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Reproductive aspects of females of *Leporinus lacustris* Campos, 1945 (Characiformes, Anostomidae) in a Neotropical floodplain

Aspectos reprodutivos das fêmeas de *Leporinus lacustris* Campos, 1945 (Characiformes, Anostomidae) em uma planície de inundação Neotropical

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Abstract: Aim: This study evaluates the reproduction and fecundity of *Leporinus lacustris* in upper Paraná River floodplain environments with the objectives to (i) recognize the germ cells of folliculogenesis and oogenesis; (ii) characterize reproductive phases; (iii) investigate oocyte diameter and evaluate if this species has group synchronous or asynchronous oocyte development and if spawning is total or batch; (iv) estimate batch fecundity; (v) establish the relationship between fecundity/ovary weight, standard length, and total weight; (vi) verify the reproductive areas of this species in the upper Paraná River floodplain. **Methods:** Sampling was carried out using gillnets in rivers, and open and closed lagoons, in March, June, September, and December 2013, 2014, 2015, 2016, 2018, and 2019 and March and September 2017. A total of 442 females were sampled and 111 subsampled, each of which had an ovary removed and fixed in Bouin solution. A subsample of 20 ovaries in the spawning capable phase were fixed in a 4% buffered formaldehyde solution to estimate the diameter of the oocytes and fecundity. The ovaries were dehydrated, embedded in historesin, cut, stained, and evaluated as regards folliculogenesis, oogenesis, development phases, and reproduction areas. **Results:** The germ cells recorded were differentiated oogonia, primary and secondary growth oocytes, fully-grown and mature oocytes, and post-ovulatory follicles that permitted the recognition of the reproductive phases. Oocyte diameter information revealed that the species has group synchronous oocyte development, determinate fecundity and batch spawning, and eliminates an average of 38,490 oocytes. **Conclusions:** The fact that *Leporinus lacustris* is reproductively successful in the Baía River and in the Fechada, Guaraná, Patos, Garças, Ventura and Ressaco do Pau Véio lagoons strengthens the importance of the areas of environmental protection of the islands and lowlands of the Paraná River, Ilha Grande National Park and Ivinheima River State Park.

Keywords: oogenesis; reproductive phases; spawning type; freshwater fish; Paraná River.

Resumo: Objetivo: Este estudo avaliou a reprodução e fecundidade de *L. lacustris* em ambientes da planície de inundação do alto rio Paraná, com os objetivos de: (i) reconhecer as células germinativas da foliculogênese e oogênese; (ii) caracterizar as fases reprodutivas; (iii) investigar o diâmetro dos oócitos e avaliar se esta espécie tem o desenvolvimento dos oócitos sincrônico em grupo ou assincrônico e se a desova é total ou parcelada; (iv) estimar a fecundidade do lote; (v) estabelecer a relação entre fecundidade/peso do ovário, comprimento padrão e peso total e (vi) verificar as principais áreas de reprodução desta espécie na planície de inundação do alto rio Paraná. **Métodos:** As amostragens foram realizadas em rios, lagoas abertas e fechadas no alto rio Paraná, com redes de espera nos meses de março, junho, setembro e dezembro de 2013, 2014, 2015, 2016, 2018 e 2019 e março e setembro de 2017. Foram amostradas 442 fêmeas e subamostradas 111, das quais foi retirada uma subamostra do ovário e fixada em solução de Bouin. Uma subamostra de 20 ovários na fase apta a desova foi fixada em solução de formaldeído tamponado a 4%, para posteriormente, estimar o diâmetro dos oócitos e fecundidade. **Resultados:** As células germinativas registradas foram: oogônias diferenciadas, oócitos de crescimento primário e secundário, oócitos de crescimento completo e maduros, e folículos pós-ovulatórios que permitiram reconhecer as fases reprodutivas. As informações do diâmetro dos oócitos revelou que a espécie tem desenvolvimento dos oócitos sincrônico em grupo, fecundidade determinada e desova parcial, e elimina no período de desova em média 38.490 oócitos. **Conclusões:** *Leporinus lacustris* reprodutivamente bem sucedido no rio Baía e nas lagoas Fechada, do Guaraná, dos Patos, das Garças, do Ventura e do Ressaco do Pau Véio reforçando a importância das áreas de proteção ambiental das ilhas e várzeas do rio Paraná, Parque Nacional da Ilha Grande e Parque Estadual do rio Ivinheima.

Palavras-chave: oogênese; fases reprodutivas; tipo de desova; peixes de água doce; rio Paraná.

