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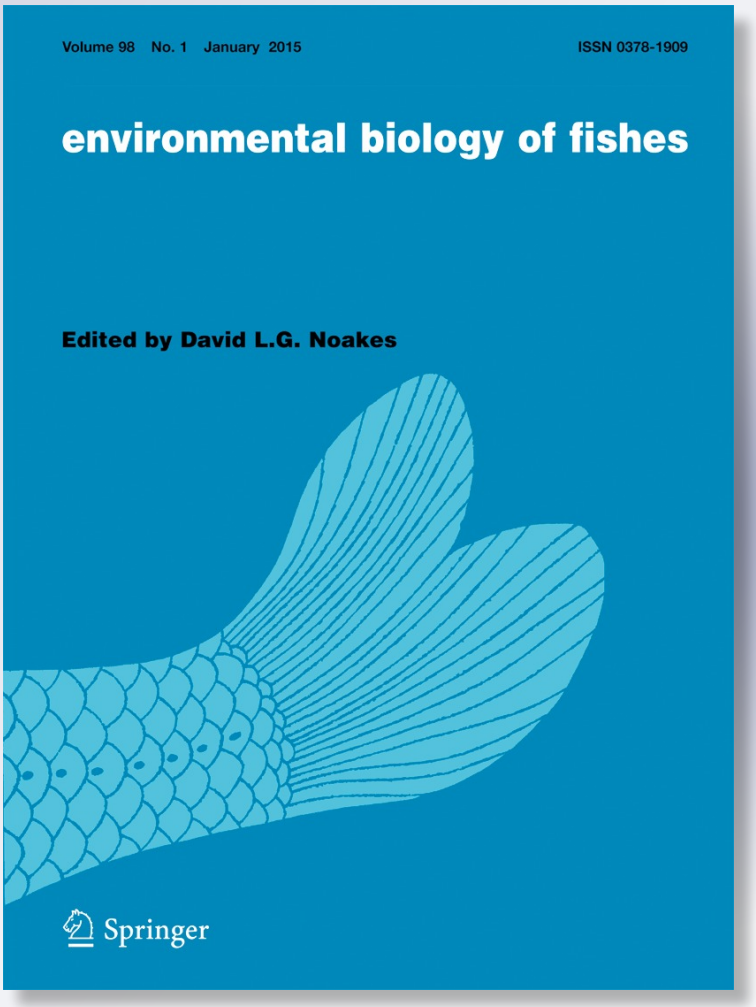

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Equilibrium reproductive strategy of the armored catfish *Hypostomus auroguttatus* (Siluriformes, Loricariidae) in a tropical river in Southeastern Brazil

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Abstract We investigated the reproductive strategy developed by the armored catfish *Hypostomus auroguttatus* Kner 1854 in a tropical river of Southeastern Brazil. A total of 173 females (157–370 mm *TL*) and 165 males (140–357 mm *TL*) were analyzed. Sex ratio (1 female: 1.05 male) was well balanced. Six stages of oogenesis and five of spermatogenesis were described. Oocyte development was synchronic in two groups, with oocyte size ranging from pre-spawning (<200 μm) to spawning (600–1,000 μm), followed by a sharp decrease in the postspawning (200–360 μm) phase. Macroscopic oocyte diameter ranged from 0.1 mm to 7.2 mm, with vitellogenic ones ranging from 4.8 to 7.2 mm. Spawning occurred throughout most of the year, peaking in September-October. Mean batch fecundity was 411 oocytes ranging from 163 to 662 vitellogenic oocytes (relative fecundity = 2.26 oocytes g^{-1}). These attributes, associated with parental care and a wide reproductive period, corresponded to an equilibrium strategy that has proved to be effective in this tropical river. The dominance of *H. auroguttatus* in rivers, compared with the congeneric *Hypostomus affinis* that dominates in impoundments, could be associated to larger egg size and lower fecundity in *H. auroguttatus*, an adaption toward equilibrium strategy that seems to be efficient to this species succeed in running waters. The hypothesis that equilibrium reproductive strategy for fish species is favored in more, predictable environments was confirmed.

Keywords Tropical fish · Fish reproduction · Reproductive strategy · Tactics

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Introduction

The armored catfishes *Hypostomus auroguttatus* is a member of the Loricariidae family widely distributed in the Paraiba do Sul River basin in Southeastern Brazil. This native iliophagous/detritivorous species has successfully adapted to the river basin that have suffering from anthropogenic activities in the last decades. Species widely distributed in different types of habitat need to be investigated to assess eventual changes in their reproductive traits. The genus *Hypostomus* comprises bottom-dwelling species associated with fast flowing lotic systems, feeding on microalgae attached to rocky substratum (Buck and Sazima 1995; Garavello and Garavello 2004). Power (1990) and Antoniassi et al. (1998) reported that species of *Hypostomus* prefer clean and running waters of the large Brazilian rivers, but can withstand the barrage events by adapting to reservoirs.

Originally described as *Hypostomus auroguttatus* by Kner (1854), this species was posteriorly designated as *H. luetkeni* by Steindachner (1877) but was repositioned to its original nomenclature in recent years.

Studies on the reproductive biology of species of the genus *Hypostomus* are scarce. Mazzoni and Caramaschi (1997a) reported that *Hypostomus luetkeni* (=*H. auroguttatus*) and *Hypostomus affinis* (Steindachner 1877) are partial spawners. Menezes and Caramaschi (1994) suggest that *H. punctatus* (Valenciennes 1840) is nest/brood guarder. Fecundity differs between these two species of *Hypostomus*, ranging from 1,235 to 4,304 oocytes for *H. affinis* (Duarte and Araújo 2002) and from 446 to 936 oocytes for *H. luetkeni* (= *H. auroguttatus*) (Mazzoni and Caramaschi 1997a).

