BOLETIM DO INSTITUTO DE PESCA
Scientific Article

Early morphological development and growth pattern in larvae and juveniles of *Cichlasoma amazonarum* (Teleostei, Cichlasomatinae): An Amazonian ornamental fish

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ABSTRACT

This study presents the first description of the larval and juvenile development of *Cichlasoma amazonarum* based on morphological, meristic, and morphometric analyses, in addition to evaluating the species' initial growth pattern. To date, this is the only study to provide information on the early development of this species of ornamental importance. The standard length of the 162 individuals analyzed ranged from 3.91 to 28.75 mm. The larvae have a rounded head, lack adhesive organs, and exhibit a short snout, an open terminal mouth, and rounded, prominent, pigmented eyes. Initially, dendritic chromatophores are distributed along the dorsal portion of the head and around the jaw, while four vertical melanophore bars are observed along the body. These bars subdivide during growth, forming eight bars in juveniles, in addition to a dark band in the prelacrimal region and a mediolateral spot located below the fifth bar. Juveniles exhibit characteristics similar to those of adults. The total number of myomeres ranges from 23 to 24 segments. Growth patterns of the variables were evaluated using three regression models, whose results partially support the hypothesis of saltatory ontogeny. The morphological characteristics observed are consistent with the ecological requirements of the species, which are associated with lentic and structurally complex environments with a high abundance of aquatic macrophytes.

Keywords: Cichlid; Early development; Color pattern; Discontinuous isometric growth; Neotropical fish.

Desenvolvimento morfológico inicial e padrão de crescimento em larvas e juvenis de *Cichlasoma amazonarum* (Teleostei, Cichlasomatinae): Um peixe ornamental amazônico

RESUMO

Este estudo apresenta a primeira descrição do desenvolvimento larval e juvenil de *Cichlasoma amazonarum* com base em análises morfológicas, merísticas e morformétricas, além de avaliar o padrão de crescimento inicial da espécie. Até o momento, trata-se do único trabalho a fornecer informações sobre essa espécie de importância ornamental. O comprimento padrão dos 162 indivíduos analisados variou de 3,91 a 28,75 mm. As larvas apresentam cabeça arredondada, sem órgãos adesivos, focinho curto, boca terminal aberta e olhos arredondados, proeminentes e pigmentados. Inicialmente, os cromatóforos dendríticos distribuem-se na porção dorsal da cabeça, ao redor da mandíbula e em quatro barras verticais de melanóforos ao longo do corpo, que se subdividem durante o crescimento, tornando-se oito barras nos juvenis, além de uma faixa escura na região pré-lacrimal e de uma mancha médio-lateral situada abaixo da quinta barra. Os juvenis apresentam características semelhantes às dos adultos. O número total de miômeros varia de 23 a 24 segmentos. Os padrões de crescimento das variáveis foram avaliados por meio de três modelos de regressão cujos resultados corroboram parcialmente com a hipótese de ontogenia saltatória. As características morfológicas observadas são consistentes com as exigências ecológicas da espécie, associadas a ambientes lênticos e estruturados, com elevada abundância de macrófitas aquáticas.

Palavras-chave: Ciclídeos; Desenvolvimento inicial; Padrão de coloração; Crescimento isométrico descontínuo; Peixe neotropical.

Received: April 22, 2026 | **Approved:** September 29, 2026

Section editor: Raniere Garcez Costa Sousa

INTRODUCTION

A large proportion of taxonomic studies on freshwater ichthyoplankton focuses on the identification of fish eggs and larvae collected in natural environments, and most of these studies report the same difficulty associated with the morphological similarities observed among different groups throughout ontogenetic development (Oliveira et al., 2022; Reynalte-Tataje et al., 2020; Santos et al., 2022). Cichlids exhibit a certain degree of parental care and can be divided into two groups: substrate spawners and mouthbrooders.

Despite developmental studies describing the early stages of species such as *Cichlasoma dimerus* (Heckel, 1840) (Meijide & Guerrero, 2000) and *Cichlasoma gadovii* (Regan, 1905) (Cabrera et al., 1988), many of these studies are entirely based on reproduction under controlled conditions and are rarely conducted in natural environments (Sefc, 2011).

Cichlasoma amazonarum, popularly known as acará, is a small-sized species that can reach up to 15 cm in total length, and commonly found in streams, floodplain lakes, rivers, and creeks of the Amazon Basin, particularly in areas with marginal vegetation that provide shelter and spawning sites (Beltrão et al., 2018; Dagosta & Pinna, 2019; Nóbrega, 2018). Adults exhibit a deep, laterally compressed body, with dull coloration and black spots distributed on the caudal fin, along the lateral surface of the body, and on the preopercle. The species is distinguished from its congeners by the presence of scales covering the base of the anal and dorsal fins, as well as by the presence of four spines in the dorsal fin (Kullander, 1983; 2003). During the reproductive period, they exhibit territorial behavior, external fertilization with demersal and fractional substrate incubation and prolonged biparental care of the offspring (Keith et al., 2000; Nóbrega, 2018). Batch spawning increases survival chances due to higher fecundity per reproductive season (Spíndola Linhares et al., 2014). Additionally, it is a benthic and opportunistic species with an omnivorous diet, consuming plants, detritus, and small invertebrates (Cavalcante et al., 2015; Carvalho & Tavares-Dias, 2017).

This native cichlid exhibits rapid growth, high reproductive output, and low production costs, and is therefore used as a forage fish in farming systems with other species of higher commercial value (Guarido, 2014; Vásquez-Silvano, 2012). It is also highly valued in the aquarium trade as an ornamental fish (Hercos et al., 2009). It is noteworthy that native ornamental fish are generally obtained through wild harvesting and therefore undergo a quarantine period prior to commercialization, a stage characterized by high mortality rates due to rudimentary transportation, handling, and husbandry methods (Ferreira et al., 2020; Ladislau et al., 2019; Moreau & Coomes, 2007). This highlights the need for further information to support the development of effective captive-breeding and rearing protocols.

Although ornamental Amazonian cichlids are popular, scientific information on their biology and early developmental processes remains limited, with most studies focusing primarily on parental care and behavioral aspects (Alonso et al., 2011; Silva et al., 2005). Specifically for *C. amazonarum*, there are no detailed descriptions of its larval and juvenile stages encompassing morphological, meristic, and morphometric characters, as well as growth patterns throughout ontogeny. Measurements, counts, and pigmentation patterns are valuable tools for reducing knowledge gaps in taxonomic and monitoring studies, particularly for species of limited commercial interest, by improving identification accuracy and reducing uncertainties regarding specimens considered morphologically similar in the literature (Reynalte-Tataje et al., 2020). This information is also essential for establishing management and conservation strategies, supporting actions aimed at protecting species in their natural habitats and reducing extraction pressure on wild stocks, as well as for developing captive-rearing protocols for the ornamental aquaculture industry, thereby reducing dependence on the capture of wild specimens for commercial purposes.

