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**Original article**

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# Early development of two commercially valuable fish from the lower Amazon River, Brazil (Characiformes: Serrasalmidae)

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We described the early development of *Myloplus asterias* and *M. lobatus*, two fish species of the Serrasalmidae using morphological, meristic, and morphometric characteristics. These herbivores serrasalmids are heavily fished because of their commercial importance in the Amazon. The individuals were collected between 2016 and 2020 in the limnetic zone of open water and macrophyte stands in the Lower Amazon River floodplain. We tested different growth models to identify the development pattern of these species. During the initial ontogeny, these two species can be differentiated mainly by the myomeres total number, 37 to 39 in *M. asterias* vs. 40 to 41 in *M. lobatus*, the pigmentation pattern, and dorsal-fin ray numbers. These characteristics are effective in distinguishing these species from other serrasalmids. The morphometric relationships were also different between these two species, showing distinct patterns in growth between the analyzed features. An identification key for larvae of some sympatric Serrasalmidae species from the Amazon basin is presented. Our expectation is that this study will contribute to the knowledge of the initial ontogeny and the biology of fish species in the Neotropical region.

Keywords: Fish larvae, Identification key, *Myloplus asterias*, *Myloplus lobatus*, Ontogeny.

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Descrevemos o desenvolvimento inicial de *Myloplus asterias* e *M. lobatus*, duas espécies de peixes da família Serrasalmidae usando características morfológicas, merísticas e morfométricas. Esses serrasalmídeos herbívoros são fortemente pescados devido à sua importância comercial na Amazônia. Os indivíduos foram coletados entre 2016 e 2020 na zona limnética de águas abertas e em bancos de macrófitas na planície de inundação do baixo rio Amazonas. Testamos diferentes modelos de crescimento para identificar o padrão de desenvolvimento dessas espécies. Durante a ontogenia inicial, essas duas espécies podem ser diferenciadas pelo número total de miômeros; 37 a 39 em *M. asterias* vs. 40 a 41 em *M. lobatus*; pelo padrão de pigmentação e número de raios da nadadeira dorsal. Essas características são eficazes para distinguir essas espécies de outros serrasalmídeos. As relações morfométricas também foram diferentes entre as duas espécies, com distintos padrões de crescimento entre as características analisadas. Uma chave de identificação para larvas de algumas espécies simpátricas de Serrasalmidae da bacia amazônica é apresentada. Nossa expectativa é que este estudo contribua para o conhecimento da ontogenia inicial e da biologia das espécies de peixes da região Neotropical.

Palavras-chave: Chave de identificação, Larvas de peixes, *Myloplus asterias*, *Myloplus lobatus*, Ontogenia.

## INTRODUCTION

Ichthyoplankton studies are of great importance for fish ecology because they shed light on the conservation status of species, assist in the determination of spawning areas and periods, and subsidize management and conservation actions related to the fishery resources (Cruz *et al*., 2016; Zacardi *et al*., 2020a; Oliveira *et al*., 2022). In Brazil, a lack of studies on the characterization of the early phases of the life cycle of several freshwater fish, creates the need for ecological research on this subject (Reynalte-Tataje *et al*., 2020).

Additionally, many fish species in the Amazon basin are synchronized in the intensity of reproductive activities and use the same areas and periods for dispersal and development of their eggs and larvae (Zacardi, Ponte, 2016; Zacardi *et al*., 2020b), which worsens the difficulties in the correct identification of species. Serrasalmids known as piranhas and pacus, which share the same breeding and growth sites, are among the species that present such characteristics (Zacardi *et al*., 2018; Oliveira *et al*., 2020a; Zacardi *et al*., 2020b).

The genus *Myloplus* Gill, 1896 is the most specious among the family Serrasalmidae, and currently represents the greatest taxonomic challenge because of its complex of species (Machado *et al*., 2018; Ota *et al*., 2020). The *Myloplus* species occur in the basins of the Amazon, Orinoco, La Plata, São Francisco, Paraguay/Paraná Rivers, and in the tributaries of the Guiana Shield (Andrade *et al*., 2016a; Nico *et al*., 2018; Silvano *et al*., 2020). They have great ecological relevance owing to their consumption of plant material and their potential role as seed dispersers (Santos *et al*., 2016; Silvano *et al*., 2017).

The species *Myloplus asterias* (Müller & Troschel, 1844) and *Myloplus lobatus* (Valenciennes, 1850) are the pacus common to upland clear and black water habitats (Kolmann *et al*., 2020; Fricke *et al*., 2021), considered sedentary fishes with external fertilization and total spawning synchronized with the rainy season during the time of rising water in rivers (Santos *et al*., 2006; Ohara *et al*., 2017). Although these species are less consumed by the Amazon population compared to other more important species such as the "Tambaqui" (*Colossoma macropomum* (Cuvier, 1816) - pacus common to lowland white-water habitats), these two *Myloplus* are widely commercialized in the ornamental fish trade of Amazon, mainly in Brazil, Colombia, and Venezuela (Cella-Ribeiro *et al*., 2016; Nico *et al*., 2018; Kolmann *et al*., 2020; Silvano *et al*., 2020).

Despite the ecological and economic relevance of these species, little is known about their phenotype during the early life cycle, in which less than 10% of the 101 valid serrasalmid species have their embryonic and/or larval phases characterization (Fricke *et al*., 2020; Reynalte-Tataje *et al*., 2020). Thus, our goal is to expand the knowledge on the early stages of Neotropical fish by presenting the detailed larvae and juveniles description of *M. asterias* and *M. lobatus* occurring in the Lower Amazon River. This study was based on morphology (shape), meristic counts and morphometric measurements, and estimated the growth patterns through the development in the early stages of life. In addition, we provided an identification key for larvae of these two *Myloplus* and including allied species from the Amazon basin. This information is essential for the conservation of Amazonian fishing stocks, by accurate identification of species in this crucial early stage of life.