1. Introduction

South America presents the richest and most diverse continental ichthyofauna on the planet, with approximately 5160 species (Reis et al., 2016). The upper Paraná River shelters a diversity of about 310 fish species (Agostinho et al., 2008), which corresponds to about 6% of the number estimated for the Neotropical region. The family Anostomidae is a fish group from the order Characiformes that occurs in South America and is represented by 15 genera and 149 valid species (Fricke et al., 2021). The upper Paraná River floodplain unites 4 genera and 13 species of this family, with *Leporinus lacustris* Campos, 1945 being one of the representatives that is distributed in the Paraná and Paraguay river basins (Ota et al., 2018; Fricke et al., 2021).

Leporinus lacustris, which reaches a maximum standard length of 23.0 cm, is a non-migratory species, with external fecundity and no parental care (Vazzoler, 1996; Agostinho et al., 2003; Agostinho et al., 2004) and lives in lagoons, channels, and rivers of the upper Paraná River floodplain (Vazzoler, 1996; Suzuki et al., 2004). The species reaches sexual maturity at 10.4 cm and 8.4 cm standard length for females and males, respectively (Suzuki et al., 2004) and has a prolonged reproductive period (September to March and May) (Vazzoler, 1996; Suzuki et al., 2004), batch spawning, and a mature oocyte diameter of 1259.2 µm (Vazzoler, 1996); however, this author does not analyze models that demonstrate this information. *Leporinus lacustris* exploits different food resources and feeds on plants (fruits and seeds), insects, and occasionally ingests microcrustaceans, bryozoans, and detritus (Resende et al., 1998).

Life history strategies of fish include essential parameters related to offspring survival, such as fecundity and reproductive period, which represent adaptive characteristics that allow the species to deal with temporal and spatial variability of abiotic conditions, food availability, and predatory pressure (Winemiller, 2005). One of the reproductive strategies of fish is the possibility that oocyte development can be synchronous in one group (semelparous species), group synchronous (iteroparous species with determinate fecundity), or asynchronous (iteroparous species with indeterminate fecundity) (Wallace & Selman, 1981; Vazzoler, 1996; Murua & Saborido-Rey, 2003; Lowerre-Barbieri, 2009). Based on the fecundity data, it is possible to evaluate many aspects of fishery stocks, such as total number of eggs produced by adults and estimate recruitment dependent on the density and total yield (Gulland, 1983). This serves as a model to administer and conserve the fishery, in addition to creating guidelines to avoid the capture of high-fecundity individuals. Thus, in order to estimate the fecundity of iteroparous species, it is necessary to investigate oogenesis to verify oocyte development (group synchronous or asynchronous) and spawning type (total or batch).

In this study, we intend to produce information about the reproductive process of *L. lacustris*, in the upper Paraná River floodplain, using long-term data. We aim to evaluate the patterns of oocyte development (group synchronous or asynchronous), fecundity type (determinate or indeterminate) and spawning behavior (total or batch), as well as preferred spawning sites. Specifically, we intend to: (i) recognize the germ cells of folliculogenesis and oogenesis; (ii) describe the reproductive phases; (iii) present the diameter of the oocytes; (iv) demonstrate the relationship between the fecundity and biometric variables of the species; (v) relate the reproductive phases to different floodplain environments.

2. Materials and Methods

2.1. Location of the sampling areas

Specimens of *L. lacustris* (Figure 1), commonly known as "piau and corró", were captured quarterly (March, June, September and December) in 2013, 2014, 2015, 2016, 2018, and 2019 and in March and September 2017. The fish were sampled at nine sites: three rivers (Paraná, Baía, and Ivinheima), four open lagoons (Patos, Guaraná, Garças, and Ressaco do Pau Véio), and two closed lagoons (Fechada and Ventura) (Figure 2).

2.2. Sampling effort

Sampling was carried out at each collection point using 11 single-walled gillnets (meshes: 2.4, 3, 4, 5, 6, 7, 8, 10, 12, 14, and 16 cm; measured between non-adjacent knots) and trammel nets (meshes: 6 and 8 cm). The nets were exposed for 24 hours and inspected in the morning (8:00 to 9:00) (M), afternoon (16:00 to 17:30) (A), and at night (22:00 to 23:30) (N).