In this context, this study describes the early ontogeny of *C. amazonarum* larvae reared under captive conditions, from the onset of the free-swimming period to the juvenile stage, using morphological, morphometric, and meristic characters and comparing them with other Cichlidae species. In addition, changes in growth rates throughout development were evaluated. We hypothesized that the species would exhibit non-gradual changes in growth, based on statistical analyses testing different regression models and on the morphological transitions observed during development. According to Balon (1984), self-organization processes are characterized by thresholds throughout growth, as observed in cichlid species such as *Mesonauta festivus* (Santos, Cajado et al., 2025) and *Satanoperca pappaterra* (Lopes et al., 2015).

MATERIAL AND METHODS

Biological material collection

Larvae of *C. amazonarum* in the free-swimming stage form a "cloud," always swimming around the parents, and were collected in the natural environment in April 2024, together with the adult individuals that were actively caring for the offspring (parental care). Capture was carried out using a hand net introduced into the limnetic zone of the flooded marginal region

dominated by floating aquatic macrophyte banks in the middle stretch of the Tapajós River (02°25'07"S–054°44'02"W and 02°25'09"S–054°44'01"W), Pará state, Brazil. After capture, the individuals were acclimated and maintained in captivity at the facilities of the Laboratório de Ecologia do Ictioplâncton e Pesca de Águas Interiores, at the Universidade Federal do Oeste do Pará (2°25'07"S, 54°44'27"W). Larvae maintained in captivity were sampled randomly, following a completely randomized experimental design.

Juvenile individuals were included in the analysis to complete the ontogenetic series, allowing the construction of a morphological scale encompassing larvae, juveniles, and adults, as well as providing more robust results for the statistical analyses performed in this study. Juvenile identification followed the criteria established for the species, and specimens were collected in the same area of occurrence, period, and time of day (crepuscular–evening period) as the larvae. However, although they originated from the same region, the larvae and juveniles cannot be considered to belong to the same population or cohort, as there is no guarantee of temporal or genetic continuity between the sampled groups. This condition represents a limitation of the present study, as it may influence the morphometric and pigmentation-pattern comparisons among the ontogenetic stages analyzed.

Juvenile individuals used to complete the ontogenetic series of this study were collected in the same sampling region using a beach seine net, locally known as "picaré," measuring 10 m in length, 1.5 m in height, and with a mesh size of 0.5 mm between opposite knots. It is noteworthy that the mesh size allows the capture of larvae, juveniles, and small adult fish associated with the marginal region of the Tapajós River. Collections were authorized by the System of Authorization and Information on Biodiversity of the Chico Mendes Institute for Biodiversity Conservation and the Brazilian Ministry of Environment, under license nº. 75,271-1/2020, issued in accordance with the Brazilian Institute of Environment and Renewable Natural Resources Normative Instruction nº. 154/2007. Juvenile and adult individuals were identified using specialized literature, Van der Sleen and Albert (2017) for the genus and Kullander (1983) for the species.

Laboratory procedures

At the time of collection, the offspring were immediately separated from their parents and housed individually in a transparent acrylic incubator (14 × 8 × 9 cm) positioned along the side of a rectangular aquarium (60 × 35 × 40 cm), facilitating the observation and monitoring of larval development for approximately 25 days. Sampling frequency and the number of individuals collected were determined entirely at random, with priority given to the developmental stage of the larvae, and sampling was terminated following the mortality of the most advanced developmental stages. The newly captured larvae showed no remaining yolk reserves and had an open and functional mouth. Therefore, they were fed two or three times daily with commercial powdered feed for ornamental fish (Alcon Alevinos), specifically formulated for this developmental stage, until the end of the sampling period. The post-hatching age of the larvae could not be determined because the specimens originated from a natural environment. The larvae were reared at a mean water temperature of 28°C, maintained using an automatic heating system coupled to a thermostat, with a pH of 6.8. The incubator had an approximate usable volume of 784 mL, corresponding to a larval density of 191.33 larvae/L. Once a week, accumulated debris at the bottom of the aquarium was removed by siphoning under continuous water flow. The room in which the aquarium was maintained was subjected to an approximately 12-h light:12-h dark photoperiod. Dissolved oxygen was not measured.

After capture, juvenile specimens were anesthetized with eugenol (0.00005 mg/L) and then fixed in 10% formalin solution buffered with calcium carbonate, a protocol that adequately preserves morphometric characteristics for subsequent analyses (Cunningham et al., 2000). All sample processing strictly followed the euthanasia protocols established by the National Council for the Control of Animal Experimentation (CONCEA, 2018). Specimens were classified according to the developmental stages proposed by Ahlstrom et al. (1976), as modified by Nakatani et al. (2001). The classification included two stages of the larval period (flexion and post flexion) and the juvenile stage, in which complete formation of the fin rays occurs, along with the appearance of scales, up to the size of first sexual maturation. The yolk-sac larval and preflexion stages were not represented because the captured larvae had pigmented eyes, an open mouth, no yolk sac, a flexed posterior end of the notochord, and developing caudal-fin rays. The early flexion/postflexion and late flexion/postflexion stages are presented solely for descriptive purposes. The description of each period was based on observation of the main morphological events and the degree of early development, as well as meristic and morphometric characteristics. Continuous vertical bars of melanophores originate from dorsal blotches (A, B, C, and D) arranged in a conserved pattern on the body, but throughout development they fragment and resegment, becoming enumerated from the caudal to the cephalic direction (1a, 1p, 2, 3, 4a, 4p, 5, 6, 7, and 8), as indicated by Říčan et al. (2005), forming 10 vertical bars in direct count.

The images captured from larvae at different ontogenetic stages corresponded to individuals from the same brood, as the developmental stages were highly synchronized among specimens, reducing the risk of obtaining images of atypical individuals that were not representative of the species. The selection of the best-preserved fixed specimens considered morphological and anatomical integrity, including fin condition, body shape, and pigmentation patterns. Only one individual from each developmental stage that best represented the characteristic patterns of the species was selected. Lighting and magnification were standardized and adjusted as necessary to improve the visualization of morphological characteristics. The side photographed was selected according to Tan (2014). Pigmentation patterns were also analyzed in all individuals.

Subsequently, the specimens were fixed in 4% formalin, placed in glass vials, and deposited in the Collection of Fish Eggs and Larvae of the Laboratório de Ecologia do Ictioplâncton e Pesca em Águas Interiores (LEIPAI) at the Universidade Federal do Oeste do Pará (https://specieslink.net/col/CROLP-LEIPAI/), under the catalog numbers: LEIPAI 00918, LEIPAI 00912, LEIPAI 00710, LEIPAI 00915, LEIPAI 00916, LEIPAI 00190, LEIPAI 00219, LEIPAI 00911, LEIPAI 00913, LEIPAI 00917, and LEIPAI 00914.

