



**SERVIÇO PÚBLICO FEDERAL  
UNIVERSIDADE FEDERAL DO PARÁ  
CAMPUS UNIVERSITÁRIO DE ALTAMIRA  
PROGRAMA DE PÓS-GRADUAÇÃO EM BIODIVERSIDADE E  
CONSERVAÇÃO**

**ELZAMARA DE CASTRO OLIVEIRA**

**DESENVOLVIMENTO INICIAL DO PACU-BRANCO *Myloplus rubripinnis*  
(MÜLLER & TROSCHER, 1844) (CHARACIFORMES: SERRASALMIDAE)  
DA BACIA DO RIO XINGU**

**ALTAMIRA**

**2023**



ELZAMARA DE CASTRO OLIVEIRA

**DESENVOLVIMENTO INICIAL DO PACU-BRANCO *Myloplus rubripinnis*  
(MÜLLER & TROSCHER, 1844) (CHARACIFORMES: SERRASALMIDAE)  
DA BACIA DO RIO XINGU**

Dissertação apresentada à Universidade Federal do Pará, como parte das exigências do Programa de Pós-graduação em Biodiversidade e Conservação para obtenção do título de Mestre em Biodiversidade e Conservação.

Orientador(a): Prof. Dr. Leandro Melo Sousa

Coorientador(a): Prof. Dr. Diego Maia Zacardi

ALTAMIRA

2023

ELZAMARA DE CASTRO OLIVEIRA

**DESENVOLVIMENTO INICIAL DO PACU-BRANCO *Myloplus rubripinnis*  
(MÜLLER & TROSCHER, 1844) (CHARACIFORMES: SERRASALMIDAE)  
DA BACIA DO RIO XINGU**

Dissertação apresentada à Universidade Federal do Pará, como parte das exigências do Programa de Pós-graduação em Biodiversidade e Conservação para obtenção do título de Mestre em Biodiversidade e Conservação.

Data da aprovação: \_\_\_\_/\_\_\_\_/\_\_\_\_

**Banca Examinadora**

---

Prof. Dr. Tommaso Giarrizzo

---

Dra. Joyce Andreia Santos

---

Profa. Dra. Karina Keyla Tondato de Carvalho

---

Profa. Dra. Andréa Bialetzki

*Dedico aos meus filhos Benício e Maria Beatriz*

## **AGRADECIMENTOS**

Aos meus pais Maria Zenilda e Benedito pelo apoio, compreensão e paciência durante esta jornada.

Meus sinceros agradecimentos ao meu orientador Prof. Dr. Leandro Melo Sousa pela orientação na realização desta pesquisa e pela confiança depositada. Sou grata ao Prof. Dr. Diego Maia Zacardi pela coorientação perspicaz, dedicação, encorajamento, disponibilidade constante neste percurso. Agradeço por acreditarem em mim e me motivarem a alcançar o meu potencial.

Aos amigos e colaboradores do Laboratório de Ecologia do Ictioplâncton e Pesca em Água Interiores (LEIPAI-UFOPA) Ruineris Cajado, Lucas Oliveira, Fabíola Silva, Zaqueu dos Santos, Letícia Aguiar e Glenda Clisla.

À empresa BIOCEV pelas logísticas de campo, em especial aos pescadores.

À Profa. Tatiana Santos e ao pessoal do LAQUAX, pela receptibilidade e boas conversas, em especial Rayane Arcanjo pelo carinho e amizade.

A Liliane Campos por me receber e dar suporte nos primeiros meses de mestrado na cidade de Altamira, Gratidão!

Aos meus colegas de mestrado Leydiane, Alice, Marina, Camila e Michel, obrigada pelas vivências e partilha, e pelo apoio emocional nos momentos mais críticos.

Muito obrigada a todos que fizeram algo por mim direta ou indiretamente durante essa jornada!

*“A preservação dos recursos aquáticos é uma tarefa complexa, mas devemos lembrar que cada ação individual contribui para a saúde desses ecossistemas.” Sylvia Earle*

## RESUMO GERAL

A espécie *Myloplus rubripinnis*, popularmente conhecida como pacu-branco, possui grande potencial ecológico como dispersora de sementes e representa importante recurso alimentar e econômico para diversas famílias ribeirinhas. Entretanto, pouco se conhece sobre a bioecologia dos adultos e não existem investigações relativas ao desenvolvimento inicial desta espécie. Neste contexto, este estudo teve como objetivo caracterizar morfologicamente as primeiras fases do ciclo de vida do *M. rubripinnis*, capturados no trecho médio do rio Xingu e identificar as principais mudanças nos padrões de crescimento através de diferentes modelos de regressão. Os indivíduos foram coletados com rede de plâncton em diversos habitats presentes no rio Xingu, durante as quatro fases do ciclo hidrológico local (enchente, cheia, vazante e seca) entre os meses de janeiro de 2021 a abril de 2022. Os espécimes depois de identificados, foram classificados de acordo com o estágio de desenvolvimento em períodos larval (larval-vitelino, pré-flexão, flexão e pós-flexão) e juvenil. Foram analisados 55 indivíduos com comprimento padrão variando de 7,21 a 35,53 mm. Durante o período larval os olhos são grandes e esféricos, a cabeça varia de pequena a grande e o corpo fusiforme variando de longo a moderado com perfil dorsal convexo. O intestino alcança a região mediana do corpo e a boca é terminal. O desenvolvimento é do tipo altricial, e inicialmente a pigmentação é escassa no corpo restringindo-se a uma faixa linear ao longo da notocorda com intensificação na parte posterior do pedúnculo caudal. Em estágios iniciais (flexão) observa-se pequenos agrupamentos de cromatóforos puntiformes na região occipital, na lateral do focinho, nos primeiros raios da nadadeira dorsal e anal, na base do ânus e dos raios da nadadeira caudal, e em estágios mais desenvolvidos (pós-flexão) formam faixas verticais irregulares pelo corpo. O número total de miômeros varia de 41 a 42 ((21 a 22 pré-anal e 20 pós-anal). A sequência completa da formação das nadadeiras e o número de raios não ramificados e ramificados são: caudal (superior iii+9-7+iiii inferior), dorsal (iii,20), anal (iii,32), ventral (i,5) e peitoral (i,10). Os modelos de crescimento indicaram maiores modificações na transição dos estágios de flexão para pós-flexão, com mudanças abruptas nas taxas crescimento relacionadas à cronologia de eventos importantes na história inicial de vida dessa espécie, como alteração no hábito alimentar, posição na coluna da água e ocupação de novos habitats. O padrão de pigmentação associado a dados merísticos são caracteres eficazes para distinguir as fases iniciais de *M. rubripinnis* de seus congêneres. Os achados desse estudo possibilitam a correta identificação de larvas e juvenis de *M. rubripinnis* em ambiente natural e, em última análise, contribuem para a compreensão dos locais e períodos de desova, bem como nas ações de manejo, conservação e sustentabilidade deste peixe Neotropical.

**Palavras-chave:** Amazônia, larva de peixe, morfologia, Myleinae, ontogenia, padrões de crescimento.



## ABSTRACT

The species *Myloplus rubripinnis*, popularly known as the white pacu, has great ecological potential as a seed disperser and represents an important food and economic resource for several riverine families. However, little is known about the bioecology of adult specimens, and there is no research on the early development of this species. In this context, the present study aimed to morphologically characterize the initial phases of the life cycle of *M. rubripinnis*, captured in the middle stretch of the Xingu River, and identify the main changes in growth patterns through different regression models. The individuals were collected using a plankton net in various habitats present in the Xingu River, during the four phases of the local hydrological cycle (flood, flood, ebb, and drought) between January 2021 and April 2022. After identification, the specimens were classified according to the developmental stage into the larval period (yolk-sac, preflexion, flexion, and postflexion) and the juvenile period. A total of 55 individuals with a standard length ranging from 7.21 to 35.53 mm were analyzed. During the larval period, the eyes are large and spherical, the head size varies from small to large, and the fusiform body ranges from long to moderate, with a convex dorsal profile. The intestine reaches the middle region of the body, and the mouth is terminal. Initially, the larvae are altricial, with pigmentation scarce in the body, limited to a linear band along the lateral line and intensifying towards the back of the caudal peduncle. In the early stages, small clusters of punctate chromatophores appear in the occipital region, on the side of the snout, in the first rays of the dorsal and anal fins, at the base of the anus, and in the rays of the caudal fin. In more developed stages, irregular vertical bands form throughout the body. The total number of myomeres ranged from 41 to 42 segments (21 to 22 preanal and 20 postanal). The complete sequence of fin formation and the number of unbranched and branched rays are as follows: caudal (superior iii+9-7+iii inferior), dorsal (iii,20), anal (iii,32), ventral (i,5), and pectoral (i,10). The growth analysis indicated greater changes during the transition from the flexion to the post-flexion stages, marking the end of larval development. It is noteworthy that the pattern of pigmentation, along with meristic data, serves as effective distinguishing characteristics for identifying the species among its congeners. This emphasizes the importance of morphological, meristic, and morphometric aspects for the accurate identification of the species in its natural environment. Additionally, this information can aid in understanding the locations and spawning periods, as well as contribute to the management, conservation, and sustainability efforts of this Neotropical fish.

**Keywords:** Amazon, fish larva, morphology, Myleinae, ontogeny, growth patterns

## SUMÁRIO

<b>1 INTRODUÇÃO GERAL</b> .....	<b>1</b>
<b>2 REFERÊNCIAS</b> .....	<b>2</b>
<b>CAPÍTULO I</b> - Early development of <i>Myloplus rubripinnis</i> (Characiformes: Serrasalminidae) from the Xingu River, Brazil.....	<b>6</b>

## 1 INTRODUÇÃO GERAL

A ictiofauna de água doce localizada na região Neotropical é a mais diversificada do planeta, abrangendo 6.200 espécies válidas (ALBERT *et al.*, 2020). Dentre essas, 2.716 (43.8%) são registradas na bacia amazônica (DAGOSTA & PINNA, 2019). No entanto, a riqueza total de espécies de peixes não é plenamente conhecida, pois muitos habitats disponíveis não foram adequadamente amostrados e, mesmo em áreas bem estudadas, muitas espécies ainda estão sendo descritas (REIS *et al.*, 2016).

A família Serrasalminidae atualmente inclui 17 gêneros e 100 espécies reconhecidas (FRICKE *et al.*, 2023), que estão distribuídas na maioria das principais bacias cisandinas, sendo mais de 70 espécies ocorrendo somente na bacia amazônica (OTA *et al.*, 2020; JÉGU, 2003; NICO *et al.*, 2018). Os serrasalmídeos vulgarmente conhecidos como pacus e piranhas (JÉGU, 2003), são facilmente identificados pelo seu corpo alto e comprimido lateralmente, além da presença de uma serra ventral formada por uma série de espinhos abdominais (GÉRY, 1997).

Dentre a ampla diversidade de Serrasalminidae, os peixes do gênero *Myloplus* Gill, 1896, pertencentes à subfamília Myleinae (Serrasalminidae), apresentam um desafio particular para os estudos de taxonomia devido à sua complexidade de espécies (OTA *et al.*, 2020; KOLMANN *et al.*, 2020). Esses peixes são encontrados em várias bacias hidrográficas da América do Sul, incluindo as dos rios Amazonas, Orinoco, La Plata, São Francisco e Paraguai/Paraná e nos afluentes do Escudo das Guianas (ANDRADE *et al.*, 2016; NICO *et al.*, 2018; SILVANO *et al.*, 2020).

*Myloplus rubripinnis* (MÜLLER & TROSCHER, 1844), conhecido como pacu - branco, desempenha um papel significativo nas comunidades ribeirinhas da região amazônica, servindo como fonte de proteína, e um importante recurso para a pesca ornamental (GARCIA-DAVILA *et al.*, 2018; 2021; BELTRÃO *et al.*, 2016; COIMBRA *et al.*, 2017). Informações sobre a ecologia desta espécie são incipientes, mas sabe-se que são herbívoros, habitam em regiões de água clara, realizam pequenas migrações e apresentam dimorfismo sexual no período reprodutivo (GARCIA-DÁVILA *et al.*, 2018). Além disso, *M. rubripinnis* desperta interesse para aquicultura devido seu grande porte (40 cm) características que podem ser exploradas de forma sustentável em atividades de criação e manejo.

Estudos relativos às características morfológicas das fases iniciais de *Myloplus* se concentram apenas na descrição dos períodos larval e juvenil de *Myloplus asterias*

(MÜLLER & TROSCHER, 1844) e *Myloplus lobatus* (VALENCIENNES, 1850) da bacia amazônica (OLIVEIRA *et al.*, 2022) e de *Myloplus tiete* (EIGENMANN & NORRIS, 1900) da bacia do rio Paranapanema (ORSI *et al.*, 2016), com indivíduos coletados em ambiente natural.