2.3. Preparation and analysis of the samples

After the harvest, the fish that were still alive were euthanized using a 2.5 to 3 ml benzocaine solution per liter of water, according to the Animal Use Ethics Committee (Comissão de Ética no Uso de Animais (CEUA)/Pró-Reitoria de Pesquisa e Pós-Graduação (PPG)/Universidade Estadual de Maringá/UEM) (CEUA protocol no. 1420221018 (ID 001974)) and according to the Brazilian Guide to Good

Figure 1. *Leporinus lacustris*, commonly known as "piau" and "corró", in the upper Paraná River floodplain (Photo: Suzuki, H.I).

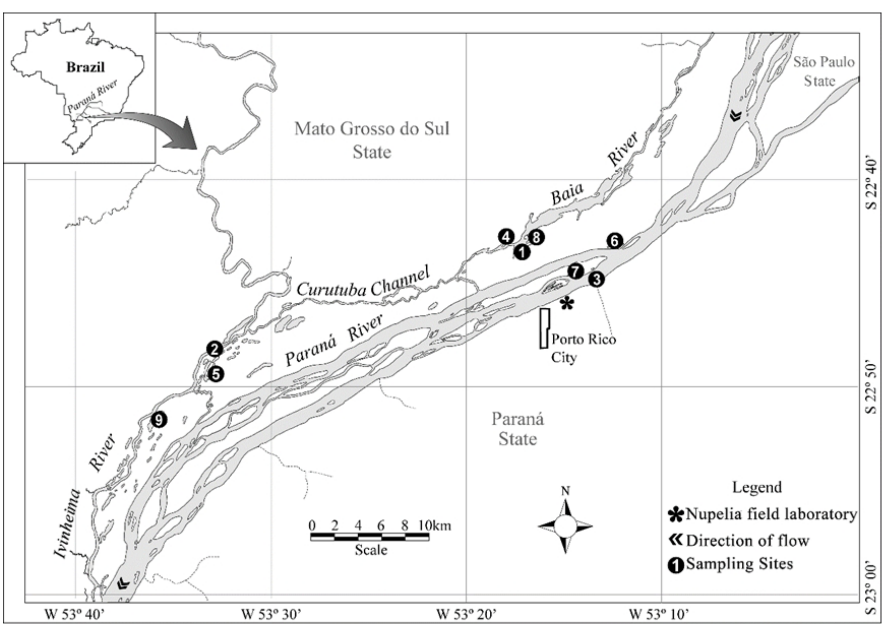

Figure 2. Sampling sites of *Leporinus lacustris* in the upper Paraná River floodplain. Ivinheima subsystem [Patos Lagoon (Lpat) (5), Ventura Lagoon (Lven) (09), Ivinheima River (Rivi) (2)], Baía subsystem [Fechada Lagoon (Lfec) (8), Guaraná Lagoon (Lgua) (4), Baía River (Rbai) (1)], and Paraná subsystem [Garças Lagoon (Lgar) (6), Ressaco do Pau Véio Lagoon (Lpve) (7), Paraná River (Rpar) (3)].

Practices in Animal Euthanasia (Conselho Federal de Medicina Veterinária, 2013).

In the laboratory, a longitudinal incision was made in the abdominal cavity and the ovaries were removed and weighed (0.01 g precision). The sex and development phase of the ovary were macroscopically attributed according to the color pattern, vascularization, visualization of oocytes, and occupation of the abdominal cavity (Vazzoler, 1996; Brown-Peterson et al., 2011; Mazzoni et al., 2020). Next, part of the ovaries was fixed in a Bouin solution for 48 h and later stored in 70% alcohol for the production of histological slides. Part of the ovaries in the spawning capable phase were fixed in a 4% buffered formaldehyde solution, to estimate fecundity.

The ovaries, preserved in 70% alcohol, were dehydrated in an alcohol series and embedded in historesin. They were cross-sectioned in a rotary microtome (thickness: 5 µm). The slides were stained using Periodic Acid-Schiff (PAS)/Iron-Hematoxylin/Metanil Yellow (Quintero-Hunter et al., 1991) and mounted in Permount resin. The documented images were captured using a light microscope (ZEISS) coupled to a digital camera. The germ cells of the ovaries were analyzed according to Grier et al. (2009), Quagio-Grassiotto et al. (2011), and Mazzoni et al. (2020) and the reproductive phases were attributed based on microscopic characteristics that follow Brown-Peterson et al. (2011) and Mazzoni et al. (2020).

The ovaries sampled in the spawning capable phase were used to estimate batch fecundity and those ovaries with post-ovulatory follicles were not considered in fecundity estimates (Murua et al., 2003). To estimate batch fecundity, a part of the ovary was dissected and weighed (0.0001 g precision). The oocytes were separated, counted, and measured under a stereoscopic microscope (Vazzoler, 1981, 1996).