Data analysis

For the morphometric analyses, the following variables were measured: head depth (HD), body depth (BD), head length (HL), snout length (SnL), standard length (SL), eye diameter (ED), and the distance from the snout to the origins of the anal (SnA), dorsal (SnD), pectoral (SnP), and pelvic (SnV) fins (Fig. 1). All measurements were taken using a binocular stereomicroscope (Leica S9i) equipped with an integrated color digital camera and image analysis software (Leica LAS EZ 4.13). In the meristic characterization, the total number of myomeres was counted from the first occipital to the region anterior to the urostyle; the pre-anal myomeres were defined as those located anterior to the vertical line passing through the anterior margin of the anal opening; the post-anal myomeres were counted posterior to the vertical line passing through the posterior margin of the anal opening, in addition to counting the number of spines (denoted in Roman numerals) and branched rays (denoted in Arabic numerals) when present in the caudal (C), dorsal (D), anal (A), pelvic (V), and pectoral (P) fins.

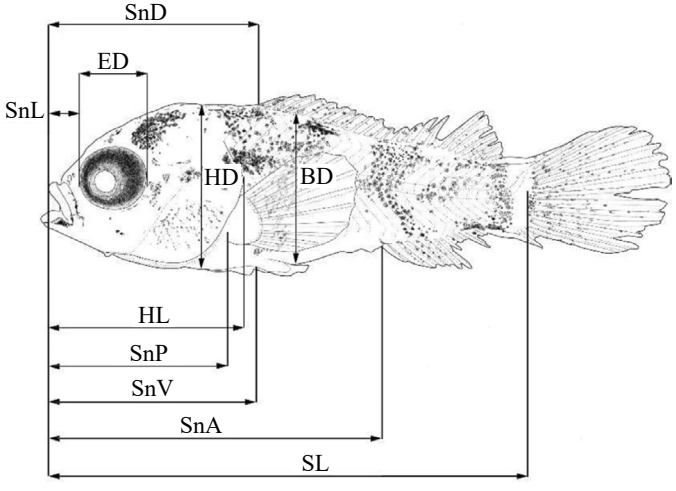

Figure 1. Morphometric measurements of *Cichlasoma amazonarum* (Cichliformes, Cichlasomatinae), larval period.

For the analysis of morphometric relationships in larvae and juveniles (expressed as percentages), the variables HD, SnL, and ED were related to head length (HL), whereas BD, HL, SnA, SnD, SnP and SnV were related to standard length (SL). The analysis of SnV was only possible when this structure was present in the individual. The body proportions of BD (BD/SL), HL (HL/SL), and ED (ED/HL) were established following the criteria proposed by Leis and Trnski (1989) and modified by Nakatani et al. (2001). To evaluate body growth patterns, regression models were used, relating response variables to SL and HL, which were considered predictor variables. These models may reflect important biological processes during the early development of the species (Kováč et al., 1999).

First, the hypothesis that body proportions exhibit continuous isometric development was tested using a simple linear regression model. In addition, two alternative hypotheses were tested: gradual allometric growth using quadratic regression, and discontinuous isometric growth using segmented linear regression, characterized by breakpoints reflecting divergent growth rates. Breakpoints were estimated using specific statistical packages designed to identify changes in the slope of the regression lines. When the R^2 values of the models were very similar, the simpler model was preferred. Missing data were excluded from the analyses. The best model for each morphometric variable, in relation to HL and SL, was selected based on the F-test (Sokal & Rohlf, 1981), using a significance level of $p < 0.05$. Regression analyses were performed using Statistica™ 7.0 software (StatSoft).

RESULTS

A total of 150 free-swimming *C. amazonarum* larvae were analyzed, comprising 85 individuals in the flexion stage and 65 in the postflexion stage, along with 12 juvenile individuals. The morphological characteristics are described below and illustrated in Fig. 2. Data on morphometric relationships and meristic counts are presented in Table 1, whereas the results of the regression analyses of larval and juvenile growth are summarized in Table 2 and Fig. 3.

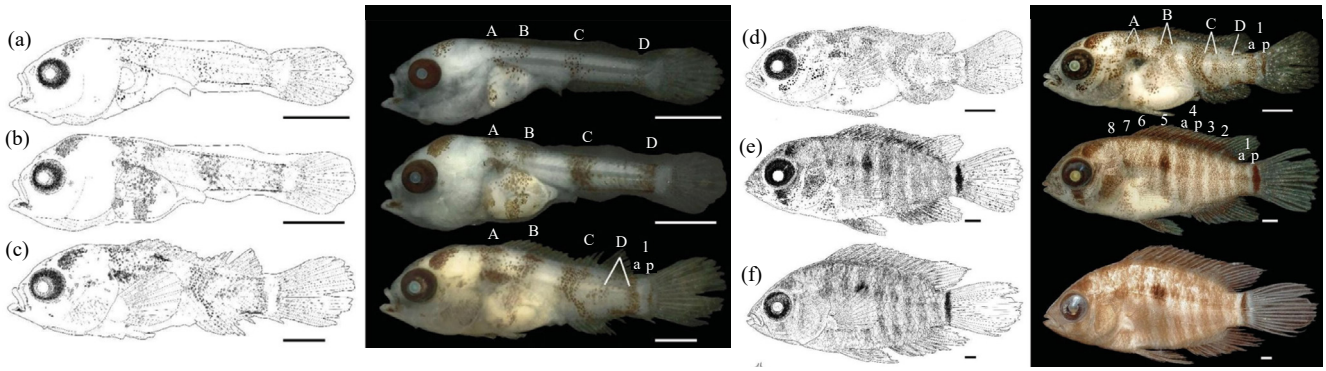

Figure 2. Larval and juvenile development of *Cichlasoma amazonarum* (Kullander 1983): (a) flexion early (3.91 mm standard lenght); (b) flexion late (4.72 mm standard lenght); (c) postflexion early (5.95 mm standard lenght); (d) postflexion late (6.58 mm standard lenght); (e) juvenile (12.62 mm standard lenght); f) juvenile (18.65 mm standard lenght). Scale bars = 1 mm.

Table 1. Main morphological events throughout the development of *Cichlasoma amazonarum*.

Stage	Characteristics	Size (mm)
Flexion	Notochord flexion	3.91
	Prominent, pigmented eyes	
	Functional mouth	
	Inflated swim bladder	
	Evident pectoral-fin bud	
Flexion	Delineation of the dorsal and anal fins, together with the appearance of the first pterygiophores	4.4
Flexion	Emergence and formation of the first pectoral-fin rays	4.6
Postflexion	Appearance of the pelvic-fin bud	5.3
	Formation of the spines and segmentation of the soft rays of the dorsal and anal fins	
Postflexion	They exhibit the complete number of rays in the pectoral and caudal fins	5.75
Postflexion	The embryonic finfold is completely absorbed.	6.58
Juvenile	The notochord is no longer visible	10.26
	Presence of conical teeth	
	All fins fully developed with spines and segmented rays	
	Presence of ctenoid scales	

Table 2. Minimum (Min), maximum (Max), mean, and standard deviation (SD) for morphometric and meristic variables (mm and %) measured in larvae and juveniles of *Cichlasoma amazonarum.*