In this study we described features of the reproductive biology of *H. auroguttatus* and assessed the tactics that this species uses to succeed in the Paraiba do Sul River middle reaches, where it is the dominant species of *Hypostomus*. We also compared its reproductive tactics with secondary information on the congeneric *H. affinis*, which is the dominant species of *Hypostomus* in impoundments of Paraiba do Sul River. We expect that this species exhibits equilibrium reproductive strategy to succeed in the river basin that has more stable physico-chemical environmental conditions compared with reservoirs.

Materials and methods

Study area

The Rio Paraíba do Sul in southeastern Brazil is a 9th order river (length 1,080 km; watershed area 57,000 km^2) draining one of the most important industrial regions in the country. Its watershed (Fig. 1) is located between parallels 20°26′ and 23°38′ S and meridians 41°00′ and 46°30′ W. The sampled area encompassed a 30-km stretch in the middle-lower reaches, downriver from several highly developed municipalities. Typical winter and summer flows are 109 m^{3}s^{-1} and 950 m^{3}s^{-1}, respectively (Araújo et al. 2003). Annual rainfall ranges from 100 to 300 cm, with the average generally over 200 cm (Carvalho and Torres 2002). The climate is mesothermic with hot and wet summers and dry winters (Barbiere and Kronemberger 1994). The studied river stretch has a maximum depth of 9 m and the substrate is predominantly rocky and sandy. The region is characterized by low mountains, low nutrient soils, fragmented semi-deciduous seasonal rain forest, and poor croplands (Carvalho and Torres 2002).

Fish collection and laboratory procedures

A total of 338 specimens (173 females, 165 males) were examined. The fish specimens were captured bimonthly by gill nets from January 2008 to February 2009. Following capture, all individuals were measured to total length (TL, nearest 1 mm), and weighted to total mass (TW, nearest 0·01 g). A ventral incision was made to expose gonads for determination of the sex and gonad development stage. Gonads were removed and weighed wet (GW, nearest 0·01 g). A portion of each gonad was preserved in Bouin's solution for histological study during 8 h. Afterwards, gonads were transferred to 70 % Ethanol for preservation. The gonads were subject to histological techniques and embedded in paraffin. Transversal sections (5 μm of thickness) were cut, mounted on glass slides and stained in haematoxylin and eosin (HE). Gonad sections collected in different regions (proximal, medium and distal) were examined and photographed using an Olympus (Tokyo, Japan) B941 microscope fitted with photographic attachment, a Nikon Coolpix 4300 digital camera. Voucher specimens were deposited in the Fish Collection of the Laboratory of Fish Ecology, University Federal Rural of Rio de Janeiro, under numbers LEP-UFRRJ 850, 851 and 852.

Data analysis

Size structure of males and females was determined by total length frequency distribution analysis. A chi-square (χ^2) test was used to assess differences in size structure between sexes and size classes. The gonad classification was adapted from West (1990) and Nuñez and Duponchelle (2009). Gonads were assigned to developmental stages, based on form, size, mass, color and vascularization; however, gonads were ultimately classified as either immature (juveniles and inactive stages) or mature (developing, spawning capable, regressing and regenerating phases) to reduce the chance of error in correctly identifying individual stages. Oocytes were classified according to their morphology, their affinity to the dyes used, and the presence of specific inclusions (lipid droplets, yolk granules, cortical alveoli). The criteria for identification of different oocyte stages and postovulatory follicles (POFs) were adapted from Brown-Peterson et al. (2011). In fishes randomly chosen from the monthly sample, the diameters of the first 50 oocytes and their nuclei were measured to the nearest 0.0001 mm. Histological identification of the various

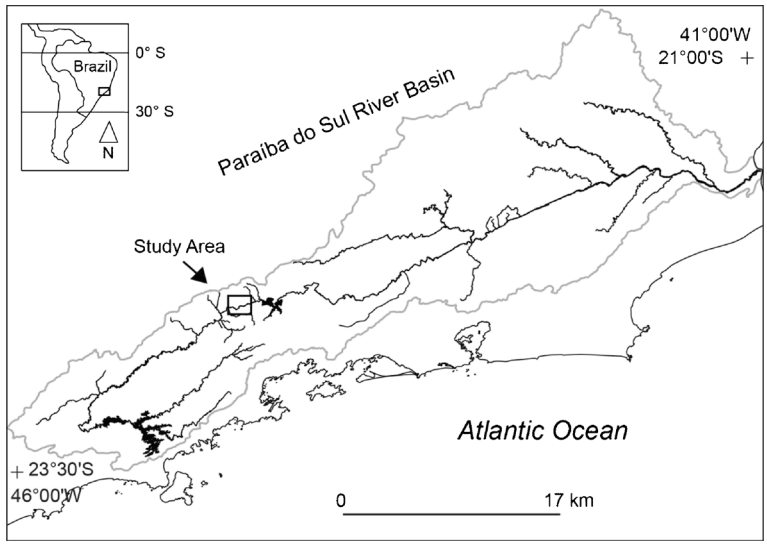

Fig. 1 Map of the Paraiba do Sul River Basin, Southeast Brazil, showing the study area

maturity stages were determined according to development of the ovary and testis and also by the presence / absence of different types of oocytes (*i.e.* whether organized by ovarian lamellae or not) and spermatocytes. Histological classification of ovaries was based on oocytes stage and the occurrence of different stages of postovulatory follicles (POFs).

