

Reproductive plasticity of *Hypostomus affinis* (Siluriformes: Loricariidae) as a mechanism to adapt to a reservoir with poor habitat complexity

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ABSTRACT. In this work we describe the gonad morphology and spawning season of *Hypostomus affinis* (Steindachner, 1877) in a tropical reservoir based on 55 males and 125 females. Our aim was to assess eventual adaptations in reproductive tactics developed by this riverine species inhabiting an oligotrophic reservoir with low habitat complexity, few rocks and few other preferred consolidated substrata. We described the stages of cells of reproductive lineage, gonadal development and some reproductive traits which were compared with information in the available literature. Cells from the spermatogenic lineage were spermatogonia, spermatocytes, spermatids and spermatozoa, and cells from the oocytarian lineage were primary oocytes, previtellogenic oocytes, cortical vesicle oocytes and yolk globules or vitellogenic. Five stages were described for the males/females according to the distribution of oocytes and spermatogenic lineage cells: resting; initial maturation; advanced maturation; partially spent/spawned; totally spent/spawn. Females outnumbered males and reached larger size. Synchronic ovary development in two groups was found with diameter of mature oocytes ranging from 2 to 3.35 mm. Indication of early maturation, a longer reproductive period and the production of smaller eggs in small clutches seems to be features of the reservoir population not found in riverine systems. Such changes in tactics may indicate a shift to an opportunistic strategy, helping the population to withstand environmental constraints and to succeed in this oligotrophic and poorly structured reservoir.

KEY WORDS. Brazil; fish reproduction; reproductive biology; reservoirs; tactics.

Knowledge on the reproductive strategy and tactics such as sex ratio, gonadal development and breeding season are essential in order to obtain a comprehensive understanding of the population dynamics of any fish species (WINEMILLER 1989, WOOTTON 1989, LASSALA & RENESTO 2007, TAMADA 2009). The balance between the advantages and disadvantages in the allocation of energy dictates the reproductive strategy and its variations (tactics). Some studies have demonstrated the plasticity of reproductive strategies in fishes confronted with changing environmental conditions, food availability and predation pressure (SUZUKI *et al.* 2000, HARDIE *et al.* 2007). Therefore, species widely distributed in different types of changeable habitats need to be investigated in order to assess eventual change in their reproductive traits.

Hypostomus affinis (Steindachner, 1877) is a detritivorous species from the Paraíba do Sul River basin that has successfully adapted to the Lajes Reservoir (DUARTE & ARAÚJO 2000), an oligotrophic environment constructed between 1905 and 1908, surrounded by well-preserved stretches of Atlantic rainforest (SANTOS *et al.* 2004). Unlike most reservoirs, the Lajes Reservoir

was built by damming only small streams with small fish adapted to high altitudes in the Atlantic Forest. The reservoir has low habitat complexity. The unprotected shoreline is composed mainly of bare soil, lacking consolidated substratum, and harboring only a few shelters due to the lack of vegetation, which was cut prior to the construction of the dams (ARAÚJO & SANTOS 2001). A large amount of the ichthyofauna in the Lajes Reservoir colonized the impounded system or was introduced into it, one of the oldest of this kind in Brazil (SANTOS *et al.* 2008).

Studies on the reproductive biology of *H. affinis* in the Paraíba do Sul River encompass sex ratio (MAZZONI & CARAMASCHI 1995), ovarian development, fecundity and spawning season (MAZZONI & CARAMASCHI 1997). They concluded that this species adopts an equilibrium (*sensu* WINEMILLER) reproductive strategy characterized by a suite of attributes associated with parental care, maturation, large eggs and seasonal reproduction. *Hypostomus affinis* is less abundant than other species in the Lajes Reservoir (ARAÚJO & SANTOS 2001) such as the Siluriformes *Loricariichthys castaneus* (Castelnau, 1855), *Trachelyopterus*

striatulus (Steindachner, 1877) and *Rhamdia quelen* (Quoy & Gaimard, 1824), the Characiformes *Astyanax paraguayae* Eigenmann, 1908 and *Oligosarcus hepsetus* (Cuvier, 1829), and the Perciformes *Cichla kelberi* Kullander & Ferreira, 2006 and *Tilapia rendalli* (Boulenger 1897).

The shortage of rocks and other preferable consolidated substrata for *H. affinis* in the Lajes Reservoir is a major environmental constraint that probably limits fish population densities (DUARTE & ARAÚJO 2000). POWER (1983) reported that loricariid catfish were six to seven times denser in sunny pools (where algae grew about seven times faster) than in shaded pools. LOWE McCONNELL (1963) identified many species of *Hypostomus* Lacepède, 1803 as common in small tributary environments with rocky bottoms in the hydrographic basin of the Rupununi River, British Guyana. Several species of *Hypostomus* known for their association with fast flowing environments are bottom-dwellers, feeding on the attached algae on rocky substratum (BUCK & SAZIMA 1995, GARAVELLO & GARAVELLO 2004); during the day, individuals remain under rocks or submerged logs (WEBER 2003). POWER (1990) and ANTONIASSI *et al.* (1998) observed the environmental preferences of *Hypostomus* species for the clean and running waters of the large Brazilian rivers, and reported that this species can survive damming. Furthermore, MAZZONI *et al.* (2010) reported that species of *Hypostomus* are normally classified as grazers, frequently inhabiting fast flowing streams in benthic areas close to rock substratum, and/or submerge wood. According to LOWE-McCONNELL (1963) species of *Hypostomus* give parental care and have low fecundity, but their reproductive strategy is rather unknown.

In this study we describe features of the reproductive biology of *H. affinis* and assess the tactics that this species uses to succeed in the Lajes Reservoir, a lentic, low structured impoundment where the preferred habitat of the species (rocks, stones and gravel) are scarce. We hypothesized that some of the reproductive tactics (e.g., sex ratio, size of oocytes, oocytes development) of our population differ from the equilibrium strategies, reported for most loricariid Siluriformes.

