Early development in the mouth-brooding cichlid fish
Satanoperca pappaterra (Perciformes: Cichlidae)

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Abstract: The Neotropical region exhibits the largest diversity of fish worldwide; however, little is known about the early development of fish species from this region. Therefore, to contribute to this knowledge, this study aimed to morphologically describe the early stages of development (eggs, larvae and juveniles) of *S. pappaterra* using morphometric and meristic traits, and to assess changes in growth rates throughout larval and juvenile development by analyzing the relationships between various morphometric traits using analytical regression models. Both juvenile and adult individuals with mouth-brooded offspring were collected along the basins of the Cuiabá and Manso Rivers in the state of Mato Grosso, Brazil between March 2000 and March 2004. After the adults were identified, the offspring were classified according to its stage (embryonic, larval or juvenile period), and various morphometric and meristic variables were individually measured (when possible). The eggs of this species are yellow in color, oval shaped, show dendritic pigmentation within their yolk, have small to moderately sized perivitelline spaces and lack a mucous membrane and oil droplets. The horizontal and vertical diameters of the sample yolks ranged from 1.43mm to 2.70mm and 1.05mm to 1.68mm, respectively. The standard length of the larval period varied from 4.30mm to 7.16mm, and the standard length of the juvenile period varied from 10.29mm to 24.57mm. Larvae exhibit yolk sacs with internal dendritic pigmentation and dark punctate pigmentation in the dorsal and ventral body regions, whereas irregular transverse spots along the flanks are observed during the juvenile period. Adhesive organs are only present during the yolk-sac stage and at the beginning of the flexion stage. The mouth is terminal during all stages of development. The myomere number varied from 22 to 29 (9 to 16 pre-anal and 10 to 16 post-anal), and the maximal numbers of fin rays and spines were as follows: dorsal, XVI+10; anal, IV+8; pectoral, 16; and pelvic, I+8. Growth analyses identified periods of important change in larval morphology (i.e., metamorphosis), particularly during the flexion and post-flexion stages and in juveniles. Therefore, the morphological development of *S. pappaterra* is consistent with the ecological requirements of this species, which primarily occurs in structured lentic environments with aquatic macrophytes. Rev. Biol. Trop. 63 (1): 139-153. Epub 2015 March 01.

Key words: ontogeny, eggs, larvae, fish, Pantanal eartheater, Paraguay River basin.

The greatest difficulty inherent to the study of freshwater ichthyoplankton is properly identifying fish eggs and larvae in their natural environments. This difficulty stems largely from the significant morphological similarities between different taxonomic groups during early stages of development (Bialetzki, Sanches, Baumgartner, & Nakatani, 1998) and because species spawn in the same areas at the same times of the year (Nakatani et al., 2001). Hence, the taxonomic characterization of early fish development could help us to better understand the ecological relationships between species during development within their natural

environments, which could yield tools for more effective environmental assessments (Oliveira, Bialetzki, Gomes, Santin, & Taguti, 2012).

Cichlidae is the second largest of the 160 characterized families within the order Perciformes, and it is composed of nearly 1 300 species worldwide and approximately 291 in South America alone (Kullander, 1998). Fish from this family exhibit parental care (generally performed by the female) and are divided into two groups: substrate spawners, which attach their eggs to a substrate and exhibit parental care by both parents, and mouth-brooders, which carry their offspring in their mouths (Ribbink, 1990). Among the substrate spawners, early development has been described in a number of species, including *Cichlasoma nigrofasciatum* (Gunther, 1868) (Martinez & Murillo, 1987); *Cichlasoma gadovii* (Regan, 1905) (Cabrera, Murillo, & Mora, 1988); *Cichlasoma dimerus* (Heckel, 1840) (Meijide & Guerrero, 2000); *Astronotus ocellatus* (Agassiz, 1831) (Nakatani et al., 2001; Paes, Makino, Vasquez, Fernandes, & Nakaghi, 2011); *Archocentrus myrnae* (Loiselle, 1997) (Puigcerver, 2007); *Amphilophus rostratus* (Gill, 1877) (Molina, 2008); *Apistogramma cacatuoides* (Hoedeman, 1951) (Alves, Rojas, & Romagnosa, 2009); *Hypsophrys nicaraguensis* (Günther, 1864) (Molina, 2011); and *Pterophyllum scalare* (Schultze, 1823) (Korzelecka-Orkisz et al., 2012). In contrast, early development in Neotropical mouth-brooders has not yet been described. Differences in the dynamics of larval and post-larval development between these two groups have been noted not only in terms of external morphology but also in terms of the maturation of several vital organs (Fishelson, 1995). According to Fishelson, the offspring of substrate spawners generally grow much faster and become self-sufficient long before mouth-brooded individuals of similar stages.

Satanoperca pappaterra (Heckel, 1840), which is commonly known as the Pantanal eartheater and locally known as 'cará' or 'acará,' is a mouth-brooding endemic species from the Amazon Basin (Rio Guaporé) and upper Paraguay River (Kullander, 2003). Within the Amazon Basin, this species co-occurs with four other species of the same genus (*Satanoperca acuticeps* (Heckel, 1840), *Satanoperca daemon* (Heckel, 1840), *Satanoperca jurupari* (Heckel, 1840) and *Satanoperca lilith* (Kullander & Ferreira, 1988), and none of these species has been characterized with respect to their early stages of development. Considering the high degree of morphological similarity within this genus as well as the spatial co-occurrence, comparative studies are required to taxonomically identify these fish during their early development. Therefore, the aims of this study were to (i) morphologically describe the early stages (eggs, larvae and juveniles) of *S. pappaterra* using morphometric and meristic traits and (ii) assess changes in the growth rates throughout larval and juvenile development by analyzing the relationships between various morphometric traits using analytical regression models.

MATERIALS AND METHODS

Study site: The samples used in this study were collected between March 2000 and March 2004 at different locations along the Cuiabá and Manso river basins (P1=14º48'27'' N - 55º38'28'' W; P2=14º52'22'' N - 55º46'28'' W; P3=14º57'07'' N - 55º42'59'' W; P4=15º06'50'' N - 55º40'38'' W; P5=15º01'20'' N - 55º32'57'' W) (Fig. 1), both of which are part of the Paraguay River hydrological basin.

