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Scientific Article

Long-term monitoring reveals a consistent female-biased sex ratio in *Pimelodus maculatus* from the Upper Uruguay River Basin

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ABSTRACT

Sex ratio is a crucial demographic parameter for the viability of natural populations, and it is commonly balanced in Neotropical freshwater fish species. This study investigated the sexual proportion of yellow-mandi *Pimelodus maculatus* in the Upper Uruguay River basin, southern Brazil, between 2000 and 2019. Fish were captured at different sites in a proportion of 2,018 females and 995 males. The total length ranged from 14 to 60 cm for females (31.8 ± 6.8 cm) and 13 to 45 cm for males (26.7 ± 13.6 cm). The frequency of females was higher from class 27 to 51 cm ($P < 0.05$), with a mean female:male sex ratio of 2.05:1, whereas a 1:1 sex ratio was found in fish shorter than 27 cm. The most important predictor explaining the dominance of females was the length, followed by year, site, and environment. Females are larger and live five years longer than males and they can become more abundant. This disparity in lifespan between females and males, the life history, and social and environmental factors may be associated with the female-biased sex ratio in *P. maculatus* population of the Uruguay River Basin.

Keywords: Neotropical freshwater fish, Lifespan, Reproductive biology, Sex deviation.

Monitoramento de longo prazo revela desvio sexual em fêmeas de *Pimelodus maculatus* da bacia do Alto Rio Uruguai

RESUMO

A proporção sexual é um parâmetro demográfico crucial para a viabilidade das populações naturais e normalmente é equilibrada nas espécies de peixes de água doce neotropicais. Este estudo investigou a proporção sexual do mandi amarelo *Pimelodus maculatus* na bacia do Alto Rio Uruguai, sul do Brasil, entre 2000 e 2019. Os peixes foram capturados em diferentes locais numa proporção de 2.018 fêmeas e 995 machos. O comprimento total variou de 14 a 60 cm para as fêmeas (31,8 ± 6,8 cm) e de 13 a 45 cm para os machos (26,7 ± 13,6 cm). A frequência de fêmeas foi maior da classe 27 para 51 cm ($P < 0,05$), com relação média de sexo feminino:sexo masculino de 2,05:1, enquanto a relação de sexo 1:1 foi encontrada em peixes com menos de 27 cm. O preditor mais importante que explica a dominância das fêmeas foi o comprimento, seguido pelo ano, local e ambiente. As fêmeas são maiores e vivem cinco anos a mais do que os machos, podendo tornar-se mais abundantes. Essa disparidade na expectativa de vida entre fêmeas e machos, a história de vida e os fatores sociais e ambientais podem estar associados ao desvio sexual feminino na população de *P. maculatus* da bacia do Rio Uruguai.

Palavras-chave: Peixes de água doce neotropicais, Expectativa de vida, Biologia reprodutiva, Desvio sexual.

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INTRODUCTION

Population biology and ecology allow us to understand how wild populations organize and develop, with significant consequences for population dynamics and biodiversity conservation (Bessa-Gomes et al., 2004), and are fundamental for advanced studies in the omics era. Reproductive data, including sex ratio, size and age at maturity, and fecundity are essential to the assessment of population structure (Nadal et al., 1996; Wilkinson and South, 2002) and status of conservation (Rieman and Allendorf, 2001). It also reflects the quality of the habitat (Zanette, 2001; Rosenfeld and Hatfield, 2006), and how mating systems evolve (Sowersby et al., 2020).

Sex ratio, which can be expressed as the proportion of females to males in a population, is a crucial demographic parameter for the viability of natural populations (Kvarnemo and Ahnesjo, 1996; Morgan, 2008; McKellar and Hendry, 2011) and the management of breeding stocks (Martínez et al., 2014). It is usually even for most Neotropical freshwater fish species (McConnell and Lowe-McConnell, 1987; Mazzoni and Caramaschi, 1995; Zaniboni-Filho et al., 2017). However, deviations from equality can occur in consequence of sex reversal (McNair Senior et al., 2015); differential mortality, growth rate, and longevity (Pathak and Jhingran, 1977; Costa Novaes and Carvalho, 2011); temporal variation in sex predominance (Costa Novaes and Carvalho, 2011); changes or restrictions in food supply (Nikolsky, 1969), predation (Raposo and Gurgel, 2001); and anthropogenic pollutants, such as domestic sewage and industrial outflow (Kidd et al., 2007).

