Temporal distribution and early development of *Moenkhausia cf. gracilima* (Lucena & Soares, 2016) (Osteichthyes, Characidae) in the upper Paraná River, Brazil

Distribuição temporal e desenvolvimento inicial de *Moenkhausia cf. gracilima* (Lucena & Soares, 2016) (Osteichthyes, Characidae) no alto rio Paraná, Brasil

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**Abstract:** Aim: To analyze temporal distribution of larvae and juveniles and the early development and of *Moenkhausia cf. gracilima*. Methods: Samples were taken quarterly in twenty-five sites in the upper Paraná River floodplain between August 2013 and May 2015. The samples were taken under the water surface at night using 0.5 mm mesh plankton nets. In the laboratory, samples were sorted, identified and separated into larval (preflexion, flexion and postflexion) and juvenile periods. Results: A total of 248 individuals was collected, mainly in the Saraiva Lagoon, suggesting that the entire life cycle of this species occurs in this environment. The reproductive period takes place between December and April, since the postflexion larvae were found until May. However, the occurrence of juveniles between February and May indicates probable batch spawning. Among the 95 individuals used for ontogenic description, 82 were larvae and 13 juveniles. Larvae may be characterized by irregular pigmentation in the upper region of the head, mouth, and body, increasing throughout development; upper lobe of the caudal fin more pigmented than the lower lobe, only visible in postflexion larvae; terminal mouth; anal opening located anterior to the median region of the body and total number of myomers ranging from 34 to 40 (15 to 20 pre and 16 to 23 postanal), while juveniles have characteristics similar to adults. The total number of fin rays is: P. 11-16, V. 7-11, D. 9-11 and A. 21-23. Conclusions: According to the distribution of developmental periods it is possible to conclude that this species reproduces in the summer, preferably in lagoons. Growth analysis indicated important alterations in larval morphology (metamorphosis) that may be associated with the ecomorphological characteristics of the species. The morphological separation of larvae of *M. cf. gracilima* from other larvae of small characids, especially at preflexion and flexion stages may be complicated by the overlap of traits, suggesting the use of other variables, mainly morphometric, for the separation of the species.

**Keywords:** fish; ichthyoplankton; ontogeny; Characidae; reproduction.
Resumo: Objetivo: Analisar a distribuição temporal de larvas e juvenis e o desenvolvimento inicial de *Moenkhausia cf. gracilima*. Métodos: Foram amostrados trimestralmente vinte e cinco estações distribuídas na planície de inundação do alto rio Paraná entre agosto de 2013 e maio de 2015. As coletas foram na subsuperfície, no período noturno, utilizando redes de plâncton com malha 0,5 mm. Em laboratório, as amostras foram triadas, identificadas e separadas em períodos larval (pré-flexão, flexão e pós-flexão) e juvenil. Resultados: Foram capturados 248 indivíduos, sendo a maioria na Laguna Saraiva, sugerindo que todo o ciclo de vida desta espécie acontece neste ambiente, e que o período reprodutivo ocorre entre dezembro e abril, uma vez que larvas em pós-flexão foram encontradas até maio. A ocorrência de juvenis entre fevereiro e maio indica provável desova parcelada. Entre os 95 indivíduos utilizados na descrição ontogênica, 82 eram larvas e 13 juvenis. As larvas podem ser caracterizadas pela pigmentação irregular na região superior da cabeça, na boca e no corpo, aumentando ao longo do desenvolvimento; lobo superior da nadadeira caudal mais pigmentado do que o inferior, só visível em larvas em pós-flexão; boca em posição terminal, abertura anal localizada anteriormente à região mediana do corpo e número total de miômeros variando de 34 a 40 (15 a 20 pré e 16 a 23 pós-anal), enquanto os juvenis apresentam características semelhantes ao adulto. O número de raios das nadadeiras é: P: 11-16, V: 7-11, D: 9-11 e A: 21-23. Conclusões: De acordo com a distribuição dos períodos de desenvolvimento, é possível concluir que esta espécie se reproduz no verão, de preferência em lagos. A análise do crescimento indicou alterações importantes na morfologia larval (metamorfoses) que podem estar associadas às características ecomorfológicas da espécie. A separação morfológica das larvas de *M. cf. gracilima* de outras larvas de caracteres pequenos, especialmente nos estágios de preflexão e flexão, pode ser complicado pela sobreposição de traços, sugerindo o uso de outras variáveis, principalmente morfométricas, para a separação das espécies.