Os estudos sobre as fases iniciais do ciclo de vida dos peixes são de grande importância para a ecologia, pois esclarecem o estado de conservação das espécies, as áreas e períodos de desova, além de auxiliarem na criação de ações de manejo e conservação relacionadas aos recursos pesqueiros (CRUZ *et al.*, 2016; ZACARDI *et al.*, 2020; OLIVEIRA *et al.*, 2022). Contudo, a grande similaridade morfológica entre as espécies, a dissimilaridade entre as larvas e os indivíduos adultos, além da falta de literatura comparativa, como chaves taxonômicas, agravam as dificuldades na identificação e tem imposto limitações ao desenvolvimento de estudos ecológicos com ovos e larvas de peixes (BIALETZKI *et al.*, 2008; NAKATANI *et al.*, 2001; ZACARDI *et al.*, 2017; SANTOS *et al.*, 2020). No Brasil, sobretudo na Amazônia, a falta de estudos sobre o desenvolvimento ontogenético inicial da maioria das espécies de peixes cria a necessidade real de pesquisas sobre o assunto (REYNALTE-TATAJE *et al.*, 2020; ZACARDI *et al.*, 2020). Dessa forma, dada a importância da correta identificação dos primeiros estágios de vida da ictiofauna e da sua relevância como subsídio a propostas de manejo e conservação desse recurso, faz-se necessário ampliar o conhecimento dos aspectos e caracteres que auxiliam no reconhecimento específico dos indivíduos. Assim, o objetivo deste estudo é caracterizar a ontogenia inicial do pacu-branco, *M. rubripinnis*, por meio da caracterização morfológica, morfométrica e merística.

## 2 REFERÊNCIAS

ALBERT, J. S., TAGLIACOLLO, V. A., & DAGOSTA, F. Diversification of neotropical 531 freshwater fishes. **Annual Review of Ecology, Evolution, and Systematics**, 51, 27–532 53. doi: 10.1146/annurev-ecolsys-011620-031032, 2020.

ANDRADE, M. C.; OTA, R. P.; BASTOS, D.A.; JÉGU, M. A new large *Myloplus* Gill 1896 from River Negro basin, Brazilian Amazon (Characiformes: Serrasalminidae). **Zootaxa**, v. 6, n. 4205, p. 571-580, 2016.

BELTRÃO, H.; MAGALHÃES, E. R. S.; YAMAMOTO, K. C. Ictiofauna da Floresta Nacional (FLONA) do Amaná, uma área de interflúvio Tapajós/Madeira (Estado do

Pará), ameaçada por garimpos de mineração. **Boletim Sociedade Brasileira de Ictiologia**, v. 117, p. 15-27, 2016.

BIALETZKI, A.; NAKATANI, K.; SANCHES, P. V.; BAUMGARTNER, G.; MAKRAKIS, M. C.; TAGUTI TL. Desenvolvimento inicial de *Hoplias* aff. *malabaricus* (Bloch, 1794) (Osteichthyes, Erythrinidae) da planície alagável do alto rio Paraná, Brasil. **Acta Sci Biol Sci**. 2008; 30:141–49. <https://doi.org/10.4025/actascibiolsci.v30i2.3608>

COIMBRA, A. B.; TERRA, A. K.; MAZUREK, R. R. S.; PEREIRA, H. S.; BELTRÃO, H.; SOUSA, R. G. C. Fishing activity of the Mura indians in the Ayapuá Lake, Low Purus River, Amazonas, Brazil. **Desafios**, v. 4, n. 1, p. 115-129, 2017.

CRUZ, P. R.; AFFONSO, I. P.; GOMES, L. C. Ecologia do ictioplâncton: uma abordagem cienciométrica. **Oecologia Australis**, v. 20, n. 4, p. 436-450, 2016.

DAGOSTA, F. C. P; PINNA, M. C.C. The fishes of the Amazon: distribution and biogeographical patterns, with a comprehensive list of species. **Bulletin of the American Museum of Natural History**, v. 2019, n. 431, p. 1-163, 2019.

FRICKE, R.; ESCHMEYER, W. N.; VAN DER LAAN, R. **Eschmeyer's Catalog of Fishes: Genera, Species, References**. 2023. Eletronic version. Disponível em: <http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp>. Acessado em 16/03/2023

GARCÍA-DÁVILA, C.; SÁNCHEZ RIVEIRO, H. FLORES SILVA, M. A., MEJÍA DE LOAYZA, E., ANGULO CHÁVEZ, C., CASTRO RUIZ, D., ESTIVALS, G., GARCÍA VÁSQUEZ, A., NOLORBE PAYAHUA, C., VARGAS DÁVILA, G., NÚÑEZ, J., MARIAC, C., DUPONCHELLE, F., & RENNO, J.-F. Peces de consumo de la Amazonía peruana. En Instituto de Investigaciones de la Amazonía Peruana. **Instituto de Investigaciones de la Amazonia Peruana (IIAP)**. Iquitos, Perú, 218 pp, 2018. <http://repositorio.iiap.gob.pe/handle/20.500.12921/369>

GARCÍA-DÁVILA, C.; ESTIVALS, G.; MEJIA, J.; FLORES, M.; ANGULO, C.; SÁNCHEZ, H.; NOLORBE, C.; CHUQUIPIONDO, C.; CASTRO-RUIZ, D.; GARCÍA, A.; ORTEGA, H.; PINEDO, L.; OLIVEIRA, C.; RÖMER, U.; MARIAC, C.;

DUPONCHELLE, F.; RENNO, J.-F. PECES ORNAMENTALES DE LA AMAZONIA PERUANA. **Instituto de Investigaciones de la Amazonia Peruana (IIAP)**. Iquitos, Perú, 503 pp, 2020. <http://repositorio.iiap.gob.pe/handle/20.500.12921/369>

GÉRY, J. Characoids of the world. T. F. H. **Publications, Neptune City**, 672 pp. 1977.

JÉGU, M. Subfamily Serrasalminae. 2003. Pp. 182–184 in: Reis, R. E., Kullander, S. O. & Ferraris Jr., C. J. (eds.), Check list of the freshwater fishes of South and Central America. Porto Alegre. **Edipucrs**.

KOLMANN, M. A.; HUGHES, L. C.; HERNADEZ, L.P.; ARCILA. D.; BETANCUR, R.; SABAJ, M. H. Phylogenomics of piranhas and pacus (Serrasalminidae) uncovers how convergent diets obfuscate traditional morphological taxonomy. **Systematic Biology**, v. 70, n. 3, p.576-592, 2020.

NAKATANI, K.; AGOSTINHO, A. A.; BIALETZKI, A.; BAUMGARTNER, G.; SANCHES, P. V.; MAKRAKIS, M; PAVANELLI, C. S. Ovos e larvas de peixes de água doce: desenvolvimento e manual de identificação. **EDUEM**: Maringá-PR, 2001.

NICO, L. G.; JÉGU, M. & ANDRADE, M. C. Family Serrasalminidae: piranhas and Pacus. 2018. Pp. 172–196 in: VAN DER SLEEN, P.; ALBERT, J. (eds.), Field Guide to the Fishes of the Amazon, Orinoco, and Guianas. **D&N Publishing, Wiltshire, UK**.

OLIVEIRA, L. S.; CAJADO, R. A.; SILVA, F. K. S.; ANDRADE, M. C.; ZACARDI, D. M. Early development of two commercially valuable fish from the lower Amazon River, Brazil (Characiformes: Serrasalminidae). **Neotropical Ichthyology**, v. 20, n. 1, p. 210024, 2022.

ORSI, M. L.; ALMEIDA, F. S.; SWARÇA, A. C.; CLARO-GARCIA, A.; VIANNA, N. C.; GARCIA, D. A. Z.; BIALETZKI, A. Ovos, larvas e juvenis dos peixes da Bacia do Rio Paranapanema uma avaliação para a conservação. **Triunfal Gráfica e Editora, Duke Energy**: Assis-SP, 2016.

OTA, R.P.; MACHADO, V.N.; ANDRADE, M.C.; COLLINS, R.A.; FARIAS, I.P.; HRBEK, T. Integrative taxonomy reveals a new species of pacu (Characiformes:

Serrasalminae) *Myloplus* from the Brazilian Amazon. **Neotropical Ichthyology**, v. 18, p. 1901-12, 2020.

REYNALTE-TATAJE, D. A.; LOPES, C. A.; MASSARO, M. V.; HARTMANN, P. B.; SULZBACHER, R.; SANTOS, J. A. State of the art of identification of eggs and larvae of freshwater fish in Brazil. **Acta Limnologica Brasiliensia**, v. 32, e6, 2020.

REIS, R.E.; ALBERT, J.S.; DIDARIO, F.; MINCARONE, M. M.; PETRY, P.; ROCHA, L.A. Fish biodiversity and conservation in South America. **Journal of Fish Biology**, v. 89, p. 12-47, 2016.

SANTOS, J. A.; SOARES, C. M.; BIALETZKI, A. Early ontogeny of yellowtail tetra fish *Astyanax lacustris* (Characiformes: Characidae). **Aquaculture Research**, v. 51, p. 4030-4042, 2020.

SILVANO, R. A. M.; NITSCHKE, P. P.; VIEIRA, K. C.; N. A. G. L. P.; MARTÍNEZ, A.T. R.; CHUCTAYA, J. A. Atlas of Fish of Tapajós and Negro Rivers I: Characiformes. In: SILVANO, R. A. M. (Ed). Fish and Fisheries in the Brazilian Amazon. People, Ecology and Conservation in Black and Clear Water Rivers 1ed. Cham: **Springer International Publishing**; p. 41-196, 2020.

ZACARDI, D. M.; BITTENCOURT, S. C. S.; QUEIROZ, H. L. Recruitment of migratory Characiforms in the different wetland habitats of Central Amazonia: subsidies for sustainable fisheries management. **Journal of Applied Ichthyology**, v. 36, n. 4, p. 431-438, 2020.

ZACARDI, D. M.; BITTENCOURT, S. D. S.; NAKAYAMA, L.; DE QUEIROZ, H. L. Distribution of economically important fish larvae (Characiformes, Prochilodontidae) in the Central Amazonia, Brazil. **Fisheries Management and Ecology**, 24(4), 283-291, 2017.

Este capítulo está formatado nas normas da revista Neotropical Ichthyology, no qual foi submetido, disponível em: <https://ni.bio.br>

Artigo 1

**CAPÍTULO I - Early development of *Myloplus rubripinnis* (Characiformes: Serrasalminidae) from the Xingu River, Brazil**



**Early development of *Myloplus rubripinnis* (Characiformes: Serrasalminidae) from the Xingu River, Brazil**

Elzamara de Castro Oliveira<sup>1,2</sup>; Lucas Silva de Oliveira<sup>2</sup>; Ruineris Almada Cajado<sup>2</sup>; Fabíola Katrine Souza da Silva<sup>2</sup>; George Yasui<sup>3</sup>; Diego Maia Zacardi<sup>1,2</sup> and Leandro Melo de Sousa<sup>1</sup>

<sup>1</sup>Programa de Pós-Graduação em Biodiversidade e Conservação, Universidade Federal do Pará, Rua, Bairro, CEP, Altamira, Pará, Brasil. (ECO)

elzamara.olliveira@gmail.com, ORCID <https://orcid.org/0000-0002-3945-4603>

(corresponding author), (LMS) leandro.m.sousa@gmail.com, ORCID

<https://orcid.org/000-002-0793-9737>.

<sup>2</sup>Laboratório de Ecologia do Ictioplâncton e Pesca em Águas Interiores, Instituto de Ciências e Tecnologia das Águas, Universidade Federal do Oeste do Pará, Rua Vera Paz, Salé, 68040-255 Santarém, PA, Brazil. (LSO) lucasmdcpa@gmail.com, ORCID <https://orcid.org/0000-0002-1631-0498>, (RAC) ruineris.cajado@gmail.com, ORCID <https://orcid.org/0000-0002-7047-0302>, (FKSS) fabiolakatrine@gmail.com, ORCID <https://orcid.org/0000-0001-7869-5437>, (DMZ) dmzacardi@hotmail.com, ORCID <https://orcid.org/0000-0002-2652-9477>.

<sup>3</sup>Laboratório de Biotecnologia de Peixes, Centro Nacional de Pesquisa e Conservação da Biodiversidade Aquática Continental, Instituto de Conservação da Biodiversidade Chico Mendes, Rodovia Pref. Euberto Nemésio Pereira de Godoy, 13630-970, Pirassununga, SP, Brazil. (GY) yasui@usp.br, ORCID <https://orcid.org/0000-0002-6105-8308>.

**ABSTRACT**

The early development of Neotropical fish *Myloplus rubripinnis* from the Xingu River Basin is described using external morphology, meristic data, and morphometric relationships. Larvae and juveniles were captured between the years 2021 and 2022 in different locations of the Xingu River, Pará, Brazil. A total of 55 individuals were analyzed, which presented a standard length ranging from 7.21 to 35.53 mm. Through the smallest individual analyzed it is suggested that the larvae of *M. rubripinnis* are altricial at hatching stage. During early ontogeny, specimens have large, spherical eyes, a head ranging from small to large, and a body from long to deep. Initially, pigmentation is scarce, but during development, chromatophores arise on the body forming incomplete bands, in addition to pigments in the first rays of the unpaired fins.

