

Life history traits of two dwarf cichlids species in the white waters of the Amazonian floodplain

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Abstract The reproductive parameters are among the most important life history aspects of fishes influenced by environmental variation. During recent years, the main life history strategies of Amazonian fish species were defined mostly by a set of reproductive parameters. In the present work, we sought to describe important life history parameters, in particular on reproductive characteristics of *Apistogramma agassizii* and *Apistogramma bitaeniata*, found in floodplain lakes of the Brazilian Amazonia. The species presented a positive sexual dimorphism, and males were significantly bigger than females. For both sexes, four developmental phase of gonad maturation were detected, and based on those it was possible to identify mature, reproductive specimens throughout the entire period of the study. From the ovaries of mature females, fecundity and spawning type were determined. Low fecundity, short spawning periods, possibly separated only by few months, and total spawning are all good indications that *A. agassizii* and *A. bitaeniata* evolved an opportunistic strategy in their life history.

Keywords Reproductive biology · *Apistogramma* · First maturity · Várzea lakes

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Introduction

The reproductive parameters of tropical fish have been broadly used in the definition of their main life history strategies (Winemiller 2005), not only for Amazonian species living in different environments (Espírito-Santo et al. 2013), but also for fish species found at other regions and latitudes (Mims and Olsen 2012). The in depth understanding of the reproductive strategies of a given population provide important information on the relationships of that population and the local habitat. Recently, studies on the reproductive biology of teleosts have revealed a broad variety of strategies that many species evolved, as result of adaptations to abiotic factors, such as temperature, photoperiod, rainfall and floodings (Guerrero et al. 2009; Godinho et al. 2010; Prudente et al. 2014; Vanin et al. 2017).

Variations in the environmental conditions demand adjustments in the reproductive strategies of fishes, to increase reproductive efficiency (Wootton 1984). Based on the pattern variations of mortality, and resource allocation in different life styles, three main types of life history strategies were proposed for neotropical fish species (Winemiller 1989; Winemiller and Rose 1992). Such reproductive strategies, that can be generically described as (1) opportunistic, adopted by fish species of small body sizes, early sexual maturation, short life span, low fecundity and partial spawning, (2) seasonal, found in species of intermediate body size, intermediate to high fecundity and total spawning, and (3) equilibrium, comprising species of large body size, late sexual maturation, long life span, high fecundity and partial

spawning. The triangular continuum model based on these three main strategies can be associated with a gradient of intermediate strategies, adapted to a gradient of environmental conditions, considering environmental stability and stochastic disturbances, and fluctuations in resource available to the fishes (Winemiller 2005). Life history strategies can also predict when the local environmental conditions will maximize the reproductive success of local species (Winemiller 2005).

Studies on the reproductive biology of cichlids carried out in várzea environment show a clear reproductive periodic cycle and the species, in general, synchronize the gonad development and sexual maturation with those moments when conditions are more adequate to spawning, insemination, fry survival and offspring development (Crampton 2008; Louca et al. 2010; Pires et al. 2015; Rangel-Serpa and Torres 2015; Silva et al. 2015). In general, cichlids are expected to show a naïve equilibrium life history strategy, both for South American (Winemiller 1989) and African cichlids (Winemiller 2005; Duponchelle et al. 2008). However, small size cichlid species can apparently develop a more opportunistic life history strategy (Winemiller 1989; Winemiller and Rose 1992).

In várzea environments, heavily seasonal, dwarf cichlids of genus *Apistogramma*, among the smallest neotropical cichlids, live in the litter of shallow littoral zones of the water bodies. This is a seasonally-flooded environment, dominated by Amazonian white waters, with sediments, high nutrient contents and high productivity (Junk et al. 2015). In these water bodies, dwarf cichlids move as the water level varies vertically. During the low water period, the fishes stay at the littoral zone, among the litter formed by dead leaves and dead vegetal matter. As the water level rises, and the riparian forest flooded, the fishes transfer to the root zone of the large aquatic macrophytes banks, formed during the flooding season (Petry et al. 2003).

