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Early Ontogeny of the *Mesonauta festivus* (Cichliformes, Cichlidae): external morphology and growth patterns

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Abstract

This study presents the early development of the Neotropical cichlid *Mesonauta festivus*, from embryogenesis through the larval and juvenile periods, based on morphological, meristic, and morphometric characters. The eggs are elliptical, dark yellow in color, with a translucent chorion, a reduced perivitelline space, and a longitudinal axis longer than the transverse axis. The larvae exhibit a hyaline embryonic membrane, a pigmented yolk sac, and adhesive organs distributed in the frontal and dorsal regions of the head. The body is elongated, with a ventral band of dense melanophores that intensify throughout development and expand dorsally along the body, the upper region of the head, and between the rays of the caudal fin. Juvenile individuals show morphology similar to that of adults and exhibit a long-based dorsal fin, extending from near the head to the caudal peduncle. The color pattern includes irregular dark vertical bands, with the third and fourth bands joined at the median portion forming a “K”, as well as light bands on the dorsal and ventral fins, separated by traces of dark pigmentation. A dark horizontal band extending from the eye to the base of the dorsal fin, and a dark blotch at the upper base of the caudal peduncle, both common to species of the genus *Mesonauta*. The number of myomeres ranges from 27 to 28 segments, and the sequence of fin ray formation is as follows: caudal (8+8), dorsal (XV, 10–11), anal (VIII, 10–14), pelvic (I, 5), and pectoral (I, 11). The larvae exhibit moderately to large eyes, a variably sized head, and an elongated body. Comparisons of larval morphology were conducted with other Neotropical cichlids that occur in syntopy. Most variables exhibited discontinuous isometric growth, except for head length in relation to standard length, which showed continuous isometric growth, probably related to the gradual change in behavior and habitat. Our results contribute to the understanding of the early life cycle of *M. festivus*, have the potential to improve captive breeding techniques, serve as a reference for phenotype assessment aiding accurate identification, and provide valuable data for basic biology that may be useful for the sustainable management and conservation of the species.

Keywords: ornamental fish; Amazonian cichlid; captive breeding; early stages of development; color pattern.

Resumo - Ontogenia inicial de *Mesonauta festivus* (Cichliformes, Cichlidae): morfologia externa e padrões de crescimento

Este estudo apresenta o desenvolvimento inicial do ciclídeo Neotropical *Mesonauta festivus*, desde a embriogênese até os períodos larval e juvenil, com base em caracteres morfológicos, merísticos e morfométricos. Os ovos são elípticos, de coloração amarelo-escura, com córion translúcido, espaço perivitelino reduzido e eixo longitudinal maior que o transversal. As larvas apresentam membrana embrionária hialina, saco vitelino pigmentado e órgãos adesivos distribuídos na região frontal e dorsal da cabeça. O corpo é alongado, com uma faixa ventral de melanóforos densos que se intensificam ao longo do desenvolvimento e se expandem dorsalmente pelo corpo, região superior da cabeça e entre os raios da nadadeira caudal. Os indivíduos juvenis apresentam morfologia semelhante à dos adultos exibem nadadeira dorsal de base longa, iniciando próximo à cabeça até o pedúnculo caudal. O padrão de coloração inclui faixas escuras verticais irregulares, sendo a terceira e a quarta unida na porção mediana formando um “K”, além de faixas claras nas nadadeiras dorsal e ventral, separadas por vestígios de pigmento escuro. Uma faixa horizontal escura, que se estende do olho até a base da nadadeira dorsal e uma mancha escura na base superior do pedúnculo caudal comum às espécies do gênero *Mesonauta*. O número de miômeros varia de 27 a 28 segmentos e a sequência

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de formação dos raios das nadadeiras é: caudal (8+8), dorsal (XV, 10-11); anal (VIII, 10-14), ventral (I, 5) e peitoral (I, 11). As larvas apresentam olhos moderados a grandes, cabeça de tamanho variável e corpo alongado. Foram realizadas comparações da morfologia larval com outros ciclídeos neotropical que ocorrem em sintopia. A maioria das variáveis revelou crescimento isométrico descontínuo, exceto o comprimento da cabeça em relação ao comprimento padrão, que apresentou crescimento isométrico contínuo, provavelmente relacionado à mudança gradual no comportamento e no habitat. Nossos resultados contribuem para a compreensão do ciclo inicial de vida de *M. festivus*, têm o potencial de aprimorar as técnicas de criação em cativeiro, servir como referência para a avaliação de fenótipos auxiliando na identificação correta, além de fornecer dados valiosos para a biologia básica que poderão ser úteis para o manejo sustentável e conservação da espécie.

Palavras-chave: peixe ornamental; ciclídeo amazônico; reprodução em cativeiro; fases iniciais de desenvolvimento; padrão de coloração.

Resumen - Desarrollo temprano del *Mesonauta festivus* (Cichliformes, Cichlidae): morfología externa y patrones de crecimiento

Este estudio presenta el desarrollo temprano del cíclido neotropical *Mesonauta festivus*, desde la embriogénesis hasta las etapas larvaria y juvenil, con base en características morfológicas, merísticas y morfométricas. Los huevos son elípticos, de color amarillo oscuro, con un corion translúcido, espacio perivitelino reducido y un eje longitudinal más largo que el eje transversal. Las larvas presentan una membrana embrionaria hialina, un saco vitelino pigmentado y órganos adhesivos distribuidos en las regiones frontal y dorsal de la cabeza. El cuerpo es alargado, con una banda ventral de melanóforos densos que se intensifican a lo largo del desarrollo y se expanden dorsalmente a lo largo del cuerpo, la región superior de la cabeza y entre los radios de la aleta caudal. Los individuos juveniles exhiben una morfología similar a la de los adultos, mostrando una aleta dorsal con una base larga, que comienza cerca de la cabeza y se extiende hasta el pedúnculo caudal. El patrón de coloración incluye franjas oscuras verticales irregulares, con la tercera y la cuarta unidas en la porción media formando una "K", además de franjas claras en las aletas dorsal y ventral, separadas por restos de pigmento oscuro. Una franja horizontal oscura se extiende desde el ojo hasta la base de la aleta dorsal, y una mancha oscura está presente en la base superior del pedúnculo caudal, común en las especies del género *Mesonauta*. El número de miómeros varía de 27 a 28 segmentos, y la secuencia de formación de los radios de la aleta es: caudal (8+8), dorsal (XV, 10-11); anal (VIII, 10-14), ventral (I, 5) y pectoral (I, 11). Las larvas tienen ojos de moderados a grandes, una cabeza de tamaño variable y un cuerpo alargado. Se realizaron comparaciones de la morfología larvaria con otros cíclidos neotropicales que se presentan en sintopía. La mayoría de las variables mostraron un crecimiento isométrico discontinuo, excepto la longitud de la cabeza en relación con la longitud estándar, que mostró un crecimiento isométrico continuo, probablemente relacionado con cambios graduales en el comportamiento y el hábitat. Nuestros resultados contribuyen a la comprensión del ciclo de vida temprano de *M. festivus*, tienen el potencial de mejorar las técnicas de cría en cautividad, sirven como referencia para la evaluación del fenotipo, lo que facilita una correcta identificación, y proporcionan datos valiosos para la biología básica que podrían ser útiles para la gestión sostenible y la conservación de la especie.

Palabras clave: pez ornamental; ciclídeo amazónico; reproducción en cautiverio; fases iniciales de desarrollo; patrón de color.