Variables	Flexion (n = 85)		Posflexion (n = 65)		Juvenile (n = 12)	
(mm)	min–max	mean ± SD	min–max	mean ± SD	min–max	mean ± SD
SL	3.91–5.09	4.59 ± 0.23	5.30–6.58	5.96 ± 0.27	10.26–28.75	19.69 ± 5.72
HL	1.37–1.90	1.70 ± 0.10	2.18–2.80	2.36 ± 0.16	4.70–10.72	8.04 ± 2.07
SnL	0.18–0.35	0.28 ± 0.03	0.26–4.57	0.54 ± 0.51	1.12–2.25	1.66 ± 0.38
ED	0.48–0.68	0.57 ± 0.03	0.66–0.98	0.79 ± 0.07	1.55–4.25	2.93 ± 0.86
HD	1.20–1.69	1.47 ± 0.09	1.82–2.37	2.06 ± 0.12	4.19–12.89	8.94 ± 2.91
BD	0.59–1.58	1.28 ± 0.11	1.09–2.34	1.89 ± 0.27	5.16–13.74	9.34 ± 2.99
SnP	1.36–1.81	1.62 ± 0.09	1.19–2.80	2.35 ± 0.24	4.81–11.61	8.36 ± 2.21
SnA	2.53–3.31	3.01 ± 0.16	3.79–4.71	4.22 ± 0.21	7.53–19.90	13.98 ± 3.87
SnD	1.42–1.98	1.78 ± 0.11	2.17–3.00	2.62 ± 0.15	4.72–10.97	7.69 ± 1.88
SnV	AF	AF	2.18–2.89	2.57 ± 0.15	4.79–12.12	8.59 ± 2.38

Continue...

Continuation.

Morphometric relationships (%)						
SnL/HL	10.76–19.31	16.31 ± 1.45	10.27–25.46	20.00 ± 2.37	17.23–24.45	20.89 ± 2.31
ED/HL	29.97–39.28	33.68 ± 1.76	30.26–39.10	33.48 ± 1.98	32.89–39.68	36.09 ± 1.99
HD/HL	74.50–101.63	86.58 ± 4.70	51.16–95.58	86.78 ± 6.20	84.23–124.28	109.19 ± 12.91
HL/SL	33.34–43.37	37.03 ± 1.72	35.43–44.39	39.51 ± 1.78	37.28–45.82	41.28 ± 2.11
BD/SL	24.56–37.63	28.08 ± 1.74	20.68–37.81	33.04 ± 2.29	40.91–50.66	47.12 ± 2.79
SnP/SL	32.01–38.98	35.32 ± 1.48	21.04–45.41	39.38 ± 3.51	40.39–46.88	42.84 ± 1.96
SnA/SL	62.47–68.99	66.32 ± 1.41	66.57–73.49	70.82 ± 1.14	69.23–73.36	71.31 ± 1.41
SnD/SL	34.36–44.75	38.89 ± 2.60	35.69–47.29	43.96 ± 1.86	36.51–45.96	39.68 ± 2.81
SnV/SL	AF	AF	39.90–46.21	43.01 ± 1.51	40.74–46.73	43.87 ± 2.05
Number of myomers (mode)						
Preanal	11–12 (11)		11–12 (11)		NV	
Postanal	12		12		NV	
Total	23–24 (23)		23–24 (23)		NV	
Number of thorns and rays (mode)						
Pectoral	NV		11–12 (12)		12	
Anal	NV		IV+9		IV+9	
Dorsal	NV		XVI+9		XVI+9	
Pelvic	NV		I+5		I+5	
Caudal	16		18		18	

SL: standard length; HL: head length; SnL: snout length; ED: eye diameter; HD: head depth; BD: body depth; SnP: snout to pectoral fin length; SnA: snout to anal fin length; SnD: snout to dorsal fin length; SnV: snout to pelvic fin length; AF: absent fin; NV: structures not fully formed visible.

Larval characterization from the free-swimming period to juvenile specimens

Flexion stage

Larvae had a SL ranging from 3.91 to 5.09 mm (mean ± standard deviation = 4.59 ± 0.23 mm), with no yolk remnants and with the posterior end of the notochord clearly flexed and visible through the transparent body. The head is rounded, and the three pairs of adhesive glands present in newly hatched larvae were not observed at this stage. The eyes are round, prominent, and fully pigmented. The nostrils are simple, and the mouth is functional and terminal, with mobile jaws and a short snout. Inflation of the swim bladder is evident. The intestine is narrow and nearly straight, with the anus located in the mid-body region. The embryonic finfold extends from the dorsal region, posterior to the head, to the ventral region near the isthmus, being narrower dorsally and broader ventrally. In individuals measuring 4.40 mm SL or more, this finfold begins to be absorbed, delineating the dorsal and anal fins, with the simultaneous appearance of pterygiophores and formation of the first fin rays. The pectoral-fin bud is evident, located laterally on the body posterior to the operculum. Initially, it has a thin, oval-shaped membrane, but in larvae larger than 4.60 mm SL, the emergence and formation of the first pectoral-fin rays were recorded. The caudal fin is rounded. At this stage, individuals exhibit the definitive total number of myomeres characteristic of the species, ranging from 23 to 24 segments, comprising 11–12 preanal and 12 postanal myomeres (Table 1). The pigmentation pattern consists of dendritic chromatophores initially distributed over the upper portion of the head, concentrated in the occipital region, around the jaw and on the isthmus, as well as dorsal clusters of melanophores that are established in an anteroposterior sequence and spread dorsoventrally, forming four vertical bars along the body (A, B, C, and D; Figs. 2a and 2b).

Post-flexion stage

Larvae showed a SL ranging from 5.30 to 6.58 mm (mean ± standard deviation = 5.96 ± 0.27 mm). The notochord flexion process is definitively completed. The head maintains the rounded shape and proportions of the previous stage, with round, prominent, and pigmented eyes, simple nares, a terminal mouth, and a short snout. The intestine remains well defined, with the anus located in the median region of the body. The embryonic membrane is completely absorbed by the end of this stage. The emergence of the pelvic fin bud is observed, as well as the formation of spines and segmentation of the soft rays composing the dorsal and anal fins. Individuals measuring 5.75 mm SL exhibit the total number of rays formed in the pectoral

and caudal fins. The total number of myomeres ranges from 23 to 24 segments, with 11–12 pre-anal and 12 post-anal (Table 1). At this more advanced larval stage, new chromatophores appear on the head, distributed around the eyes, on the maxilla, and in the opercular region. Pigmentation becomes more intense and clearly asymmetrical, spreading irregularly throughout the body, with the appearance of several combinations of transitional blotches on the flanks along the mediolateral line, resulting from the subdivisions (A, B, C, and D) that lead to the establishment of the total and definitive number of vertical phenotypic bars characteristic of the species. At the end of this stage, the first subdivision is observed, in which bars 1a and 1p derive from D in the posterior region of the caudal peduncle. Additionally, the two bars closest to the head merge in the mid-inferior section, forming a "Y"-shaped pattern, and the appearance of a cluster of melanophores at the base of the caudal fin rays creates an additional dark bar (Figs. 2c and 2d). Pigmentation is also visible between the rays of the dorsal, anal, pectoral, and caudal fins.