In the present study, we aimed to describe the reproductive biology of two dwarf cichlids species, *Apistogramma agassizii* (Steindachner 1875) and *A. bitaeniata* (Pellegrin 1936), living in a white water floodplain lake, and to unveil those reproductive traits that might define their life history strategy. We expect that the highly seasonal effects on the environment and the small body size of these species may play an important role in the definition of their life history strategy.

Materials and methods

Study site and sample collection

Members of these two species of dwarf cichlids were sampled bimonthly, from March 2011 to January 2012 at Aningal Lake, inside the Reserva de Desenvolvimento Sustentável Mamirauá (RDSM) (Fig. 1), a white water floodplain lake located at the Middle Solimões region, near the confluence of Solimões and Japurá Rivers. All RDSM water bodies are part of the Solimões river floodplains ecosystem, draining white waters, rich in sediments and nutrients, from the Andean foothills (Queiroz 2007).

In Aningal Lake, as the water level rises, it becomes useless to try sampling *Apistogramma agassizii* and *Apistogramma bitaeniata* at the litter beds in the littoral zone, but they were found in abundance at the root zone of the floating vegetation. Therefore, sampling methodology had to be seasonally adapted to these conditions, and during the low water season, we sampled these two dwarf cichlid species using hand nets (rapichés), in active searches in the flooded litter of the littoral zone. On the other hand, during the high water season we sampled these fishes with the same hand nets, but at the root zone of the floating vegetation (Fig. 2).

Sample processing

After collection, all specimens were preserved in formalin 10% and taken to further analysis in the laboratory, where they were measured and weighted. Total and standard lengths (mm) were measured with a digital caliper. All specimens were dissected with an abdominal incision to visually confirm their sex and to establish the maturation stages of their gonads. For the macroscopic analysis of the gonads we adopted a previous classification system (Brown-Peterson et al. 2011). The gonads were subjected to further microscopic analysis, to confirm macroscopic determination. Microscopic analysis followed basic standard histological techniques, where the samples were dehydrated with increasing solutions of ethyl alcohol (70 to 100%), diafanized in xylol, placed in paraffin to allow cuts of slices 5 µm thick and stained with hematoxylin-eosin (H&E).