Introduction

Fish of the genus *Mesonauta* Günther, 1862 comprise a group of cichlids native to South America, popularly known as the festive-cichlid (Queiroz et al., 2013; Oliveira et al., 2025a). Currently, the genus comprises seven valid species, namely: *Mesonauta acora* (Castelnau, 1855), *M. egregius* (Kullander & Silfvergrip, 1991), *M. festivus* (Heckel, 1840), *M. guyanae* (Schultz, 1960), *M. insignis* (Heckel, 1840), *M. karipuna* Oliveira, Britzke, Oliveira & Graça, 2025 and *M. mirificus* (Kullander & Silfvergrip, 1991) distributed across the Amazon, Amapá, Orinoco, Paraná, and middle and upper Paraguay river basins, as well as the sub-basins of the Negro, Tocantins, Xingu, Tapajós, and Essequibo rivers in Guyana (Kullander, 2003; Dagosta & Pinna, 2019; Fricke et al., 2025; Oliveira et al., 2025b). They are small-sized fish (7–12 cm in standard length) that stand out morphologically due to a coloration pattern featuring a dark transverse band extending from the snout to the posterior edge of the dorsal fin, a characteristic that makes them attractive and widely traded and valued in the ornamental fish market (Silva et al., 2015; Kullander et al., 2018; Tribuzy-Neto et al., 2020; Oliveira et al., 2025a). In addition to its use in the aquarium trade, the species is also captured by subsistence fishing carried out along the main river channels where it naturally occurs (Silva, 2013; Hallwass, 2015).

Among the seven known species of the genus *Mesonauta*, *M. festivus* (Heckel, 1840) stands out and is popularly known as the festivus-cichlid. This species exhibits broad adaptability to different biotopes, occurring in benthopelagic regions of channels, lakes, and rivers with white, clear, and black waters of the Amazon basin (Amaral et al., 2020), mainly in areas of low water flow and with a strong presence of aquatic vegetation (Pires et al., 2015). It exhibits an omnivorous feeding habit, consuming invertebrates, insects, algae, and plant material in its natural environment; in captivity, it feeds on dry and live foods (Kullander et al., 2018).

During the reproductive period, the species becomes territorial and resident, forming pairs and exhibiting a balanced life-history strategy, characterized by sexual maturation at a relatively small size (approximately 4 cm in standard length). This behavior occurs mainly during the flood season in the Amazon region (Pires et al., 2015; Sarmento, 2017; Arantes et al., 2019). The female lays small, numerous eggs in specific sites, such as rocks, leaves, or roots, which are protected by both parents, a pattern also observed in other substrate-incubating cichlids (Meijide & Guerrero, 2000; Azevedo et al., 2022; Santos et al., 2025). The larvae exhibit indirect development, following the typical pattern of the early life cycle of freshwater fishes (Zhu et al., 2018; Silva et al., 2022; Contreras-Tapia et al., 2024; Santos et al., 2025).

Despite their ecological and economic importance and wide distribution, information on the early developmental stages of *Mesonauta* species is still limited. Most studies on the genus focus on reproductive behavior, spawning strategy, and parental care (Pires et al., 2015; Silva et al., 2015, Azevedo & Araújo, 2024), and only 2% of the recorded Neotropical cichlid species have their larval stages described (Reynalte-Tataje et al., 2020). Studies on the early ontogeny of fishes are relevant to understanding the life history of species, particularly with regard to phylogenetic and systematic relationships among cichlids. In addition to describing the main changes and variations in external morphology and growth patterns throughout this ontogeny, these studies help to elucidate essential biological aspects of the species. Although there has been an increase in studies on the early ontogeny of Amazonian fishes over the last decade, most of them focus on species with planktonic eggs and larvae that are important for aquaculture and commercial fisheries, such as Characiformes and Siluriformes (Santos et al., 2022; Cajado et al., 2023; Silva et al., 2024; Santos et al., 2024).

In this context, this study aims to describe the external morphology and morphometric patterns of the embryonic, larval, and juvenile development of *M. festivus*, seeking to understand how these variations are reflected across the different early life stages. Additionally, we hypothesize that *M. festivus* exhibits a saltatory ontogeny, characterized by rapid changes in growth rates. It is expected that the results of this study will expand knowledge of the early development of this species, filling existing gaps regarding its initial stages and complementing morphological information that was previously limited to the adult phase.

Material and Methods

Collection of biological material

For fish capture, a picaré-type net (10 m in length, 1.5 m in height, and 0.5 mm mesh size between opposite knots), also known as a marginal seine net, was used. The adult specimens were collected on September 13, 2021, in the marginal area of the Tapajós River, in the state of Pará (2°28’01”S, 54°37’60”W), during the crepuscular period / at dusk. The sampling was authorized by the System of Authorization and Information on Biodiversity (SISBIO) of the Chico Mendes Institute for Biodiversity Conservation and the Brazilian Ministry of Environment (IBAMA), under license no. 75.271-1/2020, issued in accordance with IBAMA Normative Instruction no. 154/2007.

After the trawl, the fish were removed from the net and transferred to a rectangular aquarium (60 × 35 × 40 cm) at the Laboratório de Ecologia do Ictioplâncton e Pesca em Águas Interiores of the Universidade Federal do Oeste do Pará (2°25'07"S, 54°44'27"W), where they underwent an acclimation process lasting approximately 10 to 20 minutes, until the water temperature matched that of the aquarium. The mean water temperature was maintained at 27 °C using an automatic heating system coupled with a thermostat. The specimens were identified based on Kullander & Silfvergrip (1991). The individuals were kept in captivity and were fed two to three times a day with commercial flake feed specifically for adult ornamental fish. The aquarium room was maintained on a cycle of approximately 14 hours of light and 10 hours of darkness.

After eight months following capture, spontaneous spawning occurred, and the broodstock remained in the aquarium, actively providing biparental care to the offspring through a natural division of responsibilities, such as the removal of unfertilized eggs or those infected by fungi. The male focused on territorial defense, while the female directly supervised embryonic development by ensuring adequate oxygenation and removing debris through the constant movement of her pectoral fins. The eggs were collected using a Pasteur-type pipette from the first hour after fertilization until hatching. After hatching, the larvae were collected and randomly allocated, following a completely randomized experimental design. After the third day, the larvae were fed with powdered commercial feed, specifically for this developmental stage, until the end of the sampling period. All handling, care, and processing followed the euthanasia protocols established by the National Council for the Control of Animal Experimentation (CONCEA, 2018). The juveniles used in this study were collected in riverbank areas of the Tapajós River between May and August 2024, using the same methodology applied for the capture of adults (3°29’30”S/55°22’13”W; 3°50’13”S/55°32’14”W; 4°05’54”S/53°42’51”W).