Juvenile period

The juvenile individuals (Fig. 2e) analyzed had SL ranging from 10.26 to 28.75 mm (mean ± standard deviation = 19.69 ± 5.72 mm). The notochord is no longer visible due to muscular development and thickening. The head profile between the tip of the snout and the orbit is slightly curved, with large eyes and a terminal mouth, with the upper lip overlapping the lower lip at the rictus. The teeth are conical, and the snout and caudal peduncle are short. The anus remains located in the mid-body region. The lateral line is discontinuous. The origin of the dorsal fin is located at the level of the posterior margin of the operculum. All fins are fully developed, with the complete number of spines and segmented rays. The long-based dorsal fin does not exhibit a marked notch at the junction between the spines and soft rays. The body is covered with ctenoid scales, which are also present on the inter-radial membranes of the dorsal and anal fins. The caudal fin is rounded. The sequence of fin formation is as follows: caudal (18), dorsal (XVI, 9), anal (IV, 9), pectoral (12), and, finally, pelvic (I, 5) (Table 1). The pigmentation pattern is consolidated by the active development of dark vertical postcranial melanophore bars distributed along the body (1a, 1p, 2, 3, 4a, 4p, 5, 6, 7, and 8). The first bar is located on the caudal peduncle, at the posterior end of the dorsal fin, and divides into two parts (1a, 1p), with 1p becoming an additional, darker spot located posteriorly and readily identifiable at the base of the caudal-fin rays. The second bar is located at the posterior insertion of the dorsal and anal fins. The third occurs above the anal fin. The fourth bar is subdivided into 4a and 4p, with 4a located at the anterior insertion of the anal fin, beneath the anus, and 4p oriented toward the first anal-fin spines. The fifth bar is located between the anus and the pelvic fin. The sixth occurs below the anterior dorsal-fin rays, posterior to the insertion of the pectoral fin. The seventh is located anterior to the first dorsal-fin rays and extends between the opercular opening and the insertion of the pectoral fin. The eighth is situated between the seventh bar and the posterior portion of the head, extending across the opercular series (Fig. 2e), resulting in a total of 10 vertical bars based on direct counting. Bars 1a, 1p, and 2 are derived from bar D; bars 3, 4a, and 4p are derived from bar C; bars 5 and 6 from bar B; and bars 7 and 8 from bar A. Two melanophore clusters are present on the head: an indistinct spot above the orbit and an infraorbital band, in addition to the intensification of a mediolateral spot with a diffuse margin located beneath the fifth bar. The interbar regions are weakly pigmented and lighter in coloration. In the juveniles analyzed, the well-defined and dark pigmentation at the base of the caudal-fin rays (1p) still differs from the coloration pattern recorded in adults, which exhibit a dark ocellus-shaped spot restricted to the upper half of the caudal-fin base. This difference indicates that the adult pigmentation pattern develops at a later stage. The pigmentation pattern described above was observed in all juvenile individuals analyzed.

Morphometric relationships

Throughout the larval and juvenile development of *C. amazonarum*, eye size ranged from moderate to large (29.97–39.68% of HL). The head remained relatively large (33.34–45.82% of SL). BD, in turn, remained moderate (24.56–37.81% of SL) during the flexion and postflexion stages, becoming high during the juvenile period (40.91–50.66% of SL). In addition, all other measurements, including SnL and the distances from the snout to the origins of the pectoral, dorsal, anal, and pelvic fins, increased throughout development (Table 2).

Growth analyses

Most of the body variables analyzed exhibited discontinuous isometric growth, as described by segmented regression, indicating that certain body structures grow proportionally but undergo an abrupt change in growth rate after a specific point, represented by a breakpoint. For the variables ED, HD, and BD, an increase in growth rate was observed, whereas SnA, SnD, and SnV showed a decrease, with these changes occurring during the transition from the postflexion to the juvenile stage (Table 3, Fig. 3). It was also observed that only SnL increased proportionally to HL, exhibiting continuous isometric growth and maintaining a constant growth rate throughout the observed period (Table 3, Fig. 3).

