Zygote

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Embryonic development of the fire-eye-tetra *Moenkhausia oligolepis* (Characiformes: Characidae)

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Research Article

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Summary

This study describes the embryonic development of *Moenkhausia oligolepis* in laboratory conditions. After fertilization, the embryos were collected every 10 min up to 2 h, then every 20 min up to 4 h, and afterwards every 30 min until hatching. The fertilized eggs of *M. oligolepis* measured approximately 0.85 ± 0.5 mm and had an adhesive surface. Embryonic development lasted 14 h at 25°C through the zygote, cleavage, blastula, gastrula, neurula, and segmentation phases. Hatching occurred in embryos around the 30-somites stage. The present results contribute only the second description of embryonic development to a species from the *Moenkhausia* genus, being also the first for this species. Such data are of paramount importance considering the current conflicting state of this genus phylogenetic classification and may help taxonomic studies. Understanding the biology of a species that is easily managed in laboratory conditions and has an ornamental appeal may assist studies in its reproduction to both supply the aquarium market and help the species conservation in nature. Moreover, these data enable the use of *M. oligolepis* as a model species in biotechnological applications, such as the germ cell transplantation approach.

Introduction

The study of embryological development is an important tool that provides knowledge on a species life history (De Alexandre *et al.*, 2009). This phase of development comprises fish formation events from fertilization of the oocyte by spermatozoa to larval hatching (Solnica-Krezel, 2005). At this phase, the animal is more vulnerable to any environmental disturbance, which can change its morphology, cause deformities, or even result in death. Therefore, to investigate the effects of changes in climatic variables on the embryonic development of teleosts, many studies have described this phase and associated its development with abiotic factors such as temperature (Hansen and Falk-Peterson, 2001; Rodrigues-Galdino *et al.*, 2010; Arashiro *et al.*, 2018), water acidification (Villanueva *et al.*, 2011), and water dissolved oxygen content (Keckeis *et al.*, 1996), among others.

Studies on embryonic development are also important to subsidize research on phylogeny and taxonomy of species, revealing knowledge about evolutionary history and phylogenetic relationships (Godinho *et al.*, 2009; Weber *et al.*, 2012; Dos Santos *et al.*, 2016). In addition, Godinho and Lamas (2009) showed that the characteristics of eggs, when fertilized, help in the development of reproductive strategies for teleosts.

In Brazil, embryological studies focus mainly on species with an established commercial value such as Siluriformes *Pseudoplatystoma coruscans* (Cardoso *et al.*, 1995; Marques *et al.*, 2008), the Characiformes *Colossoma macropomum* (Leite *et al.*, 2013), *Brycon insignis* (Isaú *et al.*, 2011), and *Brycon cephalus* (Romagosa *et al.*, 2001; De Alexandre *et al.*, 2009), among many other large-sized animals. However, those works do not cover the diversity of species considering the abundance of described species, especially of freshwater fish (3148 species described until 2018; ICMBio, 2018).

The genus *Moenkhausia* (Eigenmann, 1903), for example, includes about 90 species of freshwater fish distributed across South America in Venezuela, Guyana, and Amazonia (Froese and Pauly, 2018), and all Brazilian watersheds (Lima and Toledo-Piza, 2001). This genus belongs to the Characiformes order, and it is currently allocated to *Incertæ sedis* in the Characidae family, due to lack of detailed research about its phylogeny. Although some taxonomic studies have already been carried out (Hojo *et al.*, 2004; Benine *et al.*, 2007, 2009; Carvalho *et al.*, 2014),

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its current classification is still unclear, as most studies are limited to the description of species of the genus.

This misclassification of the species *Moenkhausia oligolepis* (Gunther, 1864) is currently under discussion due to the wide distribution of *Moenkhausia* species coexisting and exhibiting similarities of colours and patterns. For this reason, Costa (1994) and Benine and colleagues (2009) proposed *M. oligolepis* to be a complex of species. However, according to Domingos *et al.* (2014), the coexistence and similarity between species usually results in an incorrect definition of their conservation status. While it is called black tail tetra in some areas (Matos *et al.*, 2003), this species reaches around 10 cm total length when mature (Froese and Pauly, 2018). It also presents a reticulated body colour and reddish pigmentation on the dorsal margin of the eye, giving it the popular name (fire-eye tetra), and it also has a dark spot on the stalks of the caudal fin.

Therefore, this study aimed to describe the embryonic development of *M. oligolepis* under laboratory conditions to contribute knowledge on the biology and species conservation, in addition to furthering its identification and classification. The study describes the timing of typical stages after fertilization, based on external morphology, in captive individuals of *M. oligolepis*. It was found that the embryonic development lasted 14 h at 25°C, and these stages occurred similarly to that of closely related species (e.g. *Brycon gouldingi*: Faustino *et al.*, 2011; *Astyanax bimaculatus*: Weber *et al.*, 2012; *Astyanax altiparanae*: Dos Santos *et al.*, 2016).