MATERIAL AND METHODS

The Lajes Reservoir (22°42'-22°50'S, 43°53'-44°05'W) is a major impoundment in the state of Rio de Janeiro, located at 415 m above mean sea level in the upper slopes of the Cordilheira do Mar, in southeastern Brazil. It was built between 1905 and 1908 to generate energy and has an area of 30 km² of well preserved oligotrophic system (SOARES *et al.* 2008). This reservoir has low concentrations of nitrogen (< 10 µg·L⁻¹), phosphate (< 120 µg·L⁻¹) and chlorophyll α (< 2.5 µg·L⁻¹) with a high water residence time (286 days) (SANTOS *et al.* 2004). The altitude of the reservoir and the tropical humid climate determine two distinct seasons: a wet season, from late spring to early autumn; and a dry season, from late autumn to spring (BARBIERI & KRONENBERG 1994). Surface water temperature ranges from 15.3 to 30.6°C, pH

between 6 and 8, dissolved oxygen is higher than 4.7 mg·l⁻¹ and Secchi transparency averages 2.30 m \pm 0.05 (ARAÚJO & SANTOS 2001). Fluctuation in rainfall combined with a regulated outflow results in peaks in water level in May-June, one or two months after the peak of rainfall (SANTOS *et al.* 2004). Differences in water level usually range between 3-6 m, but in extremes of flood and drawdown events can reach up to 12 m (SANTOS *et al.* 2004).

A total of 180 specimens (125 females and 55 males) were examined. Fish were collected monthly from January to December 1994 with gill nets (30 x 4 m, 3-8 cm stretched mesh size). All individuals were sexed and their total length (TL, to the nearest 0.1 mm) and total body mass (BM, to the nearest 0.1 g) were recorded. Gonads were removed and assigned to a given developmental stage, based on shape, size, weight, color and degree of blood irrigation; however, gonads were ultimately classified as either immature (1, juveniles and inactive stages); initial maturation (2a); advanced maturation (2b); partially spawned/spent (4a); and totally spawned/spent (4b); according to BAZZOLI & GODINHO (1991). Mature stages (3) are ephemeral and fish tend to release spermatozoa/oocytes when captured, being therefore hard to find (RIZZO *et al.* 2002). The diameter of oocytes was measured in a stereomicroscope fitted with an ocular micrometric (precision 0.001 mm). A cross-section from the posterior part of the gonads was fixed in Bouin solution for 4-8 hours and submitted to ordinary histological techniques. Preserved ovaries were embedded in paraffin, sectioned at 5-7 µm thickness, and stained with hematoxylin and eosin. Histological identification of the various maturity stages were determined according to germinative cellular types for females (i.e. presence/absence of different types of oocytes; whether organized by ovarian lamellae or not) and males (presence/absence of seminiferous tubules, presence/absence of spermatozoa).

The annual gonadal cycle was determined by the variations in the gonadosomatic index (GSI) = 100 (GM \times BM⁻¹), where GM is total gonad mass and BM is total body mass. Analysis of variance (ANOVA) was used to compare means of environmental variables and means of GSI among the months. When there were significant differences, an 'a posteriori' SNK test was used to identify which values were significantly different at α = 0.05 level. Raw data was previously Log₁₀(x+1) transformed to address normality and homocedasticity assumptions of ANOVA. Size structure of males and females was determined by total length (TL) frequency distribution. A chi-square (χ^2) test was used to assess differences in size structure between sexes across size classes.

RESULTS

Males ranged from 125 to 425 mm TL and females from 175 to 525 mm TL. Females larger than 275 mm TL (p < 0.05) significantly outnumbered males (Fig. 1). The overall sex ratio was unbalanced (1 male: 2.27 female) with significant predominance of females (p < 0.01, χ^2 = 32.83) compared with males.

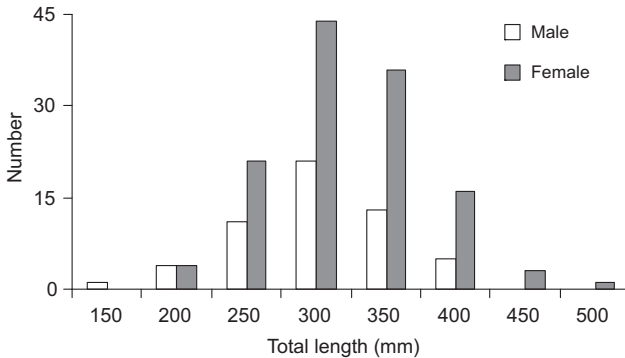


Figure 1. Length frequency distribution of males and females of *H. affinis* in Lajes Reservoir.

Gonads description

The ovaries are paired structures of different sizes located in the upper part of the coelomatic cavity. The ovaries' ducts lead to a common orifice near the anus. The right ovary is almost two times larger than the left one in advanced stages. The gonads are separated by connective tissue located ventrally to the kidneys and swim bladder.

The pair of testes are elongated, reaching the spermatic duct and do not differ morphologically from each other. The filiform testes are fairly cylindrical, flattened organs, located in the dorso-posterior area attached to the coelomic wall by the mesorc. The proximal part of the testes is thin and tubular, and the distal part changes according to the stage of the reproductive cycle.

At the beginning of the maturation, both testes and ovaries are difficult to visualize and to identify. They are translucent and easily confounded with the grizzly coloration of the peritoneum. The testes change from translucent to milky white as they mature. The ovaries, with the maturation, become laterally compressed, longitudinally voluminous, and asymmetric. A short common duct opens in the uro-genital papillae.

The testes are covered by the conjunctive albuginea tunic, flat muscular cells and blood vessels. They emit septa to the interior of the organ, forming lobules that are filled by seminiferous tubules in the testes. In the testes, the seminiferous tubules form cysts, defined by cytoplasmic projections of Sertoli cells. In each cyst, the spermatogenic cells have the same phase of development of the cells of spermatogenic lineage. Oocytes in the ovarian lamellae occur in different development phases in the ovaries. They are variable depending on the stage of the reproductive cycle.

Spermatogenesis

Spermatogonias. They are divided in primary and secondary. The primary spermatogonias (Fig. 2) are the largest cells of the spermatogenic lineage cells, having clear cytoplasm, large and prominent nucleus. They occur isolated, not forming cysts. The secondary spermatogonia appear inside the cysts. They are small cells with more condensed chromatin.

Spermatocytes. They are divided into primary and secondary (Fig. 3). The nucleus is prominent with filamentous chromatin. The secondary spermatocytes are smaller than the primary ones and the nucleus has chromatin condensed in one of the poles of the cell.

Spermatids. They originate from the secondary spermatocytes and are smaller (Fig. 3). Their cytoplasm has little affinity for dyes. The nucleus is spherical and dense.

Spermatozoa. They are the smallest cells of the spermatogenic lineage (Fig. 4). Their nucleus is round and very dense. They accumulate gradually in the tubular lumen after the breaking of the wall of the cyst. After being released in the reproductive process, there are no spermatozoa in the lumen of the seminiferous tubules and the spermatogonia appear in the wall of the tubules (Fig. 5).