The development type of the oocytes and spawning type were determined according to the frequency distribution of the oocytes by diameter class (Murua & Saborido-Rey, 2003; Murua et al., 2003; Lowerre-Barbieri, 2009).

The batch fecundity (BF) estimate of the ovary was carried out using the gravimetric method (Vazzoler, 1996). To estimate batch fecundity, only the vitellogenic oocytes, recorded from the diameter distribution of the oocytes of each ovary, were considered and determined the number to be eliminated.

Relative batch fecundity was evaluated by ovary weight (Wo, g), standard length (Sl, cm), and total weight (Tw, g). The reproductive areas were recorded by the capture frequency in different ovarian development phases through microscopic and macroscopic evaluation of the ovaries per sampling site.

3. Results

A total of 442 *L. lacustris* females were sampled and 111 specimens subsampled for histological evaluation of the germ cells and confirmation of the reproductive phases during the study period in the lagoons and rivers that compose the upper Paraná River floodplain.

3.1. Folliculogenesis and oogenesis

As regards *L. lacustris*, the germ cells from folliculogenesis and oogenesis are recorded in Figure 3A, B and Figure 3C, D, E, F, G, H, I, J, K, L, respectively.

3.2. Reproductive cycle phases

The microscopic and macroscopic description (Figure 4) of the reproductive phases of *L. lacustris* is found in Table 1. The following phases are recognized

Table 1. Microscopic and macroscopic characteristics of the ovary of *Leporinus lacustris* adapted from Vazzoler (1996), Brown-Peterson et al. (2011) and Mazzoni et al. (2020).

Phases	Macroscopic characteristics	Microscopic characteristics
Immature	Ovaries filiform, translucid, without signs of vascularization; oocytes not observed.	Presence of oogonial cysts and primary growth oocytes; without atresia (Figure 4A-C).
Developing	Large intensely-vascularized ovaries.	Start of development: primary growth oocytes (Figure 4D-F). Development: primary growth oocytes with cortical alveoli and oocytes at the start of vitellogenesis (Figure 4G-I). Oocytes fully-grown or post-ovulatory follicular complex absent. Some atresia may be present.
Spawning capable	Large ovaries occupy almost the entire coelomic cavity; oocytes visible; blood vessels prominent.	Presence of fully-grown oocytes. Some primary and secondary oocytes present (Figure 4J-L).
Regression	Ovaries flaccid and hemorrhagic; few oocytes observed.	Atresic follicles and post-ovulatory complex present. Some oocytes with cortical/vitellogenic alveoli; primary growth oocytes may be present (Figure 4M-O).
Regeneration	Small ovaries; blood vessels present, but reduced.	Primary growth oocytes, atresic follicles, and blood vessels abundant (Figure 4P-R).