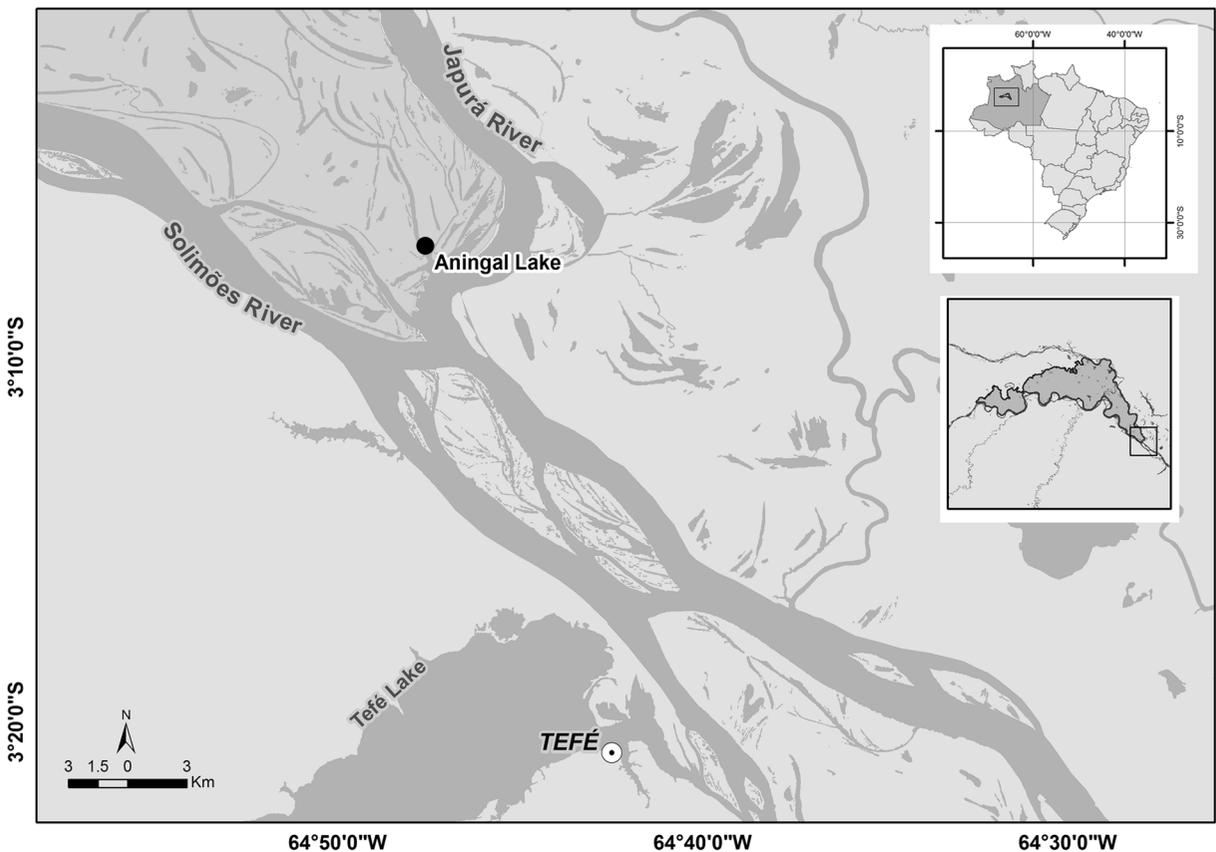


Fig. 1 Sampling sites for *Apistogramma agassizii* and *Apistogramma bitaeniata* in Aningal Lake, at Mamirauá Reserve (RDSM)

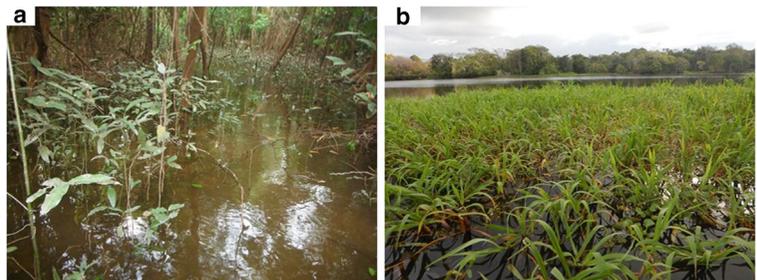
Data analysis

Size structure for both species in each environment was based on the frequency distribution of standard length classes, considering each sex separately. We established class width using Sturges' rule (Sturges 1926), or $h = R/K$ (where h = class width; R = total range of data; $K = (1 + 3.222 \times (\log n))$, and n is the sample size). In order to identify significant differences between the sexes, we applied the "t test", to a 5% contingency level, to the frequency distribution of the classes of standard

length. We performed all analysis with BIOESTAT 5.0 statistic package (Ayres et al. 2007).

The relationship between standard length and total weight was established by a non-linear regression represented by $T_W = a \times S_L^b$ (where T_W = total weight, S_L = standard, a = linear coefficient; b = angular coefficient) and adjusted by the least-squares method. Male and female linear and angular coefficients were compared by the Student's t test (Zar 2009). We used the G test, with a 5% significance level, to evaluate sex ratios bimonthly.

Fig. 2 Sampling sites, showing the littoral zone floodplain during the (a) dry season and (b) formation of floating vegetation during flood season



The reproductive period was determined based on the frequency distribution of mature stages of the gonads, and by the variation of the average values of gonadosomatic index (GSI), was determined according to $GSI = T_W - Wg * 100$ (where Wg = gonad weight, T_W = total weight).