## MATERIAL AND METHODS

The biological material used in this study comes from sampling carried out in a natural environment comprising the limnetic zone of open water (02°28'42"S 54°38'04"W) and macrophyte stands in lakes (02°43'59"S 54°35'49"W and 02°26'44"S 54°16'53"W) and channels in floodplain areas (02°12'41.56"S 54°45'42.49"W and 02°18'52.60"S 54°43'11.59"W) in the lower stretch of the Amazon River and at the mouth of the Tapajós River (02°25'30"S 54°41'23"W), Lower Amazon River, Brazil. Individuals were collected monthly throughout the years 2016, 2017, 2018 and 2020 by horizontal trawling on the subsurface of the water column using a conical-cylindrical plankton net (300 µm mesh) and a rectangular fishing sieve (500 µm mesh), like a wooden sifting screen (1.0 x 1.5 x 1.0 m area) used for sampling the submerged region of floating aquatic vegetation. Individuals in early stages such as preflexion and flexion were mostly captured in open water, while the most developed ones (*i.e*., postflexion and juveniles) were in macrophyte stands.

After capture, the specimens were euthanized with benzocaine (250 mg/L) and fixed in a 10% formalin solution buffered with calcium carbonate. In the laboratory, the fish larvae and juveniles were sorted, separating them from the plant material and plankton, then the individuals were identified at the species level. The larvae were identified using the regressive development sequence from juveniles to the smallest individuals, as suggested by Ahlstrom, Moser (1976) and modified by Nakatani *et al*. (2001). The juveniles were identified using specific literature (Andrade *et al*., 2016a,b;

2018; 2019a). After identification, the specimens were classified according to their degree of development (Ahlstrom *et al*., 1976; modified by Nakatani *et al*., 2001) into larval (preflexion, flexion, and postflexion stages) and juvenile periods.

The individuals used in this study are stored in the Collection of Larvas e Ovos de Peixes (CROLP) of the Universidade Federal do Oeste do Pará (UFOPA). Catalog numbers of the examined specimens are as follows with the number of specimens in parentheses: LEIPAI 00079 (2), LEIPAI 00080 (2), LEIPAI 00081 (2), LEIPAI 00082 (1), LEIPAI 00083 (2), LEIPAI 00084 (1), LEIPAI 00085 (6), LEIPAI 00086 (1) LEIPAI 00087 (1), LEIPAI 00088 (1), LEIPAI 00089 (1), LEIPAI 00090 (1), LEIPAI 00091 (3), LEIPAI 00092 (4), LEIPAI 00093 (7), LEIPAI 00094 (5), LEIPAI 00095 (3).

The characterization of each ontogenic period was based on the development stages and the occurrence of the main morphological events, which were recorded by pen-and-ink using the figure reflected in a camera lucida coupled with a stereoscopic microscope. For morphometric analyses, the following body measurements were obtained: standard length (SL), head length (HL), snout length (SnL), eye diameter (ED), head depth (HD), body depth (BD), snout-dorsal fin length (SnD), snout-anal fin length (SnA), snout-pectoral fin length (SnP) and snout-pelvic fin length (SnV) (Nakatani *et al*., 2001).

Photographic images and morphometric measurements in millimeters (mm) were obtained using a binocular stereoscopic microscope (Leica S9i) coupled with an integrated color digital camera for image capture and Leica LAS EZ analysis software.

The meristic data were recorded when possible, counting the myomeres total number (TNM), number of preanal myomeres (NPAM), number of postanal myomeres (NPSM), and the number of rays of the anal (A), dorsal (D), pectoral (P), and pelvic (V) fins. For the analysis of morphometric relationships (in percentage), the measures SnL, ED and HD were related to head length (HL), whereas HL, BD, SnD, SnP, SnV, and SnA were related to the standard length (SL). Body relationships between body depth (BD/SL), head length (HL/SL), and eye diameter (ED/HL) were established using the criteria proposed by Leis, Trnski (1989).

To verify the growth pattern throughout the ontogenetic development of the species, morphometric measures (response variables) were related to the standard length and head length (explanatory variables) and their relationships were analyzed by different regression models (Kováč *et al*., 1999). The hypothesis of continuous isometric growth was tested by simple linear regression. Two alternative developmental hypotheses were also tested: gradual allometric growth (quadratic regression) and discontinuous isometric growth (piecewise linear regression – characterized by breakpoints that highlight divergent growth rates). The selection of the best model for each analyzed relationship was based on the F test, with a significance level of $p < 0.05$ (Sokal, Rohlf, 1981). StatisticaTM 7.0 software was used to perform regression and F-test analyses. According to the information obtained in this study and data in Araújo-Lima *et al*. (1993) and Nakatani *et al*. (2001), we elaborated an identification key for some sympatric species of Serrasalmidae from the Amazon basin during the larval period.

## RESULTS

A total of 43 individuals were used for the descriptions, 10 of *M. asterias* (1 preflexion, 3 flexion, 5 postflexion, and 1 juvenile) and 33 of *M. lobatus* (19 flexion, 11 postflexion, and 3 juveniles). No individuals in the yolk-sac stage were analyzed for both species, and in preflexion for *M. lobatus*.

*Myloplus asterias*

Preflexion (Fig. 1A): at this stage, the specimen was 8.6 mm SL (Tab. 1). The presence of the yolk-sac is not evident, and the notochord is rectilinear and visible through transparency. The body is coated by a transparent embryonic membrane (finfold) that surrounds the entire dorsal and ventral regions, interrupted only at the anus. The eyes are large, spherical, and well pigmented. The mouth is functional and has a terminal position. The intestine is straight, and the position of the anal opening exceeds the middle region of the body. The swim bladder is inflated. On preserved specimens, it is possible to see a longitudinal band of pigmentation that extends laterally from the snout to close to the operculum. Punctiform chromatophores are present and irregularly distributed throughout the body, with clusters of pigments in the dorsal and ventral regions reaching the embryonic fin, in the anteroventral region of the finfold, and with sparse dendritic chromatophores along the digestive tract. There is no differentiation between the dorsal, caudal, and anal fins. Although evident, the pectoral fins still have no rays but are surrounded by a membrane. The myomeres total number is 37 (21 preanal and 16 postanal) (Tab. 1).

Flexion (Fig. 1B): in the three larvae analyzed, the SL ranged from 8.7 mm to 9.8 mm (Tab. 1). Larvae still have traces of the finfold, and the notochord is flexed and visible through transparency. The mouth remains in the terminal position and the nostrils are double. The intestine is straight, and the anal opening is vertically located and extends beyond the middle region of the body. The swim bladder is still visible through transparency. The pigmentation is like the preflexion stage but intensifies in the dorsal region of the head. At 8.7 mm SL, it is possible to visualize the appearance of the rays of the caudal and dorsal fins. The design and appearance of the anal-fin rays are observed at 9.8 mm SL (Fig. 1B). The myomeres total number ranges from 38 to 39, with 21 and 22 preanal and 17 in the postanal region (Tab. 1).