Oogenesis

Young Oocyte (O1). The oocyte has small diameter (mean = 150 μ m, range = 90-160 μ m), vitreous cytoplasm, basophilic, large nucleus, prominent, centralized and with outlying nucleolus (Fig. 6).

Previtellogenic oocyte (O2). Cytoplasm with fine to granulate aspect, with nucleolus attached to the nuclear wrapping. In this phase, in the cytoplasm (mean = 390, range = 350-500 μ m) the vitellinic nucleus which is a conspicuous basophilic structure, is observed (Fig. 7). The zone radiata is thin and the follicle cells are paving (Fig. 8).

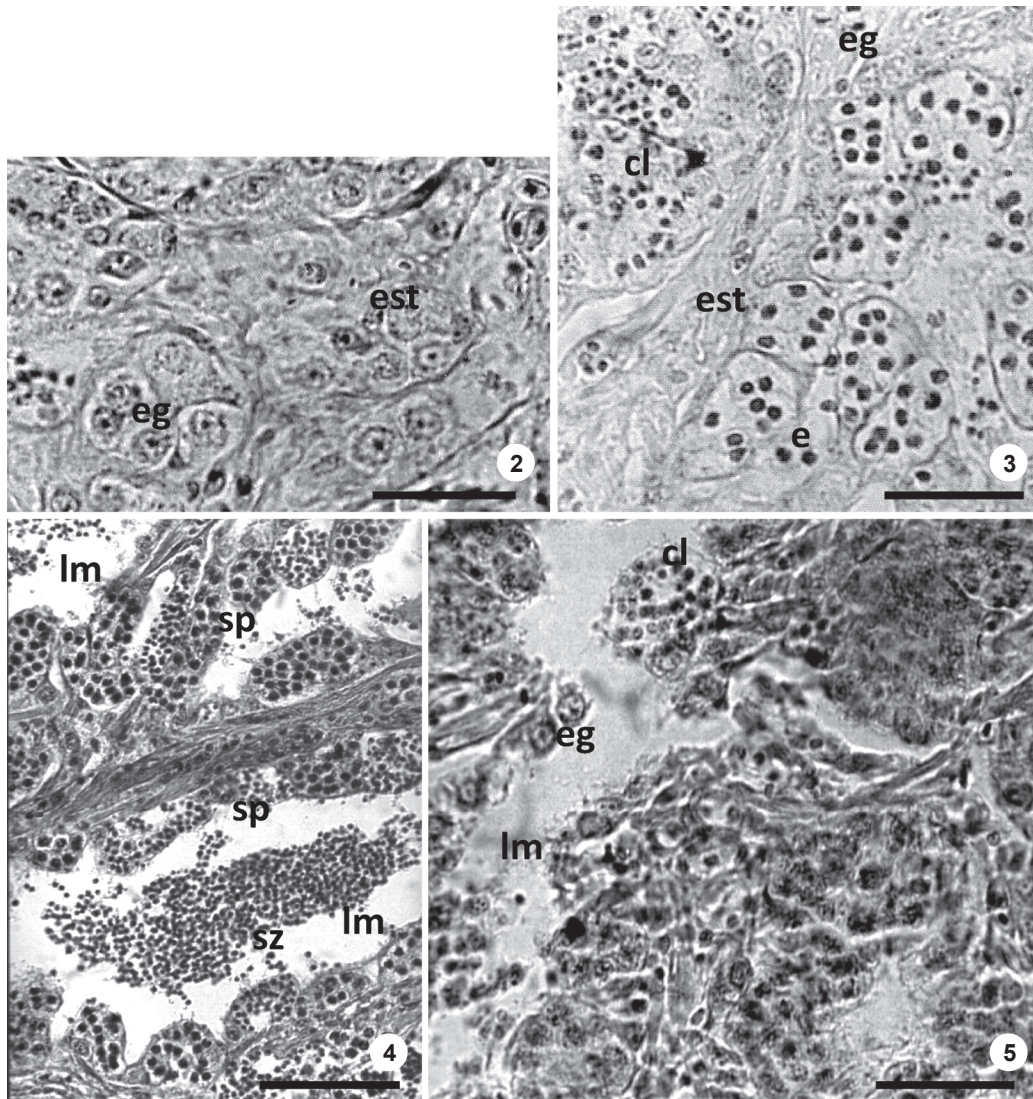
Oocyte with cortical vesicles (O3). Presence of clear vesicles in the cytoplasm. Nucleus (mean diameter = 300, range = 230-400 μ m) in central position but not well delineated and nucleolus distributed randomly (Fig. 6). The cytoplasm loses gradually the basophilic condition. The zone radiata is thin with follicle cells.

Vitellogenic oocytes (O4). Reach the largest size in this stage (mean diameter = 3050, range = 2750-3500 μ m), characterized by yolk globules in the cytoplasm. These globules initially appear in the cell periphery as small particles that increase in size as they spread throughout the cell. The striated zone radiata (width \pm 40 μ m) is thin and the cells' follicles become prismatic (Fig. 9).

Morphologic characteristics of stages of the reproductive cycle

Five stages were described for the males/females according to the distribution of oocytes and spermatogenic lineage cells: resting (1); initial maturation (2a); advanced maturation (2b); partially spent/spawned (4a); totally spent/spawn (4b). The main morphologic characteristics of the testicles and ovaries in the different stages of the reproductive cycle and the gonadosomatic indices by stage of maturation are shown in tables I and II.

Oocytes with diameter between 2 and 3.35 mm were more abundant in the advanced maturation and partially spawn stages, being totally absent in the totally spawned stage, indi-