Palavras-chave: peixes; ictioplâncton; ontogenia; Characidae; reprodução.

1. Introduction

Research on the ecology of fish eggs and larvae is of great importance to assist in the identification of spawning and nursery areas (Baumgartner et al., 2004; Bialetzki et al., 2005; Oliveira & Ferreira, 2008; Hermes-Silva et al., 2009), detection and evaluation of fish stocks and knowledge of population dynamics (Hempel, 1973; Agostinho et al., 2004), evaluation of the effects of different human interferences, such as pollution (Campagna et al., 2006), habitat Arrumado fragmentation (Sanches et al., 2006) and species introduction (Bialetzki et al., 2004, Kipper et al., 2011). In addition, the elucidation of the systematic and/or phylogenetic position of certain species or groups of species is frequently supported by information about the early stages of fish life (Bialetzki et al., 2016).

There is still little known about fish larvae systematics and studies on egg systematics are lacking; only a few species have their early developmental stages known (Bialetzki et al., 2016). This difficulty is a consequence of the lack of comparative literature, high morphological similarity of the early stages between species, and a great difference in relation to the characteristics when compared to the adult (Snyder, 1981; Fuiman, 1983; Bialetzki et al., 1998). Among the groups present in samples collected in natural environments, considering the high morphological similarity, stand out the early stages of several species of the family Characidae. Ichthyoplankton surveys conducted in different environments of Paraná River by Castro et al. (2002), Bialetzki et al. (2005) and Ziober et al. (2007) report a significant portion of the community classified in this family, mainly due to the difficulty of identification at lower taxonomic levels.

The genus *Moenkhausia* together with *Astyanax*, *Hemigrammus* and *Hypheosobrycon* represent 35% of the species of Characidae (Carvalho et al., 2014) and is formed by 77 valid species, widely distributed in South American freshwater environments (Froese & Pauly, 2016). It is characterized by presenting a combination of traits, such as the presence of five multi-cusped teeth in the internal premaxillary series, caudal fin partially covered by scales, small scales covering the anal fin base and complete lateral line (Eigenmann, 1917). Species of this genus, as well as others of the family Characidae, have been constantly revised and the taxonomic status of many of them has not yet been defined. The *Moenkhausia lepidura* (Kner, 1858) group, for example, that gathers species that have a dark upper lobe of the caudal fin, was revised by Marinho (2009). In this study, the author mentions that *Moenkhausia* sp. 2 (=*Moenkhausia cf. gracilima* personal communication of M. M. F. Marinho) is the only species of the *M. lepidura* group that occurs in the upper Paraná River basin, however, it has not yet been described in the literature.
In this context, this study intends to contribute with the knowledge about the early ontogeny of characids, aiming (i) to evaluate the temporal distribution of larval developmental stages and juveniles in the upper Paraná River floodplain, and (ii) to characterize the early development of *M. cf. gracilima*, emphasizing morphology and also morphometry and meristics.

2. Material and Methods

2.1. Study area

The study area is located in the floodplain of the upper Paraná River, downstream of the dam of Porto Primavera Hydropower Plant (HPP) and upstream of the Itaipu Reservoir. This section presents a large anastomosed channel, with reduced slope (0.09 m/km), sometimes with extensive alluvial plain and large sediment accumulation on the bed, giving rise to bars and small islands (more than 300), sometimes with large islands and more restricted floodplain (Agostinho et al., 2008). The complex anastomosis also involves numerous secondary channels, lagoons, the Baía River and the lower reaches of the Ivaí, Ivinheima, Piquiri, Amambai and Iguatemi rivers, besides the floodplains (Agostinho et al., 2008).

2.2. Sampling

Samples were taken in 25 sampling stations distributed in three biotopes: main channel of the Paraná River (upstream of the mouth of tributaries); tributaries and lagoons. The names, codes and location of each sampling site are presented in Table 1.