The annual gonadal cycle was determined by variations in the gonado-somatic index, $GSI=100(GW \times TW^{-1})$ and by eggs size-frequency distribution by gonadal maturity stages. Fulton's condition factor (K) and hepato-somatic index (I_H) were calculated as indirect indices of energy status. The Fulton's condition factor (K) was calculated with a equation $K=100(TW \times TL^{-3})$. The hepato-somatic index (*HSI*) was calculated according to the equation, $HSI=100(LW \times TW^{-1})$, where LW is the weight of the liver. One-way ANOVA and a post-hoc Tukey test (<0.05) were used to compare *GSI*, *HSI* and K among the bi-monthly period.

Batch fecundity was estimated by direct counts of fixed mature ovarian subsamples in 30 ovaries and calculated as: $F=(N \times GW) \times GWS^{-1}$, where F = fecundity, \number of mature oocytes, GW = total gonad weight and GWS = gonadal subsample weight. The diameter of oocytes was measured in a stereomicroscope fitted with an ocular micrometric (precision 0.001 mm). Relative fecundity (number of eggs per gram of total mass) was calculated to remove the effect of body size. A linear regression analysis was performed to assess relationships between fecundity and total length, total mass and gonad mass.

Results

Sex ratio

The overall sex ratio (1.05 female : 1 male) was well balanced, with no significant differences between sexes 5 (Table 1). Size for females ranged from 157 to 370 mm TL and for males ranged from 140 to 357 mm TL.

Table 1 Chi-square (χ^2) test for sex ratio comparisons of *Hypostomus auroguttatus* in the Paraíba do Sul River

Size classes (TL, mm)	Females	Males	Total	Sex ratio	$\chi 2$	Significance
140–160	1	2	3	1.0:2.0	0.33	ns
160–180	5	3	8	1.6:1.0	0.50	ns
180–200	8	7	15	1.1:1.0	0.07	ns
200–220	11	8	19	1.4:1.0	0.47	ns
220–240	21	15	36	1.4:1.0	1.00	ns
240–260	46	24	70	1.9:1.0	6.91	*
260–280	43	34	77	1.3:1.0	1.05	ns
280–300	25	36	61	0.7:1.0	1.98	ns
300–320	7	23	30	0.3:1.0	8.53	*
320–340	5	11	16	0.4:1.0	2.25	ns
340–360	1	2	3	0.5:1.0	0.33	ns
Total	173	165	338	1.0:1.0	0.29	ns

NS, non-significant; *significant at $P<0.01$. *TL*, total length

Stages of oocyte development

Oogonia, chromatin nucleolar and perinucleolar stages are present in the ovary throughout the entire annual cycle, and are referred to as primary growth oocytes (PG). Others stages of the oocyte development are Early Secondary growth, Secondary growth and Atresia and appear in mature ovary phases. A description of the different stages of oocyte development follows.