The distribution of the proportion of adults (y) by each length class (x), was adjusted by the least-squares method to a logistic curve, in order to determine the average size at first maturity (L_{50}). Data were adjusted to the logistic model using $y = 1/(1 + \exp. (- (b_1) * (x - b_2)))$, where y = proportion of mature individuals, b_1 = slope curve and b_2 = mean length of sexual maturity are parameters of the equation to be estimated by the model.

To estimate fecundity and to determine spawning type, we analyzed mature ovaries. They were immersed Gilson solution (Vazzoler 1996) and shaken gently until obtain oocyte dissociation from ovarian matrix. After separated, all oocytes had their diameter measured under a microscope-stereoscope, with micrometric ocular lens (at 0.1 mm accuracy). The frequency distribution of oocyte diameters for each of the mature ovaries enabled us to infer the spawning type for each species, and the position of the more advanced modes identified the oocyte developmental stage. We established total fecundity from the amount of vitelogenic oocytes present in each of the mature ovaries analyzed.

Results

During the sampling expeditions, 203 specimens of *A. agassizii* and 238 of *A. bitaeniata* were obtained. Females of both species reached lengths of 10 mm to 31 mm. Males of *Apistogramma agassizii* reached 14 mm to 50 mm and of *A. bitaeniata* males 10 mm to 42 mm. A positive sexual dimorphism was detected for both species. The body length distributions of males and females showed significant differences for *A. agassizii* (t -test = 3.881; $p < 0.05$), but no significant differences in the length distributions between males and females (t -test = 4.8578; $p = 2.1634$) were detected for *A. bitaeniata*. The dominant size class for *A. agassizii* was 19–22 mm, in both sexes. For *A. bitaeniata*, the dominant size class was 23–26 mm for females and 27–30 mm for males.

The parameters of the length-weight relationship, angular coefficient (b) and linear coefficient (a), showed

no significant differences between males and females of *A. agassizii*. On the other hand, significant differences were observed in those coefficients between males and females of *A. bitaeniata* (Table 1).

Annual sex ratio for *A. agassizii* was 1.11:1 (G test = 0.57) and 1.13:1 for *A. bitaeniata* (G test = 0.26). There were significant differences in the sex ratio of *A. agassizii* and *A. bitaeniata* in most of the sampled months during the period of the study (Table 2).

Gonadal development, first sexual maturation, spawning pattern and fecundity

The macroscopic evaluation of the ovaries unveiled four stages maturation. The stages “Immature”, “Developing”, “Spawning capable” and “Regressing”, were confirmed by the histological analysis.

At least some adults of both species were found in reproductive activity in all sampled periods of the seasonal cycle (Fig. 3). We also observed an increase in GSI values for both species in January, its reduction in the following months, and another increase in May for *A. agassizii* and in July for *A. bitaeniata*.

Males of both species reach sexual maturity (L_{50}) at sizes larger than those for females. For *A. agassizii*, males reached sexual maturity at 21.38 ± 1.08 mm of standard length (S_L) and females at 19.85 ± 1.13 mm (t -test = 2.0735; $p < 0.05$). Males of *A. bitaeniata* reached sexual maturity at 20.04 ± 1.1 mm S_L and females at 20.06 ± 0.7 mm (t -test = 1.9613; $p = 0.05$) (Fig. 4).

We detected the presence of two separate oocyte batches in the twenty-two mature ovaries examined. The first was the batch formed by the non-developed, non-vitelogenic oocytes. They represent a reserve lot, and will probably develop in the reproductive periods to come. The second batch was formed by vitelogenic oocytes that, once completely developed, will be spawned still in that reproductive period. This general pattern of synchronic oocital development in two groups suggests a total spawning strategy for both species (Fig. 5). The average diameters of the vitelogenic oocytes was similar for both species (t -test = 7.7711; $p = 1.1268$), 0.5–0.9 mm for *A. agassizii* and 0.5–0.8 mm for *A. bitaeniata*.