Table 1. Physiographic data of the sampling stations located in the upper Paraná River floodplain.

| Site Code | Subarea     | Geographic Coordinate |
|-----------|-------------|-----------------------|
| MPARN     | Paranapanema| 22°39'2.30"S/53°5'26.30"W |
| TPARN     | Paranapanema| 22°38'54.00"S/53°5'2.20"W |
| MBAIA     | Baía        | 22°45'38.70"S/53°19'40.60"W |
| TBAIA     | Baía        | 22°45'34.40"S/53°19'42.90"W |
| MIVIN     | Ivinheima   | 22°59'40.60"S/53°38'41.40"W |
| TIVIN     | Ivinheima   | 22°59'12.00"S/53°38'56.70"W |
| MIVIH     | Ivinheiminha| 23°14'18.50"S/53°43'3.60"W |
| TIVIH     | Ivinheiminha| 23°14'0.30"S/53°43'24.00"W |
| MIVAI     | Ivaí        | 23°18'11.80"S/53°41'54.20"W |
| TIVAI     | Ivaí        | 23°18'0.50"S/53°41'32.40"W |
| MAMAM     | Amambai     | 23°21'52.30"S/53°52'47.90"W |
| TAMAM     | Amambai     | 23°20'19.90"S/53°51'24.40"W |
| MMARA     | Maracai     | 23°26'8.29"S/53°58'0.29"W |
| TMARA     | Maracai     | 23°25'32.03"S/53°58'13.82"W |
| MPARA     | Paracai     | 23°38'51.40"S/53°56'44.30"W |
| TPARA     | Paracai     | 23°38'59.50"S/53°56'41.30"W |
| MIRPA     | Pirajui     | 23°40'18.24"S/54°3'46.97"W |
| TPIRA     | Pirajui     | 23°40'9.62"S/54°3'48.80"W |
| LSAJO     | São João    | 23°49'0.19"S/53°59'35.62"W |
| MIGUA     | Iguatemi    | 23°55'27.90"S/54°9'16.60"W |
| TIGUA     | Iguatemi    | 23°55'37.60"S/54°11'22.00"W |
| MSARA     | Saraiva     | 24°0'57.90"S/54°10'37.00"W |
| LSARA     | Saraiva     | 24°11'16.40"S/54°10'10.50"W |
| MIPQIU    | Piquiri     | 24°1'24.30"S/54°5'33.20"W |
| TPIQU     | Piquiri     | 24°1'52.20"S/54°4'38.30"W |
Quarterly samplings were performed from August 2013 through May 2015, always at night, around 20 h. For the samples, conical-cylindrical plankton nets with 0.5 mm mesh size and a mouth area of 0.1104 m² were equipped with a flowmeter (General Oceanics™ model 2030) to determine the volume of water filtered. The nets were exposed or dragged depending on the current velocity, for 10 minutes, at the subsurface (approximately 20 cm below the water surface) of the sampling stations. After, samples were stored in flasks, anesthetized and fixed with 4% formalin, buffered with calcium carbonate.

The samples were sorted, and individuals were separated and identified in the laboratory using the developmental sequence technique proposed by Ahlstrom & Moser (1976). This technique consists of comparing the morphology of smaller individuals to a known juvenile form. 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) and juvenile periods.

For the analysis of the temporal distribution, the frequency of occurrence of each stage of larval development (preflexion, flexion and postflexion) and juvenil (dependent variables) were plotted against months (independent variable).

To characterize the early ontogeny, each period was described based on the degree of development and on the occurrence of the main morphological events. The individuals that best represented these characteristics were illustrated using a camera lucida. The individuals used in this study are stored in the Ichthyology Collection of the Center for Research in Limnology, Ichthyology and Aquaculture (Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura - Nupélia) of Maringá State University (Università Estadual de Maringá - UEM), Paraná, Brazil (NUP 18375, and NUP 18376).

For morphometric variables characterization of the initial development, the following body measurements expressed in millimeters (0.01 mm precision) and measured parallel to the longitudinal axis of the body were obtained from stereomicroscope (Olympus SZ40) equipped with micrometer eyepiece (with an accuracy of 0.01 mm) and measured parallel to the longitudinal axis of the body (Ahlstrom et al., 1976): standard length (SL), snout length (SnL), eye diameter (ED), head depth (HD), head length (HL), body depth (BD) and the length from the tip of the snout to origins of pectoral (SnP), pelvic (SnV), dorsal (SnD) and anal (SnA) fins. For meristic characterization, the number of total and pre and postanal myomeres and the rays of the pectoral (P), pelvic (V), dorsal (D) and anal (A) fins were counted whenever possible. The body shape was determined according to the categories proposed by Leis & Trnaski (1989) which relate ED to HL, BD to SL, and HL to SL.