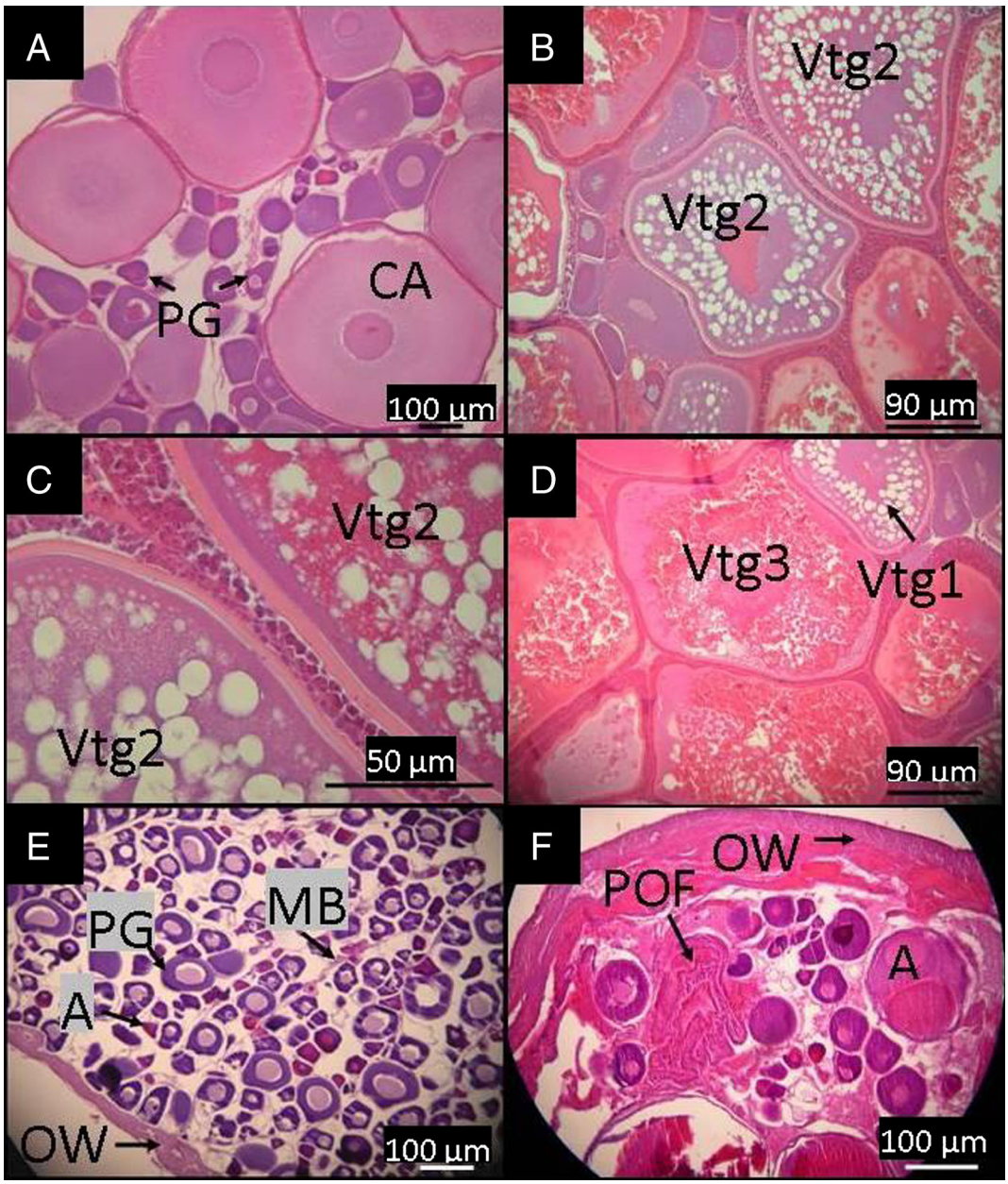

Fig. 2 Photomicrographs of ovarian histology, illustrating oocytes at different stages of development:(**a**) *PG*, Primary growth oocyte, Early secondary growth oocyte: *CA*, cortical alveolar oocytes; (**b**) and (**c**) Secondary growth oocyte: *Vtg2*, secondary vitellogenic oocytes; (**d**) Secondary growth oocyte: *Vtg1*, primary vitellogenic oocyte; *Vtg3*, tertiary vitellogenic oocyte; (**e**) Discontinuous secondary growth: *PG*, primary growth oocyte, *MB*, muscle bundle, *A*, atresia, *OW*, ovarian wall; (**f**) Discontinuous secondary growth: *POF*, postovulatory follicle complex, *OW*, ovarian wall, *A*, atresia

Primary growth (Fig. 2a and e)

Oogonia. Diameter averaging 36.1±1.8 μm (n=50). Very large nucleus (23.4±0.3 μm, n=50). **Chromatin nucleolar**. Similar to oogonia, although somewhat larger (mean diam.=87.1±2.5 μm, n=72). Large nucleus (44.6±1.6 μm, n=72). **Perinucleolar**. In the early stage, size increases (mean diam.=144.0±4.9 μm, n=95). Nucleus more conspicuous (55.9±1.8, n=95). Late stage exhibits rapid growth (mean diam.=151.4±5.9 μm, n=69) and nucleus averages to 69.2±2.7 μm, n=69.

Early secondary growth (Fig. 2a)

Cortical alveoli formation Oocytes in different stages of development. Small vesicles and alveoli appear in the periphery of the cytoplasm. Mean diameter of oocyte 277.7±9.5 μm, n=52 and nucleus 72.6±3.3 μm, n=52. Zona radiata visible, although not yet stained by eosin. Accumulation of lipid inclusions in cytoplasm has begun. Late stage exhibits vesicles and alveoli increase (mean diam.=446.7±8.2 μm, n=55 and nucleus 125.6±5.9 μm, n=55).

Secondary growth (Fig. 2b, and d)

Primary vitellogenic -Vtg1. Primary vitellogenic - Vtg1. In early stage, yolk granules small and numerous, also called yolk spheres or yolk globules containing cortical alveoli present, occupying the entire cytoplasm. Mean oocyte diameter 625±9.2 μm (n=54) and nucleus 154.0±6.4 μm (n=54). **Secondary vitellogenic (Vtg2)**. Cortical alveoli increase in size and gravitate towards the periphery as the yolk granules grow. Follicular layer and zona radiate (5–8 μm thickness) are visible, with the latter being dyed with eosin. Mean oocyte diameter 780±9.5 μm, n=54 and nucleus 170±5.9 μm, n=54. **Tertiary vitellogenic (Vtg3)**. Nucleus decreases in size. Lipid inclusions dispersed in the cytoplasm. Mean oocyte diameter 994.2±13.0 μm (n=63) and nucleus 137.1±3.8 μm, n=63.

Atresia (Fig. 2e)

The cells of the granular layer migrate to the interior of the ooplasm, absorbing the yolk; at the end of this stage the zona radiata disappears.

Table 2 Description of the phases in the reproductive cycle of female of *Hypostomus auroguttatus* in the Paraíba do Sul River

Phase	Macroscopic and histological features
Immature (never spawned)	Small ovaries, often clear, measuring 30–40 mm and weighing between 0.01 and 0.1 g, blood vessels indistinct. Only oogonia and PG oocytes present. No atresia or muscle bundles. Thin ovarian wall and little space between oocytes.
Developing (ovaries beginning to develop, but not ready to spawn)	Enlarging ovaries, measuring 28–46 mm and weighing 0.8–3.2 g, blood vessels becoming more distinct. PG, CA, Vtg1, and Vtg2 oocytes present. No evidence of POFs or Vtg3 oocytes. Some atresia can be present. *Early developing subphase*: PG and CA oocytes only.
Spawning Capable (fish are developmentally and physiologically able to spawn in this cycle)	Large ovaries, measuring 45–67 mm and weighing 9.0–34 g, blood vessels prominent. Individual oocytes visible macroscopically. Vtg3 oocytes present or POFs present. Atresia of vitellogenic oocytes may be present. Early stages of OM can be present. *Actively spawning subphase*: oocytes undergoing late GVM, GVBD or ovulation.
Regressing (cessation of spawning)	Flaccid ovaries, measuring 37–45 mm and weighing 2.9–4.4 g, blood vessels prominent. Atresia (any stage) and POFs present. Some CA and/or vitellogenic (Vtg1, Vtg2) oocytes present.
Regenerating (sexually mature, reproductively inactive)	Small ovaries, measuring 40–46 mm and weighing 1.3–6.7 g, blood vessels reduced but present. Only oogonia and PG oocytes present. Muscle bundles, enlarged blood vessels, thick ovarian wall and/or late-stage (gamma/delta) atresia or old, degenerating POFs may be present.