Average fecundity determined from mature ovaries of *A. agassizii* and *A. bitaeniata* were similar (t -test = 0.1452; $p = 0.8866$). For *A. agassizii* we found an average of 161.7 vitelogenic oocytes per gonad (\pm

Table 1 Parameters of length-weight relationship for females and males *Apistogramma agassizii* and *Apistogramma bitaeniata*, collected bimonthly from March/2011 to January/2012 in Aningal Lake. (n = individuals number; SL = standard length; TW = weight

total; a = linear coefficient; b = angular coefficient; r² = coefficient of determination; Ta = t test linear coefficient; Tb = t test angular coefficient; t test significance 5%)

		n	SL (min-max)(mm)	TW (min-max)(g)	a	Ta	b	Tb	r ²
<i>Apistogramma agassizii</i>	Females	107	13.7–33.0	0.066–1.091	-4.6046	0.2344	3.0372	0.6785	0.9655
	Males	96	15.0–47.2	0.087–3.112	-4.6573		3.0686		0.9729
<i>Apistogramma bitaeniata</i>	Females	126	12.2–34.8	0.059–1.283	3.4457	0.0118	3.2043	<0.0001	0.8942
	Males	112	12.4–40.3	0.055–1.995	3.5233		2.8423		0.9589

54.1) while for *A. bitaeniata* an average of 158.8 vitelogenic oocytes per gonad (± 19.2) was found.

Discussion

The floodplain lakes are very dynamic, seasonal water bodies, which are important breeding places for many fish species of different shapes and sizes (Carvalho de Lima and Araujo-Lima 2004). However, these environmental traits seem not to influence the life history parameters of these two dwarf cichlid species. In the present study, carried out at Aningal Lake, we demonstrate that *Apistogramma agassizii* and *A. bitaeniata* showed a group of morphologic and reproductive aspects that suggest they perform an opportunistic life history strategy, instead of the seasonal strategy expected. Aspects like total spawning, low fecundity and at least two reproductive periods in the hydrometric cycle, added to the small body sizes and strong sexual dimorphism, all are strong indications that both species have

an opportunistic strategy of life history, as defined by Winemiller (2005).

The genus *Apistogramma* is among the smallest of cichlids in the Amazon, and at study site, in the Middle Solimões region (Hercos et al. 2009). The size differences described between males and females of these two species are the biggest expressions of sexual dimorphism among fishes (Nikolsky 1963). Other relevant differences between males and females were also found in the morphology and coloration of fins, and in the proportion of the body parts in both sexes. In the present study, the males of *A. agassizii* and *A. bitaeniata* were bigger than females, as also found during other investigation with many species of this genus (Römer 2000). When males are bigger than females, it is believed they are under a stronger, more intense sexual selection, suggesting a higher degree of male-male competition and male selection by females (Arak 1988). Among many Neotropical cichlid species, bigger males tend to win other males in aggressive encounters, to conquer and maintain better quality territories and to have better access to females and to perform varied levels of

Table 2 Sex ratio by bimonthly period for *Apistogramma agassizii* and *Apistogramma bitaeniata* in Aningal Lake

<i>A. agassizii</i>				<i>A. bitaeniata</i>		
Month	% Females	% Males	G test	% Females	% Males	G test
Jan/2012	58.3	41.7	1.42	67.6	32.4	15.05*
Mar/2011	45.4	54.5	-4.44*	45.2	54.8	-8.54*
May/2011	48.8	51.2	-3.10	63.6	36.4	6.75*
Jul/2011	53.1	46.9	0.27	48.1	51.9	-0.98
Sep/2011	59.6	40.4	7.63*	64.0	36.0	7.89*
Nov/2011	51.5	48.5	0.78	47.1	52.9	-1.93
Total	52.7	47.3	0.57	52.9	47.1	1.61

Significant differences (>3.84) are indicated (*)