Pimelodus maculatus (Lacepède, 1803) is a native catfish widely distributed in South American river basins (Fowler, 1948; Ringuelet et al., 1967; Britski et al., 1986; Lundberg and Littmann, 2003). It is a gonochoristic species with direct development (Basile-Martins et al., 1975) and presents multiple spawning (i.e., asynchronous oocyte development with two or more lots of vitellogenic follicles and oocytes released in batches; Rizzo and Bazzoli, 2020) and no parental care (Agostinho et al., 2003). In males, the testes present lobes with testicular fringes (Cruz and Santos, 2004).

Although female to male ratio in *P. maculatus* populations from Paraná River was determined to be 1:1 (Sabinson et al., 2014), the long-term fish monitoring carried out in the upper Uruguay River by our group has been catching frequently more females than males, which motivated us using a 20 yearlong database to investigate:

- Whether this apparently deviation is significantly different from the expected 1:1;
- The temporal and spatial pattern of the sex ratio;
- The differences in length-frequency distribution and lifespan between sexes.

MATERIALS AND METHODS

Fish sampling

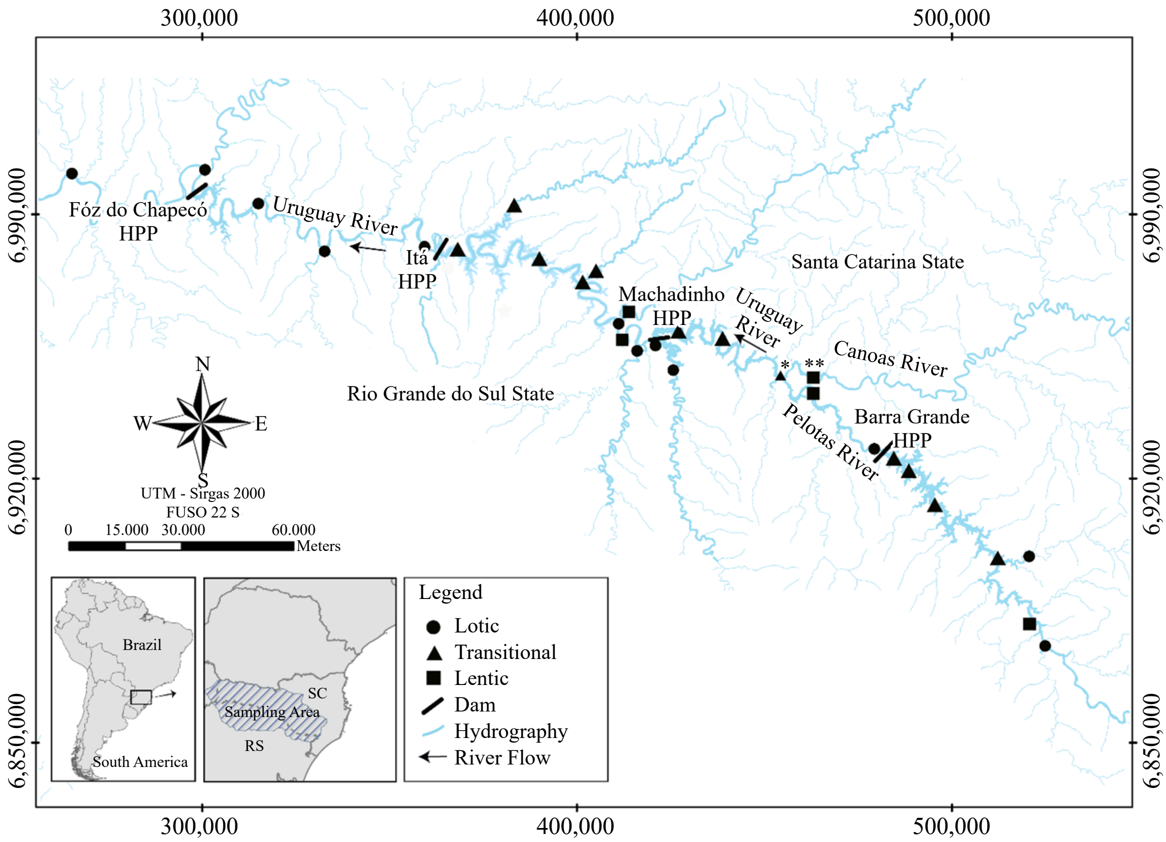
Longlines, trammel nets, and gillnet were used to sample fish in sites (n = 29) distributed in the Upper Uruguay River (Fig. 1) between 2000 and 2019, according to the methodology described in Lopes and Zaniboni-Filho (2019). These sites included lentic (hydroelectric reservoirs), lotic (river stretch consisting of rapids and waterfalls), and transitional environments (moderate-flowing tributary rivers and areas between dams comprising backwaters and pools) delimited by hydroelectric dams located in the area. The study followed the Animal Care Protocol PP00788, with voucher specimen deposited at the Zoology Museum of Universidade Estadual de Londrina (voucher number MZUEL 15606). For each *P. maculatus* captured (n = 3,013), length and sex were recorded.