Postflexion (Figs. 1C, D, E): the standard length ranged from 10.7 to 23.4 mm (Tab. 1). The notochord and the swim bladder are no longer visible by transparency because of the presence of muscle tissue and the body is laterally compressed. The mouth is terminal, the eyes remain spherical, and the anal opening remains in the posterior region of the body. The appearance of scales on the body is observed at 15.1 mm SL. At 10.7 mm SL, on preserved specimens, the pigmentation of the body becomes more conspicuous and densely pigmented, forming brownish spots through the body, head, snout, opercular region, and base of the pectoral fin. The pigmentation pattern is observed at the proximal (basal) edge of the two lobes of the caudal fin (Fig. 1C). Pigmentation in the first rays of the dorsal and anal fins does not reach their distal portions (Fig. 1E). The pelvic fin button is visible at 10.7 mm SL and all odd fins are formed (Fig. 1D). At 15.1 mm SL, there are still remnants of the finfold; it is possible to observe the adipose fin and the formation of the pelvic-fin rays. The appearance and

formation of the pectoral-fin rays are recorded in individuals from 18 mm SL. The presence of muscle tissue made the counting of myomeres impossible. The total number of spines and rays of the dorsal, anal, and pelvic fins is D. II,24-25, A. III,34-35, and V. I,6-7 (Tab. 1).

Juvenile (Fig. 1F): the analyzed individual presents 35.2 mm SL. The eyes are large, the head has a moderate convex dorsal profile, the mouth is terminal with teeth present in the jaws, and the anal opening is located beyond the middle region of the body. The body is deep and laterally compressed, with a keel forming an evident ventral serra and the presence of scales throughout the body. Despite the development of all morphological characteristics, the body shape still does not resemble an adult specimen. On preserved specimens, the pigmentation is regularly distributed and composed of an agglomeration of punctiform chromatophores covering the entire body, except

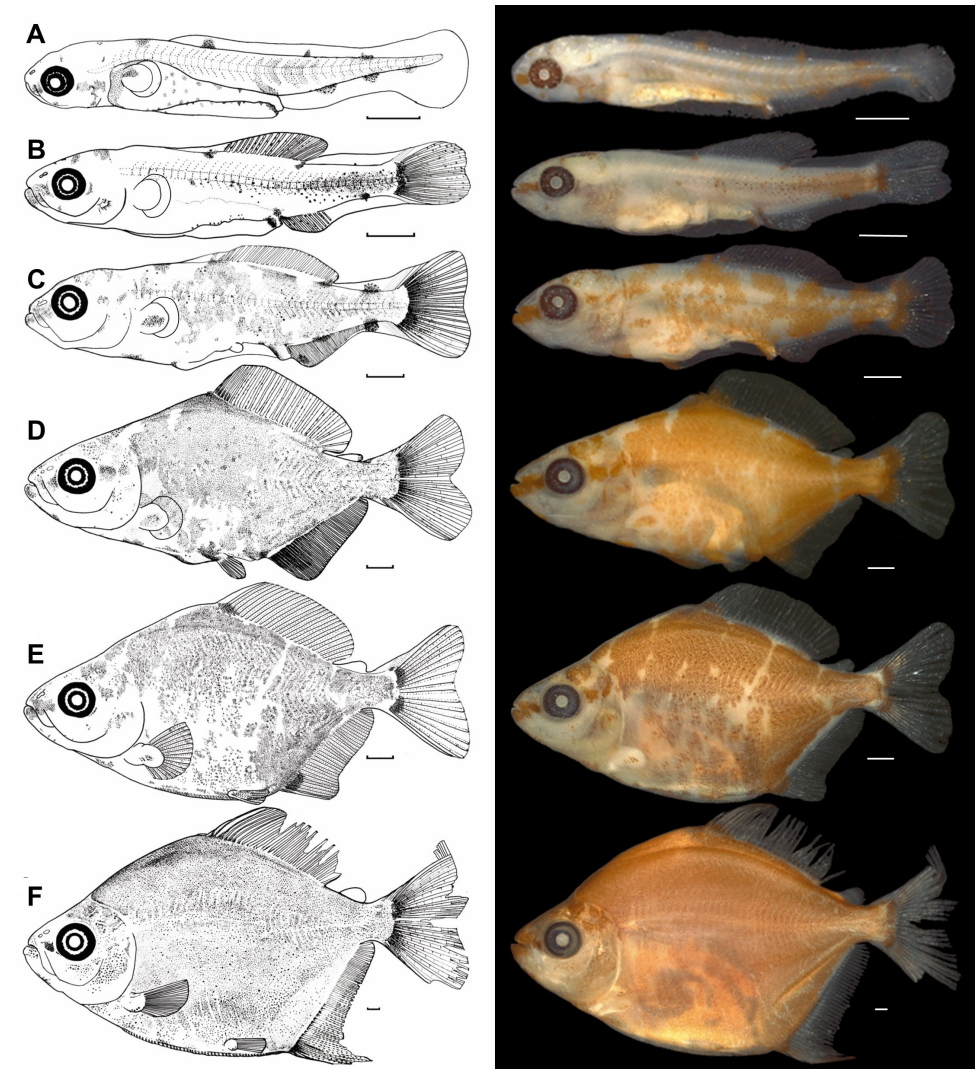


**FIGURE 1** | Larval and juvenile development of *Myloplus asterias*: **A.** Preflexion (8.6 mm); **B.** Flexion (8.7 mm); **C.** Early of postflexion (10.7 mm); **D.** Postflexion (15.1 mm); **E.** End of postflexion (21.5 mm); **F.** Juvenile (35.2 mm). Scale bar = 1 mm.