Oocyte stages code: *PG*, Primary growth oocyte; *CA*, cortical alveolar oocytes; *Vtg1*, primary vitellogenic oocyte; *Vtg2*, secondary vitellogenic oocytes; *Vtg3*, tertiary vitellogenic oocyte; *PG*, primary growth oocyte; *MB*, muscle bundle; *A*, atresia; *OW*, ovarian wall; *POF*, postovulatory follicle complex; *OW*, ovarian wall; *A*, atresia; *OM*, oocyte maturation; *GVM*, germinal vesicle migration; *GVBD*, germinal vesicle breakdown

The structure of the postovulatory follicle is recognizable by its disorganized structure, abundant vacuoles and a convoluted follicular wall surrounding an irregular cavity (Fig. 2f). Mean oocyte diameter is 278.4± 5.1 μm, n=64.

Stages of spermatocytes development

The spermatogenic cells appear in the interior of the seminiferous tubules at different stages during spermatogenesis (spermatogonia, primary and secondary spermatocytes, spermatids and spermatozoa), forming cysts. Each cyst is bound by a layer of connective tissue and contains cells at the same stage of development. In mature testes, the seminiferous tubules are filled with spermatozoa.

Phases of gonadal maturation

Ovaries and testes were assigned to one of the five developmental phases of the reproductive cycle, according to macroscopic and microscopic characterization of the gonads. Macroscopic variations were related to gonadal morphology and microscopic histology according to the composition of the oocytes and spematogenic cells (Tables 2 and 3).

Oocyte size distribution

The size-frequency distributions of *H. auroguttatus* oocytes show a characteristic pattern for each phase of maturation (Fig. 3). Reserve oocyte stock had a diameter <0.1 mm and was present in large numbers in all maturation phases; immature phases showed in the second class oocytes ranging from 0.1 to 0.2 mm in diameter. In the developing phase, oocytes ranged from 0.3 to 4.8 mm in diameter. The spawning capable phase had oocytes ranging 4.8–7.2 mm in diameter. Regressing phases showed a small number of oocytes with diameters of 0.9–4.6 mm, and a large number of reserve oocytes. The regenerating phase oocyte distribution was similar to the developing phase, with diameter ranging from 1.6 to 3.3 mm. The analysis of the frequency distribution of oocytes and the histological

Table 3 Description of the phases in the reproductive cycle of male of *Hypostomus auroguttatus* in the Paraíba do Sul River

Phase	Macroscopic and histological features
Immature (never spawned)	Small testes, often clear and threadlike. Only Sg1 present; no lumen in lobules.
Developing (testes beginning to grow and develop)	Small testes but easily identified. Spermatocysts evident along lobules. Sg2, Sc1, Sc2, St, and Sz can be present in spermatocysts. Sz not present in lumen of lobules or in sperm ducts. GE continuous throughout. *Early developing subphase*: Sg1, Sg2, and Sc1 only.
Spawning Capable (fish are developmentally and physiologically able to spawn in this cycle)	Large and firm testes. Sz in lumen of lobules and/or sperm ducts. All stages of spermatogenesis (Sg2, Sc, St, Sz) can be present. Spermatocysts throughout testis, active spermatogenesis. GE can be continuous or discontinuous. Actively spawning subphase (macroscopic): milt released with gentle pressure on abdomen. Histological subphases based on structure of GE. Early GE: continuous GE in all lobules throughout testes. Mid-GE: continuous GE in spermatocysts at testis periphery, discontinuous GE in lobules near ducts. Late-GE: discontinuous GE in all lobules throughout testes.
Regressing (cessation of spawning)	Small and flaccid testes, no milt release with pressure. Residual Sz present in lumen of lobules and in sperm ducts. Widely scattered spermatocysts near periphery containing Sc2, St, Sz. Little to no active spermatogenesis. Spermatogonial proliferation and regeneration of GE common in periphery of testes.
Regenerating (sexually mature, reproductively inactive)	Small testes, often threadlike. No spermatocysts. Lumen of lobule often nonexistent. Proliferation of spermatogonia throughout testes. GE continuous throughout. Small amount of residual Sz occasionally present in lumen of lobules and in sperm duct.

Spermatogenic stages code: *Sg1*, primary spermatogonia; *Sg2*, secondary spermatogonia; *Scs1*, primary spermatocyte *Sc2*, secondary spermatocyte; *St*, spermatid; *Sz*, spermatozoa; *GE*, germinal epithelium