Data analysis

Length histograms were constructed for females, males, and pooled sex. The interval classes were right-closed and represented by the midpoint. Two-sample Anderson-Darling test, available in *kSamples* package (Scholz and Zhu, 2019), was used to test whether male and female length distributions were the same. Deviations from a balanced sex ratio (1:1) in each length class were evaluated using Fisher's exact test.

A seasonally oscillating von Bertalanffy growth function (soVBGF) estimated the growth parameters L_{inf} (cm) and K (year^{-1}) for each sex, using electronic length-frequency analysis with the simulated annealing approach (ELEFAN_SA) available in the *TropFishR* package (Mildenberger et al., 2017). The first guesstimate of the asymptotic length (L_{inf}) was obtained through the correlation established by Froese and Binohlan (2000). Next, both L_{inf} and K were used to calculate the hypothetical age (t_0 in years) the fish would have had at zero-length (Pauly 1979). Finally, lifespan (t_{max}, in years) was estimated according to Taylor (1960), using the parameters t_0 and K.

The proportion of captured females was modeled using logistic regression with the logit link function. Following Zuur et al. (2010) data exploration protocol, 13 observations were considered truly outliers (Cook's distance of more than four times the mean), and they were dropped from the dataset. Multicollinearity was assessed using the Farrar-Glauber test (Farrar and Glauber, 1967).



*Change from a lotic to lentic environment; **change from a lotic to transitional environment, over the sample period.

Figure 1. Sampling-site locations along the Upper Uruguay River basin. Dam positions and fluviometric characteristics of each sampling station are indicated with specific symbols.

The categorical covariates used as predictors in the model were year, with 20 levels (2000 to 2019), site, with four levels (Barra Grande reservoir, downstream Itá dam, Itá reservoir, and Machadinho reservoir), environment, with three levels (lotic, lentic, and transitional), and length, with two levels (≤ 25 cm and > 25 cm), added after the length distribution analysis. Therefore, the semi-mathematical notation of the model was (Eq. 1):

$$Y_i \sim B(n_i, \pi_i)$$
$$E(Y_i) = n_i \times \pi_i \text{ and } var(Y_i) = n_i \times \pi_i \times (1-\pi_i) \quad (1)$$
$$logit(\pi_i) = Year_i + Site_i + Environment_i + Length_i$$

In which:

Yi = the count of males out of *ni* fish, and is binomial distributed with probability *πi*.

