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

Distribuição temporal e desenvolvimento inicial de *Moenkausia* 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 Lagoa Saraiva, sugerindo que todo o ciclo de vida desta espécie aconteça 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 lagoas. 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 *Hyphessobrycon* 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	Location	Biotope	Geographic Coordinate
1	MPARN	Paranapanema	Paraná River upstream of the mouth of the Paranapanema River	Main Channel	22°39'2.30"S/53°5'26.30"W
2	TPARN	Paranapanema	Paranapanema River	Tributary	22°38'54.00"S/53°5'2.20"W
3	MBAIA	Baía	Paraná River upstream of the mouth of the Baía River	Main Channel	22°45'38.70"S/53°19'40.60"W
4	TBAIA	Baía	Baía River	Tributary	22°45'34.40"S/53°19'42.90"W
5	MIVIN	Ivinheima	Paraná River upstream of the mouth of the Ivinhema River	Main Channel	22°59'40.60"S/53°38'41.40"W
6	TIVIN	Ivinheima	Ivinhema River	Tributary	22°59'12.00"S/53°38'56.70"W
7	MIVIH	Ivinheiminha	Paraná River upstream of the mouth of the Ivinheiminha River	Main Channel	23°14'18.50"S/53°43'3.60" W
8	TIVIH	Ivinheiminha	Ivinheiminha River	Tributary	23°14'0.30"S/53°43'24.00" W
9	MIVAI	Ivaí	Paraná River upstream of the mouth of the Ivaí River	Main Channel	23°18'11.80"S/53°41'54.20"W
10	TIVAI	Ivaí	Ivaí River	Tributary	23°18'0.50"S/53°41'32.40" W
11	MAMAM	Amambai	Paraná River upstream of the mouth of the Amambai River	Main Channel	23°21'52.30"S/53°52'47.90"W
12	TAMAM	Amambai	Amambai River	Tributary	23°20'19.90"S/53°51'24.40"W