Sampling: Both juveniles and mouth-brooding adults carrying eggs and/or larvae were collected using seining nets (20m length, 1cm mesh size). After capture, the adults released their offspring, which were immediately collected and placed into polyethylene bottles and fixed with 4% formaldehyde buffered with calcium carbonate.

Characterization of developmental stages: The collected individuals were separated into embryonic (early cleavage, early embryo and tail-free stages), larval (yolk-sac, flexion and post-flexion stages) and juvenile periods in accordance with the classifications proposed by
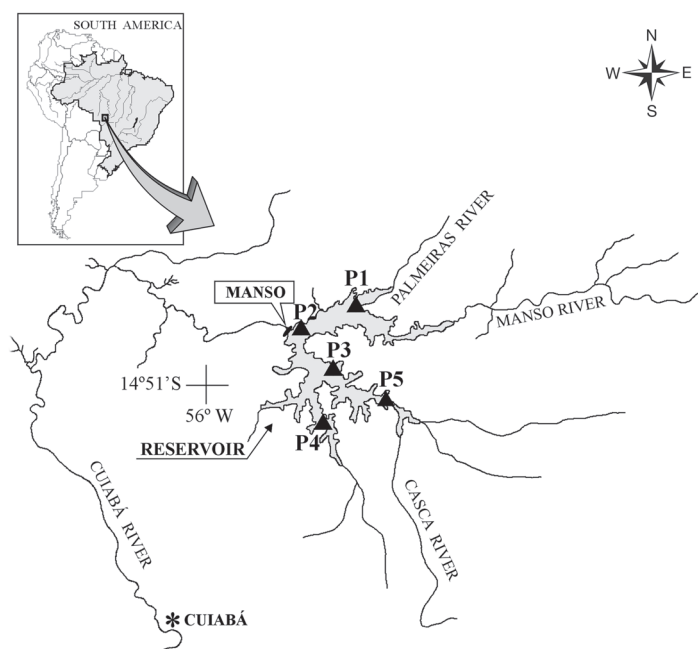
Fig. 1. Locations of the sampling points (**triangles**=P1, P2, P3, P4 and P5) along the Cuiabá and Manso river basins in the state of Mato Grosso, Brazil between March 2000 and March 2004.

Ahlstrom & Ball (1954) and modified by Nakatani et al. (2001). Each period was described based on the degree of development and occurrence of major morphological events, with representative individuals illustrated using a *camera lucida*. Individuals used in this research have been deposited in the Ichthyological Collection of the Center for Research in Limnology, Ichthyology and Aquaculture (Nupélia) at the State University of Maringá (Universidade Estadual de Maringá - UEM), Paraná, Brazil (NUP 16905 to NUP 16908 and NUP 13676).

For the morphological characterization of embryonic development, the following morphometric variables were measured (in mm) using a stereoscope equipped with an ocular micrometer: egg diameter (EgD), yolk diameter (YD) and perivitelline space (PS), with the latter categorized as narrow, moderate, large or very large based on its share of the total egg volume (Nakatani et al., 2001). For both YD and PS, the horizontal diameter was defined as the major axis corresponding to the distance between the animal and vegetal poles,

and the vertical diameter was defined as the axis with the smallest diameter. For the larvae and juveniles, the following parameters were also measured (in mm) (according to Ahlstrom, Butler, & Sumida, 1976; Nakatani et al., 2001): standard length (SL), snout length (SnL), eye diameter (EyD), head height (HH), head length (HL) body height (BH), pre-pectoral (SPcF), pre-pelvic (SPlF), pre-dorsal (SDF) and pre-anal (SAF) fin distances. Meristic characterizations were performed by counting, when possible, the number of pre- and post-anal myomeres and number of rays in the pectoral (Pc), pelvic (Pl), dorsal (D) and anal (A) fins. The body ratios for EyD, BH and HL were determined using the categories proposed by Leis & Trnski (1989).

Growth models: To identify potential ontogenic variations during the larval and juvenile periods, the morphometric variables (dependent variables) were plotted against a standard and the HL (explanatory variables), and their relationships were analyzed using

various regression models (Kováč, Copp, & Francis, 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). The significance level for the analyses was $p < 0.05$.

RESULTS

In total, 60 eggs (20 in the early cleavage, 20 in the early embryo and 20 in the tail-free stage), 88 larvae (20 in the yolk-sac, 48 in the flexion and 20 in the post-flexion stage) and 21 juveniles were analyzed. Each period is described below and illustrated in figure 2 and figure 3. Results related to morphometry, meristic counts and body ratios for the different periods are shown (Table 1, Table 2 and Table 3), and the results from the regression analyses of larval and juvenile growth are shown in table 4.

Embryonic period: In general, the eggs were yellow (apart from the internal dendritic pigmentation throughout the yolk) and oval shaped, had narrow PSs and lacked oil droplets and mucosal outer membranes (Fig. 2a and Fig. 2c). Embryos in the final stage of development were not found among the analyzed samples.

Early cleavage stage: The eggs had a mean horizontal diameter of 2.05mm and vertical diameter of 1.63mm (Table 1). The PSs ranged from narrow to moderate, with mean diameters (relative to the egg) of 6.89% horizontally and 4.86% vertically. In most cases, the egg membranes were oval shaped, which was similar to the shape of the yolk (Fig. 2a).

Fig. 2. Embryonic development of *S. pappaterra* collected from the Cuiabá and Manso river basins in the state of Mato Grosso, Brazil between March 2000 and March 2004. (**A**) Early Cleavage (1.93mm horizontal EgD and 1.67mm vertical EgD); (**B**) Early Embryo (2.07mm horizontal EgD and 1.52mm vertical EgD); and (**C**) Tail-Free (2.15mm horizontal EgD and 1.57mm vertical EgD). **EgD**=egg diameter, **PS**=perivitelline space, **BL**=blastopore, **EA**=embryonic axis, **Ta**=tail, **Ey**=eye, **Scale**=1mm.