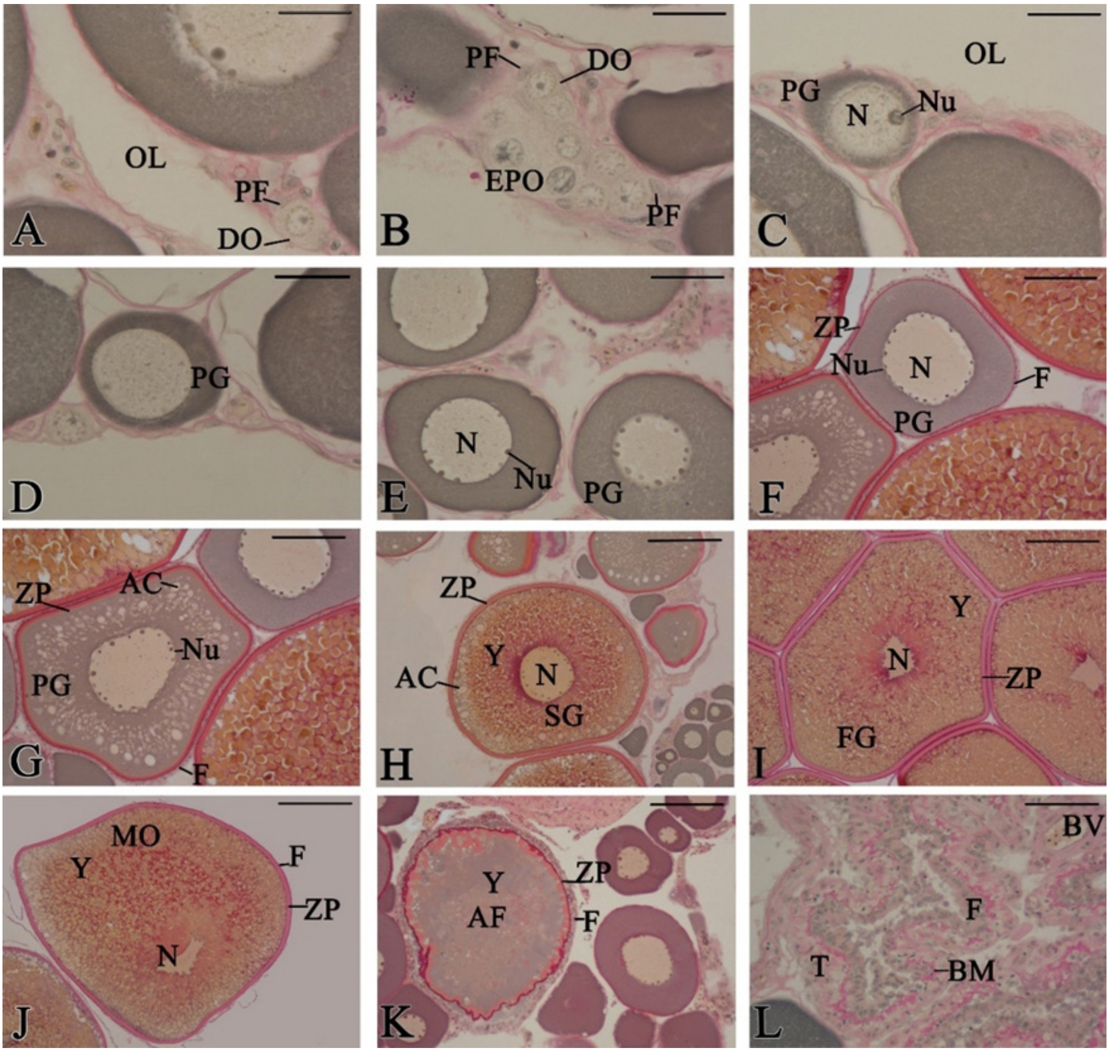

Figure 3. Folliculogenesis and oogenesis of *Leporinus lacustris* females from the upper Paraná River floodplain. (A) Differentiated oogonia (DO), bar = 25 µm; (B) Oocyte cyst in the pachytene and differentiated oogonial cysts surrounded by pre-follicle cells, bar = 25 µm; (C) Primary growth oocyte with one nucleolus, bar = 25 µm; (D) Primary growth oocyte with multiple nucleoli and scarce cytoplasm, bar = 25 µm; (E) Primary growth oocyte with perinuclear nucleoli, bar = 62.5 µm; (F) Primary growth oocyte forming a zona pellucida, bar = 125 µm; (G) Primary growth oocyte showing cortical alveoli, bar = 125 µm; (H) Secondary growth oocyte in vitellogenesis with cortical alveoli, bar = 250 µm; (I) Fully-grown oocyte with central nucleus and abundant ooplasm in yolk globules, bar = 250 µm; (J) Mature oocyte with eccentric nucleus, bar = 250 µm; (K) Irregularly-shaped atresic follicle and yolk globules partially liquified, bar = 125 µm; (L) Post-ovulatory follicle complex formed after the release of the gamete, bar = 62.5 µm; OL = ovarian lumen; PF = pre-follicular cell; DO = differentiated oogonia; EPO = early pachytene oocytes; N = nucleus; Nu = nucleolus; PG = primary growth oocytes; ZP = zona pellucida; F = follicular cell; AC = cortical alveoli; SG = secondary growth oocytes; Y = yolk; FG = fully-grown oocytes; MO = mature oocytes; AF = atresic follicle; T = theca; BM = basal membrane. Staining: PAS+Iron Hematoxylin+Metanil Yellow.

and characterized: immature, developing, spawning capable, regression, and regeneration.

3.3. Spawning type

The diameter of 12,214 oocytes was evaluated. Batch frequency varied from 400 to 900 µm, while the size of mature oocytes varied from 1000 to 1500 µm (Figure 5), indicating that *L. lacustris* presents group synchronous oocyte development, determinate fecundity and batch spawning. Batch spawning is also characterized by different groups of germ cells, such as primary and secondary growth oocytes, secondary growth oocytes in vitellogenesis and the presence of post-ovulatory follicular complexes (Figure 4M-O).