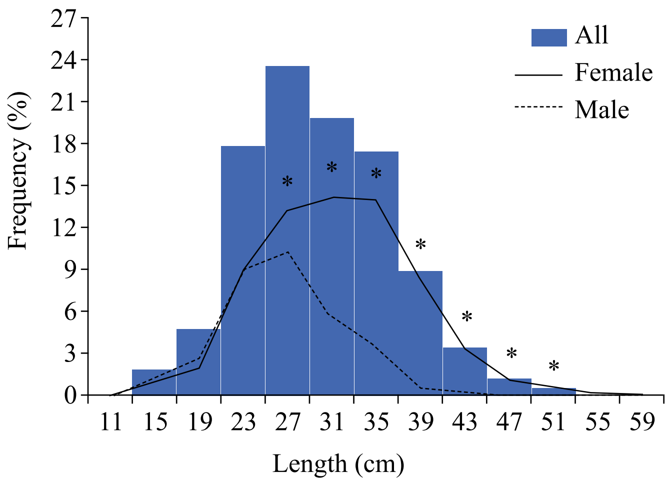
The goodness of fit analysis was performed using the Hosmer-Lemeshow test (Hosmer Jr et al., 2013). The explained variance (pseudo-R^2) was calculated according to Dobson and Barnett (2008). The predictors' relative importance (R2M) to the logistic model was determined using dominance analysis (Azen and Traxel, 2009). The odds were averaged over the other predictors' levels for each significant predictor, and Tukey's adjustment performed pairwise comparisons of the estimated marginal means. Finally, each predictor's levels were tested against an even sex-ratio null hypothesis (proportion of females = 0.5).

All tests were performed at a 0.05 significance level using R statistical software, v. 3.6.3 (R Core Team, 2020), with the odds ratio log scaled. The data were expressed as mean ± standard deviation.

RESULTS

During the 20 years, 2,018 females (377.31 ± 302.68 g) and 995 males (204.31 ± 50.40 g) (Table 1) were captured.

The total length ranged from 14 to 60 cm for females (31.8 ± 6.8 cm) and 13 to 45 cm for males (26.7 ± 13.6 cm). The largest fish captured was a female measuring 60 cm and weighing 2.1 kg. The length distribution differed between the sexes (AD = 198.8, $P < 0.05$), with greater females' frequency ($P < 0.05$) registered at length classes from 27 to 51 cm (Fig. 2). Lifespan was estimated to be 18 years for females and 13 for males (Table 2).



*Significant difference in the proportion between males and females at each length class using Fisher's exact test.

Figure 2. Length distribution of *Pimelodus maculatus* (N = 3,013) captured in the Upper Uruguay River basin between 2000 and 2019.

The logistic model fit adequately (Hosmer-Lemeshow χ^2 = 0.66, df = 4, P > 0.05) and explained 45.7% of the data variation. All explanatory variables were significant in the model (Wald χ^2, P < 0.05), with length being the most important predictor explaining the females' dominance (R^2_M = 0.150), followed by year (R^2_M = 0.031), site (R^2_M = 0.021), and environment (R^2_M = 0.019).

For fish ≤ 25 cm, the sex ratio was 1:1, whereas the odds of catching females increased 227% (P < 0.05) for fish > 25 cm (Fig. 3a). In the years 2013, 2014, 2017, 2018, and 2019, the odds of catching females were not significantly different (P > 0.05) from the odds of catching males (Fig. 3b). Except at the Barra Grande reservoir, females were more captured in all sites, and the odds were higher (P < 0.05) at downstream Itá (Fig. 3c). Females predominated in all environments, and in the transitional zone, the odds ratio increased by 37% (P < 0.05) compared to the lentic environment (Fig. 3d).

Table 1. Sampling number of females and males of *Pimelodus maculatus* sampled annually in the upper Uruguay River basin, between 2000 and 2019.