13	MMARA	Maracaí	Paraná River upstream of the mouth Maracaí River	Main Channel	23°26'8.29"S/53°58'0.29" W
14	TMARA	Maracaí	Maracaí River	Tributary	23°25'32.03"S/53°58'13.82"W
15	MPARA	Paracai	Paraná River upstream of the mouth of the Paracaí River	Main Channel	23°38'51.40"S/53°56'44.30"W
16	TPARA	Paracai	Paracaí River	Tributary	23°38'59.50"S/53°56'41.30"W
17	MPIRA	Pirajuí	Paraná River upstream of the mouth Pirajuí River	Main Channel	23°40'18.24"S/54°3'46.97" W
18	TPIRA	Pirajuí	Pirajuí River	Tributary	23°40'9.62"S/54°3'48.80" W
19	LSAJO	São João	São João Lagoon	Lagoon	23°49'01.98"S/53°59'32.62"W
20	MIGUA	Iguatemi	Paraná River upstream of the mouth of the Iguatemi River	Main Channel	23°55'27.90"S/54°9'16.60" W
21	TIGUA	Iguatemi	Iguatemi River	Tributary	23°55'37.60"S/54°11'22.00"W
22	MSARA	Saraiva	Paraná River upstream of the mouth of the Saraiva Lagoon	Main Channel	24°0'57.90"S/54°10'37.00"W
23	LSARA	Saraiva	Saraiva Lagoon	Lagoon	24°1'6.40"S/54°10'10.50"W
24	MPIQU	Piquiri	Paraná River upstream of the mouth of the Piquiri River	Main Channel	24°1'24.30"S/54°5'33.20"W
25	TPIQU	Piquiri	Piquiri River	Tributary	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 (Universidade 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 & Trnski (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.
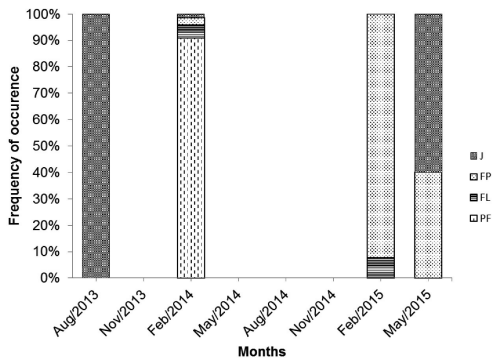
Figure 1. Monthly frequency of occurrence per stage/developmental period of *Moenkhausia* cf. *gracilima* in the Saraiva Lagoon, upper Paraná River floodplain, between August 2014 and May 2015. (PF= preflexion; FL= flexion; FP= postflexion; J= juvenile).
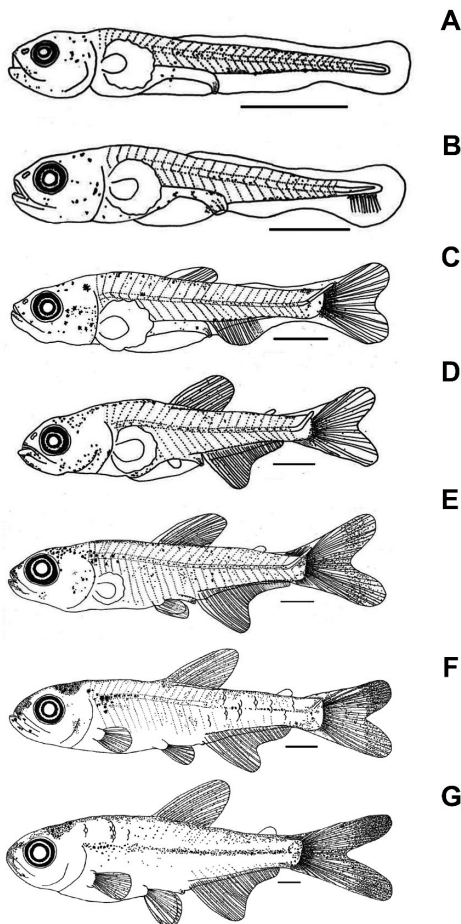