Early embryo stage: The eggs had a mean horizontal diameter of 2.01mm and vertical diameter of 1.51mm (Table 1). The PSs ranged from narrow to moderate, with mean diameters (relative to the egg) of 9.04% horizontally and 5.54% vertically. Within the yolk, formation of the embryonic axis was evident, and it extended from one pole to the other in the form of a continuous strip that bifurcated around the blastopore (Fig. 2b).

Variables (mm)	EC (n=20)		EE (n=20)		TF (n=20)	
	Min/Max	X±SD	Min/Max	X±SD	Min/Max	X±SD
Egg diameter (horizontal)	1.93-2.18	2.05±0.07	1.93-2.15	2.01±0.06	1.98-2.28	2.07±0.07
Egg diameter (vertical)	1.55-1.75	1.63±0.05	1.40-1.68	1.51±0.07	1.25-1.70	1.53±0.09
Vitellus diameter (horizontal)	1.43-2.13	1.81±0.15	1.58-2.70	1.78±0.22	1.50-1.88	1.67±0.09
Vitellus diameter (vertical)	1.38-1.68	1.50±0.07	1.30-1.63	1.41±0.08	1.05-1.60	1.38±0.11
Perivitelline space (horizontal)	0.03-0.21	0.11±0.05	0.04-0.28	0.14±0.05	0.05-0.23	0.19±0.04
Perivitelline space (vertical)	0.01-0.75	0.11±0.15	0.00-0.09	0.05±0.03	0.00-0.14	0.07±0.04
PS/EgD (%) (horizontal)	0.00-15.48	6.89±4.05	2.56-13.92	9.04±3.21	3.66-15.66	11.23±3.76
PS/EgD (%) (vertical)	0.00-10.94	4.86±2.70	0.00-15.25	5.54±3.55	0.00-14.06	9.15±2.85

n=number of eggs analyzed, **EC**=Early Cleavage, **EE**=Early Embryo, **TF**=Tail-Free, **PS**=perivitelline space, **EgD**=egg diameter.

Tail-free stage: The eggs had a mean horizontal diameter of 2.07mm and vertical diameter of 1.53mm (Table 1). The PSs ranged from narrow to moderate, with mean diameters of 11.23% horizontally and 9.15% vertically. At this stage, it is possible to observe a distinction between the body and head of the larva along the embryonic axis. The unpigmented forming eyes, notochord and punctate pigmentation within the posterior caudal region can also be observed (Fig. 2c). In the final phase of this stage, the caudal region begins to separate from the yolk, although it remains attached.

Larval period: None of the larvae examined were in the pre-flexion stage; other stages are described below.

Yolk-sac stage: In this stage, the SL ranged from 2.00mm to 4.15mm (Fig. 3a) (Table 2). Although it is possible to observe slight flexion of the notochord, the hypural bones have not yet formed. The yolk sac features internal dendritic pigmentation and is relatively large compared with the size of the larva. The eyes are elliptical and partially pigmented, and they do not undergo further shape changes during development. The mouth and anus are closed, and the snout does not yet exhibit a differentiated nasal aperture.

Within the head, the formation of bones can be observed, particularly the opercular bones, as well as two pairs of spherical adhesive glands. The pectoral fin bud is also evident at this stage, located superiorly to the yolk sac near the head. The 'finfold' surrounds the body longitudinally from the post-cephalic dorsal region to the posterior ventral margin of the yolk sac. Dendritic pigmentation is concentrated near the adhesive glands and dispersed throughout the yolk sac and in two bands of punctate pigmentation within the dorsal and ventral regions of the body. The total number of myomeres ranges from 24 to 31 (11 to 20 pre-anal and 12 to 16 post-anal) during this stage.