To identify potential ontogenic variations during the larval and juvenile periods, the morphometric variables (dependent variables) were plotted against SL and HL (explanatory variables), and their relationships were analyzed using various regression models (Kováč et al., 1999). First, we tested the hypothesis that body ratio development is continuously isometric using a simple linear regression model. In addition, we also tested two alternative hypotheses: gradual allometric growth by using a quadratic regression analysis and discontinuous isometric growth by using a piecewise linear regression analysis, which is characterized by breakpoints reflecting divergent growth rates. The optimal models for each morphometric variable relative to body and head size were determined using F tests (Sokal & Rohlf, 1981). Regression analyzes were performed using Statistica™ 7.0 software (StatSoft, 2005). The significance level for the analyses was p<0.05.

3. Results

3.1. Temporal distribution

Among the sampled sites, 99% (246 individuals) of the occurrences of M. cf. gracilima were recorded in Saraiva Lagoon. Regarding the temporal distribution, individuals of M. cf. gracilima were caught only in four of the eight months sampled. Preflexion larvae occurred only in February 2014, while flexion larvae corresponded to 5% and 8% of the samples taken in February 2014 and 2015, respectively. Postflexion larvae were recorded in February 2014 (3%) and 2015 (92%) and in May 2015 (40%). Juveniles, in turn, represented 100% of the catches in August 2015 and 60% in May 2015 (Figure 1).

3.2. Early development

For description of the early development, we analyzed 95 individuals, including 82 larvae (46 preflexion, 12 flexion and 24 postflexion) and 13 juveniles. The description of each period is presented below and illustrated in Figure 2 A-G. The results referring to morphometric and meristic variables are listed in Table 1.
3.3. Larval period

**Preflexion stage** (Figure 2A): The standard length of the larvae varies from 2.83 to 3.79 mm (mean = 3.41 mm ± 0.23). The notochord is visible by transparency, not flexed. The yolk sac is fully absorbed, the intestine is functional and the anal opening lies anterior to the body vertical line over the median region of the body. Mouth is open and terminal. Nostrils are simple. Eye is spherical and completely pigmented. The operculum is formed. Punctate and dendritic chromatophores are irregularly distributed in the upper region of the head and in the mouth; other punctate chromatophores can be seen around the body. Finfold is hyaline and is found throughout the ventral region and part of the dorsal region, extending from near the median dorsal portion of the body to the region below the pectoral fin bud. The other fins are not outlined, except the bud of the pectoral fin that is visible from the smallest individual analyzed. The total number of myomers varies from 34 to 40 (15 to 20 pre and 19 to 23 postanal).

**Flexion stage** (Figure 2B, C): The standard length of the larvae at this stage ranges from 4.69 to 6.91 mm (mean = 5.91 mm ± 0.78). The notochord is flexed and it is possible to visualize the hypural bones. The intestine is short and the anal opening is anterior to the body vertical line over the median region of the body. Mouth remains terminal. Nostrils are simple. Chromatophores are mostly dendritic and are irregularly distributed in the head and around the mouth, as well as along the body. In addition, punctate chromatophores are found at the base of the caudal fin rays. Finfold is still present, and from 6.26 mm SL, the design and onset of the formation of some caudal and anal fin rays begin. At the end of the flexion stage, with about 6.32 mm SL, it is possible to observe the first rays of the anal and dorsal fins. The total number of myomers varies from 34 to 40 (15 to 20 pre and 18 to 21 postanal).

**Postflexion stage** (Figure 2D, E, F): The postflexion larvae have the standard length ranging from 7.10 to 12.46 mm (mean = 9.75 mm ± 1.78). At this stage, the larvae present the position of the mouth and the anal opening similar to the previous stage. Nostrils are double from about 7.10 mm SL. Notochord is still visible by transparency. Larvae show intense pigmentation mainly on the back of the head and along the body. A line of pigments begins to form a longitudinal band extending from the operculum to the caudal peduncle. In the caudal fin, the chromatophores are punctate and concentrate at the base and at the top of the rays, the upper lobe is more pigmented than the lower lobe. Scales are visible from 9.96 mm SL.
Finfold is gradually absorbed and, in its place, it is possible to observe the formation of the caudal, anal, dorsal and adipose fins, but vestiges can still be observed in the ventral region up to 7.70 mm SL, at the beginning of postflexion. The pelvic fin bud is present with about 7.70 mm SL and approximately, with 9.96 mm SL it is already formed. Fin development sequence, including the segmentation of rays is caudal, dorsal, anal, pelvic and pectoral. The total number of myomers varies from 34 to 39 (15 to 20 pre and 16 to 21 postanal), but the development of muscles makes visualization difficult. The total number of fin rays in this stage is P: 9-13; V: 5-9; D: 10-15 and A: 19-23.