Laboratory procedures

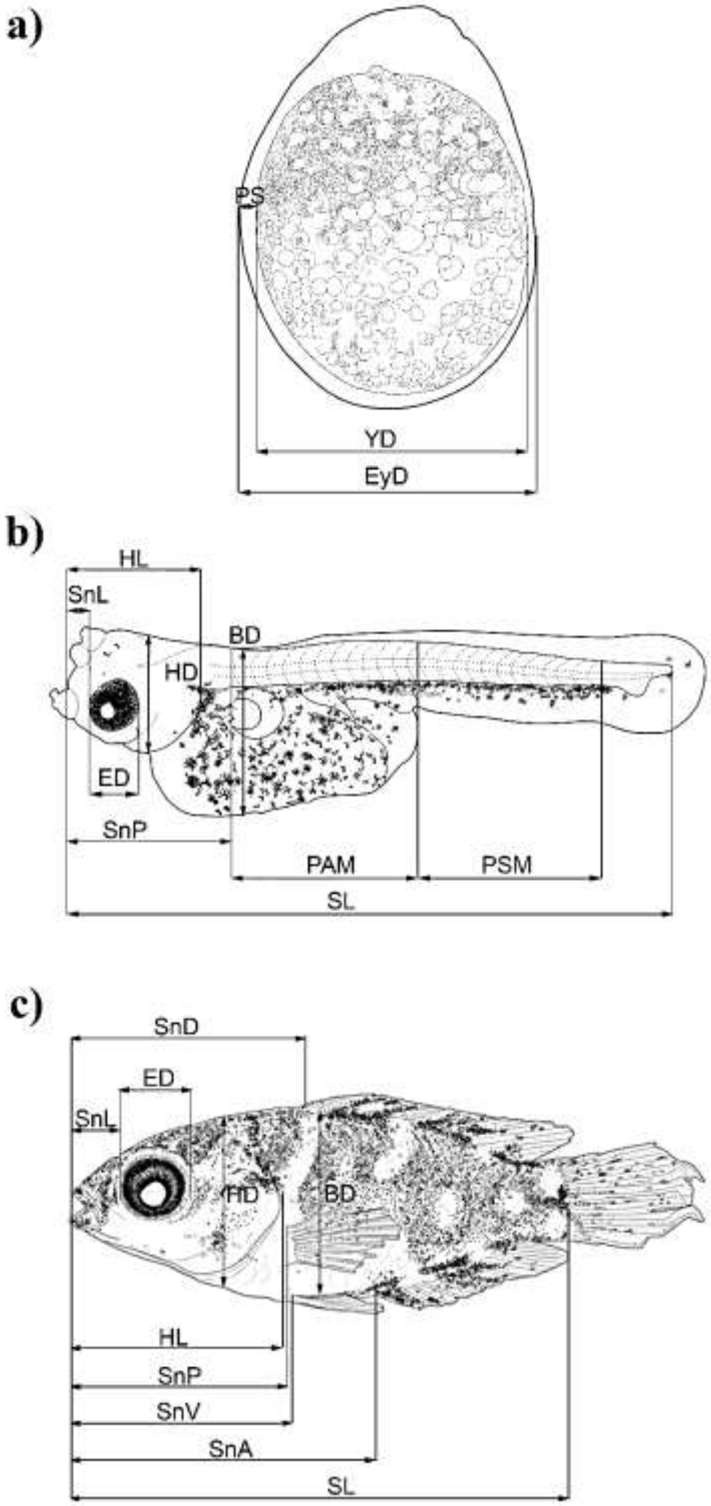
After collection, the specimens were anesthetized with eugenol and subsequently fixed in 10% formalin solution buffered with calcium carbonate, a protocol that adequately preserves morphometric characteristics for subsequent analyses (Cunningham et al., 2000). The collected eggs and larvae were classified according to the developmental stage proposed by Ahlstrom et al. (1976), modified by Nakatani et al. (2001). The classification included the embryonic period (stages of initial cleavage, early embryo, and free-tail embryo), the larval period (yolk-sac larva, flexion, and post-flexion stages), and the juvenile period, in which the rays of all fins are fully formed, scales appear, and development continues until the size at first sexual maturity. The preflexion stage was not identified because the larvae presented the posterior section of the notochord already flexed (due to the emergence of the hypural plates), in individuals whose mouths were still closed (non-functional) and with a large amount of yolk. The description of each period was based on the observation of the main morphological events and the degree of early development, as well as meristic and morphometric characteristics. The selection of the best specimens considered their integrity, such as the condition of the fins, body shape, and presence of pigmentation. Those that best represented the characteristic patterns of the species at each developmental stage were selected, fixed in 4% formalin, placed in glass vials, and deposited in the Reference Collection of Fish Eggs and Larvae of the Laboratório de Ecologia do Ictioplâncton e Pesca em Águas Interiores (CROLP LEIPAI), of the Universidade Federal do Oeste do Pará (https://specieslink.net/col/CROLP-LEIPAI/), under the numbers LEIPAI 01340 a 01352, LEIPAI 01404 e LEIPAI 01414.

The morphometric measurements (mm) were performed using a binocular stereomicroscope (Leica S9i), equipped with an integrated digital camera for image capture and analysis through the software Leica LAS EZ 4.13. Embryonic morphometric characterization was performed using the following variable: egg diameter (EyD), yolk diameter (YD) and perivitelline space (PS), this last one is categorized as restricted, moderate, broad, or very large, according to its proportion in the total volume of the egg (Nakatani et al., 2001). In the EyD, the horizontal diameter was considered the minor axis, while the vertical diameter was considered the major axis (Figure 1a). For the larvae and juveniles, ten variables were measured, following Ahlstrom et al. (1976): 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 (Figure 1b, c). Standard length (SL) measurements in specimens at the yolk-sac larval stage were taken as the greatest linear distance between the anterior tip of the upper jaw (premaxilla) and the posterior end of the notochord, and in the flexion, post-flexion, and juvenile stages, from the tip of the snout to the hypural plate (Figure 1), according to Marinho (2017) and Marinho (2023). 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 (PAM) were defined as those located anterior to the vertical line passing through the anterior margin of the anal opening; the post-anal myomeres (PSM) 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.

Data analysis

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

Figure 1. Morphometric measurements of *Mesonauta festivus* (Cichliformes, Cichlidae). a) embryonic period, b) larval period, and c) juvenile period.



The hypothesis of continuous isometric growth was tested using a simple linear regression model (equation $y = a x + b$), where "y" represents the dependent variable, "x" the independent variable, "a" the intercept, and "b" the growth slope coefficient. Two alternative hypotheses were also evaluated: gradual allometric growth, tested using a quadratic regression ($y = a x^2 + b x + c$), and discontinuous isometric growth, assessed through piecewise linear regression, characterized by breakpoints indicating changes in growth rates. The selection of the best model for each morphometric variable, in relation to head length and standard length, was performed based on the F-test (Sokal & Rohlf, 1989), adopting a significance level of $p < 0.05$. Regression analyses were conducted using Statistica™ 7.0 (StatSoft).

Results

Embryonic period

Forty eggs at different developmental stages were analyzed (12 at initial cleavage, 21 at early embryo stage, and seven at free-tail stage), illustrated in Figure 2, with the morphometric data presented in Table 1. The eggs are telolecithal and adhere to the substrate through an adhesive mucous secretion present on the chorion. The shape is elliptical, with a translucent chorion, reduced perivitelline space, and a longitudinal axis longer than the transverse axis, exhibiting a yellow coloration and diffuse internal dendritic pigmentation in the yolk (Figure 2). At the *initial cleavage* stage (Figure 2a), they exhibited a horizontal diameter ranging from 1.16 to 1.34 mm (mean: 1.23 mm ± 0.05) and a vertical diameter ranging from 1.58 to 1.83 mm (mean: 1.71 mm ± 0.08) (Table 1). The perivitelline space (PS) is limited to moderate, with an average horizontal diameter of 2.18% and vertical diameter of 10.62% (relative to the egg). The animal pole is narrower than the vegetal pole, and it is possible to observe the yolk granule cells and oil droplets, visible due to the change in cell density with more or less translucent areas.