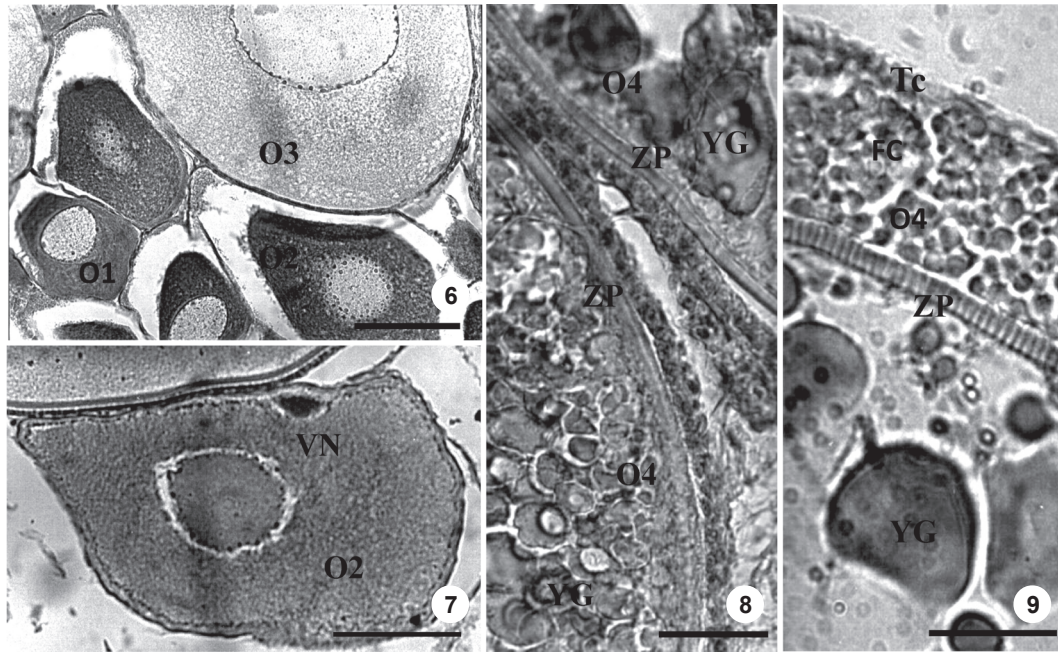


Figures 2-5. Cross section of the testis of *H. affinis* showing different phases of development, stained by Hematoxylin-Eosin: (2) testis in resting phase (stage 1) with numerous spermatogonias (eg) and lumen of the seminiferous tubules closed, scarce interstitial stroma (est); (3) testis in initial maturation (stage 2a) with spermatocytes (et) forming cysts and spermatids (sp), lineage spermatogenic cells (cl); (4) testis partially spent (stage 4a) with seminiferous tubules open containing spermatozoa (sz) and large number of the spermatids (sp); (5) testis totally spent (stage 4b), lumen (lm) with seminiferous tubules open and presence of the numerous spermatogonia (eg), spermatogenic lineage cells (cl). Scale bars: 50 μ m.

cating a total release of the vitellogenic oocytes during the reproductive season. Oocytes of the reserve stocks had diameter lesser than 1.0 mm and mode of 0.3 mm (Fig. 10). Thus, the analysis of the frequency distribution of oocytes and the histological observation unveil that spawning in this species is synchronic in two groups, that is, a group of oocytes that underwent the maturation process and another group of oocytes in which the vitellogenesis has not started yet.

DISCUSSION

The sex ratio of *H. affinis* in the Lajes Reservoir is skewed towards females, which reach larger sizes than males. This pattern is the opposite of that reported by MAZZONI & CARAMASCHI (1995) for this species in the Paraíba do Sul River, where sex ratio is balanced and males are larger than females. VIANA *et al.* (2008) did not find significant differences in the sex ratio of the



Figures 6-9. Cross section of the ovarians of *H. affinis* showing different phases of oocyte development, stained by Hematoxilin-Eosin: (6) initial maturation with young oocyte (O1) and previtellogenic oocyte (O2) and vitellogenic oocyte (O3); (7) previtellogenic oocyte (O2) with vittelinic nucleous (VN) in the region peripheric of cytoplasm; (8-9) oocyte O4 in showing the zone pellucid ou radiate (ZP), yolk globules (YG), follicular cells (FC) and teca (Tc). Scale bars: 6 = 50 μm , 7 = 120 μm , 8 = 320 μm , 9 = 160 μm .

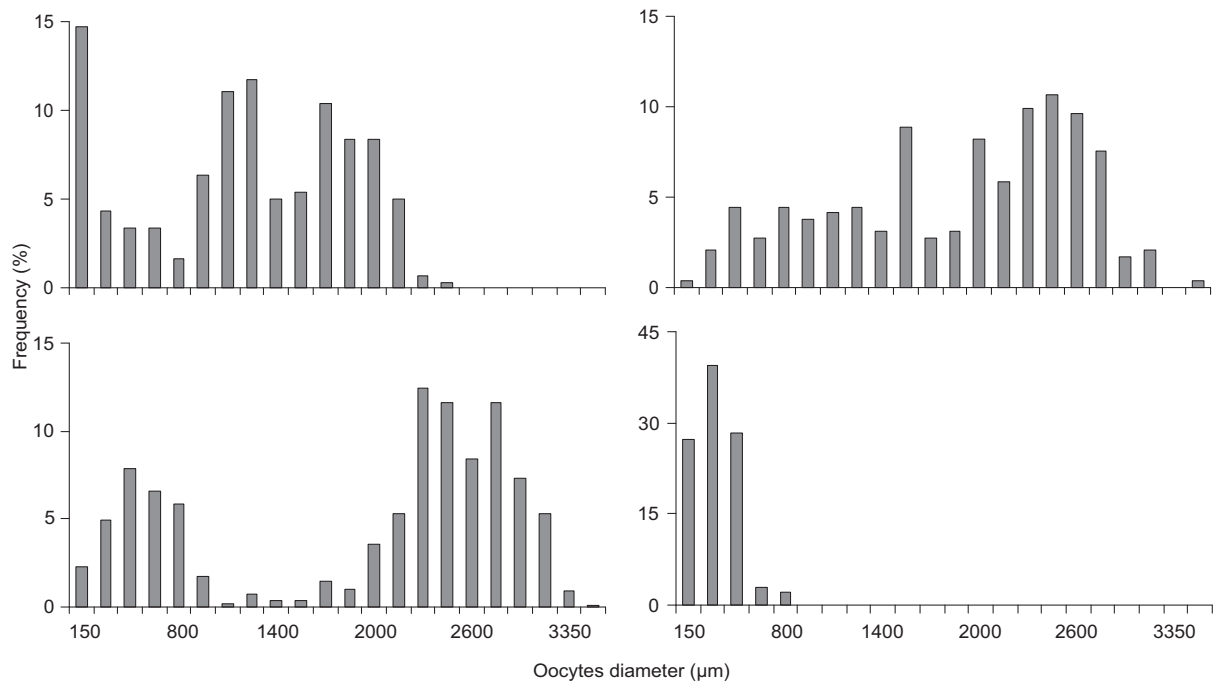


Figure 10. Diameter frequency distribution (in percentage) for oocytes of *H. affinis* in different stages of gonadal development. (N) Number of examined individuals.

Table I. Macroscopic and histological description of gonads for males and females for *Hypostomus affinis* by maturity stages.

