro, M., Suzuki, K., & Martins, R. S. (2022). Early development of pearlside *Maurolicus stehmanni* off south-eastern Brazil. *Journal of Fish Biology*, 100, 519– 531.
- Roshni, K., Renjithkumar, C. R., & Kurup, B. M. (2014). Record of a newly introduced fish, red-bellied pacu *Piaractus brachypomus* (Cuvier, 1818) (Characiformes, Serrasalminidae), in a tropical wetland system, India. *Journal of Applied Ichthyology*, 2014, 1037– 1038.
- Sanches, P. V., Baumgartner, G., Bialetzki, A., Suiberto, M. R., Gomes, F. D. C., Nakatani, K., & Barbosa, N. D. C. (2001). Caracterização do desenvolvimento inicial de *Leporinus friderici* (Osteichthyes, Anostomidae) da bacia do rio Paraná, Brasil. *Acta Scientiarum. Biological Sciences*, 23, 383– 389.
- Santos, G. M., Ferreira, E. J. G., & Zuanon, J. A. S. (2009). *Peixes comerciais de Manaus* (2nd ed.). Manaus: Editora INPA.
- Santos, J. A., Iquematsu, M. S., Soares, C. M., Galdioli, E. M., Silva, K. F., Teixeira, V. A., & Bialetzki, A. (2017). Distribuição temporal e desenvolvimento inicial de *Moenkausia cf. gracilima* (Lucena & Soares, 2016) (Osteichthyes, Characidae) no alto rio Paraná, Brasil. *Acta Limnologica Brasiliensia*, 29, e109.
- Seshagiri, B., Kumar, A., Pradhan, P. K., Sood, N., Kumar, U., Satyavati, C., ... Jena, J. K. (2022). Farming practices and farmers' perspective of a non-native fish red-bellied Pacu, *Piaractus brachypomus* (Cuvier, 1818) in India. *Aquaculture*, 547, 737483.
- Silva, F. K. S., Cajado, R. A., Oliveira, L. S., Ribeiro, F. R. V., & Zacardi, D. M. (2021). Early ontogeny of *Pimelodus blochii* Valenciennes, 1840 (Siluriformes: Pimelodidae): Neotropical catfish. *Zootaxa*, 4948, 83– 98.
- Silva, F. K. S., Cajado, R. A., Oliveira, L. S., Santos, Z., Santos, J. A., Silva, L. V. F., ... Zacardi, D. M. (2022). Early development of *Prochilodus nigricans* Spix & Agassiz 1829 (Characiformes: Prochilodontidae) in captivity. *Aquaculture Research*, 00, 1– 16.
- Silva, L. V. F. (2006). Morfologia, morfometria, distribuição de células mucosas e de cloreto em embriões e larvas de jundiá, *Rhamdia quelen* (Heptapteridae). Efeito do pH e concentração de cálcio e magnésio da água. São Carlos: Universidade Federal de São Carlos 115 pp.
- Silva, L. V. F., Fernandes, M. N., & Baldisserotto, B. (2009). Incubação e desenvolvimento de peixes aplicados à piscicultura: necessidades e cuidados. In M. Tavares-Dias (Ed.), *Manejo e Sanidade de Peixes em Cultivo* (pp. 64– 88). Macapá: EMBRAPA.
- Sokal, R. R., & Rohlf, F. J. (1989). *Biometry: the principle and practice of statistics in biological research*. New York: W. H. Freeman and Company.
- Valladão, G. M. R., Gallani, S. U., & Pilarski, F. (2018). South American fish for continental aquaculture. *Reviews in Aquaculture*, 1(2018), 351– 369.
- Vásquez-Torres, W., & Arias-Castellanos, J. A. (2013). Crescimento de juvenis de *Piaractus brachypomus* alimentados com dietas contendo diferentes perfis de aminoácidos essenciais. *Pesquisa Agropecuária Brasileira*, 48, 849– 856.

- Zacardi, D. M., Santos, J. A., Oliveira, L. S., Cajado, R. A., & Pompeu, P. S. (2020). Ichthyoplankton studies as referential for the management and monitoring of fishery resources in the brazilian amazon basin. *Acta Limnologica Brasiliensia*, 32, 1– 9.
- Zarei, F., & Rajabi-Maham, H. (2017). First record of exotic *Piaractus brachypomus* Cuvier, 1818 (Characiformes: Serrasalminidae) in Zarivar Lake, western Iran. *Journal of Applied Ichthyology*, 33, 810– 812.

ANEXO 1

CÓPIA DA PRIMEIRA PÁGINA DO ARTIGO PUBLICADO

¹Early ontogeny of the commercially valuable fish red-bellied pacu *Piaractus brachypomus* (Characiformes, Serrasalminidae) from the Amazon, Brazil



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REGULAR PAPER



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; Esmaili 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

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