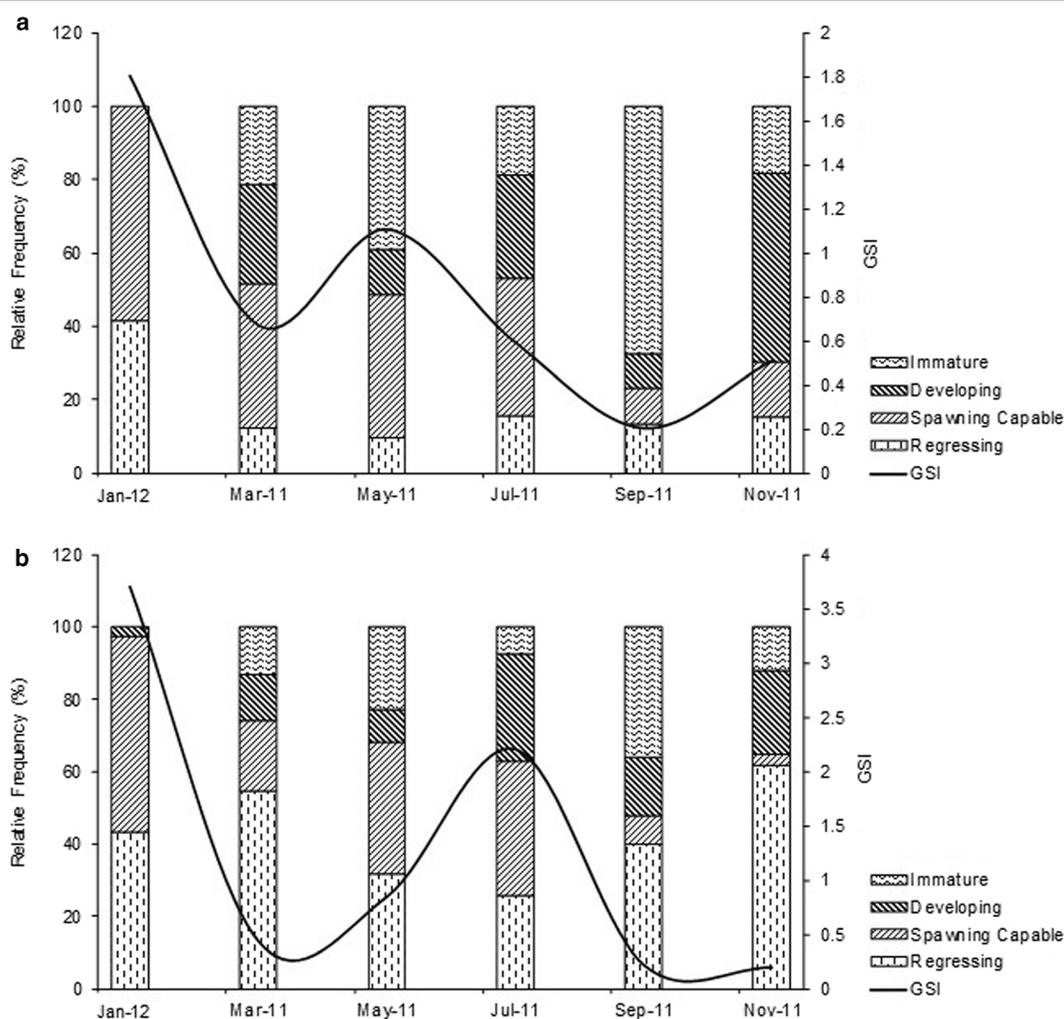


Fig. 3 Relative frequencies of gonadal development and gonadosomatic index (GSI) of *Apistogramma agassizii* and *Apistogramma bitaeniata* (males and females combined) sampled in Aningal Lake, Mamirauá Reserve

parental care (Chellappa et al. 1999; Cacho et al. 2006). The presence of enlarged male structures, that probably play the role of nuptial adornments, such as more developed dorsal, pelvic and caudal fins, gives more support to this hypothesis, but this needs an in depth investigation in the future.