Stages	Testis	Ovary
1	Filiforms and asymmetric. Numerous spermatogonia.	Whitish-yellow. Ovary takes up 32% of the cavity coelomic on the average. Weight averaging 6.8 g. Presence of O1 and O2.
2a	Aspect filiform and whitish color. The testes are thin, taking 70% of coelomic cavity. Weight up to 0.2 g. The testis presents few spermatozoa and large number of other spermatogenic lineage cells. (Fig 2.2)	Yellowish, turgid, with oocytes visible to naked eyes. Blood vessels no evident. The ovary occupies in average 40% of coelomic cavity and weights around 18.3 g. Presence of O1 and O2; few O3 oocytes (Fig. 3.1).
2b	Aspect of ribbon. White color. Turgid and voluminous. The testis taking up 85% of coelomic cavity and weights up to eye 0.4g. Predominance of spermatozoa in relation to the other spermatogenic lineage cells (Fig. 2.3).	Strong yellow coloration, voluminous, very turgid with many vitellogenic oocytes, visible to naked. Blood vessels evident. Ovary taking in mean 67% of coelomic cavity and weights approximately 47.85 g. Presence of O1 and O2 and O3. Large numbers of O4. Nucleous vitellinic in oocyte O2 (Figs. 3.2.; 3.3; 3.4).
4a	Testis white to reddish and with flaccid parts. It takes up to 85% of coelomic cavity, and weights until 0.4 g. Numerous spermatozoa when compared to the other spermatogenic lineage cells. Lumen partially empty.	Reddish, flaccid, with vitellogenic oocytes. Ovary occupies in average 70% of coelomic cavity; weights 47.0 g. Presence of O1, O2, O3, O4, and post-ovulatory follicles and atresy).
4b	Testis reddish, very hemorrhagic and flaccid, taking up to 48% of coelomic cavity, with weight averaging 0.3 g. Only spermatozoa on are found and the lumen of seminiferous tubules is open (Fig. 2.4).	Ovary dark-red and hemorrhagic, flaccid, with numerous opaque oocytes (atresic), visible to naked eye. Ovaries occupying up to 65% of coelomic cavity; weights 17.75 g. Presence of O1, O2 and many post-ovulatory follicles. Oocytes O3 and O4 when present, in atresic stage.

1) rest, 2 a) initial maturation, 2b) advanced maturation, 4a) partially spawn/spent, 4b) totally spawn/spent.

Table II. Gonadosomatic index averages (GSI) for *Hypostomus affinis* by sex in different stages of gonadal development. Values of standard deviation (s.d.), confidence interval (c.i.), and number of examined individuals (n) also showed.

Stages	Male				Female			
	n	GSI	s.d.	c.i.	n	GSI	s.d.	c.i.
1	9	0.10	0.14	0.01 – 0.19	8	1.62	1.01	0.92 – 2.32
2a	5	0.46	0.22	0.34 – 0.58	39	5.22	0.75	4.98 – 5.45
2b	8	0.57	0.12	0.49 – 0.65	30	11.36	0.76	8.75 – 13.97
4a	9	0.46	0.22	0.32 – 0.61	5	6.23	3.43	2.30 – 10.10
4b	11	0.16	0.04	0.14 – 0.18	20	2.25	0.73	1.93 – 2.57

congeneric *Hypostomus* cf. *ancistroides* in the Ivaí River Basin, state of Paraná. The reasons for such differences in sex ratio between a lentic (colonized) and a lotic (natural) system are rather unknown. In most teleosts, males are smaller than females, a strategy associated with greater reproductive investment by larger females, which can produce more oocytes. Such strategy is associated with selection toward higher fecundity (LOWE-MCCONNELL 1963, NIKOLSKY 1969, GROSS & SARGENT 1985). By contrast, larger males are associated with territorialism and interference competition by attracting more healthy females (POWER 1984).

The ecological importance of the sex ratio and size structure are still not fully explained. NIKOLSKY (1969) reported that an unbalanced sex ratio can occur between populations of a

given species, and at different times in a given population. In the Lajes Reservoir, females probably grow faster and live longer due to physiological factors, or to selection to invest more in the reproductive process, as larger females have a larger peritoneal cavity and thus can lay more eggs. Both fertility and the number of fertilized eggs increase with body size, a general pattern in teleosts (GROSS & SARGENT 1985). Additionally, individuals with a faster growth rate will undergo the most vulnerable phase (smaller size) more quickly, escaping predation in proportionally larger numbers. Smaller males may, in part, be a consequence of selection for early male maturation and reproductive effort, which reduces male growth compared to that of females (ENDLER 1983, ANDERSSON 1994).

The testes of *H. affinis* are typical of Loricariidae, thin and laterally compressed, with distal part changing according to the stage of the reproductive cycle. Only a few species have filiform or tubular testes, similar to those of *Rhinelepis aspera* (Agassiz, 1829), which was described by AGOSTINHO *et al.* (1986, 1990). The size of the testes changes markedly according to the reproductive cycle. The grey color sometimes is confused with the peritoneal layer and/or with the guts. Overall, both testes are similar in size but can also present asymmetry. Ovaries are conspicuous irrespective of their maturation stage, asymmetric, becoming irrigated by the blood during advanced maturation, with yellow color, occupying c.a. 80% of the coelomatic cavity and pressing the liver to a flattened shape. Unlikely *L. castaneus* in which ovaries are asymmetric only during the partially and totally spawned phases (DUARTE *et al.* 2007), the ovaries of *H. affinis* are asymmetric throughout the reproductive cycle.

Several cells in different phases of development occur in the tubular compartment of the testes of *H. affinis* individuals (cell of spermatogenic lineage): spermatogonia, spermatocytes, spermatids and spermatozoa. Similarly to *R. aspera* (AGOSTINHO *et al.* 1987), changes in testicular morphology occur during cell maturation. All cell of germinative lineage are contained in cysts, except spermatogonia and spermatozoa. The seminiferous tubules appear in the partially spent stage with the walls of the tubules containing spermatogonia and cysts with cells in different phases of the spermatogenesis. AGOSTINHO *et al.* (1987) reported that the germinative cells are annually replaced from a permanent stock of spermatogonia. According to AGOSTINHO *et al.* (1987), spermatozoa that occur in the spermatic ducts, similarly to those from the seminiferous tubules, are immersed in fluids produced by the cell walls. Such fluid can be associated with spermatozoa nutrition. The presence of spermatozoa throughout the year in *H. affinis* may serve as a reserve for the next reproductive cycle. HENDERSON (1962) reported that phagocytes invade the lobules and spermatic ducts to engulf residual spermatozoa. Furthermore, LOPES *et al.* (2004) reported that the spermatid may participate in the transport of spermatozoa, in the secretion of substances that form the seminal fluid, and in the re-absorption of residual spermatozoa. Resting adult males had testis with seminiferous tubules organized, with numerous spermatogonia.