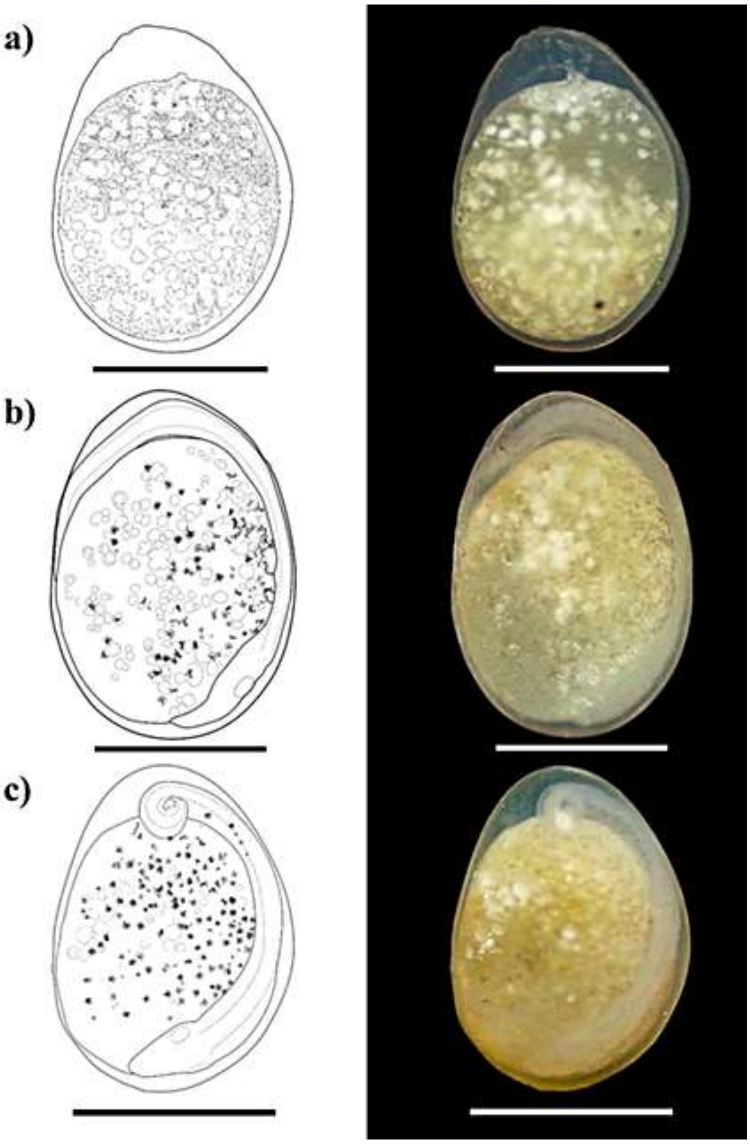
Initial embryo (Figure 2b): The eggs showed a horizontal diameter ranging from 1.12 to 1.29 mm (mean: 1.21 mm ± 0.05) and a vertical diameter ranging from 1.62 to 1.84 mm (mean: 1.73 mm ± 0.05) (Table 1). The PS remains restricted, with an average horizontal diameter of 2.53% and vertical diameter of 5.75% (relative to the egg). The yolk is composed of large oil globules of varying sizes. Observes the formation of the germ ring and the development of segmentation, including the emergence of: (I) of the somites (somitogenesis), which appear sequentially on each lateral side of the embryonic axis and will form part of the skeletal muscle and tissues, (II) from the incipient otic vesicle that began with the evagination of two lateral protrusions from the brain rudiment in the anterior region of the embryo, (III) of the caudal bud, which begins to project from the posterior end of the embryo, and (IV) of the pigmentation initially distributed in the yolk sac and, later, in the ventral region of the embryo’s body.

Free-tail embryo (Figure 2c): The eggs had a horizontal diameter ranging from 1.18 to 1.24 mm (mean: 1.21 mm ± 0.02) and a vertical diameter ranging from 1.62 to 1.75 mm (mean: 1.68 mm ± 0.05) (Table 1). The PS remains restricted, with an average horizontal diameter of 2.04% and a vertical diameter of 5.20% (relative to the egg). The posterior end of the trunk-tail was elongated, detached from the yolk, and coiled inside the chorion, in addition to the presence of an ovoid optic vesicle, oil droplets, and somite hyperplasia. Dendritic melanophores are present and distributed throughout the yolk. A wide range of pigments covers the upper part of the intestine and spreads throughout the ventral region of the embryo's body. The eggs hatch between the second and third day (approximately 52 hours post-fertilization) at an average water temperature of 27°C.

Table 1. Analyzed variables (mm), minimum values (Min), maximum values (Max), standard deviation (SD), and morphometric relationships (%) found for the morphometric variables obtained from eggs of *Mesonauta festivus*. Abbreviations: EC – initial cleavage; EE – early embryo; FTE – free-tail embryo; PS – perivitelline space; YD – yolk diameter; N – number of individuals analyzed.

Variable	EC (N=12)		EE (N=21)		FTE (N=7)	
	Min-Max	**Mean±SD**	**Min-Max**	**Mean±SD**	**Min-Max**	**Mean±SD**
Egg diameter (horizontal)	1.16-1.34	1.23±0.05	1.12-1.29	1.21±0.05	1.18-1.24	1.21±0.02
Egg diameter (vertical)	1.58-1.83	1.71±0.08	1.62-1.84	1.73±0.05	1.62-1.75	1.68±0.05
Vitellus diameter (horizontal)	1.15-1.29	1.20±0.04	1.06-1.23	1.14±0.04	1.14-1.18	1.15±0.01
Vitellus diameter (vertical)	1.47-1.77	1.61±0.09	1.34-1.72	1.50±0.11	1.40-1.59	1.57±0.07
Perivitelline space (horizontal)	0.01-0.06	0.03±0.02	0.01-0.05	0.03±0.01	0.01-0.04	0.02±0.01
Perivitelline space (vertical)	0.23-0.39	0.32±0.06	0.02-0.28	0.09±0.05	0.04-0.10	0.08±0.02
PS/EgD (%) (horizontal)	0.41-5.18	2.18±1.97	1.11-4.58	2.53±1.04	0.86-3.54	2.04±0.85
PS/EgD (%) (vertical)	7.5-17.07	0.62±2.59	1.18-20.14	5.75±3.81	2.84-6.54	5.20±1.23

Figure 2. Embryonic development of *Mesonauta festivus*: (a) initial cleavage; (b) early embryo; and (c) free-tail embryo. Scale bar = 1 mm.



Larval period

A total of 127 larvae were analyzed (52 yolk-sac larvae, 56 at flexion, and 12 post-flexion), illustrated in Figure 3. Morphometric and meristic data are presented in Table 2.

Yolk-sac larvae ((Figure 3a, b, c): Standard length ranges from 2.68 to 4.04 mm (mean ± SD = 3.68 mm ± 0.40). The newly hatched larvae have a straight notochord visible through transparency, a spherical and relatively large yolk sac (46% of body width and 25% of body height), which becomes wider on the ventral part of the trunk and narrower at the dorsal extremity, decreasing in size throughout the stage. The head is rounded, with the presence of transient adhesive organs formed by two pairs in the frontal region and one occipital pair. Otic vesicles are present in the posterior region of the head from hatching. The larvae at this stage attached to the substrate and were cared for by their parents. The formation of morphological structures at this stage begins at 3.28 mm SL, when the eye appears spherical and partially pigmented, and the presence of the mouth outline is observed, located ventrally and closed by a thin epithelial layer, but undergoes progressive migration during development, subsequently occupying a terminal position. The anus is closed and not yet functional, located in the median region of the body, along with the presence of the pectoral fin bud. At 3.99 mm SL, the pectoral fin bud is observed, surrounded by a hyaline membrane. Dendritic melanophores are distributed throughout the yolk, extending and intensifying over a broad band surrounding the ventral interface between the digestive tract, the embryonic membrane, and the terminal section of the notochord. The embryonic membrane is continuous and surrounds the body from the head-trunk junction region to the ventral area of the yolk sac. The total number of myomeres ranges from 27 to 28 (12–13 pre-anal and 15 post-anal). During this stage, the larvae remained clustered at the bottom of the aquarium and moved their tails rapidly.