In general, among fishes, males tend to mature earlier and at a smaller size, whereas females grow larger, mature later and tend to invest relatively more resources in their reproduction (Bromley 2003). However, we observed the opposite trend in this study. For some *Apistogramma* species, delayed sexual maturation may not represent an unfavorable trait in sexual selection, particularly for species where the presence of strong males becomes necessary at the time of offspring

protection (Römer 2006). In addition, the male's protective behavior could provide a good explanation for dominance of males in larger class sizes (Ituassú and Chao 2006).

In the present study, we found two batches of oocytes in the ovaries, suggesting that the occurrence of total spawning type, or complete spawning type, similar to the findings for *A. pertensis* living at Zamula (Ituassú and Chao 2006). Total spawning apparently is not a common strategy among Neotropical cichlid species. The spawning strategies of the Cichlidae family is probably best described as partial, or multiple spawning, and the ovaries of those species hold oocytes with a polymodal type of frequency distribution of their diameters (de Araújo et al. 2012). However, on the other

Fig. 4 Size at sexual maturity (L_{50}) for (—) males and (---) females of (a) *Apistogramma agassizii* and (b) *Apistogramma bitaeniata* in the Aningal Lake

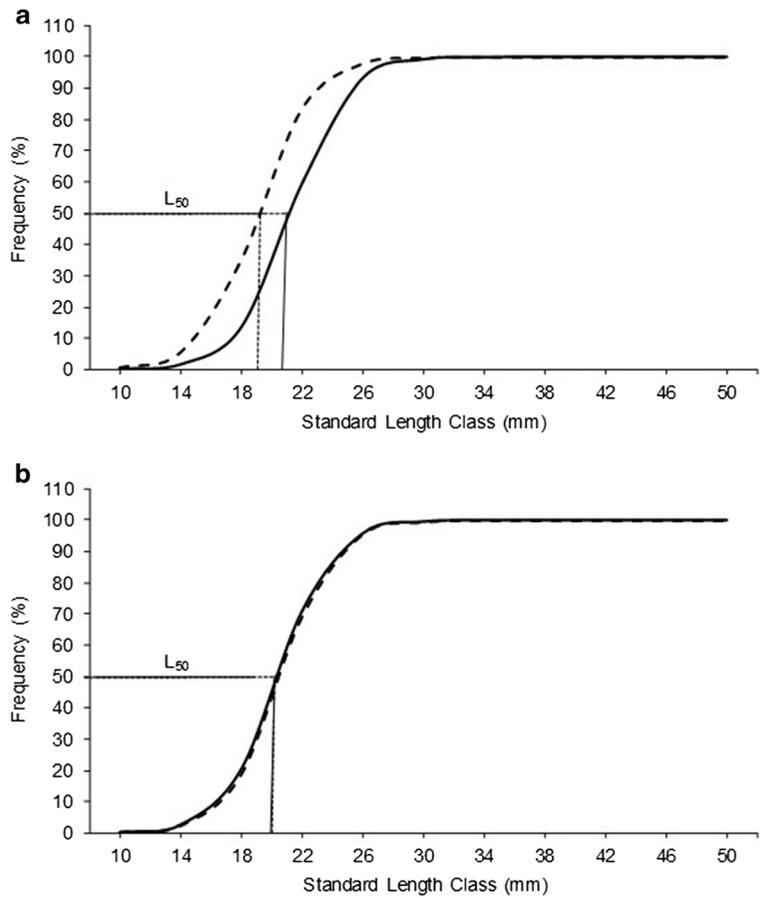
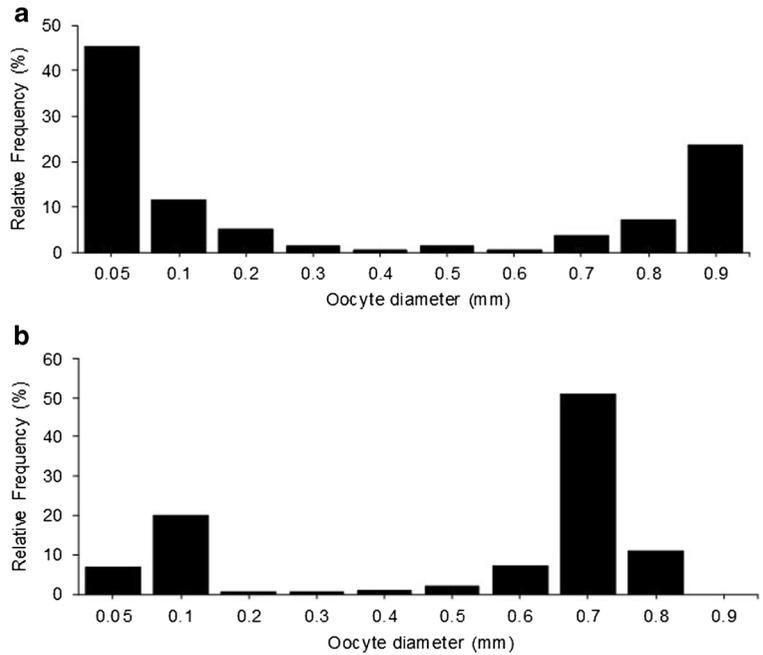