Total myomeres ranged from 41 to 42 (21 to 22 preanal and 20 postanal). The association of features including pigmentation patterns and meristic data are effective characteristics to distinguish *M. rubripinnis* larvae and juveniles from their sympatric congeners. The information provided here will assist on the early identification of this species in natural environment and will support future studies regarding reproductive biology of *M. rubripinnis*, especially in conservation strategies of Amazonian Basin.

### **RESUMO**

O desenvolvimento inicial do peixe Neotropical *Myloplus rubripinnis* da bacia do rio Xingu é descrito usando morfologia externa, dados merísticos e relações morfométricas. Larvas e juvenis foram capturados entre os anos de 2021 e 2022 em diferentes localidades do rio Xingu, Pará, Brasil. Foram analisados um total de 55 indivíduos, que apresentaram comprimento padrão variando de 7,21 a 35,53 mm. Através do menor indivíduo analisado observamos que *M. rubripinnis* apresenta desenvolvimento altricial. Durante a ontogenia inicial, os espécimes têm olhos grandes e esféricos, cabeça variando de pequena a grande e corpo de longo a profundo. Inicialmente, a pigmentação é escassa, mas durante o desenvolvimento surgem cromatóforos no corpo formando faixas incompletas, além de pigmentos nos primeiros raios das nadadeiras não pareadas. O total de miômeros variou de 41 a 42 (21 a 22 pré-anal e 20 pós-anal). A associação de características, incluindo padrões de pigmentação e dados merísticos, são características eficazes para distinguir larvas e juvenis de *M. rubripinnis* de seus congêneres simpátricos. Os resultados obtidos auxiliarão na identificação dos indivíduos em ambiente natural e subsidiarão futuros estudos sobre a biologia reprodutiva de *M. rubripinnis*, especialmente em estratégias de conservação da Bacia Amazônica.

### **KEYWORDS**

Amazon, fish larvae, morphology, Myleinae, ontogeny

### **PALAVRAS-CHAVE**

Amazônia, larva de peixe, morfologia, Myleinae, ontogenia

### **RUNNING HEAD**

Early development of *Myloplus* from the Xingu River

## INTRODUCTION

Fish species belonging to the Serrasalminae family currently comprise 17 genera (Fricke *et al.*, 2023), with a wide distribution in the Amazon, Orinoco, La Plata, and São Francisco drainages, as well as in the coastal rivers of the Guiana Shield in Brazil, Guyana, French Guiana, Suriname, and Venezuela (Jégu, 2003; Andrade *et al.*, 2018; Nico *et al.*, 2018). These fish are important for fisheries and aquaculture, with considerable social and economic relevance, providing one of the main sources of income and animal protein consumed by the populations that inhabit the surrounding area of Amazonian rivers and lakes (Isaac *et al.*, 2015; Zacardi, 2020).

The genus *Myloplus* Gill 1896, belonging to the Myleinae subfamily, is one of the most diverse among Serrasalminae, with 12 valid species (Fricke *et al.*, 2023). These fish are popularly known as “pacus” and currently represent a taxonomic challenge due to the complexity of existing critical species (Machado *et al.*, 2018; Ota *et al.*, 2020; Kolmann *et al.*, 2020). *Myloplus* species are distributed both in lotic system habitats (e.g., rapids and rivers) as well as in lacustrine environments (e.g., lakes) (Andrade *et al.*, 2016a; Nico *et al.*, 2018; Silvano *et al.*, 2020).

Among the species of the genus, *Myloplus rubripinnis* (Müller & Troschel, 1844), popularly known as “pacu-branco”, is an important resource for ornamental fish trade and local fishing, being considered an important source of food for riverside populations (Isaac *et al.*, 2015; Beltrão *et al.*, 2016; Coimbra *et al.*, 2017; Liu *et al.*, 2019).

Information regarding the biology of this species is scarce, but it is known that this species inhabits naturally restricted environments associated with clear water rivers in the Amazon basin with a preference for lentic sites and close to riparian vegetation (Ohara *et al.*, 2017). In addition, it is well known that feeding concentrates on fruits and seeds and the spawning peak occurs at the beginning of the flood (Santos *et al.*, 2006; Ohara *et al.*, 2017).

Despite the existence of some information about the ecological characteristics of *M. rubripinnis*, the reproduction and early development is still poorly understood, with emphasis on the early stages of this fish, as well as for most *Myloplus* species.

Currently, there are few studies concerning the morphological characteristics of the initial stages related to congeneric *Myloplus* species, such as: (i) Ponton and Méricoux (2001) with a description of only one stage of development of larvae of *Myloplus ternetzi* (Norman 1929) from the Sinnamary River (French Guiana); (ii) Orsi *et al.*

(2016) also characterized only one stage of development of larvae of *Myloplus tiete* (Eigenmann & Norris 1900) in the Paranapanema River basin and Oliveira et al. (2022) with the initial description contemplating a larger number of developmental stages of *Myloplus asterias* (Müller & Troschel 1844) and *Myloplus lobatus* (Valenciennes 1850) collected in the Amazon basin.

Studying the early stages of fish life is important to understand the structure of the ichthyofauna and assist areas and spawning periods - that are important information to support management, and conservation strategies related to fishing resources (Cruz et al., 2016; Zacardi et al., 2020a; Oliveira et al., 2022). In Brazil, especially in the Amazon basin, giving circumstances above, the lack of studies on the initial ontogenetic development of fish emphasize a real need for research efforts on this field (Reynalte-Tataje et al., 2020; Zacardi et al., 2020b). The panorama above is also critical because the freshwater ecosystems of the Amazon region are threatened by climate change and various anthropogenic changes, such as deforestation, overfishing and dams (Arantes et al., 2018; Latrubesse et al., 2021; Cajado et al., 2022; Röpke et al., 2022). For example, evidence indicates that the damming of the Xingu River, in the Amazon Basin, triggered an environmental filtering process, reducing the functional diversity in the region, mainly affecting species of Serrasalminidae (Kepeller et al., 2022).

Due to the ecological and economic importance of the species, the growing threats from anthropic actions and the lack of knowledge about the early life history of *M. rubripinnis*, the aim of this study was to describe the morphological, meristic, and morphometric development of this species, examining and discussing the main changes that define the ontogenetic intervals, in addition to determining the growth pattern during the initial ontogeny. These informations are important to identify wild *pacu-branco* larvae and juveniles and support management and conservation strategies for subsequent establishment of sustainable fisheries and monitoring *M. rubripinnis* population fluctuations along the Xingu River basin.

## MATERIAL AND METHODS

### *Collection and analysis of biological material*

All specimens used in this study were captured with the authorization issued by the environmental licensing board of the *Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis* – IBAMA (number 7580530) and followed the euthanasia protocols in accordance with the rules of the *Conselho Nacional de Controle*

*e Experimentação Animal* (CONCEA, 2013). Larvae and juveniles of *M. rubripinnis* were captured in environments such as backwaters, rapids, river channels and lakes adjacent to the Xingu River (3°00'S - 51°30'W to 3°40'S - 52°40'W). Samplings were carried out in two strata of the water column, subsurface (0-1 m) and half water (approximately 10 m), and in two daily cycles (daytime - 15h and nighttime - 21h). To capture the specimens, a plankton net was used, with a mechanical flowmeter coupled to measure the volume of filtered water, in horizontal trawls for approximately 10 minutes, during the ichthyoplankton monitoring campaigns that took place from January 2021 to April 2022.

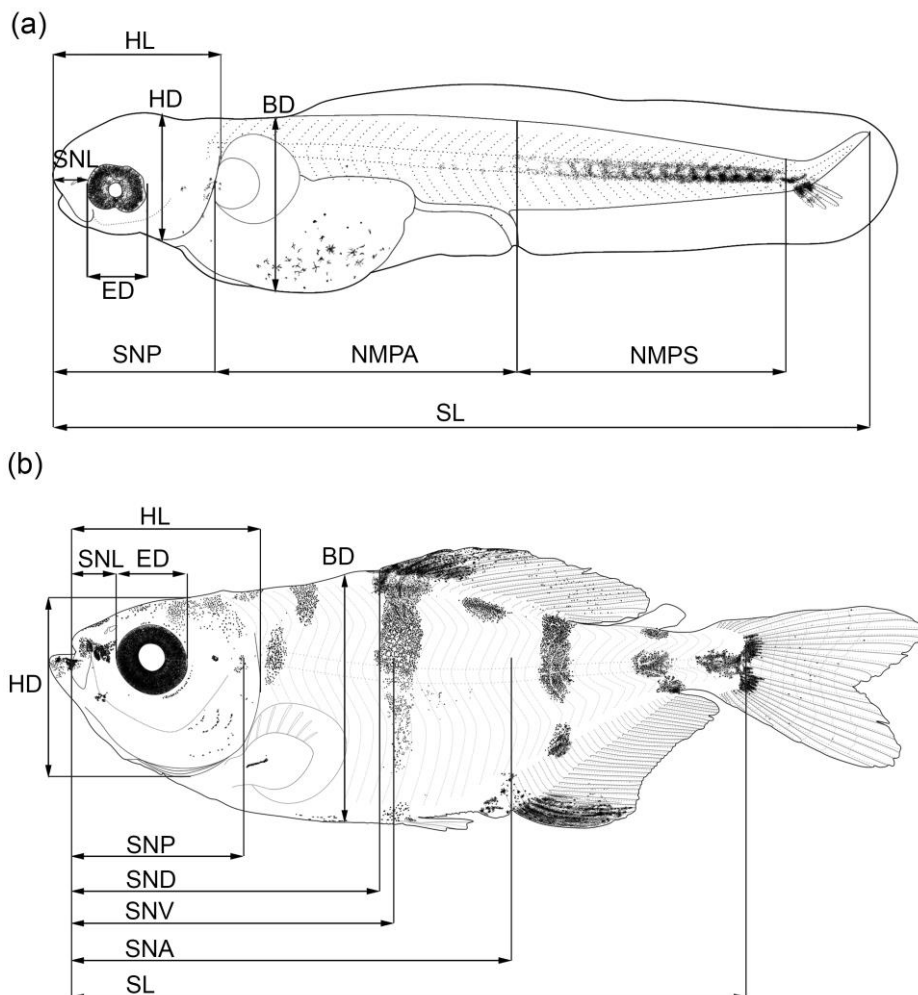
Samples were exposed in eugenol solution (30 mg/L) for approximately one minute, fixed in 10% formalin, stored in duly labeled bottles, and transported to the laboratory. In the laboratory, the samples were sorted, quantified, and identified using the developmental regressive sequence technique proposed by Ahlstrom & Moser (1976). This technique consists of identifying and grouping a series of individuals at different developmental stages, from juveniles or larvae into more advanced stages to those that have just hatched. In addition, an adult specimen of *M. rubripinnis* was defleshed for vertebrae count. The number of vertebrae is associated with the number of myomeres, thus becoming a useful tool for identifying fish larvae (Araújo-Lima & Donald, 1988). Specimens of *M. rubripinnis* were classified according to the stage of development proposed by Ahlstrom *et al.* (1976), modified by Nakatani *et al.* (2001) into (I) larval period (yolk-sac larvae, preflexion, flexion, and postflexion) and (II) juvenile period, the latter characterized by complete formation of fin rays and appearance of scales until the first sexual maturation.

Description of each period was carried out according to the appearance of the morphological characters presented in each stage. Digital images and illustrations were taken from the specimens that best represented the development during the two periods following the technique described by Faber & Gadd (1983) and Shibata (2016, 2017). All individuals were morphometrically measured using a binocular stereoscopic microscope (Leica S9i) connected to an integrated color digital camera for image capturing using the Leica LAS EZ analysis software.

Specimens analyzed are deposited at the Coleção de Ovos e Larvas de Peixes (<https://specieslink.net/col/CROLP-LEIPAI/>) of the Universidade Federal do Oeste do Pará (UFOPA). Catalog numbers are LEIPAI 00491 (3), LEIPAI 00492 (4), LEIPAI

00493 (4), LEIPAI 00494 (14), LEIPAI 00495 (14), LEIPAI 00496 (14), and LEIPAI 00497 (2).

For morphometric analyses, the following body measurements were obtained and expressed in millimeters (mm), according to Ahlstrom *et al.* (1976): standard length (SL), snout length (SNL), eye diameter (ED), head length (HL), head depth (HD), body depth (BD), and distance from the snout to the origin of the pectoral (SNP), pelvic (SNV), dorsal (SND) and anal (SNA) fins. Meristic characters were expressed by the number of total (NMT), preanal (NMPA) and postanal (NMPS) myomeres and the number of pectoral (P), pelvic (V), dorsal (D) and anal (A) fin rays, when present (Figure 1 A, B).