**TABLE 1** | Values of minimum (Min), maximum (Max) and mean length (mm) and standard deviation (SD) of morphometric and meristic variables obtained from larvae and juveniles of *Myloplus asterias*. SL: standard length; HL: head length; SnL: snout length; ED: eye diameter; HD: head depth; BD: body depth; SnD: snout-dorsal fin distance; SnA: snout-anal fin distance; SnP: snout-pectoral fin distance; SnV: snout-pelvic fin distance; NV: not visible.

| *Myloplus asterias* | | | | | | |
|---|---|---|---|---|---|---|
| **Variables (mm)** | Larval period | | | | | Juvenile period (n = 1) |
| | Preflexion (n = 1) | Flexion (n = 3) | | Postflexion (n = 5) | | |
| | Min-Max | Min-Max | Mean±SD | Min-Max | Mean±SD | Min-Max |
| SL | 8.6 | 8.7-9.8 | 9.1±0.6 | 10.7-23.4 | 17.9±5.1 | 35.2 |
| HL | 2.0 | 2.1-2.8 | 2.4±0.4 | 3.1-7.0 | 5.4±1.5 | 10.2 |
| SnL | 0.3 | 0.5-0.7 | 0.6±0.1 | 0.7-1.8 | 1.3±0.5 | 2.8 |
| ED | 0.7 | 0.8-1.0 | 0.9±0.1 | 1.1-2.5 | 1.9±0.5 | 3.7 |
| HD | 1.5 | 1.5-2.0 | 1.7±0.3 | 2.4-7.1 | 5.2±1.9 | 11.2 |
| BD | 1.5 | 1.6-2.3 | 1.8±0.4 | 2.8-13.6 | 9.1±4.3 | 21.3 |
| SnD | NV | 5.0-5.1 | 5.0±0.1 | 5.7-12.0 | 9.1±2.5 | 17.6 |
| SnA | NV | 6.8 | - | 7.4-16.6 | 12.3±3.6 | 24.7 |
| SnP | 1.9 | 2.0-2.7 | 2.3±0.4 | 2.9-6.3 | 4.9±1.3 | 9.6 |
| SnV | NV | NV | - | 5.4-11.5 | 9.3±2.5 | 18.7 |
| **Morphometric proportions (%)** | | | | | | |
| SnL/HL | 16.0 | 21.0-26.2 | 23.3±2.7 | 21.6-26.5 | 24.2±2.0 | 27.2 |
| ED/HL | 36.8 | 34.1-36.5 | 35.5±1.3 | 34.6-36.9 | 35.5±0.9 | 36.4 |
| HD/HL | 72.2 | 68.3-72.2 | 70.4±2.0 | 78.4-105.3 | 94.7±10.9 | 109.2 |
| BD/SL | 17.9 | 18.4-23.9 | 20.3±3.1 | 26.5-58.2 | 47.9±12.7 | 60.5 |
| HL/SL | 23.4 | 24.2-28.9 | 26.7±2.6 | 29.0-31.8 | 30.1±1.0 | 29.1 |
| SnD/SL | NV | 51.6-57.7 | 54.6±4.3 | 49.6-52.0 | 51.3±1.3 | 50.0 |
| SnA/SL | NV | 69.3 | - | 66.5-70.7 | 68.5±1.5 | 70.0 |
| SnP/SL | 22.2 | 23.3-27.4 | 25.2±2.1 | 26.1-29.3 | 27.4±1.2 | 27.2 |
| SnV/SL | NV | NV | NV | 48.9-55.1 | 52.4±1.6 | 53.0 |
| **Number of myomeres** | | | | | | |
| Preanal | 21 | 21-22 | 21 | NV | NV | NV |
| Postanal | 16 | 17 | 17 | NV | NV | NV |
| Total | 37 | 38-39 | 38 | NV | NV | NV |
| **Number of spines and rays** | | | | | | |
| Dorsal | NV | 7-22 | 15±7 | I,24-25 | 25±1 | II,25 |
| Anal | NV | 12-14 | 13±8 | II,34-36 | 35±1 | III,35 |
| Pelvic | NV | NV | NV | 6-7 | 7±1 | I,7 |
| Pectoral | NV | NV | NV | 17 | 17±0 | I,16 |

for those hyaline fins, but the anal and dorsal fins present the first rays pigmented throughout their latitudinal extension, and it is possible to see the pigmentation at the proximal edge of the two lobes of the caudal fin. At this period, the pectoral-fin rays are fully developed and segmented. The sequence of appearance of fin rays was caudal, dorsal, anal, pelvic, and pectoral. The total number of spines and rays is P. I,16, V. I,7, D. II,25, and A. III,35 (Tab. 1).

During the early development period, the body ranges from long to moderate in preflexion (17.9%) and flexion (18.4% to 23.9%) to moderate and deep in postflexion (26.5% to 58.2%) and deep in juvenile (60.5%); the head remains moderate (23.4% in preflexion to 29.1% in juvenile) and the eyes are large (36.8% in preflexion to 36.4% in juvenile). Most morphometric measurements increased in their proportions concerning HL and SL (HD, SnL, SnA, SnV, SnP), except SnD, which decreased (Tab. 1).

**TABLE 2** | Values of linear (L), quadratic (Q) and piecewise (S) regression analyses of morphometric variables in relation to head length (HL) and standard length (SL) of larvae and juveniles of *Myloplus asterias*. $R^2$ = coefficient of determination. BM = best model, BP = breaking point (mm), n = number of analyzed individuals. Bold values represent a significant difference ($p < 0.05$). **The n was insufficient to perform the F test.

| *Myloplus asterias* | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Relations | $R^2$ | | | Teste F | | | BM | BP | n |
| | L | Q | S | Q/L | S/Q | S/L | | | |
| SnL/HL | 0.993 | 0.994 | 0.994 | 0.75 | 0.57 | 0.63 | L | | 10 |
| ED/HL | 0.990 | 0.998 | 0.998 | 2.40 | -0.43 | 0.70 | L | | 10 |
| HD/HL | 0.996 | 0.996 | 0.998 | 0.67 | 2.41 | 1.62 | L | | 10 |
| BD/SL | 0.995 | 0.999 | 0.999 | **24.67** | 0.42 | **11.36** | Q | | 10 |
| HL/SL | 0.990 | 0.996 | 0.999 | **7.46** | **9.12** | **13.34** | S | 4.64 | 10 |
| SnD/SL | 0.998 | 0.998 | 1.000 | 0.25 | **237.00** | **126.00** | S | 9.17 | 8 |
| SnA/SL | 0.998 | 0.998 | 1.000 | 0.80 | **98.00** | **62.33** | S | 13.26 | 7 |
| SnP/SL | 0.993 | 0.994 | 0.998 | 0.57 | 4.40 | 2.65 | L | | 10 |
| SnV/SL | 0.985 | 0.994 | 0.996 | 1.50 | ** | ** | - | | 5 |

Among the morphometric variables analyzed, the HL, SnD, and SnA, related to the SL, presented isometric discontinuity during development, in which an abrupt change occurred from the postflexion stage. After this change (breakpoint), SnD and SnA increased growth rates (a1 = 0.47 and 0.64, and a2 = 0.49 and 0.72, respectively), while the development of HL decreased (a1 = 0.49, and a2 = 0.27) (Tab. 2). However, the variable BD was better represented by a quadratic regression with negative allometric growth ($b > 1$), whereas the variables SnL, ED, HD, and SnP showed continuous isometric development (linear regression) (Tab. 2; see **S1**).