Fig. 5 Oocyte size distributions from (a) ovaries of *Apistogramma agassizii* and (b) ovaries of *Apistogramma bitaeniata* in the Aningal Lake



hand, total spawning is not a rare strategy in Amazonian cichlids (Favero et al. 2010; Rossoni et al. 2010).

We infer that, at the individual level, *A. agassizii* and *A. bitaeniata*, and possibly *A. pertensis* (Ituassú and Chao 2006), mature females release a single batch of oocytes only once in each breeding season. However, at the population perspective, spawning is partial or parceled, and we found individuals at different stages of gonad development throughout the study period, indicating that the population is renewed constantly, throughout the hydrologic cycle. The presence of more than one reproductive peak, observed for both species during the study period, may be a biological response to environments with extreme seasonal changes (due to the increase in the water level). The continuous replacement of members, recruiting new young cohorts into the population, can represent a population structure restoring mechanism, ensuring the persistence and resilience of this population in that particular environment (Aranha and Caramaschi 1999).

Fecundity is a very variable parameter among the cichlids. Larger Neotropical representatives of this family, such as *Cichla monoculus*, show a batch fecundity varying from 20,720 to 24,700 oocytes (Souza et al. 2011). Other, smaller Neotropical cichlids, considered “small brood” spawners (Lowe-McConnell 1999), show proportionally lower fecundities. Among those, are placed the acará-bandeira (angelfish), *Pterophyllum scalare*, varying from 19 to 495 oocytes (Dias and Chellappa 2003), the acará-disco (discus), *Symphysodon discus*, varying from 339 to 696 oocytes (Chellappa et al. 2005) and the acará-boari (flag cichlid) *Mesonauta insignis*, with an average fecundity of 1184 oocytes (Silva et al. 2015). In this sense, the lower fecundity found for the dwarf cichlids in this study was expected. It was also expected that such small fecundities were associated with proportionately larger mature oocytes of circa 1 mm in diameter.

Overall, the results of the present study indicated that despite the seasonal variation of the water cycle in Aníngal Lake, and the important seasonal change in habitat selection and use, the dwarf cichlid species examined still benefits from the extraordinary richness of the white waters environment, and can count on abundant resources all around the hydrological cycle. Most of the morphologic and reproductive parameters studied suggest that these species have an opportunistic life history strategy, although a few of those parameters were similar to a life history strategy of equilibrium, as

found in most members of the Cichlid family. Nutrient rich white water bodies, such as the lakes in the Amazonian floodplain, are important spawning places for *Apistogramma agassizii* and *A. bitaeniata*. However, we have to build a better understanding of how the abiotic factors, and if seasonal variation, influence the reproduction of these dwarf cichlid species.

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