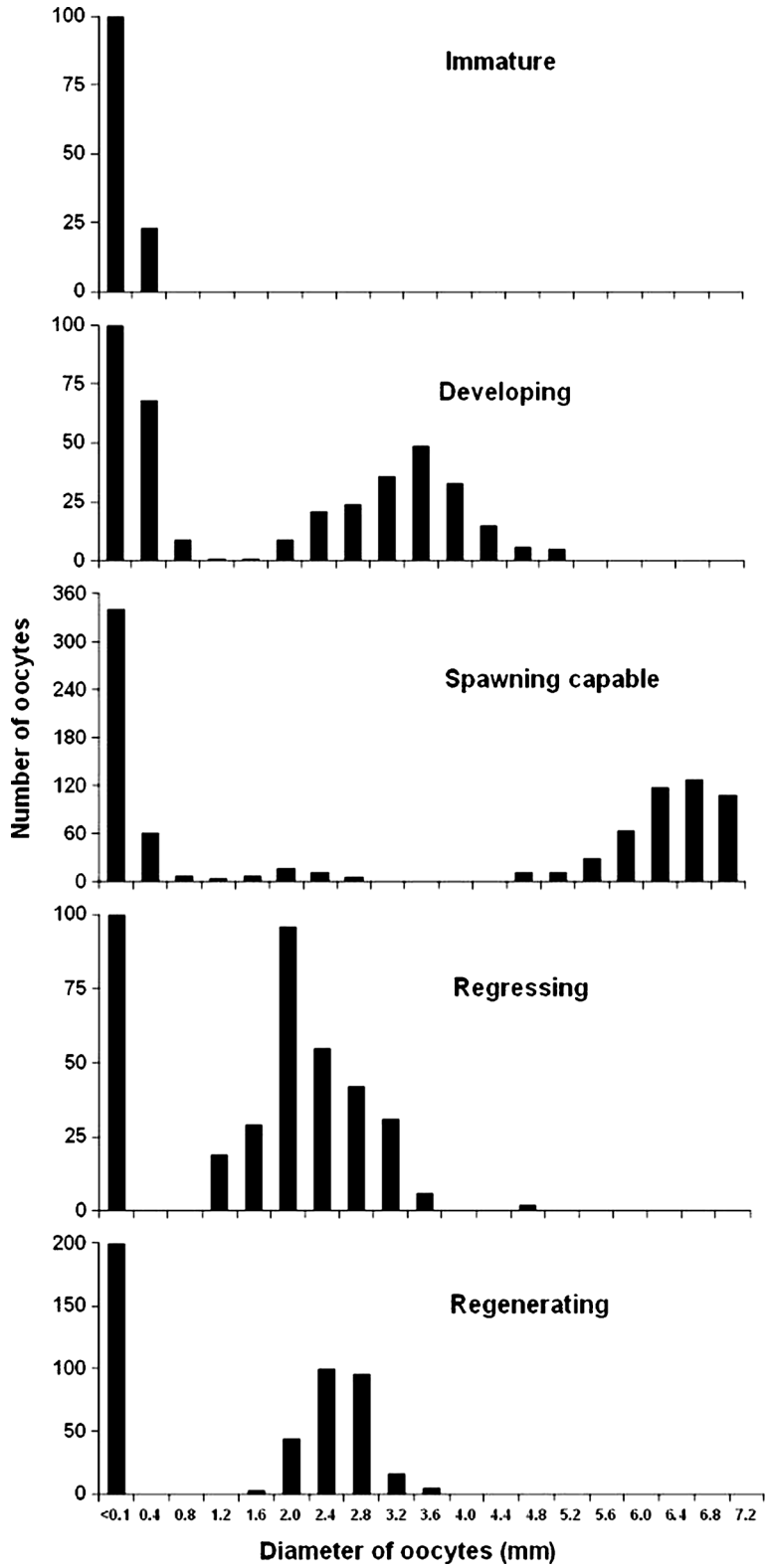

Fig. 3 Oocyte size-frequency distributions through subsequent phases of gonad development of *Hypostomus auroguttatus*

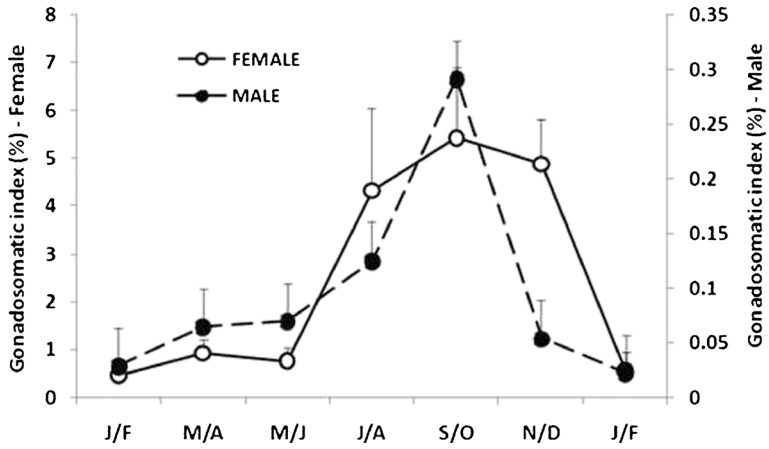

Fig. 4 Bi-monthly changes in gonado-somatic index (means + standard error) for female and male *Hypostomus auroguttatus*, in 2008/2009. J/F, January–February; M/A, March–April; M/J, May–June; J/A, July–August; S/O, September–October; N/D, November/December

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.

Spawning season

Maximum *GSI* values were recorded in September–October for females and males (Fig. 4). Females has higher significant values (F=9.67; P<0.001) between September and December compared to January to June. Males had higher significant values (F=7.8; P<0.001) in September-October compared with the remain period of the year. The percent of ovaries in the ripe stage was between 50 and 60 % in July and September (Fig. 5). In males, the percent of testes in the ripe stage ranged between 20 and 40 % in all months with exception of September–October when 100 % of the spermatocytes were ripe (Fig. 5). A well-defined reproductive period, with GSI peak in September–October for both sexes, in addition to a predominance of a particular oocyte stage inside the ovary, suggest total spawning for this species. In this type of spawning, besides large number of reserve oocytes,

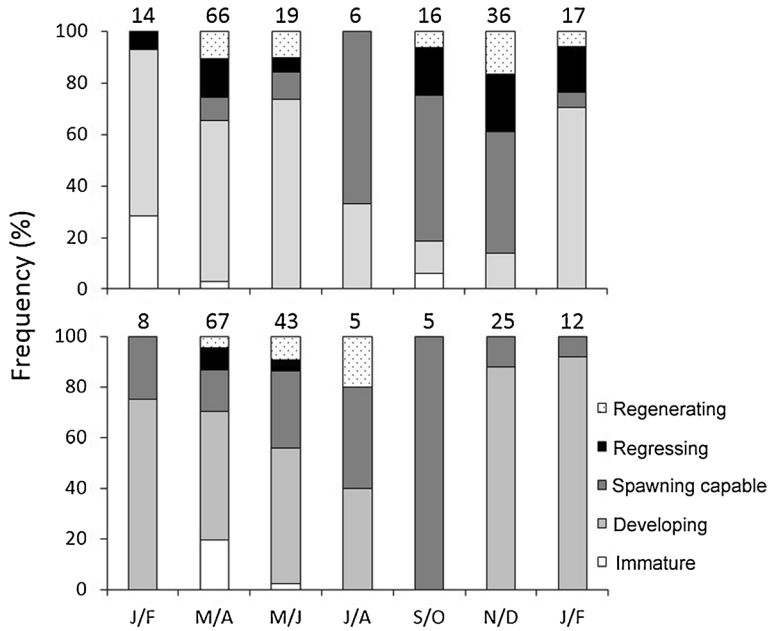

Fig. 5 Bi-monthly frequency distribution for females (above) and males (below) of *Hypostomus auroguttatus* gonadal maturity stages. Numbers above each bar = sample size. Codes of months according to Fig. 4