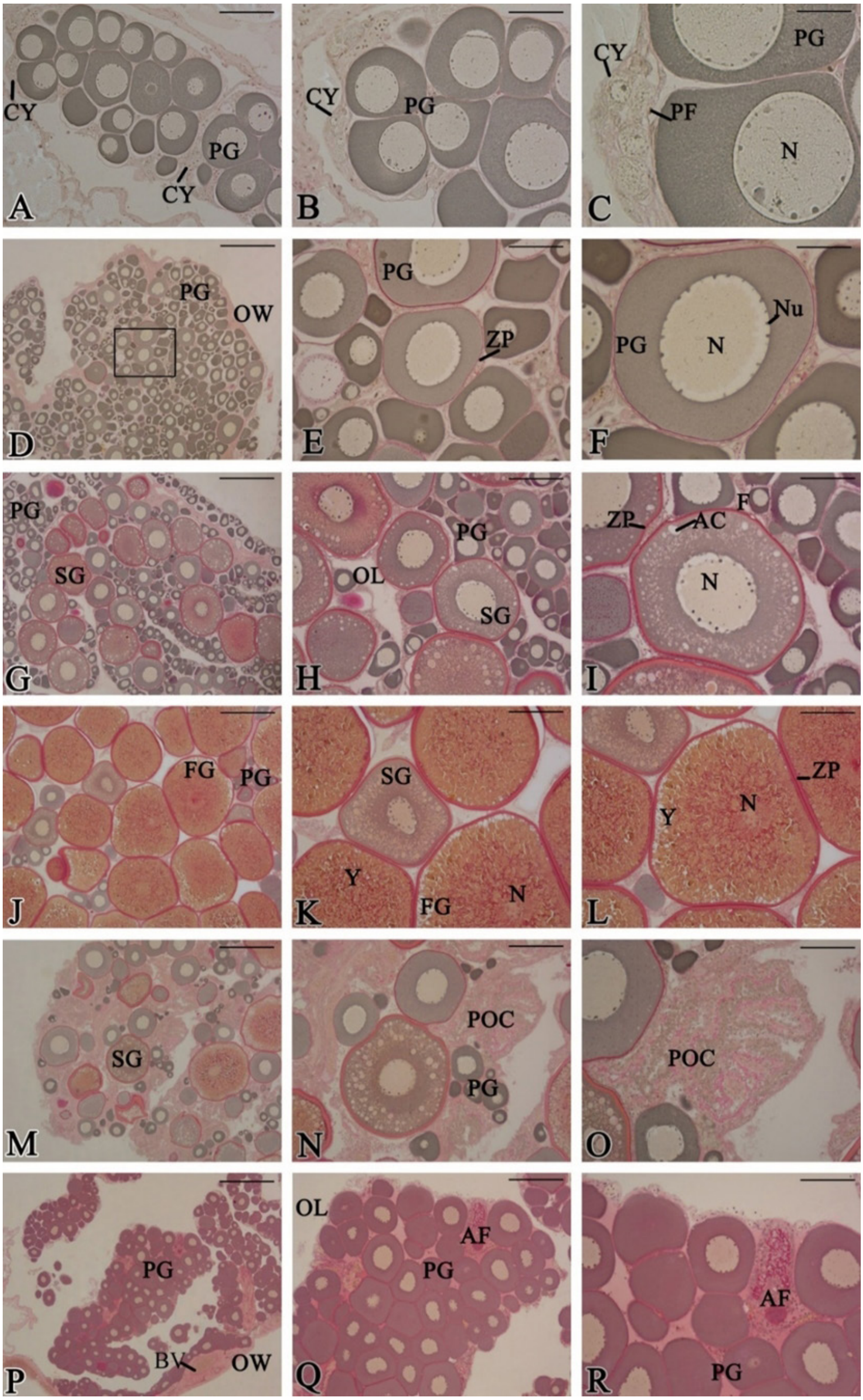

Figure 4. Reproductive phases of *Leporinus lacustris* females from the upper Paraná River floodplain. (A, B, C) Immature, bars A = 125 µm, B = 62.5 µm, C = 25 µm; (D, E, F) Start of development, bars D = 615 µm, E = 125 µm, F = 62.5 µm; (G, H, I) Developing, bars G = 615 µm, H = 250 µm, I = 125 µm; (J, K, L) Spawning capable, bars J = 615 µm, K = 250 µm, L = 250 µm; (M, N, O) Regression, bars M = 615 µm, N = 250 µm, O = 125 µm; (P, Q, R) Regeneration, bars P = 615 µm, Q = 250 µm, R = 125 µm. CY = differentiated oogonial cysts bordered by pre-follicular cells; OW = ovarian wall; N = nucleus; Nu = nucleolus; PG = primary growth oocytes; SG = secondary growth oocytes; ZP = zona pellucida; F = follicular cell; AC = cortical alveoli; FG = fully-grown oocytes; Y = yolk; POC = post-ovulatory follicular complex; AF = atresic follicle; BV = blood vessel. Staining: PAS+Iron Hematoxylin+Metanil Yellow.