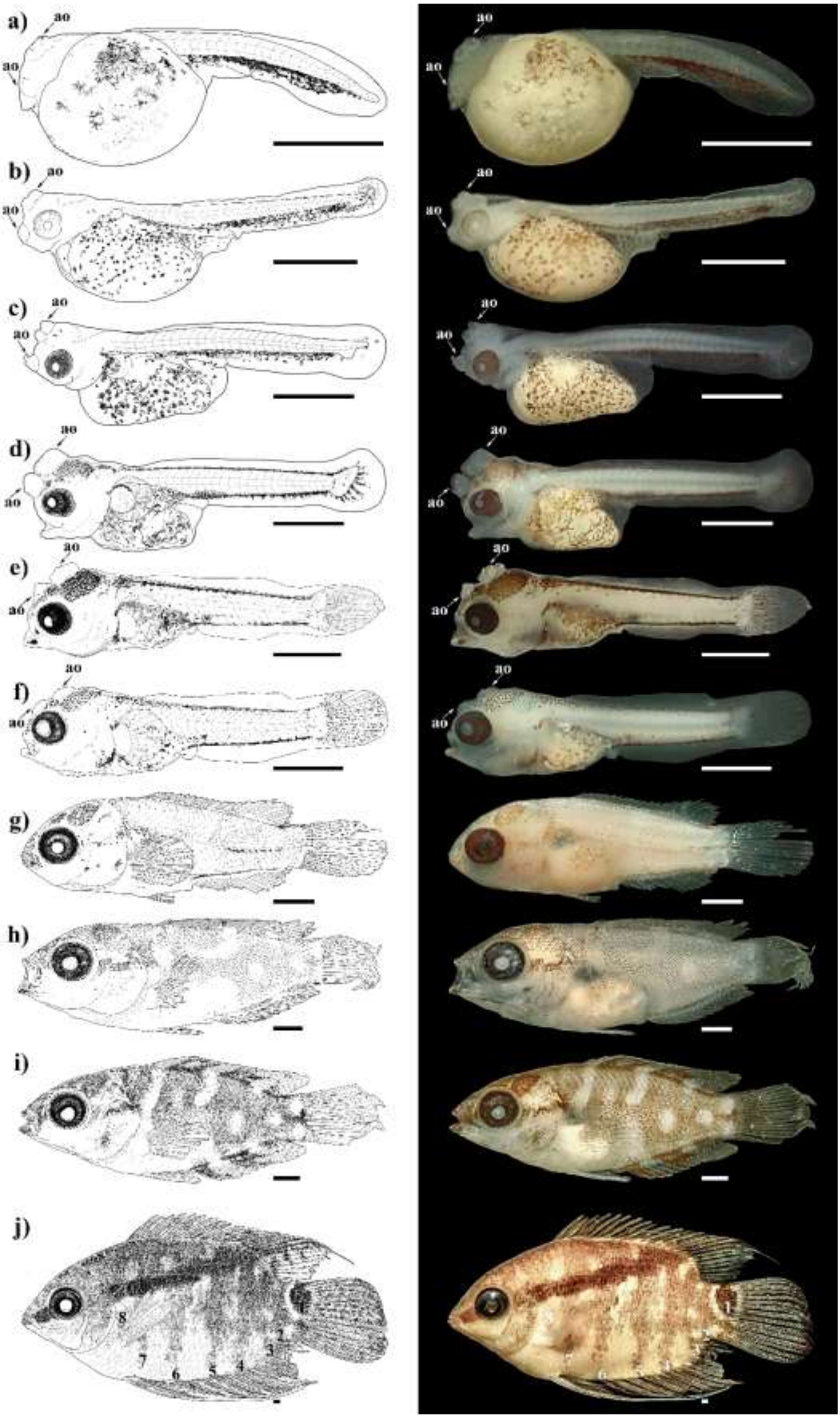


Figure 3. Larval and juvenile development of *Mesonauta festivus*: a) yolk-sac larval early (2.68 mm SL); b) yolk-sac larval (3.28 mm SL); c) yolk-sac larval late (4.04 mm SL); d) flexion early (4.09 mm SL); e) flexion (4.65 mm SL); f) postflexion early (5.00 mm SL); g) postflexion (6.68 mm SL); h) postflexion late (8.70 mm SL); i) juvenile (10.30 mm SL); and j) juvenile (14.00 mm SL); ao, adhesive organ. Scale bars = 1 mm.

Flexion (Figure 3d, e): Standard length ranges from 4.06 to 4.75 mm (mean ± SD = 4.43 mm ± 0.22). The final section of the notochord is flexed, allowing the hypural plate to be observed. The yolk sac shows a reduction in size (34.71% in width and 20.88% in depth) in individuals with 4.75 mm SL, becoming wider at the dorsal end. The nostril is simple, the eye is fully pigmented and spherical, and the mouth, in a terminal position, is open, with the lower jaw protruding from the yolk, extending the head forward (upright position), and by the end of this stage, a significant reduction of the adhesive organ is observed. The anus is open and functional, located in the median region of the body. At a standard length of 4.06 cm, the pectoral fin bud is more prominent. At this stage, the larvae inflated their swim bladder and began active swimming movements. The melanophores become more intense and are distributed over the operculum, the dorsal region of the head and body, and are also present in the yolk, the ventral region of the body, and outline the base and spaces between the rays of the caudal fin. It can be observed that the embryonic membrane extends from the dorsal region of the trunk to the ventral area of the yolk sac. The total number of myomeres ranges from 27 to 28 (12–13 pre-anal and 15 post-anal).

Postflexion (Figure 3f, g, h): Standard length ranges from 5.00 to 10.00 mm (mean ± SD = 7.73 ± 1.58 mm). The flexion of the notochord is already evident at the beginning of this stage. The yolk sac is completely absorbed in individuals with a standard length of 5.05 mm, and the head remains rounded. The adhesive organ progressively decreases, disappearing completely in individuals with a standard length of 6.68 mm. The eye remains spherical, the nostril is simple, the mouth is terminal, the snout is short, the swim bladder is inflated, and the digestive tract is positioned in the median region of the body. It is also noticeable the emergence of new pigments along the body, interspersed with unpigmented areas forming a dorsal and a ventral colorless stripe, between which traces of dark pigment remain. Furthermore, from 8.70 mm SL, a band of chromatophores can be observed located behind the eye, curving toward the beginning of the dorsal fin base. The total number of myomeres is 28 segments (13 pre-anal and 15 post-anal) (Table 2).