According to the classification by WALLACE & SELMAN (1981), *H. affinis* have synchronic oocyte development with two distinct oocyte populations occurring at the same time in the ovaries: one in the reserve stock and the other which will mature synchronically and be released during the spawning season. By contrast, MAZZONI & CARAMASCHI (1997) reported an asynchronous oocyte development for *H. affinis* in the Paraíba do Sul River, an indication of the reproductive plasticity of this species. It is expected that the events of the reproductive cycle are locked to, and synchronized with, seasonal environmental changes. AGOSTINHO *et al.* (1991), describing the reproductive cycle of *Hypostomus commersonii* (Valenciennes, 1840), found

that spawning in different periods according to size stratum is an adaptation that reduces intraspecific competition per spawning site. Limitation in spawning sites for *H. affinis* is very likely to occur in the Lajes Reservoir, where crevices in the rocky substratum are not common. We believe that such reservoir characteristics could be a constraint for the spawning activity of *H. affinis* and it could trigger plasticity in reproductive tactics.

The reproductive cycle of *H. affinis* can be classified in the following stages of gonadal development according to macro and microscopy observations: 1) resting/immature, 2a) initial maturation, 2b) advanced maturation, 4a) partially spawned/spent, 4b) totally spawned/spent. The mature stage corresponds to the climax of the gonadal maturation, the exact time of ovulation or spermiation. As this event is very brief (SELMAN & WALLACE 1989) it is hardly found and identified. Another concern is the distinction between immature and resting individuals, which are differentiated histologically by presence of the ovuligers lamellae in the later, and absent in immature females. In males, the resting testes have numerous spermatogonia and scarce interstitial stroma; by contrast, the immature stages have abundant interstitial stroma and spermatogonia randomly distributed as reported by SOARES *et al.* (1995). *Hypostomus affinis* individuals produce large oocytes (2.00-3.35 mm) and *Hypostomus* species produce the largest eggs among all teleostans of the Paraíba do Sul basins, as reported by MENEZES & CARAMASCHI (1994), MAZZONI & CARAMASCHI (1997). SUZUKI *et al.* (2000) reported that *Hypostomus ternetzi* (Boulenger, 1895) individuals produce the largest mature eggs (mean oocyte diameter = 4.36 mm) and the smallest clutches relative to adult mass in the Paraná River. MAZONI & CARRAMASCHI (1997) found larger mature eggs of *H. affinis* in the Lajes Reservoir (ranging from 3-39 mm) than the eggs we found. Presumably, *H. affinis* individuals in the Lajes Reservoir allocate their energy such as to produce the same number of eggs (average fecundity = 2374, oocyte diameter 2-3.35 mm in diameter) as populations of the Paraíba do Sul River (average fecundity = 2350, oocyte diameter 3-3.8 mm), but smaller MAZONI & CARRAMASCHI (1997) found mature eggs for *H. affinis* ranging from 3-39 mm, which are larger than our findings for this species in the Lajes Reservoir. Presumably, the energy in *H. affinis* in the Lajes Reservoir is allocated to produce the same number of eggs (average fecundity = 2374; oocyte diameter 2-3.35 mm in diameter) but more little, compared with populations of the Paraíba do Sul River (average fecundity = 2350, oocyte diameter 3-3.8 mm). The smaller size of the oocytes of *H. affinis* individuals become more obvious when we compare the maximum size reached by individuals of this species in the Paraíba do Sul River ($L_{\max} = 425$ mm males; $L_{\max} = 525$ females) with that of other species of *Hypostomus* elsewhere, such as *H. ternetzi*, in the Paraná River ($L_{\max} = 357$ mm males; $L_{\max} = 324$ mm females, SUZUKI *et al.* 2000), which are comparatively smaller than *H. affinis*. The reasons for differences in the size of the oocytes of *H. affinis* individuals between the river and the reservoir could be asso-

ciated with different types of habitats and their available resources. The Lajes Reservoir is an oligotrophic system compared with the eutrophic Paraíba do Sul River (SANTOS *et al.* 2004) and limitation in resources could shift reproductive tactics to a better use of the available energy. Furthermore, environmental stress in reservoirs, such as oxygen deficits (POTTS 1984), creates harsher living conditions. The production of comparatively smaller eggs in fishes from the Lajes Reservoir could be a mechanism to take advantage of more suitable environmental conditions (e.g., peaks of flooding with more food and shelters availability) to spawn a comparatively large number smaller eggs, thus increasing offspring survival, configuring an opportunist reproductive strategy *sensu* WINEMILLER (1989).

The absolute fecundity of *H. affinis* in the Lajes Reservoir was 2,374 oocytes (range = 1235-4304 oocytes) as reported by DUARTE & ARAÚJO (2002), and these numbers are greater than those recorded by MAZZONI & CARAMASCHI (1997) (1,784 oocytes; range = 1235-4304 oocytes). Other species of *Hypostomus* such as *P. ancistroides* (Ihering, 1911) – 970 oocytes (NOMURA *et al.* 1975), *Hypostomus luetkeni* Lacepede, 1803 – 446-936 oocytes, and *Plecostomus commersoni* – 500 oocytes (AGOSTINHO *et al.* 1991) had fecundity comparatively lower than *H. affinis*.

According to BAGENAL (1978), changes in fecundity act as a mechanism to regulate populations, depending on their densities. In spite of having high fecundity, *H. affinis* has relatively low densities in the Lajes Reservoir (SANTOS *et al.* 2008), probably associated to the lack of a rocky substratum, which provides feeding and shelter. According to POWER (1990), most of the species that belong to *Hypostomus* are limited to the bottom and forage on algae. The feeding behavior of species of *Hypostomus* is favored by a very specialized digestive tract, with a ventral mouth adapted to suck (OLIVEIRA E SILVA 1965, NOMURA & MUELLER 1980, FUGI & HAHN 1991) which prevents *Hypostomus* individuals to see their food while they are ingesting it (POWER 1983). Species of *Hypostomus* are detritivores/iliophages (FUGI & HAHN 1991) and benefit from the excess of food in epiphytic communities on submerged rocks of dammed rivers.