Flexion stage: The analyzed larvae were between 4.30mm and 5.75mm (Fig. 3b and Fig. 3c) (Table 2). The yolk is completely absorbed by approximately 5.30mm SL. At the end of this stage, the digestive system is well developed, with the mouth in a terminal position and anus open. The elliptical eyes are fully pigmented. Adhesive glands can be observed at the beginning of this stage, with a larger pair in the dorsal region of the head and smaller pair situated roughly between the eyes. The opening of the operculum and nostrils (simple) is observed at the end of this stage at approximately 5.50mm SL. Initially, the finfold has the
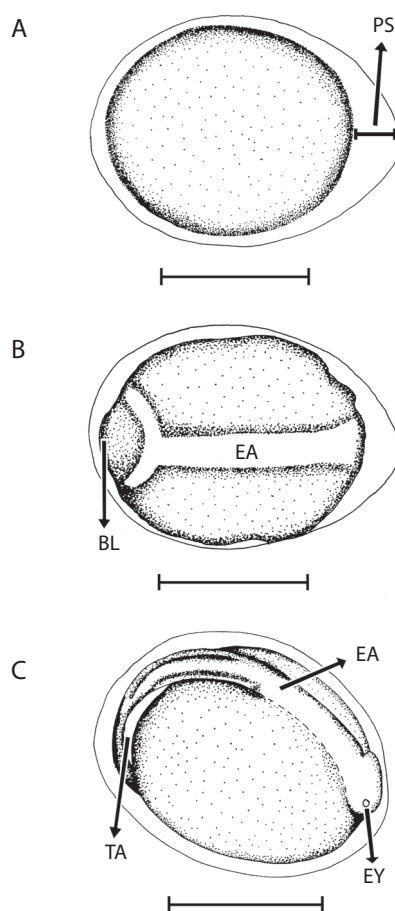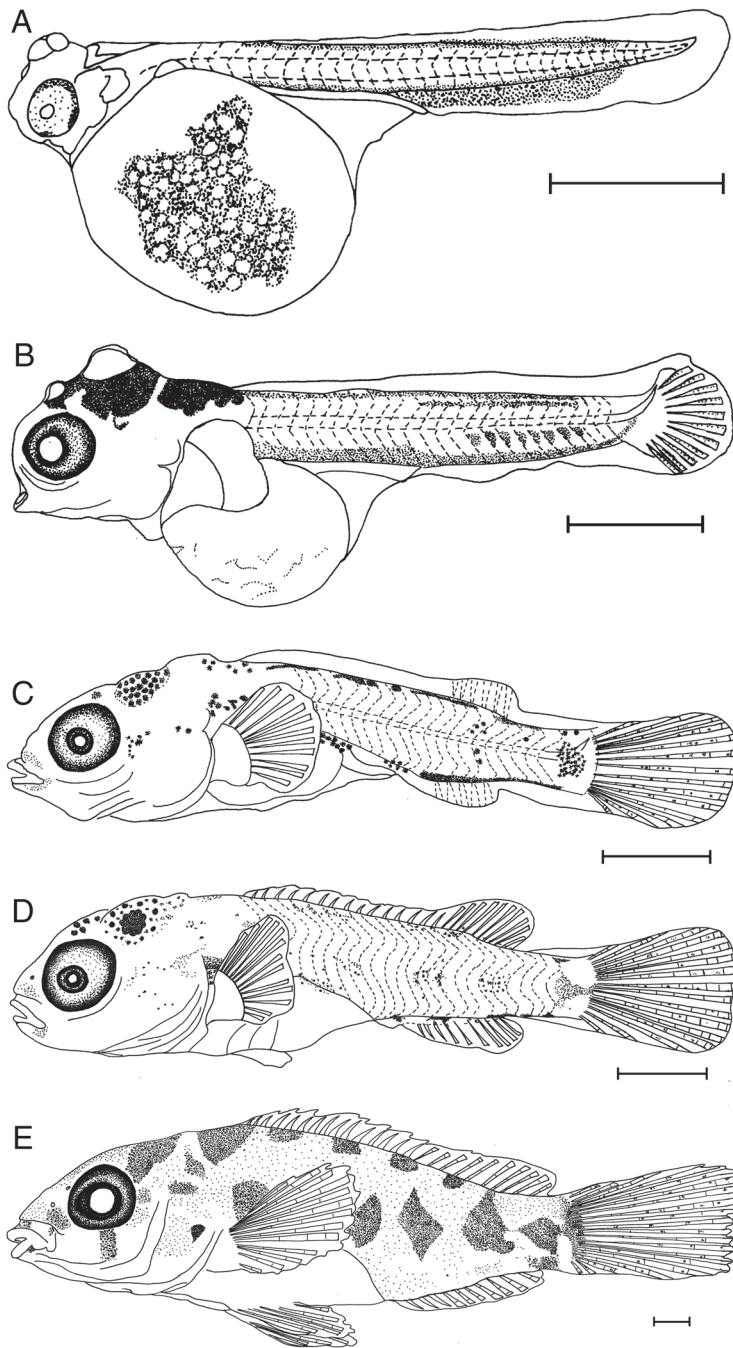
Fig. 3. Early development of *S. pappaterra* collected from the Cuiabá and Manso river basins in the state of Mato Grosso, Brazil between March 2000 and March 2004. (**A**) yolk-sac (4.05mm SL); (**B**) early flexion (5.3mm SL); (**C**) final flexion (7mm SL); (**D**) post-flexion (8.08mm SL); and (**E**) juvenile (18.4mm SL). **Scale**=1mm.

Minimum (Min), maximum (Max), mean (X) and standard deviation (SD) values for the length (mm) of the morphometric and meristic variables obtained for the larvae and juvenile *S. pappaterra* individuals

Variables (mm)	Larval Period						Juvenile Period	
	YS (n=20)		FL (n=20)		PF (n=20)		J (n=20)	
	Min/Max	X±SD	Min/Max	X±SD	Min/Max	X±SD	Min/Max	X±SD
SL	2.00-4.15	3.91±0.46	4.30-5.75	5.08±0.40	6.34-10.25	7.16±0.97	10.29-24.57	15.42±3.79
HH	0.60-0.80	0.70±0.07	0.83-1.57	1.24±0.18	1.60-2.90	1.95±0.31	2.85-6.29	4.36±0.93
HL	0.43-0.60	0.51±0.05	0.75-1.95	1.45±0.38	2.16-3.83	2.51±0.38	3.67-9.00	5.51±1.27
SnL	0.03-0.18	0.10±0.06	0.05-0.44	0.21±0.11	0.30-0.67	0.46±0.11	0.72-3.86	1.52±0.75
EyD	0.15-0.38	0.31±0.05	0.13-0.74	0.56±0.14	0.73-1.10	0.92±0.09	1.24-2.75	1.83±0.37
BH	1.48-1.68	1.57±0.05	1.17-1.74	1.46±0.15	1.67-3.00	1.99±0.36	3.10-7.71	4.93±1.10
SPcF	0.63-0.73	0.68±0.07	1.13-2.07	1.80±0.27	2.25-3.75	2.60±0.36	3.83-9.14	5.65±1.20
SPlF					2.47-4.08	2.82±0.38	4.20-8.57	5.92±1.09
SDF					2.47-3.83	2.86±0.35	3.92-8.29	5.55±1.09
SAF					2.64-9.40	4.80±1.32	6.43-16.71	10.07±2.30
Myomere								
Total	24.00-31.00	29.00±2.24	22.00-30.00	26.04±1.79	24-29	26.32±1.16		
Pre-anal	11.00-20.00	14.22±1.96	9.00-15.00	12.33±1.48	12-16	14.05±0.94		
Post-anal	12.00-16.00	15.05±1.08	12.00-16.00	13.69±1.24	10-14	12.16±1.12		
Rays								
Pc			6.00-12.00	9.04±1.80	10-14	12.20±0.95	13-16	14.76±0.62
Pl					5-6	5.71±0.49	4-8	5.43±1.08
D					8-12	9.75±1.45	8-10	9.71±0.56
A					6-8	6.9±0.45	5-8	6.48±0.81

n=number of individuals analyzed, **YS**=yolk-sac, **FL**=flexion, **PF**=post-flexion, **J**=juveniles, **SL**=standard length, **HH**=head height, **HL**=head length, **SnL**=snout length, **EyD**=eye diameter, **BH**=body height, **SPcF**=snout-pectoral fin distance, **SPlF**=snout-pelvic fin distance, **SDF**=snout-dorsal fin distance, **SAF**=snout-anal fin distance, **Pc**=pectoral, **Pl**=pelvic, **D**=dorsal, **A**=anal. Missing measurements are a result of incompletely developed larvae.