3.4. Fecundity

Relative batch fecundity was estimated in relation to ovary weight, standard length, and total weight (Figure 6A-C) from 20 reproductively active females. This species spawns, on average, 38,490 oocytes. In general, the greater the ovary weight, total length, and total weight, the greater the fecundity.

3.5. Reproduction sites

The reproduction sites of the *L. lacustris* females were evaluated through microscopic (Figure 7A) and macroscopic (Figure 7B) analysis of the ovaries and attribution of the reproductive phases. The results reveal that *L. lacustris* reproduces predominantly in the Baía River and in the Fechada and Guaraná lagoons. A low number of reproducing individuals were recorded in the Ivinheima River, while reproductive activities were recorded in the Ressaco do Pau Véio and Patos lagoons. Reproducing individuals were not found in the Paraná River; however, they were present in the Garças and Ventura lagoons.

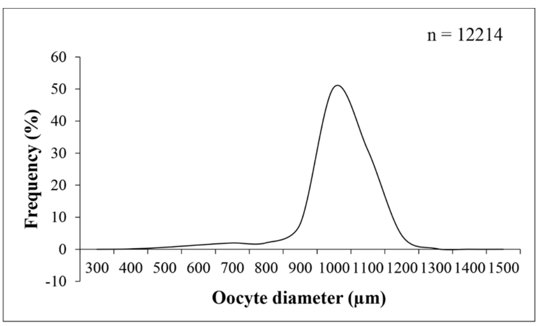

Figure 5. Oocyte diameter frequency of *Leporinus lacustris* from the upper Paraná River floodplain.

4. Discussion

The reproductive phases attributed to ovarian development receive different terminologies by the specialists. Brown-Peterson et al. (2011) record the following phases: immature, developing, spawning capable, regression, and regeneration (males and females). These authors also recognize terminological variations to describe the reproductive phases of fish. There is a tendency to standardize terminologies in Brazil, following the proposal of Brown-Peterson et al. (2011).

Leporinus lacustris is an iteroparous species and the spawning type evaluations showed that the development of the oocytes follows a group synchronous pattern (determinate fecundity with batch spawning) and, therefore, the oocytes mature