Figure 2. Early development of *Moenkausia* cf. *gracilima*. (A) preflexion larvae (3.12 mm SL); (B) early flexion larvae (4.93 mm SL); (C) flexion larvae (6.32 mm SL); (D) early postflexion larvae (7.70 mm SL); (E) postflexion larvae (9.48 mm SL); (F) late postflexion larvae (9.96 mm SL), (G) juvenile (15.00 mm SL) (scale = 1 mm).

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).

Table 2. Minimum (Min), maximum (Max) values, means (X) and standard deviation (SD) (mm and %) for morphometric and meristic variables in larvae and juveniles of *Moenkausia* cf. *gracilima*.

Variables (mm)	Larval period				Juvenile period			
	PF (n=46)		FL (n=12)		FP (n=24)		J (n=13)	
	Min/Max	X±SD	Min/Max	X±SD	Min/max	X±SD	Min/Max	X±SD
SL	2.83-3.79	3.64±0.25	4.69-6.91	5.91±0.78	7.10-12.46	9.75±1.78	13.30 -19.40	15.62±2.20
HD	0.40-0.91	0.55±0.08	0.80-1.45	1.14±0.25	1.24-2.69	1.97±0.47	2.46-4.15	3.26±0.55
HL	0.43-0.91	0.77±0.09	1.15-2.06	1.56±0.34	1.96-3.23	2.59±0.42	3.08-4.62	3.73±0.55
SnL	0.16-0.25	0.21±0.03	0.26-0.52	0.37±0.07	0.41-0.92	0.58±0.12	0.77-1.38	1.04±0.19
ED	0.20-0.33	0.26±0.03	0.35-0.68	0.52±0.13	0.62-1.38	0.98±0.23	1.23-2.00	1.58±0.24
BD	0.41-1.03	0.66±0.09	1.00-1.86	1.42±0.32	1.90-3.38	2.61±0.46	3.69-4.92	4.18±0.49
SnP	0.63-1.50	0.88±0.12	1.30-2.16	1.69±0.28	2.10-3.54	2.84±0.41	3.23-4.92	3.99±0.61
SnV	NV	NV	NV	NV	2.56-6.08	4.72±0.86	6.15-9.38	7.42±1.13
SnD	NV	NV	2.73-3.51	3.25±0.24	3.50-6.15	4.83±0.86	6.31-9.38	7.66±1.09
SnA	NV	NV	2.80-4.64	3.78±0.60	4.16-7.69	6.05±1.13	8.38-12.62	9.96±1.57
Relations (%)								
HD/HL	53.85-116.67	73.07±12.65	68.09-88.28	73.25±5.71	54.63-106.49	75.56±10.27	76.16-100.00	87.31±8.19
SnL/HL	20.51-40.32	27.90±4.53	17.26-27.78	23.77±3.61	15.75-29.41	22.60±3.04	22.78-33.44	27.79±2.61
ED/HL	25.61-51.02	34.11±4.54	27.78-46.90	33.04±5.04	27.31-53.25	37.78±5.09	36.39-46.25	42.33±3.13
HL/SL	14.48-25.41	22.52±2.19	21.99-30.13	26.14±2.82	20.02-30.35	26.81±2.44	20.57-26.49	23.91±1.65
BD/SL	12.17-32.09	19.46±2.67	18.32-27.40	23.76±2.80	21.76-30.38	26.94±1.83	23.50-30.08	26.91±1.81
SnP/SL	20.77-40.00	26.03±2.71	25.65-31.34	28.48±1.95	25.92-32.59	29.36±1.79	23.50-27.74	25.50±1.39
SnV/SL	NV	NV	NV	NV	42.25-52.01	48.50±2.25	45.10-51.99	47.43±1.88
SnD/SL	NV	NV	48.73-54.15	51.31±2.11	45.85-53.55	49.65±1.89	46.05-52.98	49.05±2.01
SnA/SL	NV	NV	51.85-67.15	61.33±4.86	46.42-66.79	62.11±3.68	60.28-69.27	63.68±2.94
Myomers								
Total	34-40	36.24±1.67	34-40	36.09±1.97	34-39	36.18±1.33	NV	NV
Preanal	15-18	16.04±0.98	15-20	17.09±1.70	15-20	17.41±1.23	NV	NV
Postanal	18-23	20.24±1.07	17-21	19.00±1.18	16-21	18.77±1.56	NV	NV
Rays								
P	NV	NV	NV	NV	9-13	10.63±1.60	14-15	14.83±0.39
V	NV	NV	NV	NV	5-9	7.2±1.00	8-11	9.17±1.11
D	NV	NV	NV	NV	10-15	10.83±1.01	10	10
A	NV	NV	NV	NV	19-23	21.13±0.87	20-23	20.58±0.90

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.

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).

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 *Moenkausia* cf. *gracilima*.