same pattern as in the previous stage; however, the finfold becomes partially absorbed during development, outlining the dorsal and anal fins, which begin to show rays at approximately 5.58mm SL. With respect to the caudal fin, rays begin to form at 4.7mm SL, and beginning at 5.25mm SL, the rays begin to segment. The first rays (6 to 12 rays) of the pectoral fin are visible at approximately 5.67mm SL. Development of the pelvic fin bud begins at approximately 5.75mm SL. Dendritic pigments are dispersed throughout the yolk sac, whereas punctate pigments are concentrated near the adhesive glands and median longitudinal lines of the dorsal and ventral regions of the larvae. Compared to the previous stage, these pigment lines become discontinuous over the course of

development. At the end of this stage, concentrations of pigment appear in the upper portion of the head, inter-orbital region and above the stomach and caudal peduncle; punctate pigment can also be observed on the mouth and operculum. The total number of myomeres varies from 22 to 30 (9 to 15 pre-anal and 12 to 16 post-anal) during this stage.

Post-flexion stage: The SL of the samples ranged from 6.34mm to 10.25mm (Fig. 3d) (Table 2). By this stage, the digestive system has formed (visible by transparency), and an anal opening is located medially to the body axis. The eyes are elliptical and pigmented, and the operculum is defined. Nasal apertures are simple. The finfold is fully absorbed, and

the dorsal and anal fins have defined shapes, with the onset of ray segmentation beginning at approximately 7.0mm SL. All rays of the caudal fin are segmented. The dorsal fin exhibits between XIII to XV spines and 10 to 12 rays, whereas the anal fin has III spines and 6 to 8 rays. From 6.67mm SL onward, the pectoral fin exhibits between 10 and 14 fully segmented rays. At the beginning of this stage, the pelvic fin is present as a bud, whereas after 7.76mm SL, rays begin to form (varying between 5 and 6) with early segmentation. Some regions of punctate pigmentation can be observed around the mouth, between the eyes and in the posterior dorsal region of the head, lobes of the head and operculum region. The punctate pigmentation pattern of the body changes over the course of development. At the beginning of this stage, 4 to 6 spots of pigment concentration are present near the dorsal region, and 4 to 5 spots are present along the body (above the stomach near the caudal region). At the end of this stage, the pigment concentration above the stomach becomes elongated longitudinally, and the remaining spots exhibit rounded shapes. Because of increased body mass and pigmentation, it was not possible to count myomeres during this stage.

Juvenile period: The SL of the samples ranged from 10.29mm to 24.57mm (Fig. 3e) (Table 2). The eyes are elliptical, and the nasal apertures are simple. In this period, individuals already possess ctenoid scales, and all of the morphological features are fully formed and adult-like. The dorsal fin exhibits between XIV to XVI spines and 8 to 10 rays, the anal fin exhibits between III to IV spines and 8 to 10 rays, the pectoral fin exhibits between 13 to 16 rays, and the pelvic fin exhibits I spine and 4 to 8 rays. The pigmentation pattern is similar to that observed during the post-flexion stage, with the addition of increased numbers of chromatophores and the formation of transverse pigment spots throughout the body.

Body ratios: Three variables were analyzed over the course of ontogenic development and standardized relative to the HL. Head height (HH) decreased during development and ranged from 138.03% to 79.49%. Snout length (SnL) decreased between the yolk-sac and flexion stages (20.74% and 13.95%, respectively) and increased during the two remaining stages (18.40% and 26.91%, respectively). Eye diameter (EyD) increased during each larval stage, ranging from moderate to large (25.00% to 76.47% during yolk-sac; 28.70% to 40.57% during post-flexion; and 30.56% to 38.10% during juvenile); however, its proportions decreased over the course of development (mean of 61.86% during yolk-sac and 33.44% during juvenile) (Table 3).

Six other variables were analyzed relative to SL. Head length (HL) showed an increase in relation to SL, ranging from small during the yolk-sac stage to large during the post-flexion stage (13.85% to 37.07%, respectively). Body height (BH) remained moderate to very large during the yolk-sac stage (36.88% to 77.5%) and moderate during the flexion through juvenile stages (varying between 28.96% and 32.02%). Snout-pectoral fin distance (SPcF) increased throughout all of the stages, ranging from 16.48% to 37.07%, whereas SP1F distance did not significantly change (39.52% during post-flexion vs. 39.07% during juvenile). Decreases in the SDF and SAF distances were observed (40.01% to 36.44% and 67.31% to 65.69%, respectively) (Table 3).

Growth models: With respect to the body growth analyses, SnL and HH showed discontinuous isometric growth (piecewise linear regression) relative to HL (from 0.50mm and 1.87mm, respectively) during development (Table 4); in particular, we observed a change in growth rate during the post-flexion stage (Appendix). Based on the slopes of the data, these variables showed higher growth rates after the breakpoint, increasing from 0.17mm to 0.37mm for SnL and from 0.54mm to 0.75mm for HL (Table 4). Eye diameter (EyD) showed continuous isometric growth (linear regression), meaning that EyD showed constant growth throughout the course of development.