Juvenile period

Seven individuals were analyzed, with standard lengths ranging from 10.30 to 14.00 mm (mean ± SD = 12.27 ± 1.43 mm), as illustrated in Figure 3 (i, j). The morphometric and meristic data are presented in Table 2. The juveniles have a laterally compressed body, with the anus located in the middle region of the body and an inflated swim bladder. The head is relatively rounded, with a moderately convex dorsal profile. The eyes are large and spherical, the nostrils are simple, the mouth is protrusible, and the snout is short. The pigmentation pattern intensifies compared to the previous stage, with the appearance of new melanophores along the body forming irregular bars or spots with a marbled/reticulated appearance, expanding dorsoventrally and mediolaterally. In individuals from 13.26 mm SL onward, the coloration becomes more characteristic of the patterns observed in adults, with emphasis on the formation of eight vertical bars, which start at the end of the caudal peduncle and extend to the anterior region of the operculum. t is noted that the third and fourth bars are joined through a “K”-shaped intersection (the bars are numbered from tail to head), that is, the first ray is always the most posterior) and the presence of a black ocellus at the base of the caudal fin. Pigments are observed between the spines and rays of the pectoral, dorsal, anal, pelvic, and caudal fins. They exhibit a depigmented gular and abdominal region, extending to the area posterior to the anus. The dorsal fin has a long base, originating near the head and extending to the caudal peduncle, while the anal fin begins in the mid-body region. The dorsal and anal rays are not much longer than the spines. At this stage, it is not possible to visualize or count the myomeres due to muscle development. The sequence of formation of the fin spines and rays was: caudal (8+8), dorsal (XV, 10-11); anal (VIII, 10-14), ventral (I, 5) and pectoral (I, 11) (Table 2).

Morphometric relationships

During the larval period, the body varied from very long (yolk-sac larvae) from long to moderate (postflexion). The head initially ranges from small to moderate and, from post-flexion onward, becomes moderate to large, remaining large in juvenile. The eyes range from moderate to large during the larval period and become large in juveniles. The other morphometric variables (SnL, HL, SnA, SnD, SnP, and SnV) showed a relative increase in their proportions throughout development (Table 2).

Table 2. Analyzed variables (mm), minimum values (Min), maximum values (Max), standard deviation (SD), and morphometric relationships (%) found for the morphometric and meristic variables obtained in larvae and juveniles of *Mesonauta festivus*. Abbreviations: HD – head depht; BD – body depht; HL – head length; SnL – snout length; SL – standard length; ED – eye diameter; SnA – snout to anal fin length; SnD – snout to dorsal fin length; SnP – snout to pectoral fin length; SnV – snout to pelvic fin length; N - number of individuals analyzed; AF – absent fin; NV – not visible.

Variables	**Larval period**						**Juvenil period**	
	Yolk-sac larvae (N= 52)		Flexion (N= 56)		Posflexão (N= 12)		Juvenile (N= 7)	
(mm)	**Min-Max**	**Mean±SP**	**Min-Max**	**Mean±SP**	**Min-Max**	**Mean±SP**	**Min-Max**	**Mean±SP**
SL	2.68-4.04	3.68±0.40	4.06-4.75	4.43±0.22	5.00-10.00	7.73±1.58	10.30-14.00	12.27±1.43
HL	0.21-0.99	0.83±0.15	1.02-1.51	1.25±0.14	1.55-3.74	2.67±0.64	3.93-5.45	4.46±0.54
SnL	0.09-0.17	0.15±0.02	0.17-0.20	0.18±0.01	0.23-0.49	0.36±0.07	0.85-1.60	1.21±0.25
ED	0.22-0.40	0.32±0.05	0.37-0.52	0.45±0.04	0.61-1.34	0.98±0.21	1.43-2.21	1.73±0.28
HD	0.32-0.67	0.46±0.06	0.51-0.66	0.59±0.05	0.76-1.95	1.40±0.37	3.29-5.24	4.08±0.64
BD	0.20-1.22	0.42±0.13	0.45-0.61	0.53±0.04	0.65-2.26	1.59±0.63	3.84-6.45	5.34±0.97
SnP	0.42-0.99	0.81±0.19	1.00-1.56	1.22±0.17	1.64-4.16	3.01±0.82	4.09-5.76	4.86±0.64
SnA	AF	AF	2.74-3.71	3.24±0.35	3.79-6.40	4.98±0.73	6.43-8.48	7.40±0.82
SnD	AF	AF	1.41-1.88	1.64±0.13	1.92-4.75	3.41±0.84	4.79-6.55	5.55±0.63
SnV	AF	AF	AF	AF	1.84-3.92	3.01±0.63	4.40-6.62	5.32±0.79
Morphometric relationships (%)								
SnL/HL	16.32-19.43	17.83±0.77	12.94-17.64	14.93±1.24	11.36-14.59	13.46±0.85	21.11-31.71	26.97±3.27
ED/ HL	32.34-45.18	38.04±3.12	31.91-40.95	36.05±1.90	31.67-39.18	37.10±1.97	35.88-41.06	38.57±1.93
HD/ HL	48.59-69.32	54.81±4.27	42.46-53.60	47.23±2.42	47.31-56.03	52.14±3.61	82.66-96.87	91.27±5.02
HL /SL	16.76-24.96	22.87±1.81	24.11-31.72	28.04±2.00	31.01-37.39	34.32±1.57	34.21-39.37	36.41±2.01
BD/ SL	7.54-36.63	10.74±1.13	11.00-13.06	12.03±0.53	12.91-24.19	19.79±4.91	37.23-46.63	43.22±3.21
SnP/ SL	13.64-25.43	22.76±3.31	22.79-32.76	27.40±2.65	32.84-41.86	38.31±3.40	34.29-42.39	39.64±2.77
SnA/ SL	AF	AF	AF	AF	59.77-75.86	65.32±5.46	57.83-64.27	60.39±2.12
SnD/ SL	AF	AF	AF	AF	38.48-47.48	43.70±2.47	43.27-48.51	45.28±1.79
SnV/ SL	AF	AF	AF	AF	36.90-41.35	38.91±1.36	39.31-48.10	43.33±3.31
Number of myomers (mode)								
Preanal	12-13 (12)		12-13 (13)		13		NV	
Postanal	15		15 (15)		15		NV	
Total	27-28 (27)		27-28 (28)		28		NV	
Number of thorns and rays (mode)								
Pectoral	NV		NV		I, 11		I, 11	
Anal	NV		NV		VIII, 10-14 (VIII, 10)		VIII, 10-14 (VIII,14)	
Dorsal	NV		NV		XV, 10-11 (XV, 11)		XV, 10-11 (XV,11)	
Pelvic	NV		NV		I, 5		I, 5	
Caudal	NV		NV		8+8		8+8	

Growth analyses

All variables exhibited discontinuous isometric growth, indicating a change in the growth rate from the inflection point observed at the post-flexion stage, except for head length, which showed continuous isometric growth. For head length, snout length, eye diameter, head depth, body depth, and distance between the snout and the pelvic fin, the growth rate of individuals accelerated after the inflection point, while for the distances between the snout and the pectoral, anal, and dorsal fins, the growth rate slowed down after this point (Figure 4, Table 3).