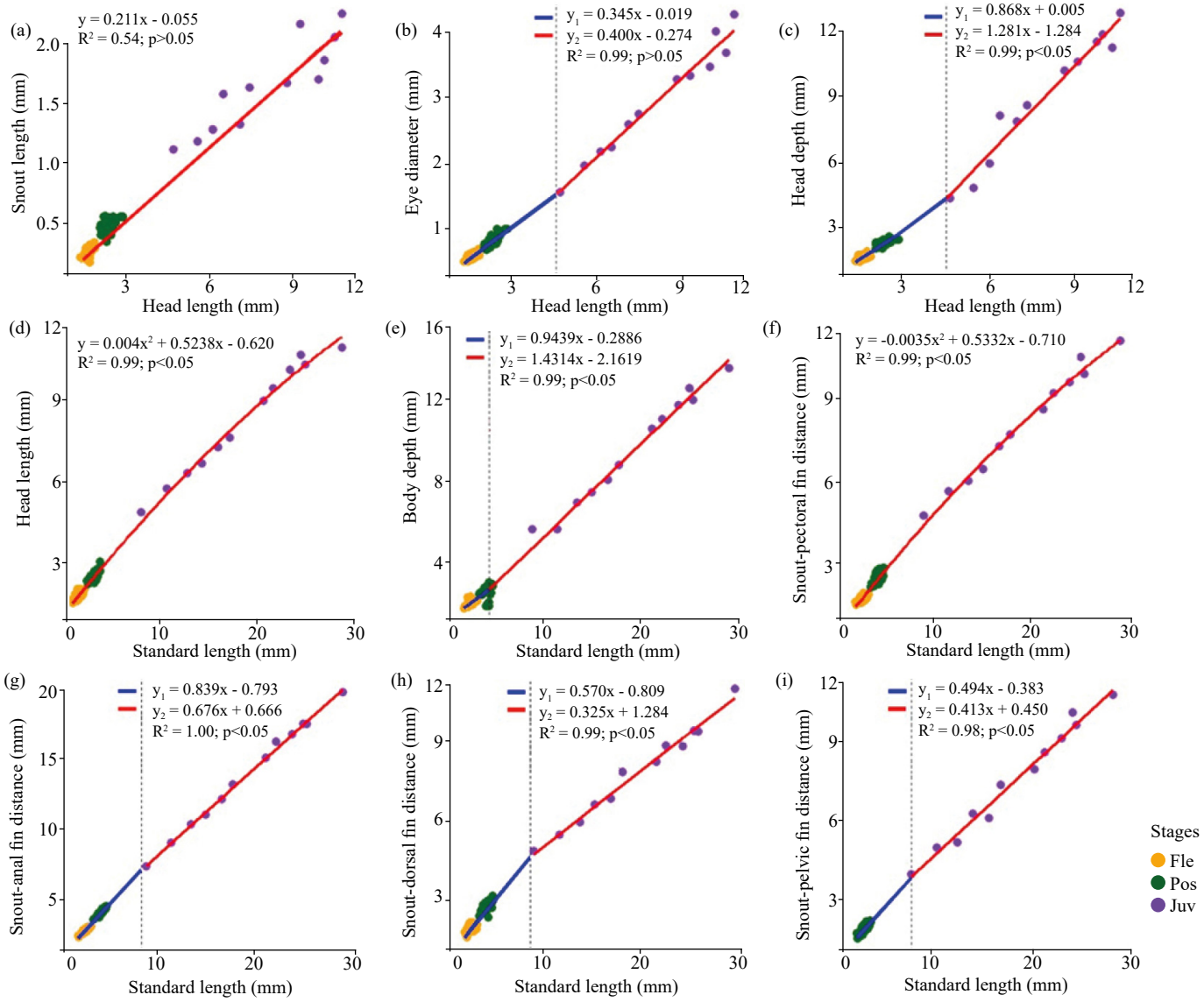

Figure 3. Head length proportions (mm) relative to (a) snout length, (b) eye diameter, (c) head depth, and (d) standard length proportions (mm) relative to head length, (e) body depth, (f) snout to pectoral fin distance, (g) snout to anal fin distance, (h) snout to dorsal fin distance, and (i) snout to pelvic fin distance during the early development of *Cichlasoma amazonarum*.

Table 3. Mathematical and statistical values of linear (L), quadratic (Q), and segmented (S) regressions for morphometric variables obtained in relation to body length and head pattern in larvae and juveniles of *Cichlasoma amazonarum*.

Variable	R^2 L	R^2 Q	R^2 S	FQ/L	p	FS/Q	p	FS/L	p	MM	BP	N
SnL/HL	0.54	0.54	0.55	2.22	0.14	2.75	0.10	2.49	0.12	L	-	162
ED/HL	0.99	0.99	0.99	38.63	0.00	16.12	0.00	29.21	0.00	S	4,56	162
HD/HL	0.98	0.99	0.99	74.11	0.00	51.74	0.00	74.75	0.00	S	4,08	162
HL/SL	0.99	0.99	0.99	44.80	0.00	0.00	1.00	21.12	0.00	Q	-	162
BD/SL	0.99	0.99	0.99	2.42	0.12	14.97	0.00	8.81	0.00	S	6,20	162
SnP/SL	0.97	0.99	0.98	11.20	0.00	0.87	0.35	6.03	0.02	Q	-	162
SnA/SL	1.00	1.00	1.00	171.70	0.00	16.82	0.00	102.8	0.00	S	8,56	162
SnD/SL	0.98	0.99	0.99	92.95	0.00	54.97	0.00	89.73	0.00	S	8,56	162
SnV/SL	0.86	0.91	0.98	97.74	0.00	470.09	0.00	428.1	0.00	S	8,56	76

SnL: snout length; HL: head length; ED: eye diameter; HD: head depth; SL: standard length; BD: body depth; SnP: snout to pectoral fin length; SnA: snout to anal fin length; SnD: snout to dorsal fin length; SnV: snout to pelvic fin length.

HL and the distance from the snout to the origin of the pectoral fin were best described by quadratic regression, indicating rapid growth during the larval stage, followed by a gradual deceleration as individuals increased in size (Table 3, Fig. 3).

DISCUSSION

The results of this study revealed rapid development of *C. amazonarum* after the onset of free swimming, characterized by the progressive formation of locomotor and feeding structures, the establishment of the pigmentation pattern, and the predominance of discontinuous isometric growth throughout ontogeny. This study provides the first description of the larval and juvenile development of the species, focusing on the morphological, morphometric, and meristic changes in individuals collected from the wild but subsequently maintained under captive conditions. As observed in several other fish species, during the transformation period—the transition from the larval stage to the juvenile phase—this cichlid exhibits accelerated growth and development of structures such as the eyes, fins, and jaws, accompanied by the loss of body translucency due to muscle thickening. These changes reflect the progressive morphological transformation associated with the acquisition of adult characteristics.

Most ontogenetic studies available for cichlids—including congeners such as *C. dimerus* (Meijide & Guerrero, 2000), *C. istlanum* (Figueroa & Torres, 2000), *C. minckleyi* (Stephens & Hendrickson, 2001), and *C. urophthalmus* (López-Ramírez et al., 2011), as well as other Amazonian species such as *Astronotus ocellatus* (Nakatani et al., 2001), *Geophagus brasiliensis* (Pandolfi et al., 2009), and *Heros severus* (Santos et al., 2025)—have been based on individuals obtained from fully controlled reproduction and rearing conditions in the laboratory, allowing continuous monitoring from the earliest yolk-sac and preflexion stages. This experimental condition represents an important methodological advantage because it enables ontogenetic events to be more accurately associated with known ages and environmental conditions.

In the present study, in contrast, individuals were collected directly from the natural environment, reflecting the inherent difficulty of obtaining newly hatched cichlid larvae due to the complexity of their ecology and reproductive behavior (Koblmüller et al., 2023), which prevented the monitoring of the earliest developmental stages (yolk-sac and preflexion). This limitation should be considered when interpreting the results presented here, particularly regarding the origin and precise age of the specimens analyzed. Nevertheless, this same difficulty in field sampling helps explain the predominance of ontogenetic, developmental, and growth studies of this group based on captive-reared individuals, reinforcing the complementary value of studies such as the present one, which document the development of *C. amazonarum* from later developmental stages obtained directly from natural populations.

A typical characteristic of cichlids is the presence of adhesive organs in the head region of larvae smaller than 3.5 mm SL, particularly in substrate-spawning species (Çelik et al., 2014; Meijide & Guerrero, 2000; Říčan et al., 2005; Santos et al., 2025). These structures help prevent dispersal by water currents, keep larvae attached to the substrate through an adhesion mechanism, and maintain them aggregated, thereby reducing predation risk and facilitating parental care and protection until they reach a more advanced developmental stage, when muscular development allows autonomous movement (Groppelli et al., 2003; Kupren et al., 2014). However, these organs are transient structures that regress and completely lose their functionality once larvae become capable of swimming or when their yolk reserves are depleted (Nelson et al., 2019; Contreras-Tapia et al., 2024). No such structures were observed in the *C. amazonarum* individuals analyzed in the present study. However, because sampling did not include the yolk-sac and preflexion stages—the developmental period during which these organs, when present, tend to be most evident—it cannot be concluded that the species lacks them; rather, they were not observed in the developmental stages analyzed. The specimens examined in this study were already larger than 3.9 mm SL, had completely absorbed their yolk reserves, functional mouths and anus, and exhibited free-swimming behavior. Under these conditions, according to the literature, adhesive organs would already have regressed even if they had been present at earlier stages. Nevertheless, the absence of these structures in the stages examined is consistent with the possibility of a short transition period from endogenous to exogenous feeding in this species. If confirmed by future studies including earlier developmental stages, this information could contribute to reducing mortality rates and preventing growth retardation during early rearing (Conceição et al., 2009; Portella et al., 2012).