Measured	R^2_L	R^2_S	R^2_Q	$F_{Q/L}$	p	$F_{S/Q}$	P	$F_{S/L}$	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		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	0.53	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; $F_{Q/L}$ = Function quadratic by linear function; $F_{S/Q}$ = Function piecewise regression by quadratic function; $F_{S/L}$ = Function piecewise regression by linear function.
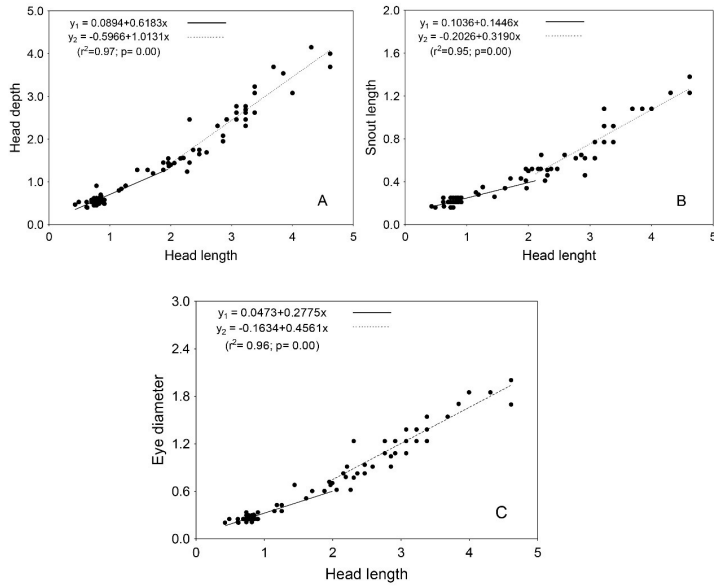
Figure 3. Morphometric relationships (mm) between head length and head depth (A), snout length (B) and eye diameter (C), during the early development of *Moenkausia* cf. *gracilima*.
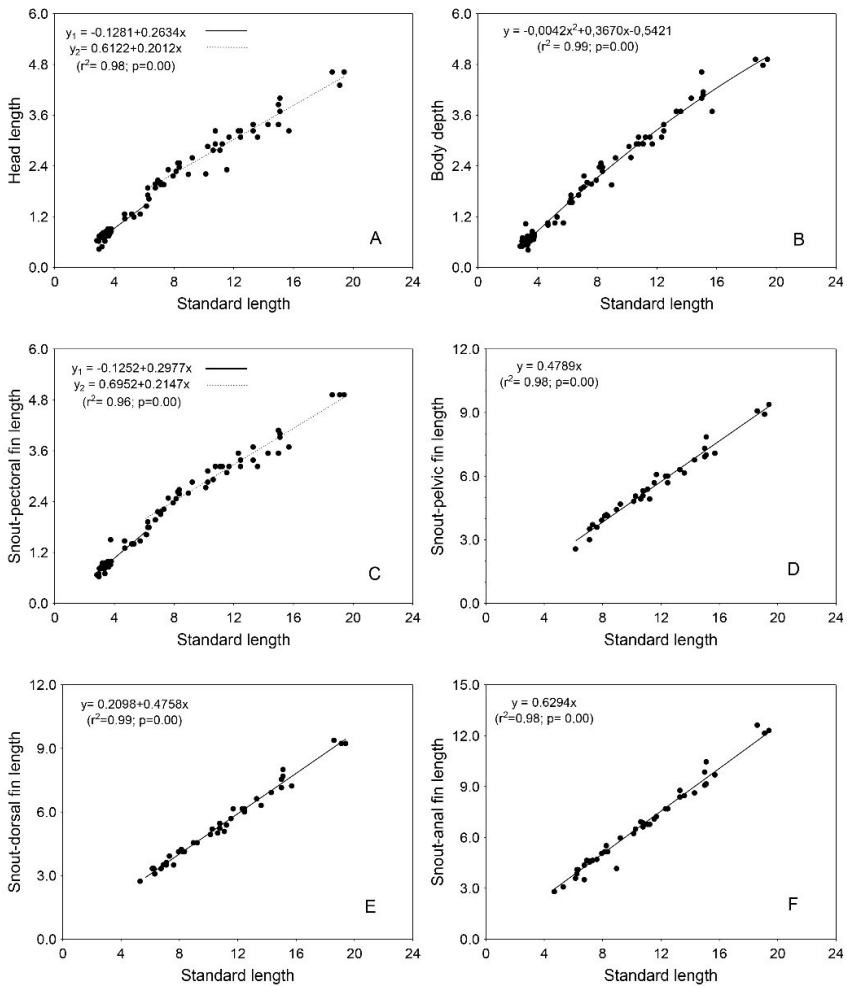

Figure 4. Morphometric relationships (mm) between standard length and: head length (A), body depth (B), snout-pectoral fin length (C), snout-pelvic fin length (D), snout-dorsal fin length (E) and snout-anal fin length (F) during the early development of *Moenkausia* cf. *gracilima*.

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) (Çelik 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 Cichlidae 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 (Koumoundouros 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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References

ABELHA, M.C.F., AGOSTINHO, A.A. and GOULART, E. Plasticidade trófica em peixes de água doce. *Acta Scientiarum. Biological Sciences*, 2001, 23, 425-434.

AGOSTINHO, A.A., GOMES, L.C. and JÚLIO JUNIOR, H.F. Relações entre macrófitas aquáticas e fauna de peixes. In: S.M. THOMAZ and L.M. BINI, eds. *Ecologia e manejo de macrófitas aquáticas*. Maringá: EDUEM, 2003, pp. 261-280.