*Myloplus lobatus*

Flexion (Figs. 2A, B): the standard length ranged from 8.5 to 10.9 mm. The notochord is already flexed. The smallest analyzed specimen presents the body surrounded by a transparent finfold. The eyes are large, spherical, and pigmented. The mouth is terminal. The intestine is straight and larvae up to 9.0 mm SL still have remnants of yolk, and there is exogenous food throughout the digestive tract. The anal opening exceeds the middle region of the body. The swim bladder is inflated and visible by transparency. The pigmentation is concentrated in the posterior region of the body near the caudal peduncle (Fig. 2A). Grouped punctiform chromatophores are present at the beginning and end of the dorsal- and anal-fin bases and where the adipose fin will appear. There are several pigments near the anal opening as well (Fig. 2B). It is possible to see a longitudinal band formed by intense pigments on the snout, mandible, and in the dorsal region of the head. At 10.4 mm SL, pigmentation becomes denser and brownish vertical bands appear throughout the body. At 8.5 mm SL, the design of the dorsal fin is observed. The appearance of the caudal, anal, and dorsal-fin rays is recorded in specimens with SL greater than 9.0 mm. The myomeres total number ranges from 40 to 41, 23 to 25 in the preanal and 16 to 17 in the postanal region (Tab. 3).

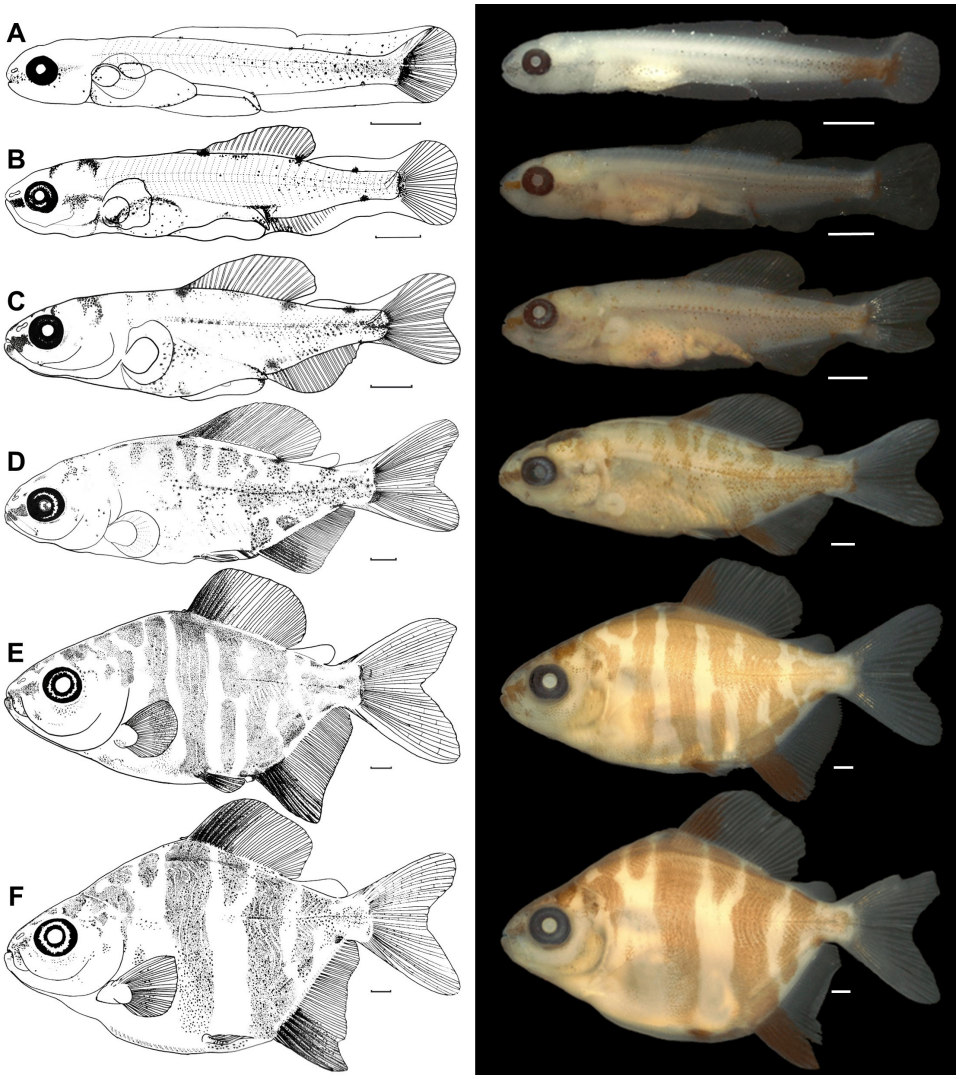


**FIGURE 2** | Larval and juvenile development of *Myloplus lobatus*: **A.** Flexion (8.5 mm); **B.** Flexion (9.7 mm); **C.** Postflexion (11.7 mm); **D.** Postflexion (15.6 mm); **E.** Juvenile (20.5 mm); **F.** Juvenile (22.8 mm). Scale bar = 1 mm.

Postflexion (Figs. 2C, D): the larvae presented SL from 11.7 to 19.3 mm. The notochord and the swim bladder are no longer visible by transparency because of the presence of muscle tissue and the laterally compressed body. The mouth is terminal, the eyes remain spherical, and the anal opening remains located in the posterior region of the body. The appearance of scales on the body is observed in specimens from 15.6 mm SL. The pigmentation throughout the body resembles the previous stage with greater intensity of the brownish vertical bands and grouping pigments that form spots on the upper part of the head and in the first rays of the dorsal, anal, and pelvic fins. The pelvic fin bud is visible at 11.7 mm SL, and from 12.6 mm SL, the first rays of this fin and the adipose fin appear. At 13.2 mm SL, all the fin rays are developed, except for the pectoral fin, which is still in development. There are still remnants of the finfold at 15.6 mm SL.