### 3.4. Morphometric relationships

In this period, the body depth varies from elongate to moderate (12.17 to 32.09%), while the head length varies from small head to moderate head (14.48 to 30.35%). Eye diameter ranges from moderate eye to large eye (25.61 to 51.02%). Snout length (20.51 to 40.32%), head depth (53.85 to 116.67%), snout-pectoral fin length (20.77 to 40.00%), snout-pelvic fin length (41.63% to 52.01%) and snout-anal fin length (46.43% to 67.15%) increase along the development, while the snout-dorsal fin length (54.15% to 45.85%) decreases (Table 2).

| VARIABLES (mm) | Larval period | Juvenile period |
|----------------|---------------|----------------|
|                | (PF n=46)     | (FL n=12)      | (FP n=24)     | (J n=13)     |
| SL             | Min/Max       | Min/Max        | Min/Max       | Min/Max       |
| HD             | 0.40-0.91     | 0.08-1.45      | 1.24-2.69     | 2.46-4.15     |
| HL             | 0.16-0.25     | 0.26-0.52      | 0.51-0.12     | 0.77-1.38     |
| ED             | 0.16-0.23     | 0.26-0.52      | 0.51-0.12     | 0.77-1.38     |
| BD             | 0.01-1.03     | 1.00-1.86      | 1.90-3.38     | 3.69-4.92     |
| SnP            | 0.63-1.50     | 1.30-2.16      | 2.10-3.54     | 3.23-4.92     |
| SnN            | NV            | NV             | 2.56-6.08     | 6.15-9.38     |
| SnD            | NV            | NV             | 3.50-6.15     | 6.31-9.38     |
| SnA            | NV            | NV             | 4.16-7.69     | 8.38-12.62    |
|                | X±SD          | X±SD           | X±SD          | X±SD          |
|                | 4.69-6.91     | 5.91±0.78      | 9.75±1.78     | 13.30-19.40   |
|                | 1.14-0.25     | 3.59-0.42      | 1.97±0.47     | 2.46-4.15     |
|                | 0.37-0.07     | 0.58±0.12      | 0.77-1.38     | 1.04±0.19     |
|                | 1.42±0.32     | 2.61±0.46      | 3.69-4.92     | 4.18-4.92     |
|                | 1.69±0.28     | 2.84±0.41      | 3.23-4.92     | 3.99±0.61     |
|                | 3.25±0.24     | 3.25±0.24      | 3.25±0.24     | 3.25±0.24     |
|                | 3.78±0.60     | 6.05±1.13      | 8.38-12.62    | 9.96±1.57     |

### Relations (%)

| VARIABLES (mm) | Total | Preanal | Postanal |
|----------------|-------|---------|---------|
| HD/HL          | 53.85-116.67 | 20.51-40.32 | 12.17-32.09 |
| SnL/HD         | 20.51-40.32 | 25.61-51.02 | 12.17-32.09 |
| SnA/HD         | 20.51-40.32 | 25.61-51.02 | 12.17-32.09 |
| SnD/HD         | 20.51-40.32 | 25.61-51.02 | 12.17-32.09 |
| SnP/HD         | 20.51-40.32 | 25.61-51.02 | 12.17-32.09 |
| SnL/HL         | 20.51-40.32 | 25.61-51.02 | 12.17-32.09 |
| SnA/HL         | 20.51-40.32 | 25.61-51.02 | 12.17-32.09 |
| SnD/HL         | 20.51-40.32 | 25.61-51.02 | 12.17-32.09 |
| SnP/HL         | 20.51-40.32 | 25.61-51.02 | 12.17-32.09 |
| SnL/SL         | 20.51-40.32 | 25.61-51.02 | 12.17-32.09 |
| SnA/SL         | 20.51-40.32 | 25.61-51.02 | 12.17-32.09 |

### Myomers

| VARIABLES (mm) | Total | Preanal | Postanal |
|----------------|-------|---------|---------|
| P              | NV    | NV      | NV      |
| V              | NV    | NV      | NV      |
| D              | NV    | NV      | NV      |
| A              | NV    | NV      | NV      |

### Rays

| VARIABLES (mm) | Total | Preanal | Postanal |
|----------------|-------|---------|---------|
| P              | 9-13  | 10.63±1.60 | 14-15  |
| V              | 5-9   | 7.2±1.00  | 8-11   |
| D              | 10-15 | 10.83±1.01 | 10     |
| A              | 19-23 | 21.13±0.87 | 20-23  |