AGOSTINHO, A.A., GOMES, L.C., VERÍSSIMO, S. and OKADA, E.K. Flood regime, dam regulation and fish in the Upper Paraná River: effects on assemblage attributes, reproduction and recruitment. *Reviews in Fish Biology and Fisheries*, 2004, 14, 11-19.

AGOSTINHO, A.A., PELICICE, F.M. and GOMES, L.C. Dams and the fish fauna of the Neotropical region: impacts and the management related to diversity and fisheries. *Brazilian Journal of Biology = Revista Brasileira de Biologia*, 2008, 68(4), 1119-1132.

AHLSTROM, E.H. and MOSER, H.G. Eggs and larvae of fishes and their role in systematic investigations and in fisheries. *Revue des Travaux de l'Institut des Pêches Maritimes*, 1976, 40(3), 379-398.

AHLSTROM, E.H., BUTLER, J.L. and SUMIDA, B.Y. 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. *Bulletin of Marine Science*, 1976, 26, 285-402.

AZEVEDO, M.A. Reproductive characteristics of characid fish species (Teleostei, Characiformes) and their relationship with body size and phylogeny. *Iheringia. Série Zoologia*, 2010, 100(4), 469-482. http://dx.doi.org/10.1590/S0073-47212010000400020.

BALON, E.K. Patterns in the evolution of reproductive styles in fishes. In: G.W. POTTS and R.J. WOOTTON, eds. *Fish reproduction: strategies and tactics*. London: Academic Press, 1984, pp. 35-53.

BAUMGARTNER, G., NAKATANI, K., GOMES, L.C., BIALETZKI, A., SANCHES, P.V. and MAKRAKIS, M.C. Identification of spawning sites and natural nurseries of fishes in the upper Paraná River, Brazil. *Environmental Biology of Fishes*, 2004, 71(2), 115-125. http://dx.doi.org/10.1007/s10641-004-0098-z.

BIALETZKI, A., GARCIA, D.A.Z. and ORSI, M.L. O estudo de ovos e larvas de peixes. In: M.L. ORSI, F.S. ALMEIDA, A.C. SWARÇA, A. CLARO-GARCÍA, N.C. VIANNA, D.A.Z. GARCIA and A. BIALETZKI, eds. *Ovos, larvas e juvenis de peixes da bacia do rio Paranapanema: uma avaliação para a conservação*. Assis: Triunfal Gráfica e Editora, 2016, pp. 17-24.

BIALETZKI, A., NAKATANI, K., SANCHES, P.V. and BAUMGARTNER, G. Eggs and larvae of the 'curvina' *Plagioscion squamosissimus* (Heckel, 1840) (Osteichthyes, Sciaenidae) in the Baía River, Mato Grosso do Sul State, Brazil. *Journal of Plankton Research*, 2004, 26(11), 1327-1336. http://dx.doi.org/10.1093/plankt/fbh123.

BIALETZKI, A., NAKATANI, K., SANCHES, P.V., BAUMGARTNER, G. and GOMES, L.C. Larval fish assemblage in the Baía River (Mato Grosso do Sul State, Brazil): temporal and spatial patterns. *Environmental Biology of Fishes*, 2005, 73(1), 37-47. http://dx.doi.org/10.1007/s10641-004-3795-3.

BIALETZKI, A., SANCHES, P.V., BAUMGARTNER, G. and NAKATANI, K. Caracterização morfológica e distribuição temporal de larvas e juvenis de *Apareiodon affinis* (Steindachner) (Osteichthyes, Parodontidae) no alto rio Paraná, Paraná. *Revista Brasileira de Zoologia*, 1998, 15(4), 1037-1047. http://dx.doi.org/10.1590/S0101-81751998000400021.

BLAXTER, J.H.S. Pattern and variety in development. In: W.S. HOAR and D.J. RANDALL, eds. *The physiology of developing fish. Pt. A. Eggs and larvae*. San Diego: Academic Press, 1988, pp. 1-58.

CAMPAGNA, A.F., ELER, M.N., ESPÍNDOLA, E.L.G., SENHORINI, J.A., RÊGO, R.F. and SILVA, L.O. Dimethoate 40% organosphosphorous pesticide toxicity in *Prochilodus lineatus* (Prochilodontidae, Characiformes) eggs and larvae. *Brazilian Journal of Biology = Revista Brasileira de Biologia*, 2006, 66(2B), 633-640. PMid:16906295. http://dx.doi.org/10.1590/S1519-69842006000400007.