**Figure 1.** Morphometric measurements in *Myloplus rubripinnis*. **A.** Flexion; **B.** Postflexion. **HD.** head deep; **BD.** body deep; **HL.** head length; **SNL.** snout length; **SL.** standard length; **ED.** eye diameter; **SNA.** distance from the snout to anal fin; **SND.** distance from the snout to dorsal fin; **SNP.** distance from the snout to pectoral fin; **SNV.**

distance from the snout to pelvic fin; **NMPA**. preanal myomeres; **NMPS**. postanal myomeres.

#### *Data analysis*

Morphometric relationships of larvae and juveniles were expressed as percentages, where the variables HD, SNL and ED were related to head length, while BD, HL, SNA, SND, SNP and SNV were related to standard length. Body relationships between body height (BD/SL), head length (HL/SL) and eye diameter (ED/HL) were established using the criteria proposed by Leis & Trnski (1989), and Nakatani *et al.*, (2001).

To verify the body growth during the initial development, regression models were applied in which the morphometric variables SNA, SNP, HL, BD (dependent variable) were plotted and related to the standard length (independent variable), and the variables SNL, DO and HD (dependent variable) related to head length (independent variable), their relationships were expressed by different growth models, which may represent different biological patterns (Kováč *et al.*, 1999). Isometric growth hypothesis was tested using a simple linear regression model. In addition, two alternative hypotheses: gradual allometric growth (quadratic regression) and discontinuous isometric growth (piecewise regression), which is characterized by unexpected changes occurring, usually marked by interruption points, which reflect divergent growth rates.

Regression models are based on mathematical functions and each model has a straight line estimated by the equation, through which it is possible to verify the body growth profile during larval development, with or without differential in growth rate (Silva *et al.*, 2022). 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). Statistica™ 7.0 software was used to perform regression analysis and F-test.

## **RESULTS**

#### *Morphological characterization*

A total of 55 individuals were analyzed (2 in yolk-sac, 42 in flexion, 4 in postflexion, and 07 juveniles). This species did not present the preflexion stage during larval development, as the final section of the notochord is flexed with individuals presenting yolk, partially pigmented eyes, and anus and mouth non-functional.

Yolk-sac (Fig. 2A): larvae ranged from 7.21 to 7.76 mm SL (mean  $7.49 \pm 0.39$ ). The body is fusiform and robust, the yolk is elliptical in shape and contained about 3.51

times in the SL. The notochord is straight and visible by transparency. The eyes are round and partially pigmented. Olfactory bulb (nostrils) and optic vesicles are visible. The anus, not opened, is positioned in the middle region of the body. Pigmentation is not very conspicuous and is distributed internally in a band parallel to the notochord, from the caudal peduncle to the beginning of the yolk. The finfold is relatively tall and surrounds the body from the posterior region of the yolk sac bypassing the caudal peduncle towards the head. Pectoral-fin buds are present and covered by a membrane and lack rays. The total number of myomeres ranges from 41 to 42 (21 to 22 preanal and 20 postanal).

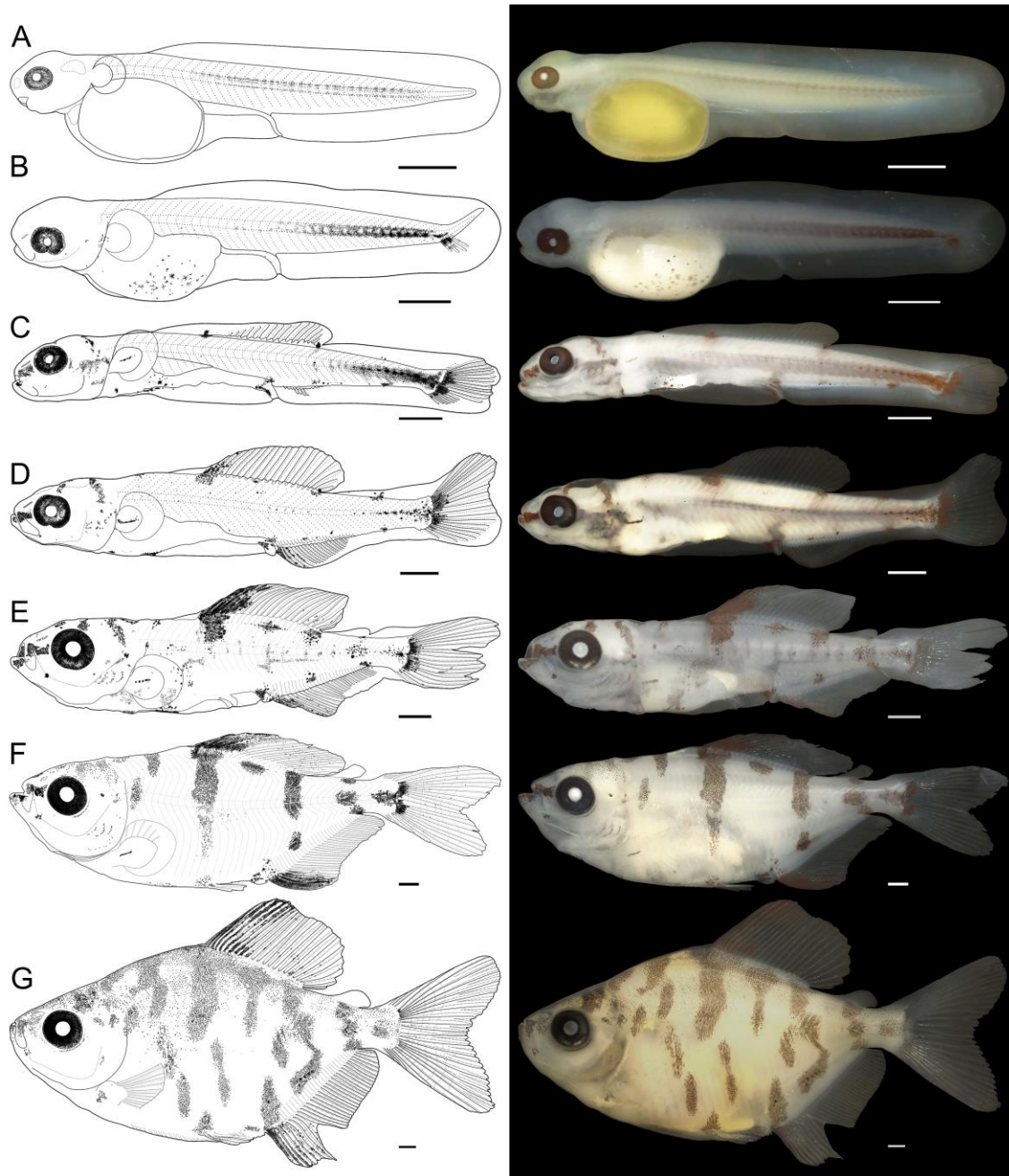
Flexion (Figs. 2B, C, D): standard length of specimens at this stage ranged from 7.80 to 12.82 mm (mean  $9.89 \pm 1.09$ ). The body is fusiform and robust. Initially, the specimens have traces of yolk, but from 9.68 mm SL it is completely absorbed. The final section of the notochord is flexed, with the hypural plate visible. The eyes are fully pigmented. The mouth is functional and in terminal position. The nostrils are simple. The swim bladder is visible through transparency and occupies a large space in the abdomen. In the smallest specimen analyzed at this stage it is evident a band of melanophores running along the notochord from the caudal rays towards the anus and dendritic pigments in the yolk and at the base of the pectoral fin. However, upon development, the band parallel to the notochord is restricted to the posterior region of the body and the base of the caudal rays. At 7.80 mm SL, chromatophores arise at the beginning and end of the dorsal and anal fins bases, towards the origin of the adipose fin and close to the anal opening. Larvae presented pigments forming a horizontal band that extends from the snout to the eyes, in addition to chromatophores in the dentary, operculum, fontanelle, occipital region and pectoral-fin bud. The pectoral-fin bud is relatively large, reaching the ventral origin of finfold. At the end of this stage, the finfold is partially absorbed and the presence of first rays of odd fins is observed. The caudal fin is forked. The total number of myomeres ranges from 41 to 42 segments (21 to 22 preanal and 20 postanal).

Postflexion (Figs. 2E, F): individuals ranged from 13.49 to 19.81 mm SL (mean  $16.68 \pm 2.74$ ). Due to the increase in muscle tissue, it is not possible to visualize the notochord and swim bladder and the myomeres count became difficult. The eyes, nostrils, position of the mouth and anal opening remain morphologically similar to the previous stage. Initially, the body is fusiform, but at later stages, it becomes partially rhomboidal. Note the presence of ventral keel in the post-pelvic region. The color pattern is similar to the



previous stage with the vertical formation of six irregular bands on the flanks. Conspicuous pigments are distributed over the first rays of the dorsal and anal fins, and irregularly over the remaining dorsal rays. At the end of this stage, the finfold is fully absorbed. The first pectoral fin rays are visible from 20 mm SL and the dorsal and anal fins have some branched rays but are not fully formed.

Juvenile (Fig. 2G): standard length ranged from 23.44 to 35.53 mm (mean  $30.48 \pm 5.18$ ). The mouth is terminal, and there are maxillary teeth, but not fully developed. The eyes are round and pigmented. The body is laterally compressed and rhomboidal in shape. The ventral keel is located in the pre- and post-pelvic region. The pigmentation pattern in vertical stripes of the “brindle” type intensifies. All the fins are well developed and with segmented rays. The sequence of formation and the number of rays is: caudal (upper iii, 9-7, iii lower lobe), dorsal (iii,19), anal (iii,33), ventral (i,6), adipose and pectoral (i,12).



**Figure 2.** Larval and juvenile development of *Myloplus rubripinnis*. **A.** Yolk-sac larvae (7.21 mm); **B.** Early flexion (7.80 mm); **C.** Flexion (9.68 mm); **D.** Late flexion (10.05 mm); **E.** Early postflexion (13.81 mm); **F.** Late postflexion (19.81 mm); **G.** Juvenile (23.44 mm). Scale bars = 1 mm.

#### Morphometric relationships

The larvae have large eyes (33.09% to 44.57% in HL), head ranging from small to large (15.35% to 36.26% in SL), while the body depth varies from elongate to moderate (10.83% to 39.36% in SL). Head depth (48.64% to 108.69%), distance from the snout to anal fin (58.71% to 66.13%), and distance from the snout to pectoral fin (17.43% to

28.78%) increased along ontogeny, but the head length and distance from the snout to dorsal fin remained stable. The distance from the snout to the ventral fin decreased (52.40% to 50.08%). For the juvenile period, these variations remained proportional, the eye large (38.95% to 43.03% in HL), the head moderate (24.22% to 27.39% in SL), and the body change to very deep (112.77% to 143.02% in SL). The distances from the snout to the anal (65.28% to 62.48%), pectoral (26.81% to 21.49%), and ventral fin (50.79% to 45.96%) decreased, while the head depth increased (112.77% to 143.02%) and the snout length (23.59% to 29.83%) remained stable, with no tendency to increase in relation to HL, only with variations between specimens (Table 1).

**Table 1.** Morphometric variables (mm), minimum values (Min), maximum values (Max), mean (X), standard deviation (SD) and morphometric ratios (%) of morphometric and meristic variables obtained in larvae and juveniles of *Myloplus rubripinnis*. **HD.** Head deep; **BD.** Body deep; **HL.** Head length; **SNL.** Snout length; **SL.** Standard length; **ED.** Eye diameter; **SNA.** Distance from the snout to anal fin; **SND.** Distance from the snout to dorsal fin; **SNP.** Distance from the snout to pectoral fin; **SNV.** Distance from the snout to pelvic fin; **N.** Number of individuals; **NA.** Fin absent; **NV.** Not visible.