At this stage, the number of spines and rays is D. II,21–23, and A. III,31–33 (Tab. 3).

Juvenile (Figs. 2E, F): the standard length ranged from 20.5 to 22.8 mm. The mouth is terminal, with teeth present in the jaws. The eyes are large, and the head features a convex dorsal profile. The body is deep and laterally compressed, with a well-marked abdominal keel (Fig. 2E). The individuals have the same pigmentation pattern as described above, but the intensity is greater. At this stage, all fins are developed and segmented (Fig. 2F) and the sequence of appearance of fin rays was caudal, dorsal, anal, pelvic, and pectoral. The total number of spines and rays is P. I,14–15, V. I,6–7, D. II,22, and A. III,32–33 (Tab. 3)

**TABLE 3** | Values of minimum (Min), maximum (Max) and mean length (mm) and standard deviation (SD) of morphometric and meristic variables obtained from larvae and juveniles of *Myloplus lobatus*. SL: standard length; HL: head length; SnL: snout length; ED: eye diameter; HD: head depth; BD: body depth; SnD: snout-dorsal fin distance; SnA: snout-anal fin distance; SnP: snout-pectoral fin distance; SnV: snout-pelvic fin distance; NV: not visible

| ***Myloplus lobatus*** | | | | | | |
|---|---|---|---|---|---|---|
| **Variables (mm)** | Larval period | | | | Juvenile period (n= 3) | |
| | Flexion (n = 19) | | Postflexion (n = 11) | | | |
| | Min-Max | Mean±SD | Min-Max | Mean±SD | Min-Max | Mean±SD |
| SL | 8.5-10.9 | 9.4±0.6 | 11.7-19.3 | 14.9±2.2 | 20.5-22.8 | 21.5±1.2 |
| HL | 2.0-3.0 | 2.5±0.3 | 1.4-5.4 | 4.1±1.1 | 6.6-6.8 | 6.7±0.1 |
| SnL | 0.4-0.7 | 0.5±0.1 | 0.8-1.4 | 1.0±0.2 | 1.4-1.6 | 1.5±0.1 |
| ED | 0.6-1.1 | 0.8±0.1 | 1.2-2.2 | 1.6±0.3 | 2.6-2.7 | 2.7±0.1 |
| HD | 1.4-2.4 | 1.7±0.3 | 2.8-6.2 | 4.9±1.0 | 7.0-7.5 | 7.2±0.3 |
| BD | 1.4-2.7 | 1.9±0.4 | 3.5-9.3 | 5.8±1.8 | 11.6-13.5 | 12.3±1.0 |
| SnD | 4.3-5.3 | 5.0±1.9 | 5.7-9.8 | 7.3±1.2 | 10.7-11.2 | 10.9±0.2 |
| SnA | 6.0-7.4 | 6.8±3.5 | 7.9-13.3 | 10.2±1.7 | 15.0-16.4 | 15.5±0.8 |
| SnP | 1.8-2.8 | 2.3±0.3 | 3.3-5.1 | 4.1±0.6 | 5.9-6.3 | 6.1±0.2 |
| SnV | NV | NV | 6.3-10.5 | 8.0±1.3 | 11.0-11.9 | 11.5±0.5 |
| **Morphometric proportions (%)** | | | | | | |
| SnL/HL | 15.5-23.5 | 19.5±2.4 | 20.0-25.2 | 22.6±1.7 | 21.5-23.6 | 22.7±1.1 |
| ED/HL | 30.6-36.3 | 32.6±1.5 | 32.8-40.3 | 35.9±1.9 | 39.4-40.4 | 40.0±0.5 |
| HD/HL | 62.6-79.7 | 69.6±4.5 | 79.6-100.9 | 90.1±6.8 | 105.3-110.1 | 107.5±2.4 |
| BD/SL | 16.2-25.6 | 19.8±3.0 | 29.8-46.9 | 38.2±6.5 | 55.0-59.3 | 57.4±2.2 |
| HL/SL | 22.2-29.1 | 26.0±2.0 | 28.7-31.8 | 31.0±1.0 | 30.0-32.2 | 31.4±1.2 |
| SnD/SL | 47.2-62.8 | 52.6±4.1 | 46.8-50.6 | 49.0±1.1 | 49.0-52.5 | 51.0±1.7 |
| SnA/SL | 64.2-70.5 | 68.5±1.6 | 66.5-71.7 | 68.9±2.0 | 71.5-73.2 | 72.1±0.9 |
| SnP/SL | 20.9-27.9 | 24.5±1.8 | 25.0-28.5 | 27.5±1.1 | 25.9-30.2 | 28.7±2.4 |
| SnV/SL | NV | NV | 49.5-57.3 | 53.8±2.3 | 52.3-54.3 | 53.4±1.0 |
| **Number of myomeres** | | | | | | |
| Preanal | 23-25 | 24±1 | 24 | 24±0 | NV | NV |
| Postanal | 16-17 | 17±0 | 16 | 16±0 | NV | NV |
| Total | 40-41 | 41±0 | 40 | 40±0 | NV | NV |
| **Number of spines and rays** | | | | | | |
| Dorsal | 3-22 | 16±5 | II,21-23 | 22±1 | II,22 | 22±0 |
| Anal | 0-28 | 11±9 | III,31-33 | 32±1 | III,32-33 | 33±1 |
| Pelvic | NV | NV | NV | NV | I,6-7 | 6±1 |
| Pectoral | NV | NV | NV | NV | I,14-15 | 14±1 |

The body ranges from long (16.2%) and moderate (25.6%) in flexion to deep in postflexion (29.8% to 46.9%) and juvenile (55.0% to 59.3%). The eye diameter ranges from moderate to large in flexion (30.6% to 36.3%) and postflexion (32.8% to 40.3%) and large in juvenile (39.4% to 40.4%). The head remained moderate (22.2% in preflexion and 31.4% in juvenile). Morphometric variables such as HD, SnL, SnA, and SnP showed an increase in their morphometric structures, while SnD showed a decrease between flexion and postflexion stages, with an increasing trend in the juvenile period. The SnV also showed a decrease in proportions over the larval and juvenile periods (Tab. 3).