TABLE 3
Minimum (Min), maximum (Max), mean (X) and standard deviation (SD) values for the body ratio (%) of the
morphometric and meristic variables from the analyzed *S. pappaterra* individuals

Relations	Larval Period						Juvenile Period	
	YS (n=20)		FL (n=20)		FP (n=20)		J (n=20)	
	Min/Max	X±SD	Min/Max	X±SD	Min/Max	X±SD	Min/Max	X±SD
HH/HL	109.09-170.59	138.03±17.8	64.99-130.00	88.87±15.3	70.68-86.46	77.70±4.2	69.84-93.96	79.49±5.4
SnL/HL	4.76-41.18	20.74±12.1	4.31-23.86	13.95±4.9	12.50-26.68	18.40±3.6	18.78-62.89	26.91±9.5
EyD/HL	25.00-76.47	61.86±11.1	13.89-50.00	39.20±5.7	28.70-40.57	37.01±2.8	30.56-38.10	33.44±1.9
HL/SL	10.49-25.61	13.85±3.5	16.07-36.82	28.13±5.6	31.83-37.97	35.06±1.6	24.54-38.98	35.96±3.2
BH/SL	36.88-77.50	41.27±8.9	22.03-37.09	28.96±4.6	24.88-30.70	27.81±1.8	24.05-35.00	32.02±2.5
SPcF/SL	15.06-17.90	16.48±2.0	29.22-39.26	34.74±2.3	33.58-42.54	36.43±1.8	26.38-46.18	37.07±3.7
SPlF/SL	-	-	-	-	35.57-44.08	39.52±1.9	28.77-49.58	39.07±4.4
SDF/SL	-	-	-	-	37.00-43.54	40.01±1.9	27.00-39.69	36.44±2.9
SAF/SL	-	-	-	-	40.62-140.30	67.31±18.5	47.24-71.88	65.69±5.1

n=number of individuals analyzed, **YS**=yolk-sac, **FL**=flexion, **PF**=post-flexion, **J**=juveniles, **HH**=head height, **HL**=head length, **SnL**=snout length, **EyD**=eye diameter, **BH**=body height, **SL**=standard length, **SPcF**=snout-pectoral fin distance, **SPlF**=snout-pelvic fin distance, **SDF**=snout-dorsal fin distance, **SAF**=snout-anal fin distance. Missing measurements are because of incompletely developed larvae.

TABLE 4
Mathematic and statistical values of the linear (L), quadratic (Q) and piecewise linear (S) regression analyses of the
morphometric variables obtained relative to the head and standard length of the *S. pappaterra* larvae

Relation	R²			F Test			BM	BP	a1	b1	a2	b2	n
	L	Q	S	Q/L	S/Q	S/L							
HH/HL	0.98	0.97	0.99	-24.20*	95.12*	24.61*	S	1.87	**0.54**	**0.46**	0.75	0.23	109
SnL/HL	0.83	0.86	0.85	21.00*	-4.00*	7.99*	S	0.50	**0.17**	**-0.02**	0.37	-0.52	107
EyD/HL	0.98	0.98	0.98	-29.95*	49.92*	2.95	L	0.83	**0.29**	**0.16**	0.30	0.20	108
HL/SL	0.95	0.92	0.96	-29.55*	106.92*	23.78*	S	2.24	**0.60**	**-1.68**	0.34	0.21	109
BH/SL	0.94	0.94	0.97	-0.09	88.22*	44.03*	S	2.25	**0.041**	**1.33**	0.31	0.15	108
SPcF/SL	0.95	0.95	0.96	2.46	15.01*	9.02*	S	3.29	**0.44**	**-0.56**	0.29	1.22	65
SPlF/SL	0.93	0.94	0.96	10.15*	15.04*	14.52*	S	4.40	**0.39**	**0.04**	0.22	2.71	41
SDF/SL	0.95	0.96	0.97	14.11*	2.45	8.56*	Q	-	**-0.005**	**0.45**	-	-	41
SAF/SL	0.88	0.89	0.94	1.30	28.99*	15.63*	S	7.50	**0.649**	**-0.10**	0.36	5.02	41

R²=coefficient of determination, **BM**=best model, **BP**=breakpoint (mm), **a** and **b**=regression parameters (a, slope coefficient; b, linear coefficient), **n**=number of individuals analyzed, **HH**=head height, **HL**=head length, **SnL**=snout length, **EyD**=eye diameter, **SL**=standard length, **BH**=body height, **SPcF**=snout-pectoral fin distance, **SPlF**=snout-pelvic fin distance, **SDF**=snout-dorsal fin distance, **SAF**=snout-anal fin distance, **(*)**=p<0.05, **bold**=values of the significant regressions.

For the variables related to SL, the results indicated that HL, BH and the SPcF, SP1F, and SAF distances showed discontinuous isometric growth during development (breakpoints=2.24mm, 2.25mm, 3.29mm, 4.40mm and 7.50mm, respectively) (Table 4 and Appendix). With the exception of BH, which showed increased growth during the post-flexion stage, the other variables decreased relative to growth rate at the beginning of either the flexion (for HL and SP1F and SAF distances) or juvenile (for SP1F distance) stages. The SDF distance showed quadratic development, meaning that it showed variable growth

that initially increased and then decreased (concave-down parabola, a1=-0.01) (Table 4 and Appendix).

DISCUSSION

The identification of ontogenic structural traits and determining their morphological changes during development is highly relevant to taxonomic studies involving fish eggs and larvae. These characteristics often provide significant information pertaining to the reproductive strategies of a species. For example, large eggs with narrow PS, such as those produced by *S. pappaterra*, are indicative of species with long larval development times (Vazzoler, 1996) and parental care (Nakatani et al., 2001). Among the cichlid species described thus far, it was not possible to define a pattern with respect to EgD. Substrate spawners (*C. nigrofasciatum,* Martinez, & Murillo, 1987); *H. nicaraguensis* (Molina, 2011); *A. rostratus* (Molina, 2008); and *Amphilophus alfari* (Meek, 1907) (Molina, 2010) produce eggs with similar dimensions to those of *S. pappaterra*, with the eggs varying from 2.00mm to 2.25mm along the horizontal axis and from 1.55mm to 1.72mm along the vertical axis; *C. dimerus* (Meijide & Guerrero, 2000) is an exception and produces smaller eggs (1.65mm±0.05mm horizontal diameter and 1.25mm±0.05mm vertical diameter). With respect to mouth-brooders, the eggs of *Oreochromis mossambicus* (Peter, 1852) are significantly larger than those of *S. pappaterra*, with a horizontal diameter of 3.04mm±0.20mm and vertical diameter of 2.19mm±0.16mm (Holden & Bruton, 1992). Therefore, the dimensions of *S. pappaterra* eggs are more similar to those of previously characterized substrate spawners than mouth-brooders. According to Kuwamura and Mihigo (1988) mouth-brooders produce fewer eggs that are of a larger size than substrate-brooders, and their young begin exogenous feeding later and at a more developed stage than the young of substrate-brooders.