Sampling year	Female	Male	Female to male ratio	Sampling year	Female	Male	Female to male ratio
2000	29	17	1.7	2010	110	53	2.1
2001	130	63	2.1	2011	112	52	2.2
2002	99	52	1.9	2012	86	55	1.6
2003	126	65	1.9	2013	52	53	1.0
2004	152	73	2.1	2014	57	25	2.3
2005	170	73	2.3	2015	62	13	4.8
2006	212	108	2.0	2016	53	13	4.1
2007	147	75	2.0	2017	43	28	1.5
2008	152	65	2.3	2018	56	23	2.4
2009	128	76	1.7	2019	42	13	3.2

Table 2. Growth parameters of the von Bertalanffy growth model (VBGM) and the *Pimelodus maculatus* estimated lifespan for this and other studies.

Reference	Sex	K	L_{inf}	t_0	Lifespan	VBGM	Site
This study	Female	0.170	62.0	-0.086	18	soVBGF	Upper Uruguay River (SC-RS, Brazil)
	Male	0.244	49.7	-0.222	13		
Fenerich et al. (1975)	Female	0.194	56.5	-0.134	15*	Ford-Walford method	Jaguari and Piracicaba rivers (SP, Brazil)
	Male	0.210	45.4	-0.145	14*		
Sabinson et al. (2014)	Female	0.171	43.9	-0.047	17*	Length frequency distribution method	Middle Paranaíba River (GO-MG, Brazil)
	Male	0.185	42.2	-0.078	16*		

*Estimated according to Taylor (1960), using the parameters t_0 and K reported in the study.