Materials and methods

Sampling of animals

Sexually mature individuals of *M. oligolepis* were collected from streams in the Tocantins Basin, located in the interior of the Amazon Forest, in the 'Fundação Zoobotânica de Marabá' – PA (collection authorization ICMBio no. 62027-1). Nylon nets (1.10 mm, 4.75 × 1 mesh, 10 cm) were used to sample the fish, which were transported to the laboratory in 30-l plastic bags filled with water and equipped with portable aerators. The species was identified in the Laboratory of Biology and Fish Genetics at the Institute of Biosciences of the Universidade Estadual Paulista (UNESP), in Botucatu of the state of São Paulo, Brazil (voucher: 25622).

Fish acclimatization lasted 4 months in glass tanks (23 × 21 cm, capacity of 13 l of water) with aeration pumps and internal bacteriological filter. The animals were fed three times a day with commercial food (4200 kcal/kg and 28% crude protein), and the tank water was partially exchanged daily.

Breeding preparation

Four males and three females were separated in a tank that had the same dimensions of the acclimatization tanks, also designed with constant circulation of water. Those animals were submitted to a monitored photoperiod cycle of 12 h of light/dark, for 45 days. During this period, the water parameters (dissolved ammonia, nitrite, dissolved O_2, pH, and temperature) were analyzed daily. The same commercial food was offered throughout the day in three rations of 0.100 g each, totalling 0.300 g of food per day.

Induction to spawning and fertilization

On the 45th day, the animals were anaesthetised with 1 ml of Eugenol solution (20 ml of Biodynamic Eugenol in 100 ml of absolute alcohol) diluted in 500 ml of water. Both males and females were injected with carp crude pituitary extract that was macerated and diluted in 0.9% saline solution. The solution was applied in the coelomic cavity at the base of the pectoral fin using an insulin syringe (1 ml) with a needle. This step was based on the protocol of Ninhaus-Silveira *et al.* (2006), in which females received two hormonal doses: the first dose was 0.5 mg/kg body weight; and after a 12-h interval, the second dose was 5.0 mg/kg body weight. Males received a single dose of 1.0 mg/kg body weight at the same time as the second dose of females.

Embryo collection and analysis

Samples were collected at the following time intervals after fertilization: every 10 min up to 2 h post fertilization (hpf); then every 20 min up to 4 hpf: and afterwards, every 30 min until hatching. The collected embryos were fixed in a solution of 2.5% glutaraldehyde sodium phosphate buffer 0.1 M, pH 7.3, and they were observed using a trinocular stereoscope (TNE-10TN Opton). The images were captured using the TC Capture program and a digital camera (Samsung A3, 2015, 8 MP) and then processed using the CorelDRAW program (version 2018).

The embryonic development of *M. oligolepis* was classified in the standard phases (zygote, cleavage, blastula, gastrula, segmentation, and hatching) based on previous studies (Arashiro *et al.*, 2018). The temperature and parameters of the water were monitored and documented during the development of the embryos.

Results and Discussion

In this study, the embryonic development of *M. oligolepis*, a Characidae of disputed taxonomic position from the Amazon, was described up to hatching. It was found that embryonic development lasted 14 h at 25°C with the described development stage occurring at similar times as that of closely related species. The ontogenetic development in fish is sensitive to changes in temperature, as its metabolic activities can be accelerated or retarded and, therefore, can alter the rhythm of the embryonic development (Santos *et al.*, 2006; Faustino *et al.*, 2011). This period is variable among species, being as short as observed in *M. oligolepis*, or it may be even shorter as observed in *M. sanctaefilomenae*, whose embryonic development lasted 13 h (Walter, 2011). Conversely, *Prochilodus lineatus* presented embryo development time similar to that of the present study at higher temperatures (28°C) (Ninhaus-Silveira *et al.*, 2006), which made clear that each species has its own relationship with abiotic factors, this observation reflects the life history and evolutionary strategy of each species.

Egg sampling and morphology

The spawning occurred seminaturally about 2 h after the application of the last hormonal doses, and the fertilized eggs measured 0.85 ± 0.5 mm (mean ± SD) in diameter. They were demersal, spherical, and translucent after fertilization, and did not present any oil droplets. The chorion had an adhesive surface, and the perivitelline spaces measured 0.1 ± 0.02 mm (mean ± SD) (Fig. 1). The diameter of the eggs was also directly related to the reproductive strategy, as small eggs are usually found in migratory species with total spawning, while the largest eggs are observed in non-migratory species (Godinho *et al.*, 2009). The diameter of *M. oligolepis* eggs is similar to those observed by Sato *et al.* (2006) and Weber *et al.* (2012) in other small Characiformes, *Astyanax bimaculatus* and *Tetragonopterus chalceus*, respectively, and these are both rheophilic species. *Astyanax bimaculatus* also reproduces in lentic waters (Webber *et al.*, 2012).