Behavioural plasticity has been recurrently mentioned for *Hypostomus* species (e.g., BUCK & SAZIMA 1995, CASATTI *et al.* 2005). VIANA *et al.* (2008) found that *H. ancistroides* seemed to be associated with the physiographical features of the Bonito River. The fast and slow flowing stretches, the rocky substratum, with little sediment deposition, and the depths not exceeding 1.5 m throughout most of the year, constituted a favorable environment for the macro algae to settle and develop. In conclusion, *H. affinis* change some reproductive tactics in the Lajes Reservoir by decreasing oocyte size and increasing fecundity. Moreover, females reach larger sizes than males and have synchronic oocytes development. Such changes in tactics configure a trend from the equilibrium to the opportunistic strategy, and it is reasonable to suppose that it is a probable mechanism to withstand environmental constraints and to get success in this oligotrophic and poorly structured reservoir.

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LITERATURE CITED

- AGOSTINHO, A.A.; G. BARBIERI; J.R. VERANI & C.S. AGOSTINHO. 1986. Ciclo reprodutivo e primeira maturação de *Rhinelepis aspera* (Agassiz, 1829), (Teleostei – Loricariidae) no rio Paranapanema. **Revista Unimar** 8 (1): 17-27.
- AGOSTINHO, A.A.; M.C. BARBIERI; C. AGOSTINHO & G. BARBIERI. 1987. Biologia reprodutiva de *Rhinelepis aspera* (Agassiz, 1829) (Teleostei, Loricariidae) no rio Paranapanema. I. Estrutura dos testículos e escala de maturidade. **Revista Brasileira de Biologia** 47 (3): 309-317.
- AGOSTINHO, A.A.; G. BARBIERI; J.R. VERANI & N.S. HAHN. 1990. Variação do fator de condição e do índice hepatossomático e suas relações com o ciclo reprodutivo em *Rhinelepis aspera* (Agassiz, 1829) (Osteichthyes, Loricariidae) no rio Paranapanema. **Ciência e Cultura** 42 (9): 711-714.
- AGOSTINHO, A.A.; N.S. HAHN & C.S. AGOSTINHO. 1991. Ciclo reprodutivo e primeira maturação de fêmeas de *Hypostomus commersonii* (Valenciennes, 1840) (Siluriformes, Loricariidae) no reservatório Capivari-Cachoeira, PR. **Revista Brasileira de Biologia** 51 (1): 31-37.
- ANDERSSON, M. 1994. Sexual selection, p. 595-624. *In*: J. KREBS & T.T. CLUTTON-BROCK (Eds). **Monographs in behavior and ecology**. Princeton, NJ, Princeton University Press, 599p.
- ANTONIASSI, L.E.; A.A. AGOSTINHO; L.C. GOMES & N.S. HAHN. 1998. Ecologia trófica de peixes em dois riachos da bacia do Rio Paraná. **Revista Brasileira de Biologia** 58 (2): 273-285.
- ARAÚJO, F.G. & L.N. SANTOS. 2001. Composition and structure of the fish community in the Lajes Reservoir, RJ. **Revista Brasileira de Biologia** 61 (4): 1-6
- BAGENAL, T.B. 1978. Aspects of fish fecundity, p. 75-101. *In*: S.D. GERKING (Ed.). **Ecology of freshwater fish production**. Oxford, Blackwell Scientific Publications, 348p.
- BARBIERI, E.B. & D.M.P. KRONENBERGER. 1994. Climatologia do Litoral Sul – Sudeste do Estado do Rio de Janeiro. **Caderno de Geografia** 12: 57-73
- BAZZOLI, N. & H.P. GODINHO. 1991. Reproductive biology of the *Acestrorhynchus lacustris* (Reinhard, 1874) (Pisces, Characidae) from Três Marias Reservoir Brazil. **Zoologischer Anzeiger** 226