The variables SnL, SnA and SnV were better represented by the piecewise linear regression model, which has discontinuous isometric growth with changes in growth in the postflexion stage. Thus, SnV decreased its growth rate (a1 = 0.44 and a2 = 0.43), while SnL and SnA increased (a1 = 0.15 and 0.65 and a2 = 0.23 and 0.79, respectively) (Tab. 4). The variables showed allometric growth, with BD, ED, HD, and SnD being positive (b > 1) and HL and SnP being negative allometry (b < 1) (Tab. 4; see **S2**).

**TABLE 4** | Values of quadratic (Q) and piecewise (S) regression analyses of morphometric variables in relation to head length (HL) and standard length (SL) of larvae and juveniles of *Myloplus lobatus*. $R^2$ = coefficient of determination. BM = best model, BP = breaking point (mm), n = number of analyzed individuals. Bold values represent a significant difference ($p < 0.05$).

| *Myloplus lobatus* | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Relations | R2 | | | | Teste F | | BM | BP | n |
| | L | Q | S | Q/L | S/Q | S/L | | | |
| SnL/HL | 0.962 | 0.962 | 0.988 | 0.08 | **58.41** | **29.32** | S | 0.75 | 33 |
| ED/HL | 0.989 | 0.989 | 0.991 | **13.56** | -2.52 | **4.70** | Q | | 33 |
| HD/HL | 0.989 | 0.989 | 0.996 | **43.85** | 1.36 | **22.88** | Q | | 33 |
| BD/SL | 0.982 | 0.982 | 0.991 | **36.71** | 2.68 | **20.76** | Q | | 33 |
| HL/SL | 0.987 | 0.987 | 0.992 | **16.31** | -1.17 | **6.96** | Q | | 33 |
| SnD/SL | 0.971 | 0.971 | 0.981 | **8.63** | 3.03 | **6.16** | Q | | 30 |
| SnA/SL | 0.994 | 0.994 | 0.996 | **4.78** | **4.75** | **5.21** | S | 9.39 | 24 |
| SnP/SL | 0.974 | 0.974 | 0.978 | **4.32** | 1.27 | 2.82 | Q | | 33 |
| SnV/SL | 0.969 | 0.969 | 0.994 | 2.09 | **26.61** | **17.02** | S | 8.67 | 14 |

**Identification key for some Serrasalmidae species from the Amazon basin during larval period**

**1.** Dorsal region of the head and the ventral region from the isthmus to the abdomen densely pigmented..... Serrasalminae
**1'.** Dorsal region of the head and the ventral region from the isthmus to the abdomen lacking densely pigments.....(Myleinae) 2
**2.** Anterior and posterior regions of dorsal, anal, and adipose fins with punctiform chromatophores; presence of melanophores at anterior and posterior regions of the anus; more than 20 dorsal-fin rays; edge of the anal fin not convex .....3
**2'.** Absence of punctiform chromatophores in dorsal, anal, and adipose fins; melanophores at anterior portion of the anus only; less than 20 rays on dorsal fin; edge of anal fin convex with anterior rays longer the posterior .....4
**3.** Presence of irregular pigments forming spots along body that are intensifying through development; 24 or more dorsal-fin rays; myomeres total number ranging from 37 to 39 (mode 38), with 21 to 22 preanal segments .....*Myloplus asterias*
**3'.** Presence of pigments forming vertical bands along body (brindled pattern) that are intensifying through development; less than 24 dorsal-fin rays; myomeres total number ranging from 40 to 41 (mode 41), with 23 to 25 preanal segments. ..... *Myloplus lobatus*
**4.** Posterior part of body with large and branched melanophores with concentrated pigments (individuals captured in aquatic vegetation may show greater intensity in the pigmentation pattern than specimens captured in the limnetic zone of open water); ocellus absent at flanks and anal fin densely pigmented.....*Mylossoma aureum*
**4'.** Posterior part of the body without pigments, melanophores evident smaller in regions of caudal peduncle and anus. Individuals that are captured in aquatic vegetation have melanophores concentrated in the anterior part of body, ocellus present in flanks and anal fin not densely pigmented..... *Mylossoma albiscopum*

## DISCUSSION

The integrative approach presented to distinguish these *Myloplus* species during their early stages of development proved effective. Throughout the initial ontogeny, *M. asterias* and *M. lobatus* showed common characteristics of the Serrasalmidae family, such as a body ranging from long to deep, eyes from moderate to large eyes, terminal mouth, and the presence of a ventral keel (Nakatani *et al*., 2001; Jégu, 2003; Ortí *et al*., 2008). Despite these similarities, both species have characteristics that allow their proper identification and reflect ecological and morpho-functional adaptations to the environment.

*Myloplus asterias* larvae in the preflexion stage do not present remnants of yolk, whereas *M. lobatus* in flexion still has traces of endogenous nutrition, but it has started an exogenous feeding activity. This process of simultaneous exogenous and endogenous feeding is considered a critical period (Kamler, 1992). This period provides energy reserves to the larvae, which display feeding plasticity by searching for suitable exogenous foods, which ensures survival during larval development (Bialetzki *et al*., 2008; Kamler, 2008; Aruho *et al*., 2019). The presence of yolk in *M. lobatus* larvae in flexion indicates that this species, compared to *M. asterias* larvae, has greater chances of survival and growth, as observed by Bialetzki *et al*. (2001; 2008) in *Auchenipterus osteomystax* (Miranda Ribeiro, 1918) and *Hoplias* aff. *malabaricus* (Bloch, 1794), respectively. This condition can be corroborated by the fact that *M. lobatus* is also more abundant than *M. asterias* in some environments, as reported by Soares *et al*. (2017) in an important tributary of the Amazon River.

The onset of exogenous feeding is associated with simultaneous events such as eye pigmentation and mouth opening (Lasker *et al*., 1970; Faustino *et al*., 2015; Santos *et al*., 2016). The well pigmented and relatively large eyes in the early larval stages of *M. asterias* and *M. lobatus* are essential to the efficiency of obtaining food because vision is a crucial sense for the capture of food items, as well as for enabling escape from predators (Gatz, 1979; Winemiller, 1991). The larvae and juveniles of the two *Myloplus* species showed characteristics related to the trophic guild of herbivorous/omnivorous fishes such as the terminal mouth, long intestine, and differences in pigmentation patterns (Andrade *et al*., 2019b). These characteristics indicate the individuals of these *Myloplus* species, since their initial stages, present a tendency to these trophic guilds.