Within the family Cichlidae, internal pigmentation of the yolk during the embryonic period appears to be a reliable taxonomic characteristic of this group. For example, *A. ocellatus,* which was described by Nakatani et al. (2001) and Paes et al. (2011), shows strong pigmentation within the yolk sac from the embryonic period until full absorption, which is similar to what was observed for *S. pappaterra*; the same pigmentation occurs during the embryonic stages of the species *C. gadovii* (Cabrera et al. 1988)), *C. dimerus* (Meijide & Guerrero, 2000) and *Oreochromis niloticus* (Linnaeus 1758) (Nakatani et al., 2001; Fujimura & Okada, 2007), although the pigmentation is less intense.

Characterizing the shape and distribution of pigmentation is also widely used in taxonomic studies to identify larvae and juveniles (Nascimento & Araújo-Lima, 1993; Meijide & Guerrero, 2000; Godinho, Santos, & Sato, 2003; Oliveira et al., 2012). In the cichlids *A. ocellatus* (Nakatani et al., 2001; Paes et al., 2011), *O. niloticus* (Nakatani et al., 2001; Fujimura & Okada, 2007), *C. nigroasciatum* (Martinez & Murillo, 1987), *H. nicaraguensis* (Molina, 2011) and *S. pappaterra*, the presence of dendritic pigments in the upper region of the head at the onset of the larval period appears to be a common trait. With respect to body pigmentation, *S. pappaterra* larvae differ from other species by the presence of pigmented regions in the dorsal and ventral regions. At the beginning of the juvenile period, *S. pappaterra* has 5 or 6 transverse spots, *C. nigrofasciatum* has 8 or 9 transverse spots (Martinez & Murillo, 1987) and *O. niloticus* has 7 transverse spots (Nakatani et al., 2001; Fujimura & Okada, 2007). In contrast, *H. nicaraguensis* does not have spots on its body and shows only a blotch on the caudal peduncle (Molina, 2011), whereas *A. ocellatus* shows intense pigmentation throughout its entire body as well as between the rays of its fins (Nakatani et al., 2001; Paes et al., 2011).

From an ecological perspective, pigmentation patterns may play protective roles against predation. Therefore, the absence of pigmentation on the bodies of larvae during early developmental stages suggests that they do not require camouflage, which is perhaps because

they are cared for by their parents. However, as larvae continue to develop (post-flexion larvae and juveniles), pigmentation increases and bands appear, allowing larvae to camouflage themselves in their environment. For *A. ocellatus*, Machado-Allison (1987) observed that the larvae develop a highly disruptive pigmentation pattern in natural environments, which allows a perfect camouflage against predators when the larvae are hidden among macrophyte roots. Indeed, this behavior has been observed in larvae from a variety of species (e.g., *Hoplias malabaricus, Hoplosternum littorale* and *Prochilodus lineatus*), which has been described by Nakatani, Baumgartner and Cavicchioli (1997) and Nakatani, Bialetzki, Baumgartner, Sanches and Makrakis (2004).

With respect to larval development, a slight flexion of the notochord could be observed during the yolk-sac stage prior to the formation of the hypural bones in *S. pappaterra*. This phenomenon occurs extremely early and is unusual at this stage of development compared with other species. In addition, of the analyzed larvae, specimens in the pre-flexion stage were not found. Therefore, we believe that the pre-flexion stage in *S. pappaterra* may be short or even absent, which could be useful for identifying larval individuals.

The presence of adhesive glands is also an important characteristic for species identification. For example, *C. dimerus* (Meijide & Guerrero, 2000), *A. ocellatus* (Nakatani et al., 2001; Paes et al., 2011) and *H. nicaraguensis* (Molina, 2011) exhibit three pairs of adhesive glands – two pairs on the upper region and a third on the frontal region of the head – whereas *S. pappaterra* possesses two pairs – a single pair of glands on the upper region of the head and another on the frontal region. Jones (1972) reported that the larvae of certain substrate-spawner species have three pairs of adhesive glands on their heads, whereas mouth-brooder larvae possess only rudimentary glands. Therefore, it is likely that the single pair of adhesive glands possessed by *S. pappaterra* is rudimentary, although this was not shown by our study. Within the family Cichlidae, *S. pappaterra*

differs from *O. niloticus* (Nakatani et al., 2001; Fujimura & Okada, 2007) by the lack of adhesive glands. In sedentary species and those with parental care, these organs play a protective role by preventing the dispersal of larvae, leading to better parental care. Meijide and Guerrero (2000) reported that within their first five days, *C. dimerus* larvae attach themselves to substrates using mucous secretions released by their adhesive organs. In *S. pappaterra*, these organs are likely used by larvae to attach themselves within the mouth of their parent when threatened.

Myomere number is another widely used characteristic in identifying fish larvae, which can be useful up to and including the species level. Nevertheless, this characteristic is rarely reported in studies, hindering the utility of comparative analyses. With respect to the larvae of described cichlids species, we could only find mention of this characteristic in the literature for *A. ocellatus* (Nakatani et al., 2001). *Satanoperca pappaterra* possesses 22 to 30 myomeres (9 to 15 pre-anal and 12 to 16 post-anal), which is similar to the 28 to 30 myomeres (13 to 14 pre-anal and 14 to 16 post-anal) observed in *A. ocellatus* larvae. Therefore, the use of this trait for differentiating between these two species would only be effective if used in conjunction with other traits.