CARVALHO, F.R., SARMENTO-SOARES, L.M. and MARTINS-PINHEIRO, R.F. Redescription of *Moenkhausia doceana* (Steindachner, 1877) (Ostariophysi: Characiformes): a characid from the Northeastern Mata Atlântica ecoregion, Brazil. *Neotropical Ichthyology*, 2014, 12(2), 377-388. http://dx.doi.org/10.1590/1982-0224-20140006.

CASTRO, R.J., NAKATANI, K., BIALETZKI, A., SANCHES, P.V. and BAUMGARTNER, G. Temporal distribution and composition of the ichthyoplankton from Leopoldo's Inlet on the upper Paraná River floodplain (Brazil). *Journal of Zoology*, 2002, 256(4), 437-443. http://dx.doi.org/10.1017/S095283690200047X.

CAVICCHIOLI, M. and LEONHARDT, J.H. Estudo do desenvolvimento morfológico de larvas de curimbatá, *Prochilodus scrofa* (Steindachner, 1882), obtidas de reprodução induzida. *Revista Unimar*, 1993, 15, 109-124. Supplement.

CELIK, I., CELIK, P., CIRIK, S., GÜRKAN, M. and HAYRETDAĞ, S. Embryonic and larval development of black skirt tetra (*Gymnocorymbus ternetzi*, Boulenger, 1895) underlaboratory conditions. *Aquaculture Research*, 2012, 43(9), 1260-1275. http://dx.doi.org/10.1111/j.1365-2109.2011.02930.x.

DIBBLE, E.D., KILLGORE, K.J. and HARREL, S.L. Assessment of fish-plant interactions. In: L.E. MIRANDA and D.R. DEVRIES, eds. *Multidimensional approaches to reservoir fisheries management*. Bethesda: American Fisheries Society, 1996, pp. 357-372.

DUFFY, K.C. and BALTZ, D.M. Comparison of fish assemblages associated with native and exotic submerged macrophytes in the lake Pontchartrain estuary, USA. *Journal of Experimental Marine Biology and Ecology*, 1998, 223(2), 199-221. http://dx.doi.org/10.1016/S0022-0981(97)00166-4.

EIGENMANN, C.H. The American Characidae. Part I. *Memoirs of the Museum of Comparative Zoology*, 1917, 43, 1-102.

FROESE, R. and PAULY, D., eds. *FishBase* [online]. 2016 [viewed 2016 Nov 16]. Available from: http://www.fishbase.org

FUIMAN, L.A. Growth gradients in fish larvae. *Journal of Fish Biology*, 1983, 23(1), 117-123. http://dx.doi.org/10.1111/j.1095-8649.1983.tb02886.x.

GALUCH, A.V., SUIBERTO, M.R., NAKATANI, K., BIALETZKI, A. and BAUMGARTNER, G. Desenvolvimento inicial e distribuição temporal de larvas e juvenis de *Bryconamericus stramineus* Eigenmann, 1908 (Osteichthyes, Characidae) na planície alagável do alto rio Paraná, Brasil. *Acta Scientiarum*, 2003, 5(2), 335-343.

HEMPEL, G. On the use of ichthyoplankton surveys. *FAO Fisheries Technical Paper*, 1973, 122, 1-2.

HERMES-SILVA, S., REYNALTE-TATAJE, D. and ZANIBONI-FILHO, E. Spatial and temporal distribution of ichthyoplankton in the upper Uruguay River, Brazil. *Brazilian Archives of Biology and Technology*, 2009, 52(4), 933-944. http://dx.doi.org/10.1590/S1516-89132009000400017.

HOJO, R.E.S., SANTOS, G.B. and BAZZOLI, N. Reproductive biology of *Moenkhausia intermedia* (Eigenmann) (Pisces, Characiformes) in Itumbiara Reservoir, Goiás, Brazil. *Revista Brasileira de Zoologia*, 2004, 21(3), 519-524. http://dx.doi.org/10.1590/S0101-81752004000300015.