The pigmentation in the initial development of these *Myloplus* can act as camouflage while using structured environments such as aquatic vegetation (Machado-Allison, 1987; Nakatani *et al*., 1997). However, we found no differences in the intraspecific pigmentation pattern between open water habitats and macrophyte stands. At the flexion stage, *M. asterias* larvae present pigments that intensify and distribute themselves as spots throughout the body until reaching a homogeneous pattern in juveniles, while in the *M. lobatus* larvae, vertical bands begin to emerge and intensify over its development. This variation in pigmentation associated with the meristic data allows the correct separation of the two *Myloplus* species mainly from the postflexion stage. These pigmentation patterns differentiate them from the larvae of *Mylossoma aureum* (Spix & Agassiz, 1829), which has pigments concentrated on the posterior part of the body with large and branched melanophores, and *Mylossoma albiscopum* Cope, 1872 (*sensu* Mateussi *et al*., 2018), which has smaller melanophores concentrated in the anterior part of the body (Araújo-Lima *et al*., 1993).

The pigmentation pattern of the two species can differentiate them from juvenile individuals of other serrasalmids such as *Tometes kranponhah* Andrade, Jégu & Giarrizzo, 2016. *Tometes kranponhah* has a well-defined humeral spot in the anterior part of the body and the presence of weak spots in the flanks ranging from vertically elongated to circular blotches, being more conspicuous in the ventral part of the flanks (Andrade *et al*., 2016c). These also differ from the larvae of *Serrasalmus* Lacépède, 1803 that have a high concentration of pigments in the upper region of the head and snout (Nakatani *et al*., 2001).

The caudal-fin rays are the first to appear in several Characiformes (Oliveira *et al*.,

2012; Mattox *et al*., 2014; Santos *et al*., 2017; Cajado *et al*., 2021). This characteristic is related to active swimming and movement into the water column searching for food or escaping from predators (Osse, Van den Boogaart, 1999; Silva *et al*., 2021). The sequence of fin formation in *M. asterias* and *M. lobatus* was similar to that observed in other Characiformes larvae – caudal, dorsal, anal, pelvic, and pectoral fins (Araújo-Lima *et al*., 1993; Nascimento, Araújo-Lima, 1993; Nakatani *et al*., 2001; Bialetzki *et al*., 2008; Oliveira *et al*., 2012). However, the number of rays on the dorsal and anal fins of juveniles *M. asterias* was not similar to those found by Jégu *et al*. (2004). This difference could be related to the non-monophyletism of these species (Machado *et al*., 2018).

The number of myomeres can certainly be used to diagnose *M. asterias* (37–39) from *M. lobatus* (40–41) during the first development stages, as well as the number of dorsal-fin rays in more developed specimens from 10.7 mm SL (24 to 25 *vs.* 21 to 23). The myomeres total number of *M. lobatus* does not distinguish it only from *M. asterias*, it also differentiates it from other congeneric and sympatric species as *Myloplus arnoldi* Ahl, 1936 and *Myloplus torquatus* (Kner, 1858), which have fewer than 38 myomeres based on vertebrae count (Araújo-Lima, Donald, 1988; Andrade *et al*., 2016b). Nevertheless, the meristic counts are not enough to taxonomically separate individuals of *M. asterias* from species *M. arnoldi* and *M. torquatus*, generating cryptic biodiversity in ichthyoplankton studies.

*Myloplus asterias* and *M. lobatus* have a body ranging from elongated in their first larval stages to deep-bodied during postflexion, which is the same pattern found in the early stages of other serrasalmids (Araújo-Lima *et al*., 1993; Nakatani *et al*., 2001). Among the Serrasalmidae characteristics (*e.g.*, laterally compressed body, presence of a pre-dorsal spine – except for *Colossoma* Eigenmann & Kennedy, 1903, *Mylossoma* Eigenmann & Kennedy, 1903 and *Piaractus* Eigenmann, 1903; and a ventral keel composed of modified abdominal scales), the deep body characterizes the Serrasalmidae family (Jégu, 2003; Ortí *et al*., 2008). This suggests that there are changes in habitat use from lentic waters to lotic systems such as lakes to the flowing waters of a river. In that case, the earlier larvae stages are represented by an elongated body, which suggests less drag in the water currents, and the deep body in bigger juveniles assists in performing maneuvers in flowing waters (Andrade *et al*., 2019b).

The processes of delay or acceleration in the growth of specific body parts reflect adaptive ontogenetic development as a response to functional requirements (Kováč *et al*., 1999; Oliveira *et al*., 2020b; Cajado *et al*., 2021). In many fish species, a reduction in the growth coefficients of various organs and tissues occurs at similar body lengths and it is correlated with typical morphogenetic events (Urho, 2002; Osse, Van den Boogaart, 2004). Concerning the growth of the body variables of these two *Myloplus*, only SnA was similar for both species, while the remaining were different. This may a result from the low number of individuals analyzed, mainly due to the need for a large sampling effort in different seasonal periods and landscape environments to capture all stages and periods of development (Taguti *et al*., 2009; Oliveira *et al*., 2020a). The allometric growth observed in body depth indicates a great transformation of the body shape, which may be directly related to the change in feeding habits and locomotion of the species. Furthermore, the interruptions in the growth of the variables HL, SnD, and SnA of *M. asterias* and SnL, SnA, and SnV of *M. lobatus* that occurred in the postflexion stage suggest that most remodeling of the body external shape takes place at this stage of development.

In conclusion, larvae, and juveniles of *M. asterias* and *M. lobatus* can be distinguished from each other and from other Serrasalmidae by combining characteristics such as pigmentation pattern, number of myomeres, and number of dorsal-fin rays. The greatest modifications of the two *Myloplus* species during the initial ontogeny occur in the postflexion stage, which may result from greater interactions with the environment, such as foraging in aquatic macrophyte stands. Despite the difficulty in identifying species during larval stages, the information presented here is useful as a tool for the description and recognition of these two species of commercially valuable fish.

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**Marcelo Costa Andrade:** Investigation, Methodology, Visualization, Writing-review and editing.
**Diego Maia Zacardi:** Conceptualization, Investigation, Methodology, Visualization, Writing-original draft, Writing-review and editing.

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## ETHICAL STATEMENT

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## COMPETING INTERESTS

The authors declare no competing interests.

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