Analysis of the morphological ontogeny of *S. pappaterra* larvae and juveniles revealed that of seven of the nine variables considered (SnL, HH, HL, and BH as well as SPcF, SP1F and SAF distances) showed variable growth rates (i.e., breakpoints), particularly during the flexion and post-flexion stages and in juveniles. According to Kováč et al. (1999), a breakpoint can be considered significant if it is associated with certain morphological, physiological and/or survival events. In this case, changes in head morphology during ontogenic development may reflect changes in the ecology of the species because this breakpoint (i.e., increase in growth rate) coincides with changes in the feeding habits of *S. pappaterra*, as described by Cassemiro, Rangel, Pelicice and Hahn (2008).

Finally, with respect to body-related changes, these are likely associated with increased locomotion during development (Kováč et al., 1999). Furthermore, Gatz Jr. (1979) proposed that body height is inversely related to maximal water velocity and directly related to the ability to perform vertical maneuvers and rotate around the body axis. Therefore, the morphological development of *S. pappaterra* is consistent with the ecological requirements of this species, which primarily occur in structured lentic environments with aquatic macrophytes (Casatti, Mendes, & Ferreira, 2003).

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RESUMEN

Desarrollo temprano en el pez cíclido *Satanoperca pappaterra* **(Perciformes: Cichlidae)**. La región Neotropical exhibe la mayor diversidad de peces en todo el mundo. Sin embargo, poco se sabe sobre el desarrollo temprano de las especies de peces de esta región. Para contribuir a este conocimiento, este estudio tuvo como objetivo describir morfológicamente las primeras etapas de desarrollo (huevos, larvas y juveniles) de *S. pappaterra* usando rasgos morfométricos y merísticos. Además de evaluar los cambios en las tasas de crecimiento en el desarrollo larval y juvenil, mediante el análisis de las relaciones entre los diferentes rasgos morfométricos utilizando modelos de regresión analíticos. Tanto los individuos juveniles y adultos con crías de incubación bucal se recogieron a lo largo de las cuencas de los ríos Cuiabá y Manso en el estado de Mato Grosso, Brasil, entre marzo 2000 y marzo 2004. Después de identificar los adultos, las crías se clasificaron de acuerdo a su etapa (embrionaria, período larval o juvenil), y diversas variables morfométricas y merísticas se midieron de forma individual (cuando fue posible). Los huevos de esta especie son de color amarillo, ovalados, muestran pigmentación dendrítica dentro de su yema, tienen espacios perivitelinos de tamaño pequeño a moderado y carecen de una membrana mucosa y gotas de aceite. Los diámetros horizontales y verticales de las yemas oscilaron entre 1.43-2.70mm y 1.05-1.68mm, respectivamente. La longitud estándar del período larval varió de 4.30-7.16mm, y la longitud estándar del período juvenil varió entre 10.29-24.57mm. Las larvas exhibieron sacos vitelinos con pigmentación dendrítica interna y pigmentación puntiforme oscura en las regiones dorsal y ventral del cuerpo, mientras que se observaron manchas transversales irregulares a lo largo de los flancos durante el periodo juvenil. Órganos adhesivos solo estan presentes durante la etapa de saco vitelino y al comienzo de la etapa de flexión. La boca es terminal durante todas las etapas de desarrollo. El número de miomeros varió entre 22 y 29 (9 a 16 pre-anal y 10 a 16 post-anal), y los números máximos de radios de las aletas y espinas fueron los siguientes: dorsal, XVI+10; anal, IV+8; pectoral, 16; y pélvica, I+8. El análisis del crecimiento identificó periodos de cambios importantes en la morfología larval (es decir, la metamorfosis), especialmente durante las etapas de flexión y post-flexión y en los juveniles. Por lo tanto, el desarrollo morfológico de *S. pappaterra* es consistente con las exigencias ecológicas de esta especie, que se encuentran principalmente en ambientes de estructura léntica con macrófitos acuáticos.

Palabras clave: ontogenia, huevos, larvas, peces, incubación bucal, Río Paraguay.

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APPENDIX

$y_1 = 0.46 + 0.54x$ ($r^2 = 0.91$, p = 0.00)
$y_2 = 0.23 + 0.75x$ ($r^2 = 0.96$, p = 0.00)

A — Head height (mm) vs Head length (mm)

$y_1 = 0.02 + 0.17x$ ($r^2 = 0.75$, p = 0.00)
$y_2 = 0.52 + 0.37x$ ($r^2 = 0.64$, p = 0.00)

B — Snout heigth (mm) vs Head length (mm)

$y_1 = 0.14 + 0.31x$ ($r^2 = 0.98$, p = 0.00)

C — Eye diameter (mm) vs Head length (mm)

$y_1 = -1.68 + 0.60x$ ($r^2 = 0.79$, p = 0.00)
$y_2 = 0.21 + 0.34x$ ($r^2 = 0.92$, p = 0.00)

D — Head length (mm) vs Standard length (mm)

$y_1 = 1.33 + 0.04x$ ($r^2 = 0.06$, p = 0.03)
$y_2 = 0.15 + 0.31x$ ($r^2 = 0.91$, p = 0.00)

E — Body height (mm) vs Standard length (mm)

$y_1 = -0.56 + 0.42x$ ($r^2 = 0.86$, p = 0.00)
$y_2 = 1.22 + 0.29x$ ($r^2 = 0.80$, p = 0.00)

F — Snout-pectoral fin distance (mm) vs Standard length (mm)

$y_1 = 0.04 + 0.39x$ ($r^2 = 0.95$, p = 0.00)
$y_2 = 2.71 + 0.22x$ ($r^2 = 0.67$, p = 0.00)

G — Snout-pelvic fin distance (mm) vs Standard length (mm)

$y_1 = -0.38 + 0.51x - 0.01x^2$ ($r^2 = 0.67$, p = 0.00)

H — Snout-dorsal fin distance (mm) vs Standard length (mm)

$y_1 = -0.10 + 0.65x$ ($r^2 = 0.85$, p = 0.00)
$y_2 = 5.02 + 0.36x$ ($r^2 = 0.61$, p = 0.00)

I — Snout-anal fin distance (mm) vs Standard length (mm)

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