KELSO, W.E., KALLER, M.D. and RUTHERFORD, D.A. Collecting, processing, and identification of fish eggs and larvae and zooplankton. In: A.V. ZALE, D.L. PARRISH and T.M. SUTTON, eds. *Fisheries techniques.* 3rd ed. Bethesda, Maryland: American Fisheries Society, 2012, pp. 363-452.

KENDALL JUNIOR, A.W., AHLSTROM, E.H. and MOSER, H.G. Early life history stages of fishes and their characters. In: H.G. MOSER, W.J. RICHARDS, D.M. COHEN, M.P. FAHAY, A.W. KENDALL JUNIOR and S.L. RICHARDSON, eds. *National Marine Fisheries Service; American Society of Ichthyologists and Herpetologists. Ontogeny and systematics of fishes: based on International Symposium dedicated to the memory of ELBERT HALVOR AHLSTROM*. Lawrence: American Society of Ichthyologists and Herpetologists, 1984. pp. 11-22.

KIPPER, D., BIALETZKI, A. and SANTIN, M. Composição taxônomica da assembleia de larvas de peixes no reservatório de Rosana, Rio Paranapanema, Brasil. *Biota Neotropica*, 2011, 11(1), 421-426.

KOUMOUNDOUROS, G., DIVANACH, P. and KENTOURI, M. Osteological development of *Dentex dentex* (Osteichthyes: Sparidae): dorsal, anal, paired fins and squamation. *Marine Biology*, 2001, 138(2), 399-406. http://dx.doi.org/10.1007/s002270000460.

KOVÁČ, V., COPP, G.H. and FRANCIS, M.P. Morphometry of the stone loach, *Barbatula barbatula*: do mensural characters reflect the species' life history thresholds? *Environmental Biology of Fishes*, 1999, 56(1/2), 105-115. http://dx.doi.org/10.1023/A:1007570716690.

LEIS, J.M. and TRNSKI, T. *The larvae of Indo-Pacific shorefishes*. Honolulu: University of Hawaii Press, 1989, 371 p.

LOURENÇO, L.S., MATEUS, L.A. and MACHADO, N.G. Synchrony in the reproduction of *Moenkhausia sanctaefilomenae* (Steindachner) (Characiformes: Characidae) in the Cuiabá River floodplain, Pantanal of Mato Grosso, Brazil. *Revista Brasileira de Zoologia*, 2008, 25(1), 20-27. http://dx.doi.org/10.1590/S0101-81752008000100004.

MACHADO-ALLISON, A. *Los peces de los llanos de Venezuela: un ensayo sobre su historia natural.* Caracas: Universidad Central de Venezuela, 1987, 144 p.

MARINHO, M.M.F. Análise filogenética e revisão taxonômica as espécies de *Moenkhausia* Eigenmann, 1903 do grupo M. *Lepidura* (Ostariophysi: Characiformes: Characidae) [Dissertação de mestrado em Biologia Animal]. São José do Rio Preto: Universidade Estadual Paulista, 2009.

MATTOX, G.M., HOFFMANN, M. and HOFFMANN, P. Ontogenetic development of *Heterocharax macrolepis* Eigenmann (Ostariophysi: Characiformes: Characidae) with comments on the form of the yolk sac in the Heterocharacinae. *Neotropical Ichthyology*, 2014, 12(2), 353-363. http://dx.doi.org/10.1590/1982-0224-20130107.

MEIJIDE, F.J. and GUERRERO, G.A. Embryonic and larval development of a substrate-brooding cichlid *Cichlasoma dimerus* Heckel, 1940 under laboratory conditions. *Journal of Zoology*, 2000, 252(4), 481-493. http://dx.doi.org/10.1111/j.1469-7998.2000.tb01231.x.

MILLER, B.S. and KENDALL JUNIOR, A.W. *Early life history of marine fishes.* Berkeley: University of California Press, 2009, 364 p.