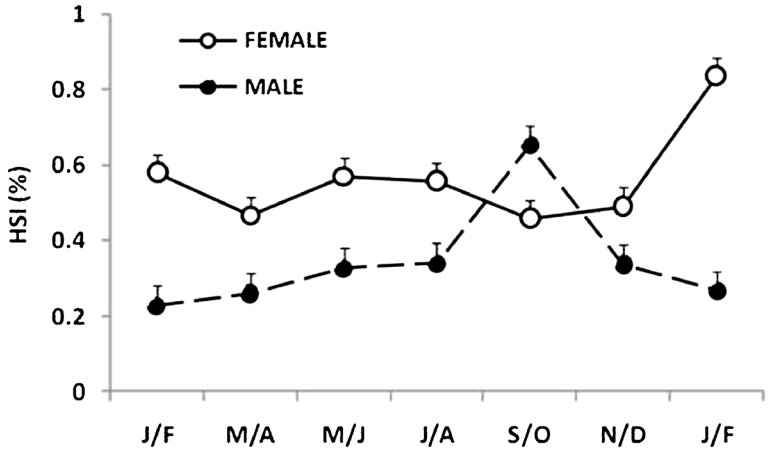

Fig. 6 Bi-monthly changes in hepato-somatic index (means + standard error) for female and male *Hypostomus auroguttatus*. Codes of months according to Fig. 4

a second group of oocytes in a given stage of development is found.

Overall, *HSI* values for females were higher than those for males all over the year, with exception of September/October when males had higher *HSI* than females. Peaks of *HSI* differed between females and males (Fig. 6). Highly significant temporal differences (F=5.7; P<0.0001) were recorded for females that had higher *HSI* in January/February compared to March to June and September to December 2008. For males, comparatively higher *HSI* values (F=3.4, P=0.003) was found in September-October compared with the remaining periods. Moreover, we found indication of significant inverse relationship between GSI and HSI for females (R=0.21; P<0.05) whereas a significant positive correlation (R=0.27; P<0.05) was found for males.

The Fulton's condition factor (K) changed slightly along the year with a tendency for lowest values in males and females between September and December (Fig. 7). However, no significant (females, F=2.3, P=0.05; males, F=0.4, P=0.9) differences were found among the studied period.

Fecundity

Batch fecundity ranged from 163 to 662 ripe oocytes (relative fecundity=2.26 oocytes g^{-1}), averaging 411 oocytes for the 30 examined females, with a total of 1,492 measured oocytes averaging 6.30 mm (±0.57 standard deviation). Fecundity tended to increase linearly with total length, total mass and gonad mass, but the only significant relationship (R^2=0.56; P<0.05) was found between the batch fecundity and gonad mass. The equations that relate these parameters are shown in Table 4.

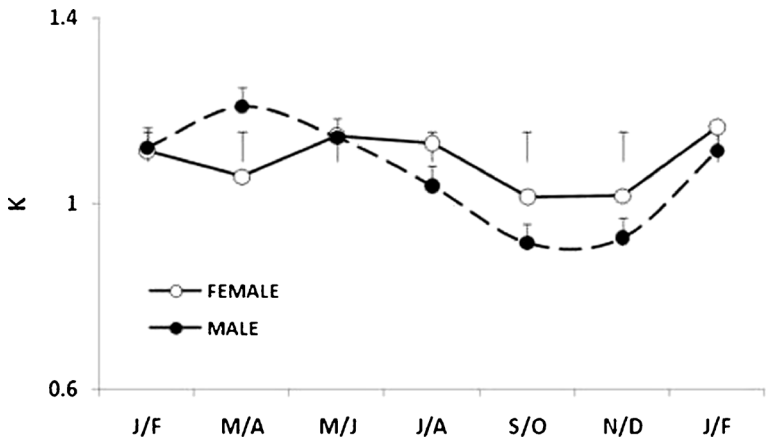

Fig. 7 Bi-monthly changes in condition factor (means + standard error) for female and male *Hypostomus auroguttatus*. Codes of months according to Fig. 4

Table 4 Regression parameters (a, b) for relationship between batch fecundity (y, dependent variable) and parameters of total length (TL), total mass (TW) and gonad mass (GW) (x, independent variables) for *Hypostomus auroguttatus* in the Paraiba do Sul River

Relationship	*n*	Range of x	*a*	*b*	r^2
Fecundity vs TL	30	245–290 mm	566.23	3.67	0.14
Fecundity vs TW	30	121–290 g	243.63	0.92	0.06
Fecundity vs GW	30	7.7–34.1 g	89.72	17.31	0.56

n, sample size, R^2 =coefficient of determination

Discussion

Hypostomus auroguttatus has an equilibrium strategy sensu Winemiller and Rose (1992) in Paraiba do Sul River characterized by a well balanced sex ratio, total spawning, low fecundity and large oocytes. According to Winemiller (1989, 2005), equilibrium-type life history strategies are associated with higher juvenile survivorship as result of greater parental investment in individual progeny. To some extent, this association of life history traits agrees with the "K-strategy" as originally proposed by Pianka (1970). We did not record parental care for this species, but indications of parental care were reported by Mazzoni and Caramaschi (1997b) that suggest that males are less prone to be captured during the spawning season. Suzuki et al. (2000) reported that the congeneric *Hypostomus ternetzi* (Boulenger 1895) males guard nests after spawning.