**PF** = preflexion; **FL** = flexion; **FP** = postflexion; **J** = juveniles; **NV** = not visible; **n** = number of individuals analyzed; **SL** = standard length; **HD** = head depth; **HL** = head length; **SnL** = snout length; **ED** = eye diameter; **BD** = body depth; **SnP** = from the tip of the snout to origins of pectoral; **SnV** = from the tip of the snout to origins of pelvic; **SnD** = from the tip of the snout to origins of dorsal and **SnA** = from the tip of the snout to origins of anal; **P** = ray of the pectoral fin; **V** = ray of the pelvic fin; **D** = ray of the dorsal fin; **A** = ray of the Anal fin.

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3.5. Juvenile period

Juveniles present a standard length of 13.30 to 19.40 mm (mean = 15.62 ± 2.20). In this period, the individuals present characteristics similar to the adult, such as for example, the intestine reaching the median region of the body, terminal mouth and presence of scales. Pigmentation is concentrated in the superior region of the head, formed by dendritic and punctate chromatophores. In addition, punctate chromatophores are also present in the region of the mouth and around the nostrils. In the region of the lateral line, the chromatophores are dendritic and punctate, forming a longitudinal band extending to the median caudal rays. Besides that, pigments are also found in the caudal fin, where they are concentrated at the base and at the top of the rays; the upper lobe is more pigmented by punctate chromatophores than the lower lobe. All fins are fully formed, including segmented rays, distributed as follows: pectoral (11-16), pelvic (7-11), dorsal (9-11) and anal (21-23) (Figure 2G).

3.6. Morphometric relationships

In this period, the body depth and head depth remain moderate, varying from 23.50 to 30.80% and 20.57 to 26.49%, respectively, while the eye diameter is large (36.39 to 46.25%). The head length (76.16 to 100.00%), the snout length (22.78 to 33.44%), the snout-pectoral fin length (23.50 to 27.74%), snout-pelvic fin length (45.10 to 51.99%) and snout-anal fin length (60.28% to 69.27%) increases during development, while the snout-dorsal fin length (46.05% to 52.98%) decreases (Table 2).

3.7. Body relations

Among the morphometric variables analyzed, all variables related to head length, snout length (breakpoint: 2.11mm), eye diameter (breakpoint: 1.44mm) and head depth (breakpoint: 1.57mm) were better represented by a piecewise linear regression model, that is, there was an initial growth similar to the independent variable and an abrupt change, after the breakpoint (Table 3; Figure 3 A-C).

Among the variables related to standard length, head length (breakpoint: 5.49mm) and snout-pectoral fin length (breakpoint: 4.86mm) were better represented a piecewise linear regression model (Table 3, Figure 4A and C). Body depth (Table 3, Figure 4B). was better described by a quadratic regression model, that is, it presented an allometric growth, in this case, negative (b <1), while the snout-pelvic fin length, snout-dorsal fin length and snout-anal fin length were better represented by a linear growth model (Table 3, Figure 4D, E, F).

| Measured | R^2 | R^2 | R^2 | F_{cb} | p | F_{pq} | P | F_{sb} | p | BM | BP | N |
|----------|-----|-----|-----|--------|----|--------|---|--------|----|-----|-----|---|
| SnL/HL   | 0.93| 0.95| 0.95| 47.06  | 0.00| -4.95  | 0.03| 19.51  | 0.00| S   | 0.43| 95 |
| ED/HL    | 0.96| 0.97| 0.97| 10.71  | 0.00| 17.42  | 0.00| 15.03  | 0.00| S   | 0.66| 95 |
| HD/HL    | 0.96| 0.97| 0.97| 16.89  | 0.00| 7.48   | 0.00| 12.79  | 0.00| S   | 1.33| 95 |
| HL/SL    | 0.97| 0.98| 0.98| 41.56  | 0.00| 22.46  | 0.00| 36.91  | 0.00| S   | 1.70| 95 |
| BD/SL    | 0.98| 0.99| 0.99| 26.85  | 0.00| 3.49   | 0.06| 15.53  | 0.00| Q   | 0   | 95 |
| SnP/SL   | 0.97| 0.99| 0.98| 57.79  | 0.00| 25.73  | 0.00| 49.61  | 0.00| S   | 1.87| 95 |
| SnV/SL   | 0.98| 0.98| 0.98| 0.40   | 0.03| 0.07   | 0.80| 0.23   | 0.63| L   |     |    |
| SnD/SL   | 0.99| 0.99| 0.99| 0.10   | 0.75| 2.19   | 0.15| 1.15   | 0.29| L   |     | 44 |
| SnA/SL   | 0.98| 0.98| 0.98| 4.26   | 0.05| -0.05  | 0.83| 2.05   | 0.16| L   |     | 45 |