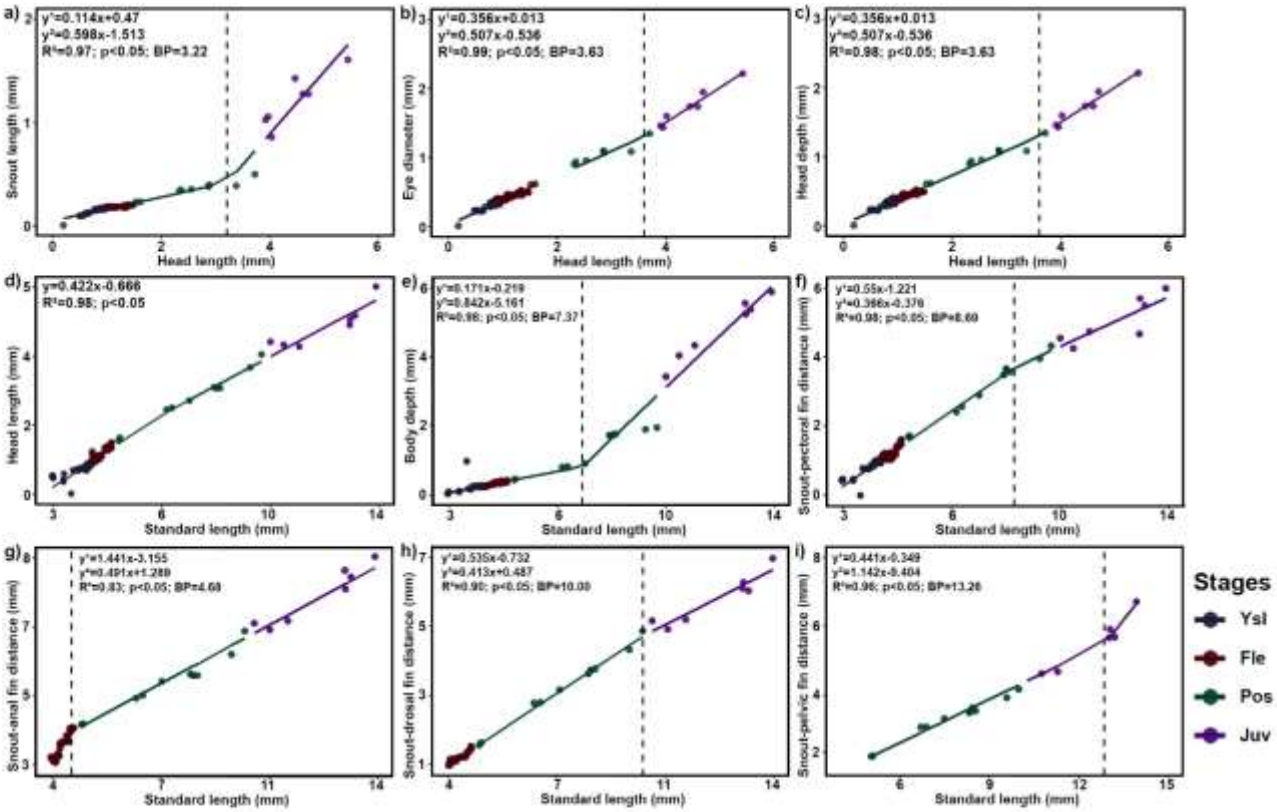


Figure 4. Head length proportions (mm) relative to snout length (**a**), eye diameter (**b**), head depth (**c**), and standard length proportions (mm) relative to head length (**d**), body depth (**e**), snout to pectoral fin distance (**f**), snout to anal fin distance (**g**), snout to dorsal fin distance (**h**), and snout to pelvic fin distance (**i**) during the early development of *Mesonauta festivus*.

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

Variables	**Body Growth of** *Mesonauta festivus*											
	R^2_L	R^2_Q	R^2_S	$F_{Q/L}$	**p**	$F_{S/L}$	**p**	$F_{S/Q}$	**p**	**MM**	**BP**	**N**
SnL/HL	0.85	0.95	0.97	236.55	0.00	235.84	0.00	81.52	0.00	S	3.22	127
ED/ HL	0.99	0.99	0.99	38.61	0.00	27.85	0.00	13.27	0.00	S	3.63	127
HD/ HL	0.90	0.97	0.98	350.00	0.00	190.27	0.00	8.73	0.00	S	2.62	127
HL /SL	0.99	0.99	0.99	14.49	0.00	9.36	0.00	3.88	0.05	L	-	127
BD/ SL	0.91	0.98	0.98	389.40	0.00	239.11	0.00	22.21	0.00	S	7.37	127
SnP/ SL	0.98	0.99	0.99	43.94	0.00	30.53	0.00	12.91	0.00	S	8.68	127
SnA/ SL	0.66	0.74	0.83	37.93	0.00	58.93	0.00	61.45	0.00	S	4.75	75
SnD/ SL	0.85	0.88	0.90	35.94	0.00	34.37	0.00	25.66	0.00	S	5.15	75
SnV/ SL	0.93	0.93	0.96	2.01	0.16	44.44	0.00	85.50	0.00	S	4.33	19

Discussion

The recording of morphological characteristics and changes, functional adaptations, and the rate of growth processes during fish larval development is essential for understanding larval survival strategies and provides relevant information for taxonomic studies, as it contributes to the detection of specific differences, including heterochrony, which may play a crucial role in phenotypic divergence, as reported by Marconi et al. (2023). Although the larvae are quite different in appearance from the adults, they still possess distinctive features that allow their identification. This study examined the morphological, meristic, and morphometric changes of the Amazonian ornamental fish *M. festivus* during its early ontogeny (e.g., yolk sac shape, number of myomers, fin spines and rays, coloration patterns, and body proportions), and growth patterns were estimated.

The species exhibits embryonic development with characteristics similar to other Neotropical cichlids, including elliptical eggs with little perivitelline space and a mucous secretion that ensures adhesion and fixation of the eggs at the spawning site (Rizzo et al., 2002; Piesiewicz et al., 2024; Santos et al., 2025). This secretion acts as a protective barrier against impacts and suspended particles, safeguarding the embryonic structure during early development (Sefc, 2011). The characteristics of the egg are related to the species' non-migratory reproductive behavior and follow the phylogeny of the substrate-brooding group, with parental care (Meijide & Guerrero, 2000; Kullander, 2003; Contreras-Tapia et al., 2025), as a way to protect the spawning from predators and to aid in the development and growth of the larvae. The morphological characteristics of *Mesonauta* eggs had not yet been described, but they are consistent with the characteristics observed at the family level.

The egg size of *M. festivus* showed slight variations compared to other freshwater cichlids, such as *Astronotus ocellatus*, *Cichlasoma dimerus*, *Heros severus*, and *Pterophyllum scalare*, which have substrate incubation (Meijide & Guerrero, 2000; Groppelli et al., 2003; Paes et al., 2012; Santos et al., 2025). While cichlid species that practice mouthbrooding have larger eggs throughout embryonic development (Fujimura & Okada, 2007; Lopes et al., 2015). The size of fish eggs is considered physiologically important, as it is related to oocyte quality and the fecundity of the breeders, as well as to larval survival and growth rates (Thorsen & Kjesbu, 2001; McDonough et al., 2003). The ellipsoidal (oval) shape increases the surface area (surface-to-volume ratio), facilitating gas exchange and improving embryo oxygenation, an advantage in aquatic environments with slower water flow, low oxygen levels, and high organic matter (Kamler, 1992; Strathmann & Strathmann, 1995; Kochhann & Chapman, 2023). This type of shape facilitates organization and adherence to the substrate in rows or egg masses (deposition of more eggs in the same space), fitting better between rock crevices, plants, branches, stones, and logs, thereby reducing the chances of being swept away by currents or predated (Riehl & Patzner, 1998; Wootton, 1998, Johnston & Leggett, 2002). In addition to maximizing resistance to compression by sediments and vegetation in environments with unstable substrates (Zhu et al., 2025).