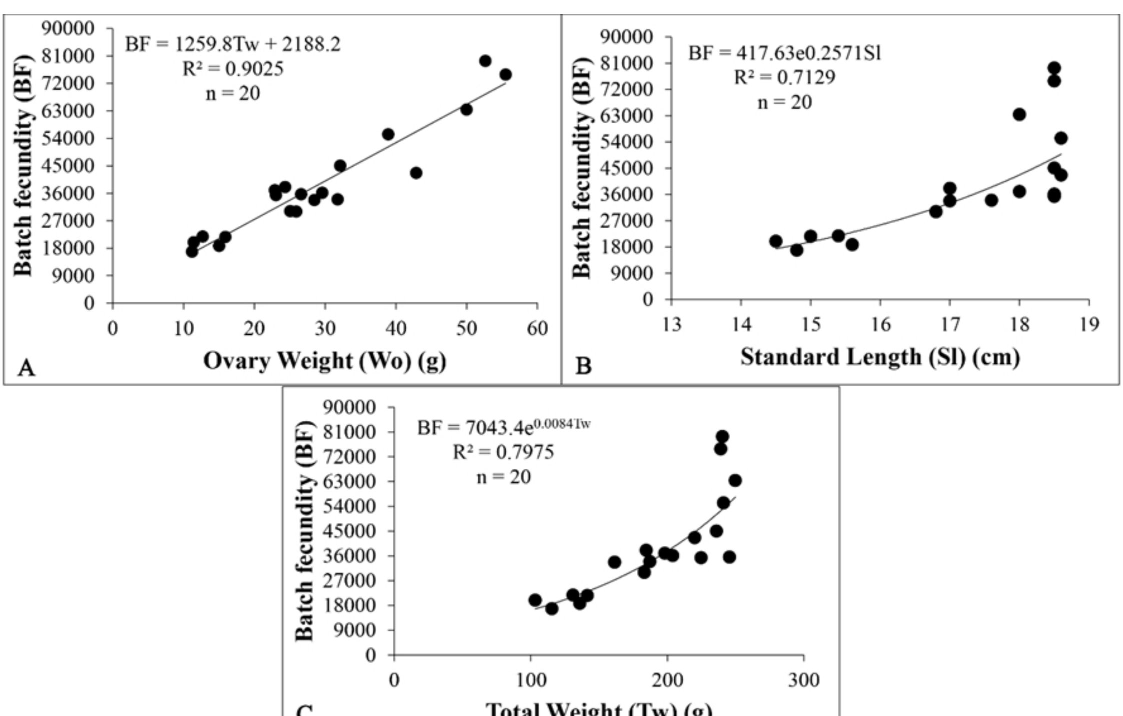

Figure 6. Relationship between relative oocyte fecundity and the (A) ovary weight, (B) standard length, and (C) total weight of *Leporinus lacustris* females captured in the upper Paraná River floodplain.

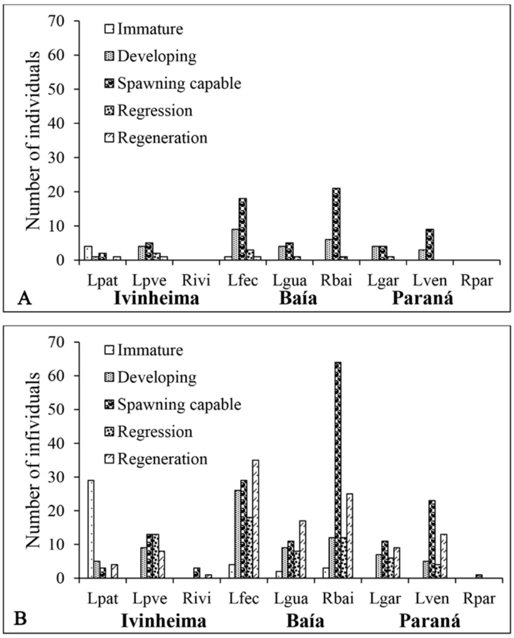

Figure 7. Number of females per reproduction site of *Leporinus lacustris* from the upper Paraná River floodplain. Microscopic (A) and macroscopic (B) evaluation of the ovaries. Lpat = Patos Lagoon; Lpve = Ressaco do Pau Véio Lagoon; Rivi = Ivinheima River; Lfec = Fechada Lagoon; Lgua = Guaraná Lagoon; Rbai = Baía River; Lgar = Garças Lagoon; Lven = Ventura Lagoon; Rpar = Paraná River.

simultaneously and are eliminated at the same time during spawning. The oocytes from the less developed reserve stock have smaller diameters and have to mature synchronously in groups to be eliminated in the spawning period.

An important study about reproductive strategies of the teleost community of the upper Paraná River showed that species that migrate to spawn with external fecundity and no parental care had high fecundity (194,000 to 2,600,000 oocytes), while the non-migrators with external fecundity and no parental care had low fecundity (3,200 to 130,000 oocytes). Non-migratory species with external fecundity and parental care had low fecundity (3,000 to 61,000), the same as species with internal fecundity (10,330 to 14,950) (Vazzoler, 1996). *Leporinus lacustris* is a non-migratory species, has external fecundity and no parental care and had a mean fecundity of 38,490 oocytes (minimum of 16,869 and maximum of 79,391 oocytes).

Evaluation of fish reproduction in the upper Paraná River basin (Vazzoler, 1996; Suzuki et al., 2004) has shown that *L. lacustris* reproduces from September to March (and May) and spawns intensely (≥ 30%) in the Ivinheima, Baía, and Iguaçu rivers, Corutuba Channel, and Guaraná, Pousada das Garças, and Fechada lagoons and moderately (≥ 10 - < 30%) in Patos Lagoon. This study showed that *L. lacustris* continues to reproduce successfully in the Baía River and Fechada, Guaraná, Pau Véio, Patos, Garças, and Ventura lagoons. Few individuals reproduced in the Ivinheima River and no reproductive activity was recorded in the Paraná River.

Leporinus lacustris fecundity, spawning type, and reproductive success in the Baía River and in the Fechada, Guaraná, Pau Véio, Patos, Garças, and Ventura lagoons strengthens the importance of the areas of environmental protection of the islands and lowlands of the Paraná River, Ilha Grande National Park and Ivinheima River State Park. The upper Paraná River floodplain and adjacent areas house 211 species (Ota et al., 2018); therefore, there should be more effort to study the reproduction and fecundity of the fish.

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