<i>Myloplus rubripinnis</i>								
Variables (mm)	Yolk-sac (N=2)		Flexion (N=42)		Postflexion (N=4)		Juvenile (N=7)	
	Min-Max	X ± SD	Min-Max	X ± SD	Min-Max	X ± SD	Min-Max	X ± SD
SL	7.21-7.76	7.49±0.39	7.80-12.82	9.89±1.09	13.49-19.81	16.68 ±2.74	23.44-35.53	30.48±5.18
HL	1.38-1.47	1.42±0.07	1.20-3.38	2.21±0.55	3.91-5.19	4.46±0.57	6.42-8.82	7.73±1.00
SnD	0.32-0.36	0.34 ±0.03	0.24-0.67	0.44±0.12	0.76-1.19	0.95 ±0.18	1.68-2.62	2.05±0.33
ED	0.58-0.59	0.58±0.01	0.49-1.36	0.88±0.22	1.56-2.09	1.81±0.23	2.50-3.61	3.15±0.40
HD	1.20-1.24	1.22±0.02	1.03-2.78	1.66±0.40	3.31-5.64	4.39±1.09	7.24-12.61	10.09±1.98
BD	1.39-1.41	1.40±0.01	1.05-2.96	1.52±0.41	4.09-7.80	5.66±1.84	11.87-21.69	17.03±4.00
SnP	1.44-1.59	1.52±0.11	1.44-3.63	2.41±0.54	3.93-5.28	4.58±0.60	6.23-7.88	7.26±0.64
SnA	4.56-4.65	4.60±0.06	4.46-8.16	6.11±0.85	8.64-12.40	10.29±1.71	15.30-23.07	19.64±3.21
SnD	NA	NA	3.33-6.27	4.86±0.59	6.64-9.31	7.90±1.20	11.61-17.02	14.42±2.10
SnV	NA	NA	NA	NA	7.24-9.92	8.51±1.25	11.91-16.83	14.71±2.18
Morphometric proportions (%)								
SNL/HL	17.78-20.59	19.19±1.98	16.46-25.89	20.78±1.92	18.32-23.53	21.33±2.40	23.59-29.83	26.56±2.51
ED/HL	35.65-38.99	37.32±2.36	33.09-44.57	40.19±2.48	40.00-41.10	40.62±0.45	38.95-43.03	40.81±1.56
HD/HL	75.32-83.09	79.21±5.49	48.64-94.49	76.37±8.63	84.71-108.69	97.42±12.69	112.77-143.02	129.47±9.70
HL/SL	17.60-17.63	17.61±0.02	15.35-36.26	22.17±4.03	25.47-28.27	26.85±1.26	24.22-27.39	25.53±1.21
BD/SL	18.79-21.02	19.90±1.57	10.83-23.11	15.28±3.03	27.63-39.36	33.29±5.56	50.30-61.03	55.31±4.02
SnP/SL	18.56-22.04	20.30±2.46	17.43-28.45	24.24±3.39	26.66-28.45	27.56±0.99	21.49-26.81	24.13±2.25
SnA/SL	58.71-64.43	61.57±4.04	56.62-66.13	61.64±2.95	60.48-62.59	61.68±1.06	62.28-65.28	64.49±1.08
SnD/SL	NA	NA	33.14-51.67	47.20±3.66	46.73-48.07	47.43±0.67	45.33-49.84	47.52±1.84
SnV/SL	NA	NA	NA	NA	50.08-52.40	51.11±0.97	45.96-50.79	48.43±1.63
Myomeres								
	Min-Max	Mode	Min-Max	Mode	Min-Max	Mode	Min-Max	Mode
Pre-anal	21 - 22	22	21 - 22	22	NV	-	NV	-
Post-anal	20 - 20	20	20 - 20	20	NV	-	NV	-
Total	41 - 42	42	41 - 42	42	NV	-	NV	-
Rays								

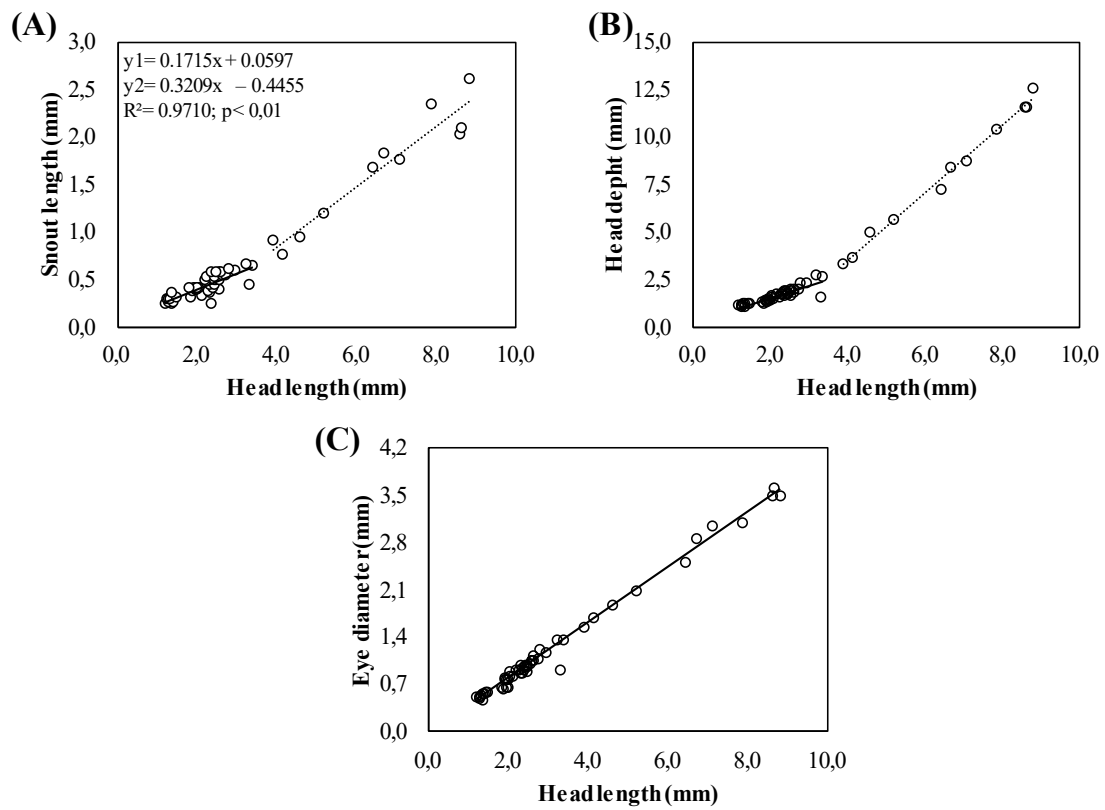
Pectoral	NA	-	NA	-	i, 12	-	i,12	i,12
Anal	NA	-	NA	-	iii, 33	-	iii,33	iii,33
Dorsal	NA	-	NA	-	iii, 19	-	iii,19	iii,19
Pelvic	NA	-	NA	-	NV	-	i,6	i,6

### Growth analysis

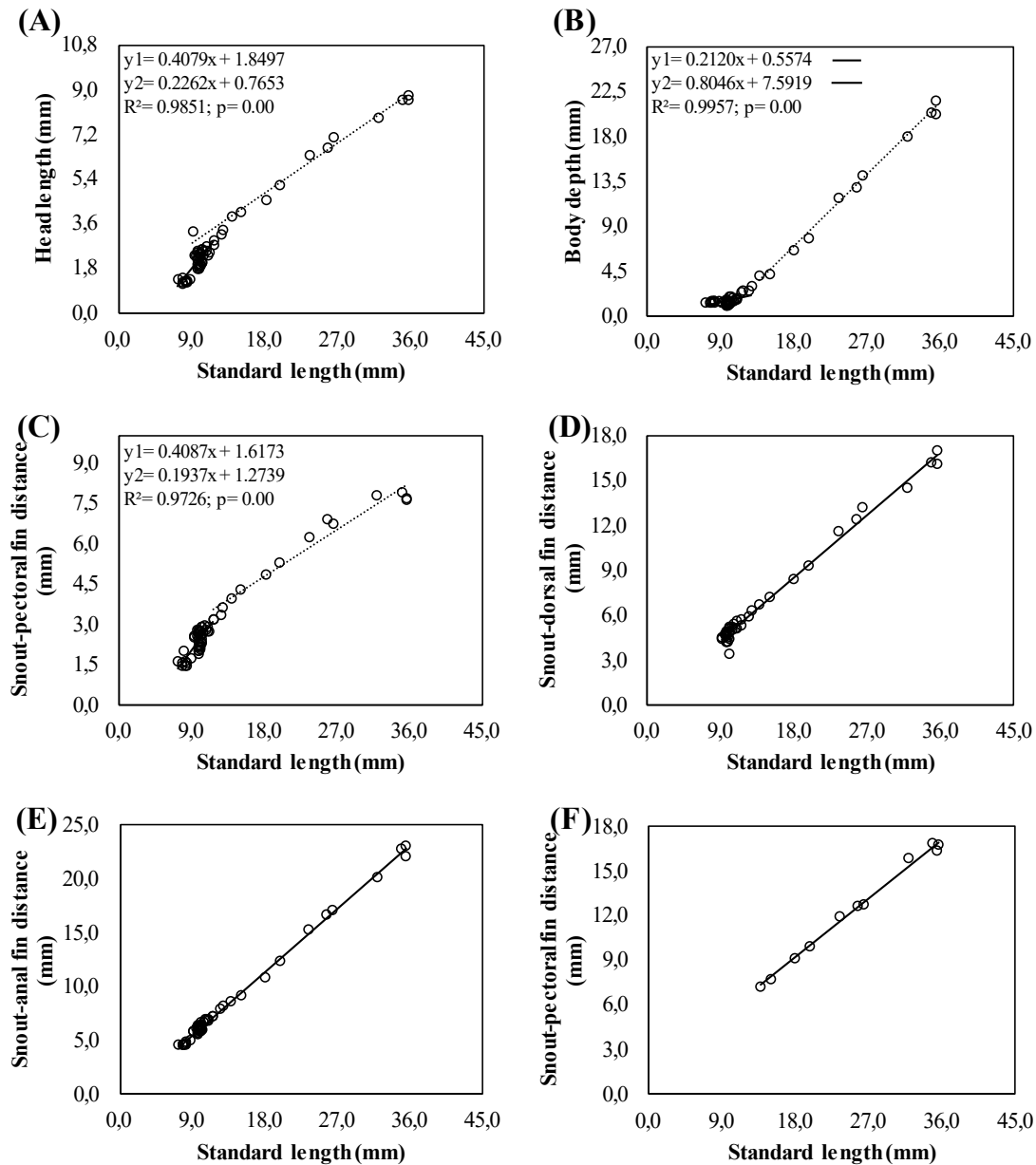
The snout length and head depth showed discontinuous isometric development (piecewise linear regression). This indicates that the snout and head deep initially grow at the same rate as head length. An abrupt change in the growth of these variables occurred during the transition between flexion and postflexion stages (breakpoint = 0.68 mm and 2.91 mm, respectively) (Table 2). After this breakpoint, the snout and head depth increased their growth rate. Eye diameter showed continuous isometric growth (simple linear regression), growing at the same rate as the head. Body depth and distance from the snout to the pectoral fin showed a discontinuous isometric growth (piecewise regression; breakpoint = 3.05 mm and 3.16 mm. respectively) (Table 2; Fig. 3). After the breakpoint, the head and distance from the snout to the pectoral fin growth rate decreased, while the body deep increased in the flexion stage. The distances from the snout to dorsal, anal, and pelvic fins showed continuous isometric growth (simple linear regression) (Fig. 4).

**Table 2.** Mathematical and statistical values of linear (L), quadratic (Q) and piecewise linear (S) regressions for morphometric variables obtained in relation to head length and standard length in larvae and juveniles of *Myloplus rubripinnis*. **R<sup>2</sup>**. Coefficient of determination; **BM**. Best model; **BP**. Breakpoint in the dependent variable; **L**. Simple linear regression; **Q**. Quadratic Regression; **S**. Piecewise regression; **N**. Number of individuals; **p**. significance value. Note =Values in bold showed p <0.05.

Body growth of <i>Myloplus rubripinnis</i>												
Variables	R <sup>2</sup> <sub>L</sub>	R <sup>2</sup> <sub>Q</sub>	R <sup>2</sup> <sub>S</sub>	F <sub>Q/L</sub>	p	F <sub>S/Q</sub>	p	F <sub>S/L</sub>	p	BM	BP	N
SNL/HL	0.95	0.96	0.97	<b>14.21</b>	0.00	<b>5.77</b>	0.00	<b>10.66</b>	0.00	S	0.68	55
ED/HL	0.98	0.98	0.99	0.00	1.00	<b>4.59</b>	0.03	2.29	0.13	L	-	55
HD/HL	0.96	0.99	0.99	<b>184.04</b>	0.00	<b>21.43</b>	0.00	<b>139.61</b>	0.00	S	2.91	55
HL/SL	0.96	0.97	0.98	<b>24.47</b>	0.00	<b>24.76</b>	0.00	<b>30.32</b>	0.00	S	3.05	55
BD/SL	0.98	0.99	0.99	<b>37.33</b>	0.00	<b>63.58</b>	0.00	<b>73.36</b>	0.00	S	3.79	55
SnP/SL	0.94	0.98	0.97	<b>79.21</b>	0.00	<b>-14.00</b>	0.00	<b>20.95</b>	0.00	S	3.16	55
SnD/SL	0.98	0.98	0.99	-1.41	0.62	3.14	0.08	0.82	0.36	L	-	41
SnA/SL	0.99	0.99	0.99	1.54	0.21	1.71	0.20	1.64	0.20	L	-	55
SnV/SL	0.99	0.99	0.99	1.56	0.25	-0.19	0.67	0.55	0.48	L	-	11



**Figure 3.** Body relationships (mm) of head length to **A.** snout length, **B.** head depth, and **C.** eye diameter during early development of *Myloplus rubripinnis*.



**Figure 4.** Body ratios (mm) between standard length and head length **A.** body deep **B.** distance from the snout to pectoral fin **C.** distance from the snout to dorsal fin **D.** distance from the snout to anal fin **E.** and distance from the snout to pelvic fin **F.** during early development of *Myloplus rubripinnis*.