Mouth opening and the macroscopic depletion of the yolk sac are considered important morpho-anatomical events marking the onset of exogenous feeding in fish larvae (Cuenca-Soria et al., 2013; Gisbert & Williot, 2002). Because the present study did not monitor hatching or directly measure the time elapsed until complete yolk absorption, it is not possible to accurately determine the duration of the endogenous feeding phase in *C. amazonarum*. However, the fact that all individuals analyzed

already had a functional mouth and no residual yolk at the time of collection indirectly suggests that this species may reach these developmental milestones earlier than other neotropical cichlids with a mouthbrooding strategy, which tend to absorb the yolk sac more slowly and exhibit a prolonged period of endogenous dependence (Lopes et al., 2015; Saemi-Komsari et al., 2018; Siddique et al., 2023). This inference, however, should be interpreted with caution and confirmed by future studies that monitor the earliest developmental stages, including hatching and the progressive absorption of the yolk sac.

The sequence of appearance and development of morphological structures, such as the early and rapid formation of the caudal fin, the emergence of pectoral-fin rays prior to the formation of the pelvic fin, and the regular and simultaneous development of the dorsal and anal fins, represents a pattern similar to that observed in other cichlid species (Contreras-Tapia et al., 2025; Meijide & Guerrero, 2000). However, the sequence of fin formation in *C. amazonarum* larvae differs from that observed in Characiformes, in which the pectoral fin is the last fin to develop, as reported for *Brycon falcatus* (Silva-Cajado et al., 2025), *Bryconops gracilis* (Oliveira et al., 2024), *Rhytiodus microlepis* (Santos et al., 2024), *Triportheus albus*, *T. angulatus*, and *T. auritus* (Cajado et al., 2021, 2023). These differences may reflect distinct adaptations and ecological responses among species.

The changes in body organization observed in *C. amazonarum* coincide with the replacement of temporary embryonic structures by definitive structures and are associated with the development of the feeding system (functional jaws), digestive system (differentiation of the digestive tract into stomach and intestine), and locomotor system. These changes represent an important period of morphological reorganization and functional adaptation (Korzelecka-Orkisz et al., 2012; Kupren et al., 2014), facilitating the behavioral transition of this species to a free-swimming pelagic phase characterized by exogenous foraging and the ability to exploit different habitats and substrate types (Arnold et al., 2025; James Cooper et al., 2020). These findings support the idea that functional demands emerge gradually in response to different ecophysiological conditions.

The distribution pattern of pigmentation is considered an important taxonomic feature for the systematic identification of fish larvae, and its usefulness is well established despite its dynamic and transient nature and the multiple variations that may occur during its formation, including the presence, absence, distribution, number, shape, position, and size of chromatophores, which can differ among species and developmental stages (Correia et al., 2010; Zacardi & Bittencourt, 2017). This pattern contributes to distinguishing groups at different taxonomic levels, from families to species, and plays a fundamental role in fish adaptation, speciation, and social and behavioral interactions (Irion & Nüsslein-Volhard, 2019; Patterson & Parichy, 2019). In this context, the pigmentation pattern observed in *C. amazonarum* represents a relevant contribution to the taxonomic characterization of the species, particularly regarding the origin, timing of establishment, and number of vertical bars, as well as the presence of the mediolateral spot.

The increase in the number of vertical bars observed in *C. amazonarum*—a conspicuous coloration pattern of the species—is primarily formed by an increase in melanophore density and the accumulation of melanin, which already occurs during the larval stages. According to Liang et al. (2020), in African cichlids, this process begins as early as the first three weeks after egg fertilization and is determined by spatial variation in the pigmentary and structural properties of the tissue, including the dynamic regulation of melanophore density, melanin synthesis, and melanosome dispersion. In these species, melanophore migration begins in the dorsal region and gradually expands in a dorsoventral direction, establishing the vertical bars along the body.

In contrast, among Neotropical cichlids, the timing of pigmentation establishment varies considerably. In *Astronotus ocellatus*, *Heros severus*, and *M. festivus*, larval pigmentation appears earlier and with greater intensity (Paes et al., 2011; Santos et al., 2025), whereas in *Geophagus brasiliensis*, *Pterophyllum scalare*, *Symphysodon discus*, and *S. pappaterra*, pigmentation develops gradually throughout early ontogeny (Eagderi et al., 2017; Lopes et al., 2015; Mattos et al., 2015; Ota et al., 2021; Pandolfi et al., 2009). *C. amazonarum* resembles the latter group but exhibits even more pronounced changes and a later establishment of the pigmentation pattern elements compared with the other species examined, representing one of the distinctive features highlighted here. Regarding the origin of the pigmentation pattern, following the classification proposed by Říčan et al. (2005; 2016), pigmentation development in *C. amazonarum* corresponds to type B, in which there is no trace of a mid-lateral band; instead, the pattern begins as a mottled pigmentation and proceeds directly to the formation of vertical bars. Regarding the number of bars, considerable variation occurs among Neotropical cichlids. *Satanoperca pappaterra* exhibits five or six bars (Lopes et al., 2015; Ota et al., 2021), whereas species of the genera *Acaronia*, *Aequidens*, *Bujurquina*, *Heros*, and *Krobia*, which have fewer postcranial vertical bars (Říčan et al., 2005), have a total of eight bars based on direct counting. *C. amazonarum* differs from both groups by

exhibiting 10 vertical bars along the body—the highest number recorded among the species compared.

Regarding the mediolateral spot, its position also distinguishes taxonomic groups. In *C. amazonarum*, as in all cichlasomatines, the spot is located beneath the fifth bar, differing from heroines, in which the strongly pigmented mediolateral spot is located beneath the fourth bar. This structure is absent in *S. pappaterra* (Lopes et al., 2015; Ota et al., 2021) and *M. festivus* (Santos et al., 2025). Other pigmentation characteristics observed in closely related genera are also absent in *C. amazonarum*. More advanced larvae and juveniles of *Acaronia*, *Bujurquina*, and *Krobia* exhibit a dorsally inclined horizontal mediolateral band behind the vertical bars, whereas larvae of *Laetacara* display horizontal pigmentation interconnected with the vertical bars dorsally, mediolaterally, and ventrally, forming a series of X-shaped structures interspersed with small unpigmented circles arranged in two rows (Říčan et al., 2005). Taken together, these differences in the number of bars, the origin of the pigmentation pattern, and the presence and position of the mediolateral spot reinforce the taxonomic value of the pigmentation pattern described for *C. amazonarum*. This pattern may be shaped both by the ecological adaptations of each cichlid species and by their reproductive strategies and evolutionary history (Sefc, 2011; Takahashi, 2003).

Initially, pigmentation in *C. amazonarum* larvae may not be essential for protection against predators, as the larvae are guarded by their parents. However, as development progresses and pigmentation intensifies, this trait may be associated with a potential defense mechanism, as disruptive coloration tends to break up the body outline, which may contribute to mimicry and camouflage strategies against predators, particularly in visually complex habitats. A similar pattern of habitat use has been observed in species such as *M. festivus*, *Acaronia nassa*, and *Heros* sp., which also shelter among the roots of floating aquatic macrophyte beds (Prado et al., 2010). This suggests that strategies associated with these microhabitats could hypothetically enhance larval survival. Nevertheless, because the present study did not directly assess predation, camouflage, or antipredator behavior, this potential ecological function of pigmentation should be regarded as a hypothesis to be tested in future studies rather than as an established conclusion regarding its role in recruitment, reproductive success, or the replenishment of natural stocks of the species.