Hypostomus auroguttatus is the predominant member of the *Hypostomu*s genus in the middle reaches of the Paraiba do Sul River but occurs in low abundance in reservoirs compared with the congeneric *H. affinis* that is the abundant Hypostominae in lentic systems. Reproductive traits could be responsible for such differential occurrence of these close related species in different habitats, since species relative abundance is highly dependent on reproductive success over time (Arantes et al. 2013). There are some differences in the reproductive tactics between *H. auroguttatus* and *H. affinis*. For example, in Lajes Reservoir, a tropical impoundment in Southeastern Brazil (Duarte et al. 2011), *H. affinis* has unbalanced female biased (2 female : 1 male) sex ratio, females reach larger size than males, smaller eggs (average diameter=3 mm) and higher fecundity (1,235–4,275 eggs) compared with our findings for *H. auroguttatus* in the Paraíba do Sul River. According to Mazzoni and Caramaschi (1995) *H. luetkeni* (=*H. auroguttatus*) is restricted to habitat with rocks, while *H. affinis* is able to colonize different types of microhabitat. Because of this pattern of distribution and higher and lower reproductive effort of *H. affinis* and *H. luetkeni*, respectively, Mazzoni and Caramaschi (1995) suggest that *H. affinis* is an opportunistic species (sensu Winemiller) when compared to *H. luetkeni*.

The more stable physico-chemical environmental conditions in the Paraíba do Sul River compared with nearby reservoirs (Klapper 1998) could favor the equilibrium strategy in this system compared with more changeable conditions in reservoirs, where physico-chemical environmental variables (*e.g.*, dissolved oxygen, temperature, pH, nutrients and algae blooms) change widely on daily and seasonal basis (Soares et al. 2008), thus favoring opportunist strategy. Mims and Olden (2012, 2013) found that equilibrium strategists were positively related to predictability in water flow and that a high proportion of equilibrium species is favored in more stable environments. 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 not only withstand the barrage events but could also benefit by the luminous environments below the dam. The fast and slow flowing stretches, the rocky substrate 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. According to Power (1990), most of the species that belong to the genus *Hypostomus* are limited to the bottom and forage on algae. Overall species with larger oocytes are less fertile (Duarte and Alcaraz 1989; Adebisi 1990) and tend to produce large oocytes and in low numbers (Winemiller and Rose 1992; Kolm and Ahnesjö 2005). Reduced fecundity is compensated by the high energy invested in caring for and protecting the eggs, as they take longer to hatch.

According to Lowe-McConnel (1987), species of *Hypostomus* had wide spawning period that last from the end of dry season to peak of wet season, lay the eggs in holes and crevices next to the shoreline and both sex care of offspring. Extended spawning period are an important reproductive tactic to recruitment success as they disperse the mortality risk of the early developmental stages (Begg and Marteinsdottir 2000). Our findings corroborated that *Hypostomus auroguttatus* has a long reproductive period in Paraiba do Sul River.

We found that *H. auroguttatus* has ovarian development as synchronic in two groups of oocytes. Mazzoni

and Caramaschi (1997a) reported that *H. luetkeni (=H. auroguttatus*) has oocyte development different from both asynchronic and group-synchronic (sensu Wallace and Selman 1981), and named oocyte development as "two batches group-synchronous" because after a first recruitment of oocytes into secondary phase, two batches of oocytes in different phases of development grow together being released subsequently after the complete maturation. They also reported that the ovarian development of *H. luetkeni* oocytes differs from its sympatric and congeneric species *H. affinis* which, in contrast, exhibits an asynchronous development. These last findings coincide with those from Duarte and Araújo (2002) that found asynchronic development for *H. affinis* in Lajes reservoir. Asynchronous spawning of small batches of ova throughout the reproductive season ensures that some reproduction occurs regardless of environmental conditions, without sacrificing the ability of large numbers of fish to spawn in synchrony during periods of elevated rainfall when conditions for survival of offspring are optimal (Durham and Wilde 2008).

GSI and frequency of maturity stages analyses for *H. auroguttatus* in this study suggests a spawning period from July to December. The increased *HSI* values in January-February for females suggest that reserves were restored after the spawning efforts. On the other hand, males had close direct relationship with reproductive period suggesting that they are physiologically well prepared for reproduction during the spawning season. A non-significant correlation between *K* with both *GSI* and *HSI* for both sexes is evidence that the vitellogenesis and spermatogenesis are not directly related to the depletion of hepatic reserves or to the decrease in condition factor. These findings are in accordance with Chellappa et al. (1995), that reported the Fulton's condition factor (*K*) and hepato-somatic index (*HSI*) as poor predictors of energy reserves in fish.

The hypothesis that equilibrium reproductive strategy for fish species is favored in more stable, predictable environments was confirmed. The findings of the present study indicate total spawning and equilibrium strategy for *H. auroguttatus* and can be interpreted as being adaptive with respect to better environmental conditions of the riverine system where this species reach high abundance. On the other hand, the congeneric *H. affinis* that is the predominant Hypostominae species in reservoirs seems to be adapted to copy with more harsh conditions of reservoirs, where physico-chemical environmental constraints and food availability are more variable. Further studies on this subject are still required in tropical areas. A research that encompasses different river and reservoirs and between-year variations should be implemented to corroborate this study's findings.

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