## DISCUSSION

Our study provides the first description of the main external morphological events and meristic and morphometric data that occur during the initial development of *M. rubripinnis* and establishes a reference for their correct identification during the larval and juvenile periods. The occurrence of different intervals in the process of

morphological development and growth of *M. rubripinnis* is directly related with the requirements for survival and adaptation ability in different periods of the initial life history. However, each step is characterized by sequential changes in size, morphology, ecological habit, and relationship with the environment, and therefore, they seek to reach functional thresholds through the sequence of formation of elements, structures, and organs of the systems (Solomon *et al.*, 2017; Moteki *et al.*, 2017). Understanding these factors is essential to elucidate the functional and behavioral modifications of the species.

*Myloplus rubripinnis* larvae have a altricial development, poorly developed, with incomplete functional systems, partially pigmented eyes, large amount of endogenous yolk reserves, finfold covering the entire body, with non-functional mouth and anus, as with most freshwater teleost larval species (Santos *et al.*, 2016; Santos *et al.*, 2020; Lima *et al.*, 2021; Santos *et al.*, 2022b).

When compared to other Serrasalminidae larvae *Myloplus rubripinnis* have relatively tall and wide finfold (Nakatani *et al.*, 2001; Santos *et al.*, 2022b). The finfold plays an important role in breathing (Van Den Boogaart *et al.*, 2012) and on the ability of individuals to move, especially during drift in the intermediate flow regime between river systems and growth areas (Muller *et al.*, 2004; Pavlov *et al.*, 2008; Van Leeuwen *et al.*, 2015). This involves a behavioral component and a functional explanation for the presence of this structure which is gradually absorbed and replaced by caudal, dorsal, and anal fins throughout development (Li *et al.*, 2016).

The low number of larvae of *M. rubripinnis* at the yolk-sac stage analyzed was due to the difficulty of capturing this stage in the natural environment, probably because most of these yolk-sac larvae are far from the surface of the water. Through the experimental spawning from wild *M. rubripinnis* breeders induced in captivity on the banks of the Xingu River, it was observed that the eggs are demersal and in the first post-hatching moments the larvae remain close to the substrate (unpublish data). Only a few days later (3 to 4 days), the larvae begin to occupy the most superficial strata of the water column, being able to be collected by plankton nets. This behavior may be a strategy used by the species that seems to have seasonal spawning, releasing a low number of eggs (300 to 400 eggs) with restricted perivitelline space (personal observation). These characteristics are common to species whose reproduction is associated with lentic and semi-lentic environments (Sato *et al.*, 2003). They can be deposited at the bottom of

rivers or reservoirs and allow the larvae access to higher concentrations of food and consequently, faster initial growth rates (Rizzo & Bazzoli, 2020).

The yolk-sac larvae of *M. rubripinnis* are, comparatively, larger and more robust (> 40%) than the larvae of *Mylossoma* (Serrasalminidae) found drifting in the channel of whitewater rivers in the preflexion stage (Araújo-Lima *et al.*, 1993). Our results show the morphological and morphometric difference in development between species belonging to the same family. However, the analyzed specimens share characteristics similar to other *Myloplus* such as terminal mouth, intestine reaching the median region of the body, initially fusiform and elongated body that becomes deep and laterally compressed with a lozenge shape in more developed stages, vertical bands of dense melanophores and brownish on the side of the body, in addition to a small horizontal stripe extending from the snout to the eye and the presence of a ventral keel with small spines (Ponton & Mérioux, 2001; Orsi *et al.*, 2016; Oliveira *et al.*, 2022).

Early larvae of *M. rubripinnis* have only a linear band of internal pigments along the body, located on the notochord and scattered spots in the yolk region. In this case, although the pigmentation intensifies throughout development, they differ from the pattern described in larvae of *Mylossoma* (Araújo-Lima *et al.*, 1993), *Piaractus* (Santos *et al.*, 2022a), *Serrasalmus* (Nakatani *et al.*, 2001) and other species of *Myloplus* as observed by Oliveira *et al.* (2022). The most notable difference between *M. rubripinnis*, *M. asterias* and *M. lobatus* is in the pigmentation pattern, *Myloplus asterias* has densely pigmented spots scattered along the body, while *M. lobatus* and *M. rubripinnis* have a brindle phenotype, characterized by vertically elongated irregular dark spots of melanophores, but the pattern is distinguished between the two species in terms of shape, quantity, color, and distribution in the body.

The well-defined pigmentation in the first larval stages of *M. rubripinnis* differs from that found in other species of the Serrasalminidae family, such as *P. brachypomus*, *M. aureum* and *M. albiscopum* (Santos *et al.*, 2022a; Araújo-Lima, 1993), however it is similar to that observed for species of the genus *Myloplus* (Oliveira *et al.*, 2022; Garcia *et al.*, 2016; Ponton & Merigoux, 2001). This indicates camouflage mechanisms associated with the environment that these species colonize in the early stages of life.

For example, initially, the first species are essentially pelagic and transparent (Zacardi *et al.*, 2020) the pigmentation in this period represents an adaptive camouflage strategy in the water column and avoids attracting the attention of visual predators (Sanches *et al.*, 2001; Cajado *et al.*, 2021). While *Myloplus* larvae are associated with lentic and



structured sites with the presence of vegetation, where pigmentation is essential to mimic the environment and avoid visual predators (Oliveira *et al.*, 2022).

In general, *M. rubripinnis* present a clear ecological transition between the larval and juvenile period, similar to that found in several Amazonian species with a pelagic larval phase (drifting) and, later, colonization of structured environments (aquatic vegetation) (Araújo-Lima *et al.*, 1993; Zacardi *et al.*, 2020; Cajado *et al.*, 2018, 2021). This transition between development periods is called recruitment in ecology and is associated with the metamorphosis of larvae into juveniles and has a direct implication on the fitness of the species. This can be considered critical in the adaptation of individuals, allowing crucial processes of maturation and acquisition of functional and sensory skills to colonize suitable habitats for food and refuges against predators (Sánchez-Botero & Araújo-Lima. 2001; Pinheiro *et al.*, 2016; Oliveira *et al.*, 2020). reflecting the lifestyle and feeding strategies of the *M. rubripinnis*.

Larvae are divided into ontogenetic developmental stages corresponding to the developmental sequence of the fins, their supporting elements and other characteristics (Ahlstrom *et al.*, 1976; Nakatani *et al.*, 2001; Kelso *et al.*, 2012). However, *M. rubripinnis* does not present the preflexion stage, passing from yolk-sac larvae stage into flexion stage, with the formation of the caudal fin and the appearance of the hypural bones, still with significant endogenous reserve. This process together with the establishment of eye pigmentation, mouth opening and swim bladder inflation, implies the need for individuals to increase visual performance, as well as active swimming ability and propulsion. In addition, it favors the larvae to move vertically and horizontally, exploring the pelagic zone (niche alteration), in addition to maximizing success in capturing prey during the beginning of mixed and exogenous feeding (Fuiman & Magurran. 1994).

On the other hand, the presence of larvae with a large and lasting yolk sac (endo-exogenous feeding) can be a compensatory alternative for possible deficits or difficulties faced during exogenous feeding (Fiala & Spurny, 2001; Nowosad *et al.*, 2021) and reflects a high parental investment in offspring by *M. rubripinnis*. This strategy seems to ensure the maintenance of adequate development of internal and skeletal organs, indicating a trade-off in growth and a longer window of time to start exogenous feeding, optimizing the potential for survival in the natural environment during this larval stage (Stephen *et al.*, 2007). Especially when the availability of food can be sporadic due to the low amount of nutrients in clear water rivers, with low

sediment content and high transparency (Junk *et al.*, 2011; Gregory-Bogotá *et al.*, 2020).

The early formation of caudal-fin structures in *M. rubripinnis* larvae enables accelerated swimming, reducing the risk of predation and several other performance criteria (Van Leeuwen *et al.*, 2015), even if their maneuverability is limited due to the absence of paired fins. The development of swimming performance and high propulsive movements require prepared and optimized muscles, therefore, they require intensive mass gain (Rome, 2006). This may explain the rapid axial muscular development observed in *M. rubripinnis* larvae. Also, in the flexion stage, the digestive tract, which was initially straight, now presents a torsion of the stomach and separation of the intestine into a middle and posterior portion. This fact may be associated with increasing nutritional requirement and subsequent search for new food items (Taguti *et al.*, 2009; Santos *et al.*, 2020).

*Myloplus rubripinnis* larvae began the postflexion stage when the posterior portion of the notochord completes its flexion, pelvic fin buds appear, the embryonic membrane disappears, dorsal and anal fin rays establish, and the caudal fin becomes forked. At this stage of development, swimming actions are more constant and stable, which is necessary after the depletion of energy reserves in the yolk sac, since the larvae are now totally dependent on external food and require more efficient skills for foraging (Solomon *et al.*, 2017). Fin development corresponds to the needs of functional and ecological changes, optimizing several essential swimming and feeding actions, such as exploration of the environment, capture of prey and avoidance of predators, as indicated by Potthoff & Tellock (1993). This transition on the ontogenetic priorities, changes in behavior and way of life is one of the factors that ensures adaptability at each stage and an increase in the probability of larval survival (Osse & Van Den Boogaart, 2004; Peña & Dumas, 2009; Zhao *et al.*, 2020).

Changes in the formation and structure of the fins were accompanied by an increase in the pre-anal and pre-pectoral distance, with a decrease in the pre-ventral distance, and it coincides with the transformation of the body from long to moderate and deep in juvenile, becoming compressed laterally. These changes are considered common to serrasalmids (Makrakis *et al.*, 1997; Nakatani *et al.*, 2001; Santos *et al.*, 2022a). The complete formation of the pectoral fins only at the end of the initial ontogeny suggests that their use, mainly in species with a compressed body and pelagic habit, is not limited only as swimming stabilizers (balance), but to agility (maneuverability) and

displacement in places with great availability of shelters by roots and trees (Santos, 2017). This represents the changes in fish locomotor performance as a function of different environmental characteristics.

After the structural completion of the fins, individuals reach juvenile stage and begin to present the complete number of rays. although there are individual variations in the counts. Anyway, the incompatibility between fin ray numbers may be related to non-monophyly between species, as discussed by Oliveira *et al.* (2022). The sequence of appearance of fin rays in *M. rubripinnis* was caudal, dorsal, anal, pelvic, and pectoral, a basic pattern found for this group of fish (Nakatani *et al.*, 2001; Oliveira *et al.*, 2022; Santos *et al.*, 2022a).

For *M. rubripinnis*. the total number of myomeres (41 to 42 segments) corresponds to the number of vertebrae in adult individuals and represents a fundamental character to differentiate the species from other congeners such as *M. asterias* (37 to 38 myomeres), *M. schomburgkii* (37 myomeres), and *M. arnoldi* (34 myomeres) in early stages. Furthermore, the combination with the number of rays (branched and unbranched) present in the dorsal fin can be considered important elements to distinguish congeners from the Amazon basin in more advanced stages, see Table 3.

**Table 3.** Meristic data for some of the *Myloplus* species occurring in the Amazon basin based on Andrade *et al.* (2016a) and Oliveira *et al.* (2022). \*estimated number based on the total number of vertebrae and \*\*myomeres.

Meristic data	Some species of <i>Myloplus</i> from Amazon basin					
	<i>M. asterias</i>	<i>M. lobatus</i>	<i>M. arnoldi</i>	<i>M. rubripinnis</i>	<i>M. schomburgkii</i>	<i>M. torquatus</i>
Myomeres	37-38	40-41	34*	40-42	37*	37*
Vertebrae	36-37	39-40	38	39-40	36	36
Dorsal rays	iii-iv, 24-30	iii-iv, 19-23	iii, 21-24	iii, 19-25	iii, 18-23	iii, 24-25
Anal rays	iii, 30-37	iii, 31-35	iii, 29-31	iii, 30-36	iii, 29-35	iii, 30-37
Pectoral rays	i, 11-15	i, 12-15	ND	i, 10-15	i, 13-15	i, 12-15
Pelvic rays	i, 6-7	i, 5-7	ND	i, 5-7	i, 6-7	i, 6-7

Our study shows that the morphometric growth pattern of *M. rubripinnis* exhibits strong changes in the flexion to postflexion stages. It includes an initial phase of growth stagnation with low variation in the morphological characteristics of snout length and head deep, which can be attributed to lower dependence, in early ontogeny, on the central nervous system, sense organs, and structures related to food capture. The delay

or decrease of morphometric and growth relationships acts as a response to functional requirements (Kováč *et al.*, 1999; Oliveira *et al.*, 2020; Cajado *et al.*, 2021). While, in later developmental stages, the increased variation in head and body size parameters found in *M. rubripinnis* larvae, suggests a driving force to potentiate the acquired skills for swimming and prey capture, synergistically decrease predation-based mortality (Franz *et al.*, 2021). This indicates that body changes and proportions are related to bioecological adaptations, as observed for other Characiformes (Bialetzki *et al.*, 2008; Taguti *et al.*, 2009; Santos *et al.*, 2020; Cajado *et al.*, 2021).