NAKATANI, K., AGOSTINHO, A.A., BIALETZKI, A., BAUMGARTNER, G., SANCHES, P.V., MAKRAKIS, M. and PAVANELLI, C.S. *Ovos e larvas de peixes de água doce: desenvolvimento manual de identificação de ovos e larvas de peixes brasileiros de água doce*. Maringá: EDUEM, 2001, 378 p.

NAKATANI, K., BAUMGARTNER, G. and CAVICCHIOLI, M. Ecologia de ovos e larvas de peixes. In: A.E.A.M. VAZZOLER, A.A. AGOSTINHO and N.S. HAHN, eds. *A planície de inundação do alto rio Paraná: aspectos físicos, biológicos e econômicos.* Maringá: EDUEM, 1997, pp. 281-306.

NORTON, S.F. A functional approach to ecomorphological patterns of feeding in cottid fishes. *Environmental Biology of Fishes*, 1995, 1995(44), 61-78. http://dx.doi.org/10.1007/BF00005907.

OLIVEIRA, E.C. and FERREIRA, E.J. Spawning areas, dispersion and microhabitats of fish larvae in the Anavilhanas Ecological Station, rio Negro, Amazonas State, Brazil. *Neotropical Ichthyology*, 2008,

6(4), 559-566. http://dx.doi.org/10.1590/S1679-62252008000400003.

OLIVEIRA, E.F., LUIZ, E.A., AGOSTINHO, A.A. and BENEDITO-CECILIO, E. Fish assemblages in littoral areas of the upper Paraná River floodplain, Brazil. *Acta Scientiarum*, 2001, 23(2), 369-376.

OSSE, J.W.M. and VAN DEN BOOGAART, J.G.M. Dynamic morphology of fish larvae, structural implications of friction forces in swimming, feeding and ventilation. *Journal of Fish Biology*, 1999, 55, 156-174.

ROSSI, L.M. and PARMA DE CROUX, M.J. Influencia de la vegetación acuática en la distribución de peces del rio Paraná, Argentina. *Ambiente Subtropical*, 1992, 2, 65-75.

SANCHES, P.V., NAKATANI, K., BIALETZKI, A., BAUMGARTNER, G., GOMES, L.C. and LUIZ, E.A. Flow regulation by dams affecting ichthyoplankton: the case of the Porto Primavera dam, Paraná River, Brazil. *River Research and Applications*, 2006, 22(5), 555-565. http://dx.doi.org/10.1002/rra.922.

SNYDER, D.E. Myomere and vertebrae counts of the North America cyprinids and catostomids. In: R.D. HOYT (Ed.) *Proceedings of Third Symposium on Larval Fish*. Bowling Gree: Western Kentucky University, 1979, pp. 53-69.

SNYDER, D.E. *Contributions to a guide to the cypriniforms fish larvae of the upper Colorado River system*. Denver: Bureau of Land Management, 1981. Biological Sciences Series, vol. 3.

SOKAL, R.R. and ROHLF, F.J. *Biometry. The principles and practice of statistics in biological research*. San Francisco: W. H. Freeman and Company, 1981, 859 p.

STATSOFT. *Statistica: data analysis software system. Version 7.1* [online]. Cary: Statsoft Inc., 2005 [viewed 18 Oct. 2016]. Available from: www.statsoft.com

SUIBERTO, M.R., GALUCH, A.V., BIALETZKI, A. and NAKATANI, K. Ontogenetic shifts in the digestive tube and diet of *Bryconamericus stramineus* Eigenmann, 1908 (Osteichthyes, Characidae). *Acta Limnologica Brasiliensia*, 2009, 21(4), 465-472.

TÓFOLI, R.M., HAHN, N.S., ALVES, G.H.Z. and NOVAKOWSKI, G.C. Uso do alimento por duas espécies simpátricas de *Moenkhausia* (Characiformes, Characidae) em um riacho da Região Centro-Oeste do Brasil. *Iheringia. Série Zoologia*, 2010, 100(3), 201-206. http://dx.doi.org/10.1590/S0073-47212010000300003.

ZIOBER, S.R., BIALETZKI, A., GOMES, L.C. and KIPPER, D. The importance of a marginal lagoon as a fish nursery in the upper Paraná River floodplain. *Acta Limnologica Brasiliensia*, 2007, 19(4), 369-381.