R^2 = coefficient of determination; Q = quadratic regression; L = linear regression; S = piecewise regression; BM = best model; BP = breakpoint; N = number of individuals analyzed. Bold values presented p <0.05. SL = standard length; HD = head depth; HL = head length; SnL= snout length; ED = eye diameter; BD = body depth; SnP = from the tip of the snout to origins of pectoral; SnV = from the tip of the snout to origins of pelvic; SnD = from the tip of the snout to origins of dorsal and SnA = from the tip of the snout to origins of anal; F_{cb} = Function quadratic by linear function; F_{pq} = Function piecewise regression by quadratic function; F_{sb} = Function piecewise regression by linear function.

Table 3. Linear, quadratic and piecewise regression statistics for the morphometric variables in relation to the standard length and head of the larvae and juveniles of Moenkhausia cf. gracilima.
Figure 3. Morphometric relationships (mm) between head length and head depth (A), snout length (B) and eye diameter (C), during the early development of *Moenkausia cf. gracilima*.

Figure 4. Morphometric relationships (mm) between standard length and: head length (A), body depth (B), snout-pectoral fin length (C), snout-pelvic fin length (D), snout-dorsal fin length (E) and snout-anal fin length (F) during the early development of *Moenkausia cf. gracilima*.
4. Discussion

The type of reproductive strategy used by the parents, that is, from the way the egg is fertilized (internally or externally) to the type of initial development (direct or indirect) directly conditions fish ontogeny (Balon, 1984). Species with indirect development have altricial larvae, which are small, transparent and poorly developed at hatching; non-functional mouth, anus and gills; unpigmented eyes; relatively large yolk sac and finfold around the trunk in the median position (Bialetzki et al., 2016). *Moenkhausia cf. gracilima* presents this model of life cycle and its early development can be classified as indirect, with the presence of free-living organisms with different developmental stages (egg, larvae or juvenile) (Miller & Kendall Junior, 2009).

The occurrence of larvae and juveniles of *M. cf. gracilima* was predominantly observed in the Saraiva Lagoon; possibly its entire life cycle may be occurring in this environment. Oliveira et al. (2001) mention that, in littoral areas of rivers and lakes, there is predominance of small characids. This group is favored by the presence of macrophyte stands that provide adequate substrates for spawning, abundant food resources and shelter from predators (Rossi & Parma de Croux, 1992; Dibble et al., 1996; Duffy & Baltz, 1998; Agostinho et al., 2003; Ziober et al., 2007). In addition, some species of sedentary fish use macrophyte stands to develop the entire life cycle (Ziober et al., 2007).

In agreement with Azevedo (2010), several species of small characids show seasonal reproductive period between September and April, relatively high fecundity and total spawning. Nonetheless, Hojo et al. (2004) investigated the reproduction of *Moenkhausia intermedia* Eigenmann, 1908 and reported that this species presents reproduction throughout the year and batch spawning, while *Moenkhausia sanctaefilomenae* (Steindachner, 1907) exhibits split spawning between late December and early January related to the rainy period and flood (Lourenço et al., 2008). For *M. cf. gracilima* the results suggest that the reproductive period of this species occurs between December and April, once postflexion larvae were found until May. On the other hand, the occurrence of juveniles between February and May indicates that, possibly, the spawning of this species can be batch.

Initial development of *M. cf. gracilima* showed a total absorption of the yolk sac before the preflexion stage indicates an early onset of exogenous feeding, with less than 2.83 mm. Suiberto et al. (2009) observed that larvae of *Bryconamericus stramineus* Eigenmann, 1908 onset its captured food in preflexion stage. In the same way, larvae of *Aphyocharax anisitsi* Eigenmann & Kennedy, 1903, *Astyanax altiparanae* Garutti & Britski, 2000, and *Hemigrammus marginatus* Ellis, 1911 (Nakatani et al., 2001), *Gymnocorymbus ternetzi* (Boulenger, 1895) (Celik et al., 2012) and *Heterocharax macrolepis* Eigenmann, 1912 (Mattox et al., 2014) also present early yolk absorption, suggesting a strategy and a characteristic common to the group.