Previous studies have indicated that morphometric changes can describe potential alterations in the morphological characteristics of an organism throughout body growth, reflecting phenotypic plasticity under specific environmental conditions (Osse & van den Boogaart, 2004; Shingleton et al., 2007). According to Balon (1999), fish larvae do not grow gradually but rather through saltatory developmental patterns resulting from processes of morphofunctional self-organization. In *C. amazonarum*, larval growth was characterized predominantly by discontinuous isometric growth, as observed in ED, HD and BD, and the distances from the snout to the origins of the anal, dorsal, and pelvic fins, with breakpoints identified during the postflexion stage. However, it is important to emphasize that the low number of juvenile individuals sampled and the absence of specimens within the 6.58–10.26 mm SL interval limit the precision with which these breakpoints can be determined and may affect the resolution of ontogenetic transitions identified within this size range. Therefore, the results obtained should be interpreted as providing partial support for the saltatory ontogeny hypothesis proposed by Balon (1999) for *C. amazonarum*. Future studies with larger juvenile samples and more continuous coverage of size classes are recommended to further test and refine this interpretation.

The growth and variation in eye size, ranging from moderate to large, were described by a segmented growth model (S) for the ED/HL ratio, with a breakpoint at 4.56 mm SL. This pattern may be related to the functional demands of vision, particularly during the transition to exogenous feeding, when larvae have not developed all sensory structures yet (Härer et al., 2019; Miranda et al., 2020) and therefore need to rapidly complete ocular development. This process may influence feeding preferences and trophic level from this size onward (Cavalcante et al., 2015). These results indicate that the development and maturation of the visual system in *C. amazonarum* represent critical physiological processes concentrated around 4.56 mm SL, coinciding with the larval transition phase and potentially contributing to overcoming the critical period and achieving autonomous survival in the aquatic environment.

The head also exhibited a segmented growth model (S) for the HD/HL ratio, with a breakpoint at 4.08 mm SL, remaining proportionally large throughout early development, similarly to the pattern observed in other *Cichlasoma* species (Meijide & Guerrero, 2000; Stephens & Hendrickson, 2001). This marked increase in HD around 4 mm SL—close to the breakpoint identified for ED—may be associated with structural development of the central nervous system and skull, expansion and consolidation of the branchial apparatus and oral structures (premaxillae and maxillae), and the prioritization of vital functions and processes such as the transition from cutaneous to

branchial respiration, enabling more efficient water pumping and gas exchange, and the ossification of oral structures, including the jaws, which is essential for maximizing food capture and preventing starvation (DeLaurier, 2019; Le Pabic et al., 2009; Pan, 2024). The temporal proximity between the breakpoints for ED (4.56 mm SL) and HD (4.08 mm SL) suggests that these physiological and structural events may act in an integrated manner, promoting both head development and enlargement and the subsequent stabilization of growth rates relative to body size (Silva et al., 2022).

The distances related to fin insertion—from the snout to the origins of the anal (SnA/SL), dorsal (SnD/SL), and pelvic (SnV/SL) fins—all exhibited a segmented model (S), with a coincident breakpoint at 8.56 mm SL. This size is considerably larger than the breakpoints observed for the eye and head and is consistent with the postflexion stage. This result indicates that changes in growth rate associated with the development and completion of fin rays, together with the replacement of the initial transient structure (embryonic finfold) by the definitive fins, both paired and unpaired, occur in a concentrated manner around 8.56 mm SL, meeting critical functional demands for survival in a fluid and dynamic environment. The formation and consolidation of these structures within the same size range were accompanied by the differentiation of myomeres (segmental musculature). This set of integrated morphological changes, concentrated from 8.56 mm SL onward, enables the force generated by the body to be converted into directional movement, allowing rapid changes in direction, enhancing swimming performance, and contributing to braking and stabilization—actions that are essential for prey capture (Feilich, 2016; Osse & Van den Boogaart, 2004) and for resisting hydrodynamic forces generated by microcurrents (Li et al., 2016; Menzer et al., 2026), thereby reducing the likelihood of larvae being displaced away from their parents. It is noteworthy that the HL/SL ratio followed a purely quadratic model (Q), without a discrete breakpoint, suggesting that proportional head growth relative to standard length occurred continuously rather than abruptly throughout ontogeny.

CONCLUSION

This study provides the first description of the early ontogeny of *C. amazonarum*, contributing essential information on the larval and juvenile developmental mechanisms of the species. The results demonstrated rapid growth following the onset of free swimming, characterized by the progressive formation of locomotor and feeding structures, the establishment of a pigmentation pattern with taxonomic value—defined by the number of vertical bars, the origin of the mottled pattern (type B), and the position of the mediolateral spot—and the predominance of a discontinuous isometric growth model, with breakpoints identified at specific sizes for the eyes, head, and fins. These coordinated morphological changes may be associated with the acquisition of new functional capacities by individuals, potentially related to the use of aquatic environments such as ponds, shallow and marginal river zones, isolated watercourses, flooded areas, and regions covered by stands of aquatic macrophytes, which are recognized habitats for the species, as well as to the exploitation of food resources. However, these associations were not directly tested in the present study. The data presented here help fill gaps in the bioecological knowledge of *C. amazonarum* and provide a morphological basis for future investigations into the factors influencing individual fitness and niche specialization throughout development.

CONFLICT OF INTEREST

Nothing to declare.

DATA AVAILABILITY STATEMENT

All data were generated or analyzed in this study.

AUTHORS' CONTRIBUTIONS

Conceptualization: Mota, G.C.L., Zacardi, D.M.; **Investigation:** Mota, G.C.L., Santos, L.A., Zacardi, D.M., Vasconcelos, A.C.C.; **Writing – original draft:** Mota, G.C.L., Santos, L.A., Zacardi, D.M.; **Project Administration:** Mota, G.C.L., Zacardi, D.M.; **Supervision:** Zacardi, D.M.; **Final approval:** Mota, G.C.L., Zacardi, D.M.

FUNDING

Not applicable.

DECLARATION ON USE OF ARTIFICIAL INTELLIGENCE TOOLS

Artificial intelligence tools were used only for minor language corrections in the manuscript translation. All scientific content, data analysis, and interpretation remain the sole responsibility of the authors.

ACKNOWLEDGMENTS

The authors acknowledge the collaboration of the Universidade Federal do Oeste do Pará, through the Laboratório

de Ecologia do Ictioplâncton e Pesca em Águas Interiores, and the Universidade Federal do Oeste do Pará for their support during the stages of collection, sorting, and identification of the specimens analyzed in this study, especially Zaqueu Santos for preparing the species illustrations.

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