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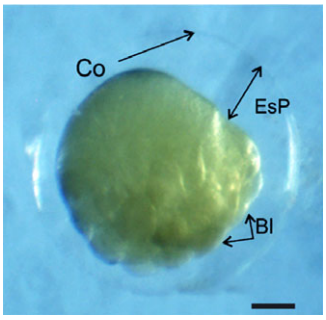

Figure 1. Morphological characteristics of *M. oligolepis* eggs. Presence of chorion (Co), perivitelline space (EsP), and initial cleavage, blastomeres (Bl). Scale bar, 0.25 mm.

It was also observed that the eggs of *M. oligolepsis* showed characteristics of adhesiveness. According to Kolm and Ahnesjö (2005), adhesive eggs are a characteristic of the species with partial spawning and parental care. Godinho and colleagues (2010) also observed higher adhesiveness in eggs of lentic species with multiple spawning, whereas lotic species presented free eggs and total spawning. Judging the characteristics of the environment in which the matrices of this study were collected, it can be suggested that *M. oligolepis* is a species that spawns in lentic waters, however it is different from other species with adhesive eggs as there was no evidence of parental care in this *M. oligolepis*.

Egg adhesion to the substrate contributes to the viability and protection of the offspring in the natural environment but, in captivity, it may cause high mortality of the embryos, as egg and embryo agglomeration impairs gas exchange between the developing embryo and the external environment. Moreover, egg adhesion can contribute to proliferation of fungi and bacteria, causing death or malformation in the embryos. Many techniques have been developed to mitigate such damage (Siddique *et al.*, 2014) such as incubators equipped with a closed water recirculation system to promote the circulation of water and embryos, therefore preventing their deposit and agglomeration at the bottom of the tank (Luz *et al.*, 2001). In the studied species, it was observed that, although the eggs fixed to each other or the aquarium walls presented strong adhesiveness to forming embryo clusters, the aerator was sufficient to keep them suspended in the water, eliminating the need for more elaborate techniques.

Another important structure in the embryological staging of fish is the chorion, as hydration of the egg causes it to expand to form the perivitelline space (Siddique *et al.*, 2014), and this will aid in embryo development, protecting it from external injuries often caused by water flow. This vulnerability makes eggs with large perivitelline spaces characteristic of species that reproduce in agitated waters. Conversely, smaller perivitelline spaces suggest eggs that spawn in calm waters, an aspect that reflects different species adaptations to their environment (Yamagami *et al.*, 1992; De Alexandre *et al.*, 2009; Ribeiro and Guimarães, 2012; Yang *et al.*, 2014). *M. oligolepis* presents pelagic eggs similar to other Characiformes such as *Acestrorhynchus* spp., *Hoplias lacerdae*, *Prochilodus* spp., and *Leporinus* sp. that were observed by Rizzo *et al.* (2002).

Embryogenesis

Phases, stages, and time of development of *M. oligolepis* embryogenesis are listed in Table 1.

Table 1. Phases and time of embryonic development in *M. oligolepis* at the temperature of 25°C

Phase	Stage	Time (h)	Figure
Zygote		0.12	2A
Cleavage	2 cell	0.20	2B
	4 cell	0.25	2C
	8 cell	0.30	2D
	16 cell	0.35	2E
	32 cell	0.45	2F
	64 cell	0.55	2G
Blastula	128 cell	1:10	2H
	256 cell	1:20	2I
	512 cell	1:30	2J
	Dome	1:40	2K
Gastrula	50% epiboly	2:00	2L
	75% epiboly	2:40	2M
	90% epiboly	3:30	2N
	95%/epiboly	4:00	2O
	Initial neurula	4:20	2P
Neurula	100% epiboly	5:30	3A
Segmentation	5 somites	5:50	3B
	8 somites	6:30	3C
	17 somites	9:30	3D
	27 somites	11:30	3E
Hatching	30 somites	14:00	3F

Zygote phase

An increase of the perivitelline space and formation of the blastodisc was observed, defining the animal and vegetal poles and evidencing a great quantity of yolk (Fig. 2A).

Cleavage phase

Cleavage followed the pattern of discoidal meroblastic division, noting the presence of 2, 4, 8, 16, 32, and 64 consecutive blastomeres (Fig. 2B–G). This phase took approximately 30 min.

Blastula phase

This phase was initiated at the sixth cleavage, doubling the number of cells in the sequences of 128, 256, and 512 blastomeres, which was achieved at 1 h 30 min after fertilization (AF). The dome phase was reached at 1 h 40 min AF, and was characterized by the organization of thousands of blastomeres in several layers at the top of the yolk (Fig. 2H–K).