The pigmentation pattern of *M. cf. gracilima* is commonly found in fish species living among macrophytes (Machado-Allison, 1987), with macules and other marks on the body and in the head region. According to Nakatani et al. (1997), this intense pigmentation is probably associated with camouflage to prevent predation. Pigmentation can be used to identify Cichilidae embryos and larvae (Meijide & Guerrero, 2000), however, among some Characidae from the upper Paraná River (A. altiparanae, H. marginatus and Hyphessobrycon eques (Steindachner, 1882)) studied by Nakatani et al. (2001), this characteristic does not distinguish them from these species, since they all show similar color during development. The exception is the postflexion larvae that already present darker upper lobe than the lower lobe, allowing identification at a specific level.

Fin development is an important characteristic during early fish ontogeny, as it is closely correlated with changes in swimming mode and speed, feeding techniques and preferences, and predation escape (Kendall Junior et al., 1984; Osse & van den Boogaart, 1999), besides supporting the anatomical and functional needs of skeletal formation (Koumourdoulos et al., 2001). Fin development sequence observed in *M. cf. gracilima* is similar to other Characiformes (Nakatani et al., 2001), where preflexion larvae show pectoral fin bud and finfold which in turn is gradually replaced by the unpaired, caudal, dorsal, anal and adipose fins. The formation of the dorsal fin rays before the anal fin is not a trait shared by all members of the family Characidae, and in some species, the anal fin appears in development before the dorsal fin, as in *H. macrolepis* (Mattox et al., 2014).

The total or partial number of myomers is considered an important trait in the identification of fish larvae (Snyder, 1979; Kelso et al., 2012). Comparing the total number of myomers found in *M. cf. gracilima*, 34 to 40, to those observed in small...
characids of the upper Paraná River basin with early ontogeny known, we found that there is overlap with *A. altiparanae* (32 to 37), *H. eques* (29 to 35), *A. cf. anisitsi* (33 to 36) (Nakatani et al., 2001) and *B. stramineus* (35 to 40) (Galuch et al., 2003) and small separation from *H. marginatus* (29 to 33) (Nakatani et al., 2001). On the other hand, when comparing the pre (15 to 20) and postanal (16 to 23) myomers, only with *H. eques* there is no overlap in the pre-anal myomers (10 to 14), for the other species, there is overlap with one or the other, or in both partial counts. This result demonstrates that this trait is not efficient to distinguish species, unless it is associated with others traits, such as pigmentation, morphology and development of the fins. Moreover, the lack of studies on ontogeny for the other Characidae species of the basin reduces the reliability of this trait in the separation of species.

The relationships between the variables that showed abrupt growth, that is, with breakpoints, are considered significant if associated with some morphological, physiological and/or survival event (Kováč et al., 1999). In this case, head depth, snout length and eye diameter in relation to head length exhibited disruption of growth, suggesting that, in this interval, most of the remodeling of the external morphology occurs. The modifications of head-related structures are probably due to the formation of the brain of larvae, which leads to the diversification of motor and sensory abilities (Cavicchioli & Leonhardt, 1993; Bialetzki et al., 1998; Galuch et al., 2003). Changes in the snout length may be related to the onset of exogenous feeding (Blaxter, 1988) and also to the feeding habit of the species (Norton, 1995). Different diets within the same species are usually found according to the stages of development of the individuals, due to differences in energy demand and morphological limitations (Abelha et al., 2001). In the case of two species of the genus *Moenkhausia* as adults, feeding is mainly invertivore (Tófoli et al., 2010), nevertheless, the change in the size of the snout and in eye diameter possibly imply differentiated diets during the development.

Small characids share many traits during ontogeny making species and genera identification difficult in samples taken in natural environments. Few studies have been conducted with the goal of knowing the early development of this group, probably due to the difficulty in obtaining series of development, due to the complexity of establishing a protocol for induced reproduction and also due to the low commercial interest of most species. However, advances in the ichthyoplankton study in different river basins are extremely dependent on these descriptions and efforts should be directed to minimize this problem.

*Moenkhausia cf. gracilima* has seasonal reproduction and possibly batch spawning, completing its entire life cycle in the Saraiva Lagoon. Growth analysis indicated important alterations in larval morphology (metamorphosis) that may be associated with the ecomorphological characteristics of the species. The morphological separation of larvae of *M. cf. gracilima* from other larvae of small characids, especially at early developmental stages (preflexion and flexion stages) may be complicated by the overlap of traits, suggesting the use of other variables, mainly morphometric, for the separation of the species.

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