The larvae of *M. festivus* are altricial, as they exhibit little morphological development, with unpigmented eyes, nonfunctional mouth and anus, absence of the pectoral fin bud, and presence of a spherical yolk sac proportionally large relative to standard length, as well as adhesive organs. It was not possible to observe larvae in the preflexion stage, suggesting that this stage is very short or even nonexistent. The flexion stage is reached early, before the complete absorption of the yolk. Other neotropical cichlids, such as *Cichlasoma dimerus* and *Symphysodon aequifasciatus*, also exhibit slower and later yolk absorption up to the final flexion stage (Meijide & Guerrero, 2000; Satoh et al., 2017), and *Pterophyllum scalare* and *Nannacara anomala*, extending until the end of postflexion (Korzelecka-Orkisz et al., 2012; Kupren et al., 2014). On the other hand, mouthbrooding species, such as *Oreochromis niloticus* (Fujiwara & Okada, 2007), they exhibit a much larger yolk sac and an even longer extension of the endogenous nutrition phase. The presence of prominent cephalic adhesive organs in early larvae of *M. festivus* has also been described for other cichlid (Lopes et al., 2015; Kratochwil et al., 2015; Santos et al., 2025) and are considered a temporary and transient gland that secretes mucus and functions as a mechanism for attachment, adhesion, and/or aggregation of larvae on the substrate during early development (Maurakis & Maurakis, 2017), a life strategy to remain together and under parental care. However, the number, shape, location, function, or absence of these glands may vary among species and groups of fish (Prusińska et al., 2009; Pottin et al., 2010; Nelson et al., 2019; Oliveira et al., 2025b).

Mesonauta festivus larvae at early developmental stages exhibit a pigment pattern similar to that described for most Neotropical cichlids, with dendritic melanophores concentrated on the yolk and forming an intense ventral stripe that extends along the interface between the digestive tract and the embryonic membrane, reaching the terminal region of the notochord (Kupren et al., 2014; Contreras-Tapia et al., 2024; Santos et al., 2025). In the most developed larval stage (late postflexion) and in juvenile individuals, changes in the intensity and formation of new chromatophores become more evident throughout the body. This new remodeling in the increase and intensification of pigmentation, making the individuals more conspicuous, may indicate an adaptive response to the habitat, favoring camouflage and mimicry in environments with aquatic vegetation and more protected microhabitats, helping to reduce predation and functioning as a defense mechanism (Sugimoto, 2002; Liang et al., 2020; Marconi et al., 2024; Prazdnikov, 2024), in specific fish behaviors, such as social status (Barlow & Siri, 1994; Korzan et al., 2008) or indicate an intraspecific signal that helps reduce aggression and assist in the establishment of a dominance hierarchy (Miyai et al., 2011). However, the color pattern, characterized by the dispersion or concentration of melanophores on the body, is an attribute commonly used in taxonomic studies involving cichlids (Ready et al., 2006; Rodrigues et al., 2009).

By comparing the external morphological characteristics of *M. festivus* with the larval development of other neotropical cichlids reported in the literature. It is noted that the total number of myomeres (27 to 28) overlaps with the values found in larvae of *Astronotus* (28–30) and *Satanoperca* (24–30), which occur syntopically in Amazonian water bodies. However, *Astronotus* larvae have a moderately deep body (28.35% to 35.79% SL) and an inferior mouth that becomes terminal during development (Nakatani et al., 2001), whereas *M. festivus* has a long body, with depth ranging from 12.00 to 12.97% of SL, and a mouth always in a terminal position that becomes protrusible in the juvenile stage. *Satanoperca* larvae have a moderately sized and more robust body (27,81% a 41,27% SL), terminal mouth that becomes subterminal in later stages and elliptical eye (Lopes et al., 2015), differing from *M. festivus*, which has a spherical eye that ranges from moderate to large. *Crenicichla* larvae also have large, spherical eyes and a terminal mouth, but they exhibit distinctive features compared to *M. festivus*, including a moderately more elongated and low body, a large head, a concave snout, and a total myomeric count ranging from 32 to 33 segments (Ponton & Mérigoux, 2001; van der Sleen & Albert, 2018). More developed individuals of *M. festivus* can be distinguished and identified using morphological characters such as the shape and size of the head, snout, body, and caudal fin, as well as pigmentation patterns and meristic data, including the number of spines and rays in the dorsal and anal fins, as presented in Table 4.

Table 4. Comparative data of meristic and morphological values reported in the literature among different genera of Neotropical Amazonian cichlids.

Genus	Characters						
	Spines and rays (dorsal fin)	Spines and rays (anal fin)	Caudal fin shape	Body shape	Pigmentation bars on the body	Myomeres	Vertebrae
Acarichthys	XII-XIII+11-12	III, 8-9	emarginate	Deep body with a straight and steep predorsal contour	absent	26-27*	25-26
Acaronia	XII-XIV+9-10	III, 7-9	rounded	elongated and deep body	absent	25*	24
Astronotus	XII-XIV, 19-22	III, 15-17	rounded	moderate body	wavy bands and/or irregular spots	28-30	29-31*
Caquetaia	XV-XVI, 10-13	V-VI, 9-10	rounded	strongly compressed body	absent	-	-
Cichlasoma	XIII-XVIII, 8-12	III-VI, 7-9	rounded	moderate body	absent	-	-
Geophagus	XV-XIX, 9-13	III, 7-9	emarginate	moderate body	absent	33-34*	32-33
Heros	XV-XVI, 12-14	VII-VII, 11-13	rounded	strongly compressed and deep body	regular vertical bars (6–7)	-	-
Mesonauta	XV, 10-11	VIII, 10-14	rounded	deep and laterally compressed body	irregular bars	28-29	29-30*
Satanoperca	XII-XVII, 8-14	III, 6-9	truncated or subtruncated	long snout and small mouth	dorsal melanophore spots (4 a 7)	29-30*	28-29
Symphysodon	VIII-X, 28-33	VI-IX, 27-31	subtruncated	body strongly compressed and deep - rounded	regular vertical bars (9)	-	-

* The meristic and morphological data used for comparison were taken from Nakatani et al. (2001), Lopes et al. (2015), and Van der Sleen & Albert (2017).

The growth of body parts was isometric and continuous, with abrupt changes between the larval period (postflexion stage) and juvenile stage, indicating high morphometric and morphological variation during development. This suggests an adaptive response to the species' morphophysiological and behavioral changes, involving the loss of larval traits and the acquisition of adult characteristics. Initially, the larvae of *M. festivus* concentrate their growth in the head region, while the body develops more slowly. These changes reflect visual and feeding adaptations, marking the transition from endogenous to exogenous feeding and the formation of a more functional head. The development of the fins occurs after the flexion of the posterior section of the notochord and the appearance of the hypurals that support the rays of the caudal fin, followed by the formation of the rays of the dorsal, anal, ventral, and pectoral fins, indicating an increase in swimming capacity, maneuverability, and propulsion with growth. Thus, the individuals are able to shift their vertical distribution from the benthopelagic to the mesopelagic layer, which ensures better morphofunctional performance throughout early development, necessary to escape predators and obtain food, thereby increasing their chances of survival (Osse et al., 1997; Osse & Van den Boogaart, 2004). This transformation occurs when individuals reach a standard length greater than 8.5 mm, accompanied by changes in eye diameter growth and muscle development, resulting in a shift from an elongated body to a more robust profile and an intensification of body pigmentation. Additionally, the appearance of teeth during the juvenile period suggests a greater ability to grasp food. Some authors state that ontogenetic changes in habitat use are associated with alterations in the morphometric proportions of structures related to swimming and feeding (Machado-Evangelista et al., 2015; Moteki et al., 2017), consistent with the ecological information for this cichlid, which occurs in areas with low current and abundant aquatic vegetation (Azevedo & Araújo, 2024).

The results allow a better understanding of the ontogenetic changes that occur in *M. festivus*, following a long sequence of stable stages interrupted by a rapid shift in its development, associated with some morphological, physiological, ecological, or behavioral event of the species (Balon, 1984; Kovác et al., 1999). Furthermore, it provides support for future studies on the genus *Mesonauta*, contributing to comparative research with other Neotropical cichlids and their congeners.

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