Information on *M. rubripinnis* growth patterns strengthen the hypothesis of growth priorities in which the most essential organs develop first, followed by those of lower priority for survival.

These findings provide a basis for determining the complete ontogeny of *M. rubripinnis*. This information will be able to help in the correct identification of *M. rubripinnis* larvae in a natural environment and help in studies to monitor the ichthyofauna, essential for monitoring population fluctuations of larvae and juveniles of this species along the Xingu River basin, under strong anthropic influence.

#### ACKNOWLEDGEMENTS

The authors would like to thank the colleagues from the Laboratório de Ecologia do Ictioplâncton e Pesca em Águas Interiores (<https://leipaiufopa.com>) of Universidade Federal do Oeste do Pará for their assistance in the sorting and identification of the biological material used in this study. This study is part of the Master Thesis of the first author (ECP) at the Programa de Pós-Graduação em Biodiversidade e Conservação of Universidade Federal do Pará. We are grateful to Norte Energia S/A for the Research and Development Project ANEEL (P&D-07427-0121/2020) and to Universidade Federal do Pará. We are especially grateful to Zaqueu Santos for scientific illustrations.

#### REFERENCES

Ahlstrom EH, Moser HG. Eggs and larvae of fishes and their role in systematic investigation and in fisheries. *Rev Trav Inst Peches Marit.* 1976; 40(3-4):379-98. Available from: <https://archimer.ifremer.fr/doc/00000/1996/>

Ahlstrom EH, Butler JL, Sumida BY. Pelagic stromateoid fishes (Pisces. Perciformes) of the eastern Pacific: kinds, distributions, and early life histories and observations on five of these from the northwest Atlantic. *Bull Mar Sci.* 1976; 26(3):285-402.

Andrade MC, Jégu M, Gama CS. A new species of *Myloplus* Gill (Characiformes: Serrasalminidae) from the Tumucumaque Mountain Range, Brazil and French Guiana, with comments on *M. rubripinnis*. *Zootaxa.* 2018; 4403(1):111-22. <https://doi.org/10.11646/zootaxa.4403.1.6>

Andrade MC, Jégu M, Giarrizzo T. A new large species of *Myloplus* (Characiformes: Serrasalminidae) from the Rio Madeira basin, Brazil. *ZooKeys.* 2016b. 571:153-67. <https://doi.org/10.3897/zookeys.571.5983>

Andrade MC, Jégu M, Giarrizzo T. *Tometes kranponhah* and *Tometes ancylorhynchus* (Characiformes: Serrasalminidae), two new phytophagous serrasalmids, and the first *Tometes* species described from the Brazilian Shield. *J Fish Biol.* 2016c; 89(1):467-94. <https://doi.org/10.1111/jfb.12868>

Andrade MC, Ota RP, Bastos DA, Jégu M. A new large *Myloplus* Gill 1896 from River Negro basin Brazilian Amazon (Characiformes: Serrasalminidae). *Zootaxa.* 2016a; 4205(6):571-80. <http://doi.org/10.11646/zootaxa.4205.6.5>

Arantes CC, Winemiller KO, Petrere M, Castello L, Hess LL, Freitas CE. Relationships between forest cover and fish diversity in the Amazon River floodplain. *Journal of Applied Ecology.* 2018; 55: 386-395. <https://onlinelibrary.wiley.com/doi/10.1111/1365-2664.12967>

Araújo-Lima CARM, Donald E. Número de vértebras de Characiformes do rio Amazonas e seu uso na identificação de larvas do grupo. *Acta Amazon.* 1988; 18:351-58. <https://doi.org/10.1590/1809-43921988182358>

Araújo-Lima CARM, Kirovsky AL, Marca AG. As larvas dos pacus *Mylossoma* spp. (Teleostei; Characidae) da Amazônia Central. *Rev Bras Biol.* 1993; 53(2):591-600.

Beltrão H, Magalhães ERS, Yamamoto KC. Ictiofauna da Floresta Nacional (FLONA) do Amaná. uma área de interflúvio Tapajós/Madeira (Estado do Pará). ameaçada por garimpos de mineração. Boletim Sociedade Brasileira de Ictiologia. 2016; 117: 15-27.

Bialetzki A, Baumgartner G, Sanches PV, Galuch AV, Luvisuto MA, Nakatani K *et al.* Caracterização do desenvolvimento inicial de *Auchenipterus osteomystax* (Osteichthyes, Auchenipteridae) da bacia do rio Paraná, Brasil. Acta Sci Biol Sci. 2001; 23:377-82. <https://doi.org/10.4025/actasciv23i0.2692>

Bialetzki A, Nakatani K, Sanches PV, Baumgartner G, Makrakis MC, Taguti TL. Desenvolvimento inicial de *Hoplias* aff. *malabaricus* (Bloch, 1794) (Osteichthyes, Erythrinidae) da planície alagável do alto rio Paraná. Brasil. Acta Sci Biol Sci. 2008; 30:141-49. <https://doi.org/10.4025/actascibiols. v30i2.3608>

Blaxter JHS. Pattern and variety in development. In: Hoar. W.S.; Randall. D.J. (Ed.). Fish physiology. London: Academic Press. 1988; 11:1-58.

Bogotá-Gregory JD, Lima FCT, Correa SB *et al.* Biogeochemical water type influences community composition, species richness, and biomass in megadiverse Amazonian fish assemblages. Scientific Reports. 2020; 20(1):15349. <https://doi.org/10.1038/s41598-020-72349-0>

Borges MEE, Nakatani K, Bialetzki A, Felis MEG. Diferenciação do número de vértebras de algumas espécies de Characiformes (Osteichthyes) da bacia do Rio Paraná, Brasil. Acta Sci Biol Sci. 2000; 22(2):539-544.

Cajado RA, Oliveira LS, Silva FKS, Zacardi DM, Andrade MC. Effects of anomalous climatic events on the structure of fish larvae assemblages in the eastern Amazon. Front Environ Sci. 2022; 10:1064170. <https://doi:10.3389/fenvs.2022.1064170>

Cajado RA, Oliveira LS, Silva FKS, Zacardi DM. Early development of the Neotropical fish known as long sardine *Triportheus auritus* (Valenciennes, 1850) (Characiformes, Triporthidae). J Appl Ichthyol. 2021; 37(5):759-69. <https://doi.org/10.1111/jai.14228>

Coimbra AB, Terra AK, Mazurek RRS, Pereira HS, Beltrão H, Sousa RGC. Fishing activity of the Mura Indians on Lake Ayapuá, Lower Purus River, Brazil. *Revista Desafios*. 2017; 4(1):115-129.

Cruz PR, Affonso IP, Gomes LC. Ecologia do ictioplâncton: Uma abordagem cienciométrica. *Oecol Aust*. 2016;20(4):436-50. <https://doi.org/10.4257/oeco.2016.2004.04>

Faber DJ, Gadd S. Several drawing techniques to illustrate larval fishes. *Transactions of the American Fisheries Society*. 1983; 112: 349-353.

Fiala J, Spurny P. Intensive rearing of the common barbel (*Barbus barbus*) larvae using dry starter feeds and natural diet under controlled conditions. *Czech Journal of Animal Science-UZPI (Czech Republic)*. 2001; 320-326.

Franz GP, Lewerentz L, Grunow B. Observations of growth changes during the embryonic-larval-transition of pikeperch (*Sander lucioperca*) under near-natural conditions. *J Fish Biol*. 2021;99(2):425-436. <https://doi.org/10.1111/jfb.14734>

Fricke R, Eschmeyer WN, Fong JD. Eschmeyer's catalog of fishes: species by family/subfamily [Internet]. San Francisco: California Academy of Science; 2023. Available from: <http://researcharchive.calacademy.org/research/ichthyology/catalog/SpecieByFamily.asp>

Fricke R, Eschmeyer WN, Van Der Laan R. Eschmeyer's Catalog of Fishes: genera, Species [Internet]. San Francisco: California Academy of Science; 2023. Available from: <http://researcharchive.calacademy.org/research/ichthyology/catalog/SpecieByFamily.asp>. Acessado em 04/03/2023.

Fuiman LA, Magurran AE. Development of predator defences in fishes. *Rev Fish Biol Fish*. 1994; 4:145-183. <https://doi:10.1007/BF00044127>

Garcia DAZ, Claro-Garcia A, Costa ADA, Bialetzki A, Casimiro ACR, Swarça AC *et al*. Composição ictiofaunística e desenvolvimento inicial das espécies. In: Orsi ML, Almeida FS, Swarça AC, Claro-Garcia A, Vianna NC, Garcia DAZ *et al.*, editors. Ovos, larvas e

juvenis dos peixes da Bacia do Rio Paranapanema: uma avaliação para a conservação. 1st ed. Assis: Triunfal Gráfica e Editora; 2016.

Isaac VJ, Almeida MCD, Cruz REA, Nunes LG. Artisanal fisheries of the Xingu River basin in Brazilian Amazon. *Brazilian Journal of Biology*; 2015; 75: 125-137.

Jégu M. Subfamília Serrasalminae (Pacus and Piranhas). In: Reis RE, Kullander SO, Ferraris CJJ, editors. Check list of the freshwater fishes of South and Central America. Porto Alegre: Edipucrs; 2003. p.182-96.

Junk WJ, Piedade MTF, Schöngart. J, Cohn-Haft M, Adeney J M, Wittmann FA. Classification of major naturally occurring Amazonian lowland wetlands. *Wetlands*. 2011;31: 623-640. <https://doi.org/10.1007/s13157-011-0190-7>

Kelso WE, Kaller MD, Rutherford DA. Collecting, processing, and identification of fish eggs and larvae and zooplankton. *Fisheries techniques*. 2012; 363-451.

Keppeler FW, Andrade MC, Trindade PA, Sousa LM, Arantes CC, Winemiller KO *et al.* Early impacts of the largest Amazonian hydropower Project on fish communities. *Science of The Total Environment*. 2022; 838; 155951. <http://doi.org/10.1016/j.scitotenv.2022.155951>

Kolmann MA, Hughes LC, Hernandez LP, Arcila D, Betancur R, Sabaj MH *et al.* Phylogenomics of piranhas and pacus (Serrasalminidae) uncovers how convergent diets obfuscate traditional morphological taxonomy. *Syst Biol*. 2020; 70(3):576-92. <https://doi.org/10.1093/sysbio/syaa065>

Kováč V, Copp GH, Francis MP. Morphometry of the stone loach, *Barbatula barbatula*: Do mensural characters reflect the species' life history thresholds? *Environ Biol Fish*. 1999; 56:105-115. <https://doi.org/10.1023/A:1007570716690>

Latrubesse EM, D'Horta FM, Ribas CC, Wittmann F, Zuanon J, Park E *et al.* Vulnerability of the biota in riverine and seasonally flooded habitats to damming of Amazonian rivers. *Aquat Conserv: Mar Freshwater Ecosyst*. 2020; 31(5):1136–1149. <https://onlinelibrary.wiley.com/doi/10.1002/aqc.3424>



Leis JM, Trnski T. The larvae of Indo-Pacific shorefishes. Honolulu: University of Hawaii Press; 1989.

Li G, Muller UK, Van Leeuwen JL, Liu H. Fish larvae exploit edge vortices along their dorsal and ventral fin folds to propel themselves. *J. R. Soc. Interface.* 2016; 13(116): 20160068. <http://dx.doi.org/10.1098/rsif.2016.0068>

Lima DLG, Cajado RA, Silva LVF, Maia JLS, Zacardi DM. Descrição morfológica do desenvolvimento inicial de *Brycon amazonicus* (Characiformes, Bryconidae) do Baixo Amazonas, Pará. *Biota Amaz.* 2021; 11(1):60-67.

Liu X, Jiang J, Li C, Bai X, Ma L, Liu K. Two complete mitochondrial genomes of *Myloplus rubripinnis* and *Metynnis hypsauchen* (Characiforme, Serrasalminidae). *Mitochondrial DNA Part B.* 2019; 4(2): 3874-3875.

Machado VN, Collins RA, Ota RP, Andrade MC, Farias IP, Hrbek T. One thousand DNA barcodes of piranhas and pacus reveal geographic structure and unrecognised diversity in the Amazon. *Sci Rep.* 2018; 8:8387. <https://doi.org/10.1038/s41598-018-26550-x>

Mateussi NTB, Oliveira C, Pavanelli CS. Taxonomic revision of the Cis-Andean species of *Mylossoma Eigenmann & Kennedy, 1903* (Teleostei: Characiformes: Serrasalminidae). *Zootaxa.* 2018; 4387(2):275-309. <https://doi.org/10.11646/zootaxa.4387.2.3>

Moteki M, Tsujimura E, Hulley PA. Developmental intervals during the larval and juvenile stages of the Antarctic myctophid fish *Electrona antarctica* in relation to changes in feeding and swimming functions. *Polar Science.* 2017;12:88-98.