Gastrula phase

This phase began approximately 2 h AF. The blastoderm cells of started the epiboly movement, moving toward the yolk and gradually evolving. At 2 h 40 min, a germinative ring was observed (Fig. 2L). At 4 h AF, 90% of the yolk was surrounded by the blastula, and the blastopore was observed (Fig. 2M–P).

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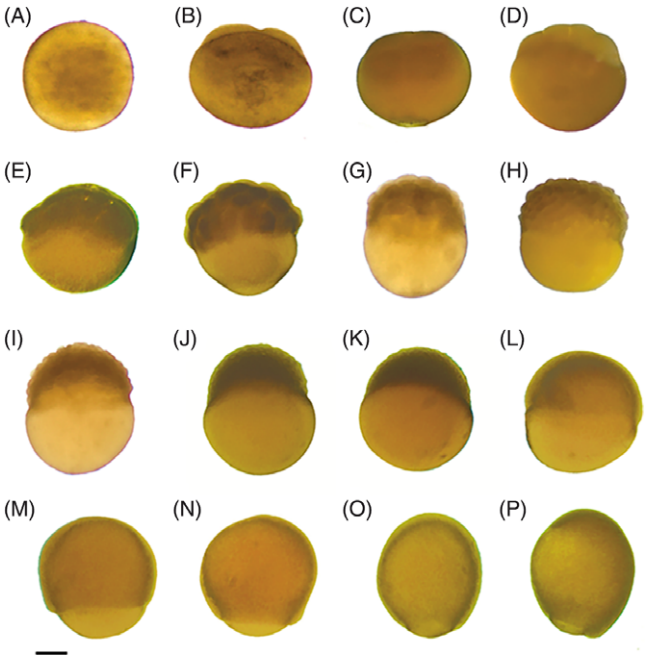

Figure 2. Embryonic development of *Moenkhausia oligolepis* after fertilization. Zygote, cleavage, blastula, gastrula, epiboly, and neurula phases. Scale bar, 0.25 mm. See Table 1 for key.

Neurula

This stage occurred at 5 h and 30 min AF. It was characterized mainly by 100% epiboly, whose blastoderm completely envelops the yolk (Fig. 3A).

Segmentation

The segmentation phase is the last phase of embryonic development. It represents the differentiation of the cephalic and caudal poles, and it also includes the appearance of somites, vesicles, and some external and internal organs of the embryo, extending until the moment of hatching. Segmentation lasted about 8 h 10 min. The embryo presented the first somite around 5 h 50 min AF, eight somites at 6 h 30 min, and at 7 h 30 min, it was possible to visualize the optical vesicle. At 7 h 40 min AF, there were 17 somites, and 8 h 10 min AF, the appearance of the Kupffer vesicle was observed, followed by the appearance of the otic vesicle at 9 h AF. At 11 h 30 min AF, there were 27 somites, and after that, there were about 30 somites just before hatching (Fig. 3B–F).

Hatching phase

The embryo presented a free tail at 12 h 30 min AF, followed by larvae hatching at 14 h AF with about 30 somites (Fig. 3F).

Considering that this is only the second embryological study of the genus *Moenkhausia*, this work brings important data about the embryology of *M. oligolepis*. It is noted that although much information has been revealed and supported, some of the data needed more detailed and elaborate assessments. The use of such data to clarify the incomplete picture in species and genus classification is encouraged. As suggested by Webber *et al.* (2012), studies like this one are important to support future studies on reproduction, phylogeny, and taxonomy.

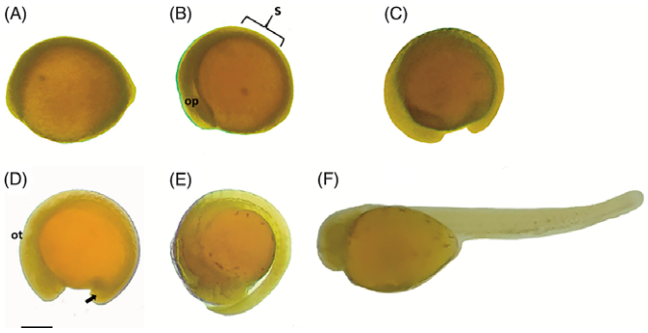

Figure 3. Embryonic development of *Moenkhausia oligolepis* after fertilization. Segmentation and hatching phases. s: somites, op: optic vesicle, ot: otic vesicle; arrow: Kupffer vesicle. Scale bar, 0.25 mm. See Table 1 for key.

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Conflict of interest. The authors declare that they have no conflict of interest.

Ethical standards. The authors assert that all procedures contributing to this work comply with the ethical standards of the relevant national and institutional guidelines on the care and use of laboratory animals.

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