- (5/6): 285-299.
- BUCK, S. & I. SAZIMA. 1995. An assemblage of mailed catfishes (Loricariidae) in southeastern Brazil: distribution, activity, and feeding. *Ichthyology Exploration of Freshwaters* 6 (4): 325-332.
- CASATTI, L.; F.C. ROCHA & D.C. PEREIRA. 2005. Habitat use by two species of *Hypostomus* (Pisces, Loricariidae) in Southeastern Brazilian streams. *Biota Neotropica* 5 (2): 1-9.
- DUARTE, S. & F.G. ARAÚJO. 2000. Distribuição espacial e temporal de *Hypostomus affinis* na Represa de Ribeirão das Lajes. *Acta Biologica Leopoldensia* 22: 261-276.
- DUARTE, S. & F.G. ARAÚJO. 2002. Fecundity of the *Hypostomus affinis* (Siluriformes, Loricariidae) in the Lajes Reservoir, Rio de Janeiro, Brazil. *Revista de Biologia Tropical* 50 (1): 193-197.
- DUARTE, S.; F.G. ARAÚJO; A. SALES & N. BAZZOLI. 2007. Morphology of gonads, scale of maturity and spawning season of *Loricariichthys spixii* (Siluriformes, Loricariidae), in a subtropical reservoir, Rio de Janeiro, Brazil. *Brazilian Archives of Biology and Technology* 50 (6): 1019-1032.
- ENDLER, J.A. 1983. Natural and sexual selection on color patterns in Poeciliid fishes. *Environmental Biology of Fishes* 9: 173-190.
- FUGI, R. & N.S. HAHN. 1991. Espectro alimentar e relações morfológicas com o aparelho digestivo de três espécies de peixes comedores de fundo do rio Paraná, Brasil. *Revista Brasileira de Biologia* 51 (4): 873-879.
- GARAVELLO, J.C. & J.P. GARAVELLO. 2004. Spatial distribution and interaction of four species of the catfish genus *Hypostomus* Lacepède with bottom of Rio São Francisco, Canindé do São Francisco, Sergipe, Brazil (Pisces, Loricariidae, Hypostominae). *Brazilian Journal of Biology* 64 (3): 591-598.
- GROSS, M.R. & R.C. SARGENT. 1985. The evolution of male and female parental care in fishes. *American Zoologist* 25: 807-822.
- HARDIE S.A.; R.W.G. WHITE & L.A. BARMUTA. 2007. Reproductive biology of the threatened golden galaxias *Galaxias auratus* Johnston and the influence of lake hydrology. *Journal of Fish Biology* 71: 1820-1840.
- HENDERSON, N.E. 1962. The annual cycle in the testis of the eastern brook trout, *Salvelinus fontinalis* (Mitchill). *Canadian Journal of Zoology* 40: 631-641.
- LASSALA, M.D.P. & E. RENESTO. 2007. Reproductive strategies and genetic variability in tropical freshwater fish. *Genetics and Molecular Biology* 30: 690-697.
- LOPES, D.C.J.R.; N. BAZZOLI; M.F.G. BRITO & T.A. MAIA. 2004. Male reproductive system in the South American catfish *Conorhynchus conirostris*. *Journal of Fish Biology* 64: 1419-1424.
- LOWE MCCONNELL, R.H. 1963. The fishes of the Rupununi savanna district of British Guiana, South America. Part 1. Ecological groupings of fish species and effects of the seasonal cycle of the fish. *Journal of the Linnean Society, Series Zoology*, 45 (304): 103-144.
- MAZZONI, R. & E.P. CARAMASCHI. 1995. Size, structure, sex ratio and onset of sexual maturity of two species of *Hypostomus*. *Journal of Fish Biology* 47: 841-849.
- MAZZONI, R. & E.P. CARAMASCHI. 1997. Spawning season, ovarian development and fecundity of *Hypostomus affinis* (Osteichthyes, Loricariidae). *Revista Brasileira de Biologia* 57 (3): 455-462.
- MAZZONI, R.; C.F. REZENDE & L.R. MANNA. 2010. Feeding ecology of *Hypostomus punctatus* Valenciennes, 1840 (Osteichthyes, Loricariidae) in a costal stream from Southeast Brazil. *Brazilian Journal of Biology* 70: 569-574.
- MENEZES, M.S. & E.P. CARAMASCHI. 1994. Características reprodutivas de *Hypostomus* grupo *H. punctatus* no rio Ubatiba, Marica, RJ (Osteichthyes, Siluriformes). *Revista Brasileira de Zoologia* 54 (3): 503-513.
- NIKOLSKY, G.V. 1969. *Theory of fish population dynamics*. Edimburgh, Oliver & Boyd, V+323p.
- NOMURA, H. & I.M.M. MUELLER. 1980. Biologia do cascudo, *Plecostomus hermanni* Ihering, 1905. do rio Mogi guaçu. São Paulo (Osteichthyes, Loricariidae). *Revista Brasileira de Biologia* 40 (2): 267-275.
- NOMURA, H.; M.J. OLIVEIRA; A.M.P. LELLIS & B.E. CALDO. 1975. Caracteres merísticos e biologia do cascudo bugio *Plecostomus ancistroides* Ihering, 1911 (Pisces, Loricariidae). *Científica* 3 (2): 231-245.
- OLIVEIRA E SILVA, S.L. 1965. Aspectos histológicos do tubo digestivo de *Plecostomus* sp (Pisces, Actinoptergii, Loricariidae) Rio de Janeiro. *Acta da Sociedade de Biologia* 4: 63-68.
- POWER, M.E. 1983. Grazing responses of tropical freshwater fishes to different scales of variation in their food. *Environmental Biology of Fishes* 9 (2): 103-115.
- POWER, M.E. 1984. The importance of sediment in the grazing ecology and size class interactions of an armored catfish, *Ancistrus spinosus*. *Environmental Biology of Fishes* 10: 173-181.
- POWER, M.E. 1990. Resource enhancement by indirect effects of grazers: Armored Catfish, Algae, and Sediment. *Ecology* 71, 897-904.
- POTTS, G.W. 1984. Parental behavior in temperate marine teleosts with special reference to the development of nest structures, p. 223-244. *In*: G.W. POTTS & R.J. WOOTON (Eds). *Fish reproduction: strategies and tactics*. San Diego, Academic Press, 424p.
- RIZZO, E.; Y. SATO; B.P. BARRETO & H.P. GODINHO. 2002. Adhesividade and surface pattern of eggs in neotropical freshwater teleosts. *Journal of Fish Biology* 61: 615-632.
- SANTOS, A.F.G.N.; L.N. SANTOS & F.G. ARAÚJO. 2004. Water level influences on body condition of *Geophagus brasiliensis* (Perciformes, Cichlidae) in a Brazilian oligotrophic reservoir. *Neotropical Ichthyology* 2: 151-156.
- SANTOS, L.N.; F.G. ARAÚJO & D.S. BROTO. 2008. Artificial structures as tools for fish habitat rehabilitation in a neotropical reservoir. *Aquatic Conservation* 18: 896-908.
- SELMAN, K. & R.A. WALLACE. 1989. Review cellular aspects of oocyte growth in teleosts. *Zoological Scientist* 6: 211-231.
- SOARES, M.G.; A.C. DABES; Y. SATO & N. BAZZOLI. 1995. Tamanho da primeira maturação sexual do *Schizodon knerii* e do *Leporinus piau* (Teleostei, Anostomidae) na represa de Três

- Marias, MG. **Arquivo Brasileiro de Medicina Veterinária e Zootecnia** **48**: 47-54.
- SOARES, M.C.S.; M.M. MARINHO; V.L.M. HUSZAR; C.W. BRANCO & S.M.F.O. AZEVEDO. 2008. The effects of water retention time and watershed features on the limnology of two tropical reservoirs in Brazil. **Lakes Reservoir Research Management** **13**: 257-269.
- SUZUKI H.I.; A.A. AGOSTINHO & K.O. WINEMILLER. 2000. Relationship between oocyte morphology and reproductive strategy in Loricariid catfishes of the Parana River, Brazil. **Journal of Fish Biology** **57**: 791-807.
- TAMADA, K. 2009. Variations in clutch and egg sizes in the amphidromous goby *Rhinogobius* sp. CB along a river course and within a spawning season. **Ichthyology** **56**: 69-75.
- VIANA, D.; L.L. WOLFF; T. ZALESKI; S. ROMÃO; G. BERTOLDI & L. DONATTI. 2008. Population structure and somatic indices of *Hypostomus* cf. *ancistroides* (Siluriformes, Loricariidae) collected from the Bonito River, Ivaí River Basin, Turvo, Paraná. **Brazilian Archives of Biology and Technology** **51** (3): 493-502.
- WALLACE, R.A. & K. SELMAN. 1981. Cellular and dynamic aspects of oocyte growth in Teleost. **American Zoologist** **21**: 325-343.
- WEBER, C. 2003. Subfamily Hypostominae, p. 351-372. *In*: R.E. REIS; S.O. KULLANDER & C.J. FERRARIS-JR. (Orgs). **Check list of the freshwater fishes of South and Central America**. Porto Alegre, Editora da Pontifícia Universidade Católica do Rio Grande do Sul, 729p.
- WINEMILLER, K.O. 1989. Patterns of variation in life history among South American fishes in seasonal environments. **Oecologia** **81**: 225-241.
- WOOTTON, R.J. 1989. Introduction: strategies and tactics in fish reproduction, p. 1-12. *In*: G.W. POTTS & M.N. WOOTTON (Eds). **Fish reproduction: strategies and tactics**. San Diego, Academic Press, 424p.

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