Müller UK, Van Leeuwen JL. Swimming of larval zebrafish: ontogeny of body waves and implications for locomotory development. *J Exp Biol.* 2004;207(5):853-868. <https://doi:10.1242/jeb.00821>

Nakatani K, Agostinho AA, Bialecki A, Baumgartner G, Sanches PV, Makrakis M *et al.* Ovos e larvas de peixes de água doce: desenvolvimento e manual de identificação. Maringá: EDUEM; 2001.

Nakatani K, Baumgartner RG, Cavicchioli M. Ecologia de ovos e larvas de peixes. In: Vazzoler AEAM, Agostinho AA, Hahn NS, editors. A planície de inundação do alto rio Paraná: aspectos físicos, biológicos e econômicos. Maringá: EDUEM;1997; p.281-306.

Nico LG, Jégu M, Andrade MC. Family Serrasalminidae - Piranhas and Pacus. In: Van der Sleen P, Albert JS, editors. Field guide to the fishes of the Amazon, Orinoco, and Guianas (Princeton Field Guides). Princeton: Princeton University Press; 2018. p.172–96.

Nowosad J, Kupren K, Biegaj M, Kucharczyk D. Allometric and ontogenetic larval development of common barbel during rearing under optimal conditions. *Animal*; 2021; 2:100107. <https://doi.org/10.1016/j.animal.2020.100107>

Ohara WM, Lima FCT, Salvador GN, Andrade MC. Peixes do rio Teles Pires: diversidade e guia de diversidade e identificação. Goiânia: Gráfica e Editora Amazonas; 2017.

Oliveira CC, Suzuki MAL, Oliveira LS, Zacardi DM. Description of the initial development and temporal distribution of *Microphilypnus tapajosensis* larvae and juveniles in a reservoir in the Eastern Amazon. *Cienc Nat*. 2020; 42-49. <https://doi.org/10.5902/2179460X41542>

Oliveira FG, Bialez A, Gomes L C, Santin M, Taguti T. Desenvolvimento larval de *Brycon hilarii* (Characiformes. Characidae). *Lheringia. Ser Zool*. 2012;102(1):62-70. <https://doi.org/10.1590/S0073-47212012000100009>

Oliveira LS, Cajado RA, Silva FKS, Andrade MC, Zacardi DM. Early development of two commercially valuable fish from the lower Amazon River, Brazil (Characiformes: Serrasalminidae). *Neotrop Ichthyol*; 2022; 20(1):e210024. <https://doi.org/10.1590/1982-0224-2021-0024>

Orsi ML, Almeida FS, Swarça AC, Claro-Garcia A, Vianna NC, Garcia DAZ *et al*. Ovos, larvas e juvenis dos peixes da Bacia do Rio Paranapanema: uma avaliação para a conservação. Triunfal Gráfica e Editora. Duke Energy: Assis-SP. 2016.

Ortí G, Sivasundar A, Dietz K, Jégu M. Phylogeny of the Serrasalminidae (Characiformes) based on mitochondrial DNA sequences. *Genet Mol Biol*. 2008; 31:343-51. <https://doi.org/10.1590/S1415-47572008000200030>

Osse JWM, Van Den Boogaart JGM. Allometric growth in fish larvae: timing and function. In: Govoni JJ, editor. The development of form and function in fishes and the question of larval adaptation. Bethesda: American Fisheries Society Symposium; 2004. p.167-94.

Osse JWM, Van Den Boogaart JGM. Dynamic morphology of fish larvae, structural implications of friction forces in swimming. feeding and ventilation. J Fish Biol. 1999; 55:156-74. <https://doi.org/10.1006/jfbi.1999.1071>

Ota RP, Machado VN, Andrade MC, Collins RA, Farias IP, Hrbek T. Integrative taxonomy reveals a new species of pacu (Characiformes: Serrasalminidae: *Myloplus*) from the Brazilian Amazon. Neotrop Ichthyol. 2020; 18:e190112. <https://doi.org/10.1590/1982-0224-20190112>

Pavlov D, Mikheev V, Lupandin A, Skorobogatov M. Ecological and behavioural influences on juvenile fish migrations in regulated rivers: a review of experimental and field studies. Hydrobiologia. 2008; 609. 125-138. <https://doi.org/10.1007/s10750-008-9396>

Peña R, Dumas S. Development and allometric growth patterns during early larval stages of the spotted sand bass *Paralabrax maculatofasciatus* (Percoidei: Serranidae). Scientia Marina. 2009; 73(S1):183-189.

Pinheiro DT, Corrêa JMS, Chaves CS, Campos DPF. Diversidade e distribuição da ictiofauna associada a bancos de macrófitas aquáticas de um lago de inundação amazônico estado do Pará, Brasil. Acta of Fisheries and Aquatic Resources. 2016; 4(2): 59-70.

Ponton D, Mérigoux S. Description and ecology of some early life stages of fishes in the River Sinnamary (French Guiana. South America). Folia Zool; 2001; 50: 1-116.

Potthoff T, Tellock JA. Osteological development of the snook. *Centropomus undecimalis* (Teleostei: Centropomidae). Bulletin of Marine Science.1993; 52(2): 669-716.

Reynalte-Tataje DA, Lopes CA, Massaro MV, Hartmann PB, Sulzbacher R, Santos JA *et al.* State of the art of identification of eggs and larvae of freshwater fish in Brazil. *Acta Limnol Bras.*2020; 32: e6. <https://doi.org/10.1590/s2179-975x5319>

Rizzo E, Bazzoli N. Reproduction and embryogenesis. In: *Biology and physiology of freshwater neotropical fish.* Academic Press. 2020; 287-313. <https://doi.org/10.1016/B978-0-12-815872-2.00013-0>

Rome LC. Design and function of superfast muscles: new insights into the physiology of skeletal muscle. *Annu Rev Physiol.* 2006; 68: 193-221. <https://doi.org/10.1146/annurev.physiol.68.040104.105418>

Röpke C, Pires TH, Zuchi N, Zuanon J, Amadio S. Effects of climate-driven hydrological changes in the reproduction of Amazonian floodplain fishes. *Journal of Applied Ecology*; 2022; 59(4): 1134–1145. <https://doi.org/10.1111/1365-2664.14126>

Sánchez-Botero JI, Araujo-Lima CARM. As macrófitas aquáticas como berçário para a ictiofauna da várzea do rio Amazonas. *Acta Amazonica.* 2001;31(3):437-447. <https://doi.org/10.1590/1809-43922001313447>

Santos GM, Ferreira EJG, Zuanon JAS. Peixes comerciais de Manaus. Editora INPA. IBAMA. PróVárzea. 2006.

Santos JA, Soares CM, Bialezki A. Early ontogeny of yellowtail tetra fish *Astyanax lacustris* (Characiformes: Characidae). *Aquac Res.* 2020;51(10):4030-4042. <https://doi.org/10.1111/are.14746>

Santos JE, Sales NG, Santos ML, Arantes FB, Godinho HP. Early larvae ontogeny of the Neotropical fishes: *Prochilodus costatus* and *P. argenteus* (Characiformes: Prochilodontidae). *Rev Biol Trop.* 2016; 64:537-46. <https://doi.org/10.15517/rbt.v64i2.19052>

Santos LA, Oliveira EC, Oliveira LS, Zacardi DM. Larval Development of *Boulengerella cuvieri* (Characiformes: Ctenoluciidae) in the Middle Tapajós River. Eastern Amazon. Brazil. *Int J Zool Animal Biol.* 2022b; 5(6): 000411

Santos LL. Relações atributos ecomorfológicos - variáveis ambientais em assembleias de peixes de riachos amazônicos. Dissertação apresentada ao Programa de Pós-Graduação em Ecologia Aquática e Pesca da Universidade Federal do Pará. 58p. 2017.

Santos Z, Oliveira LS, Cajado RA, Silva FKS, Silva LV, Zacardi DM. Early ontogeny of the commercially valuable fish red-bellied pacu *Piaractus brachypomus* (Characiformes. Serrasalminidae) from the Amazon. Brazil. J Fish Biol. 2022;102(1):214-224. <https://doi.org/10.1111/jfb.15253>

Sato Y, Fenerich-Verani N, Nuñez APO, Godinho HP, Verani JR. Padrões reprodutivos de peixes da bacia do São Francisco. In: GODINHO HP, GODINHO AL editors. Águas. peixes e pescadores do São Francisco das Minas Gerais. Belo Horizonte. PUC Minas. 2003: p. 229-274.

Shibatta OA. Introdução à ilustração de peixes 3: Arte finalização em preto e branco com o uso da técnica do pontilhismo. Boletim Sociedade Brasileira de Ictiologia. 2016a: 119: 12-17.

Shibatta OA. Introdução à ilustração de peixes 5: Desenho de larvas de peixes com auxílio de microscópio estereoscópio com câmera clara. Boletim Sociedade Brasileira de Ictiologia. 2017b; 121:20-27.

Silva FKS, Cajado RA, Oliveira LS, Ribeiro FRV, Zacardi DM. Early ontogeny of *Pimelodus blochii* Valenciennes, 1840 (Siluriformes: Pimelodidae): Neotropical catfish. Zootaxa. 2021; 4948 (1):83-98. <https://doi.org/10.11646/zootaxa.4948.1.4>

Silva FKS, Oliveira LS, Santos Z, Santos JÁ, Silva LVF, Zacardi DM. Early development of *Prochilodus nigricans* Spix & Agassiz 1829 (Characiformes: Prochilodontidae) in captivity. Aquac Res. 2022;53(12):4540-55. <https://doi.org/10.1111/are.15951>

Silvano RAM, Hallwass G, Juras AA, Lopes PFM. Assessment of efficiency and impacts of gillnets on fish conservation in a tropical freshwater fishery: Assessment of efficiency and impacts of gillnets in a tropical fishery. Aquat Conserv. 2017; 27:521-33. <https://doi.org/10.1002/aqc.2687>

Silvano RAM, Nitschke PP, Vieira KC, Nagl P, Martínez ATR, Chuctaya JA *et al.* Atlas of Fish of Tapajós and Negro Rivers In: Characiformes. In: Silvano RAM, editor. Fish and Fisheries in the Brazilian Amazon. People, Ecology and Conservation in Black and Clear Water Rivers 1ed. Cham: Springer International Publishing; 2020. p.41-196.

Sokal RR, Rohlf FJ. Biometry. The principle and practice of statistics in biological research. San Francisco: WH Freeman; 1981.

Solomon FN, Rodrigues D, Gonçalves EJ, Serrão EA, Borges R. Larval development and allometric growth of the black-faced blenny *Tripterygion delaisi*. J Fish Biol; 2017; 90(6). 2239–2254. <https://doi:10.1111/jfb.13286>

Stephens DW, Brown JS, Ydenberg RC. (Eds.). Foraging: behavior and ecology. University of Chicago Press; 2007.

Taguti TL, Kipper D, Bialecki A, Sanches PV, Makrakis MC, Baumgartner G *et al.* Desenvolvimento inicial de *Pyrrhulina australis* Eigenmann & Kennedy. 1903 Characiformes. Lebiasinidae). Biota Neotrop. 2009; 9(4):59–65. Available from: <https://www.scielo.br/j/bn/a/xmVmM6MfZm4FhHRGmqHm5DQ/?format=pdf&lang=pt>

Urho L. Characters of larvae what are they? Folia Zool. 2002; 51:161-86.

Van Den Boogaart JGM, Muller M, Osse JWM. Structure and function of the median finfold in larval teleosts. Journal of Experimental Biology; 2012; v. 215(14). p. 2359–2368. <http://doi:10.1242/jeb.065615>

Van Leeuwen JL, Voosenek CJ, Müller UK. How body torque and Strouhal number change with swimming speed and developmental stage in larval zebrafish. J R Soc. Interface. 2015; v.12 n. 110. p 20150479. <http://doi:10.1098/rsif.2015.0479>

Zacardi DM, Bittencourt SCS, Queiroz HL. Recruitment of migratory Characiforms in the different wetland habitats of Central Amazonia: subsidies for sustainable fisheries management. J Appl Ichthyol. 2020b 36(4):431-38. <https://doi.org/10.1111/jai.14040>

Zacardi DM, Santos JA, Oliveira LS, Cajado RA, Pompeu PS. Ichthyoplankton studies as referential for the management and monitoring of fishery resources in the Brazilian

Amazon basin. *Acta Limnol Bras.* 2020a; 32:1-09. <https://doi.org/10.1590/s2179-975x6619>

Zacardi DM. A pesca artesanal em áreas de inundação no baixo Amazonas, Pará: técnicas de captura e composição pesqueira. In: Oliveira AC, editor. *Aquicultura e Pesca: Adversidades e Resultados* 3rd ed. Ponta Grossa: Atena; 2020.p.1-16.

Zhao Z, Li G, Xiao Q, Jiang HR, Tchivelekete GM, Shu X, Liu H. Quantification of the influence of drugs on zebrafish larvae swimming kinematics and energetics. *PeerJ.* 2020 ;8:e8374.[https://doi: 10.7717/peerj.8374](https://doi:10.7717/peerj.8374). PMID: 31938582; PMCID: PMC6954687