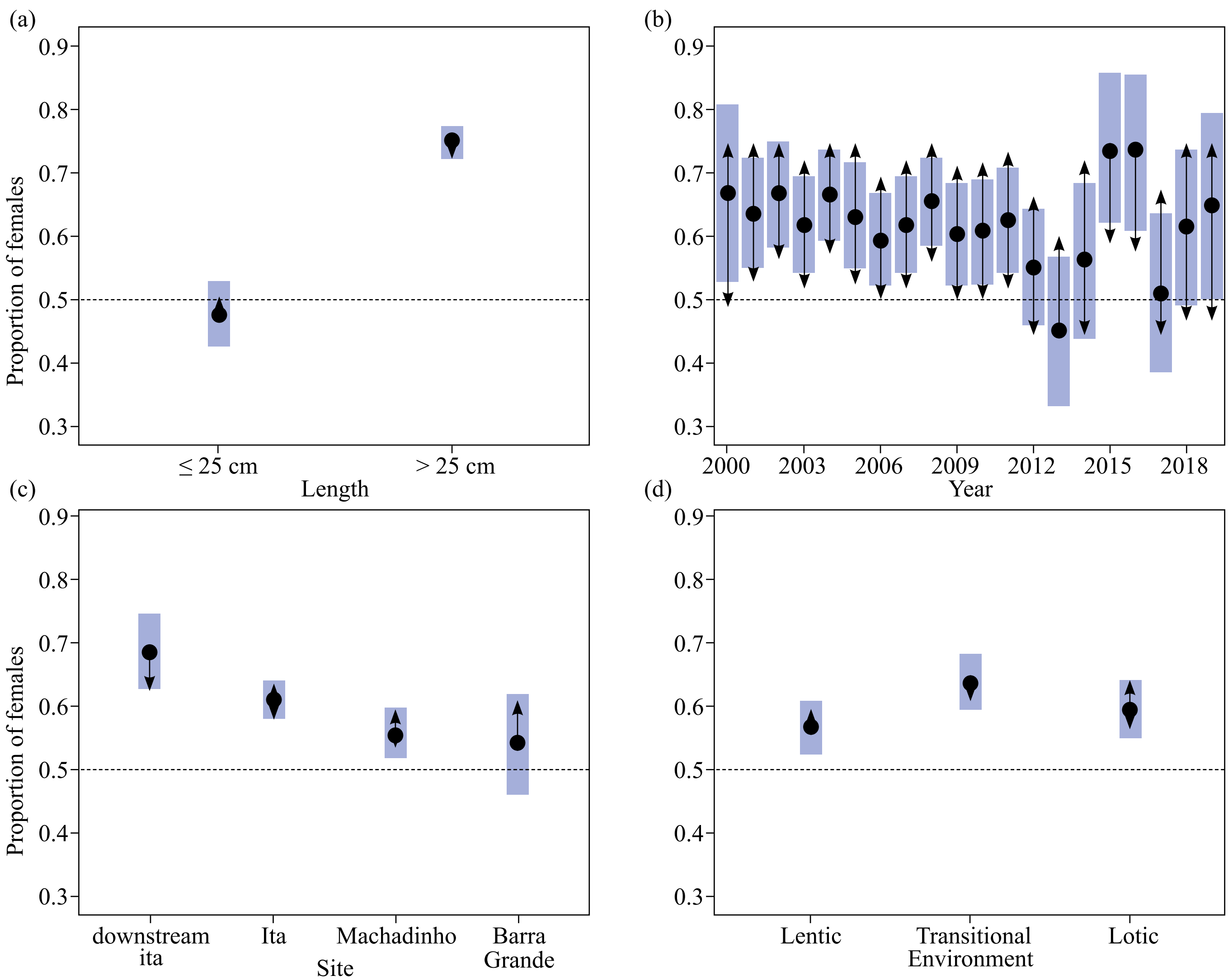


Figure 3. Estimated marginal means (circles) of the proportions of *Pimelodus maculatus* females in the logistic model for the predictors (a) length, (b) year, (c) site, and (d) environment. Grey bars represent confidence intervals. Two means differed significantly if their respective comparison arrows did not overlap (Tukey's multiple comparison test, P < 0.05).

DISCUSSION

As with most Neotropical freshwater fish, *P. maculatus* populations have been reported to have an even sex ratio in both free-flowing rivers (Basile-Martins et al., 1986) and dammed rivers (Sabinson et al., 2014). Indeed, the gender equality in fish ≤ 25 cm may be evidence of a 1:1 sex ratio at hatching that persists into the juvenile stage and at least one moment into adulthood for *P. maculatus* from the Upper Uruguay River (Fenerich et al., 1975; Deitos et al., 2002). However, our long-term data showed consistent and striking differences in the sex ratio both spatio-temporal and size biased in favor of females.

Deviations from equality in sex ratios related to age and length stratification were found locally but not in the whole population, as we observed. According to Basile-Martins et al. (1986), males of *P. maculatus* were more abundant among juvenile fish in some stretches, and females predominate among adult fish in another stretches. Further, Sabinson et al. (2014) argued that a higher proportion of males in the intermediate classes of size distribution and a higher proportion of females in classes of greater size could result from differences in growth rates between the sexes. Adult females of *P. maculatus* females dominated the larger-size classes and were more abundant than adult males, suggesting that other factors such as adult survival rates (Veran and Beissinger, 2009), dispersal (Hutchings and Gerber, 2002), and lifespan (Vandeputte et al., 2012) may be promoting deviations in the sex ratio.

The induced breeding of captive *P. maculatus* requires euthanasia of males for collection of semen directly from testes due to the anatomical shape of testes that makes hand-stripping impossible. However, background information on the reproduction of fish in the wild does not support reproduction or spawning-related mortality (Maia et al., 2007; Paschoalini et al., 2013; Sabinson et al., 2014). Also, sex-biased dispersal seems not to be the case in the Upper Uruguay River because we conducted a comprehensive study in which the data were periodically collected for 20 years, using varied fishing gear and adequate spatial coverage of the sampling sites.

Some hypotheses could explain the deviation in the sex ratio over 25 cm. The greater longevity observed for *P. maculatus* females would be the most likely one. The 5-year difference in lifespan between the sexes was remarkable in the Upper Uruguay River compared to the 1-year difference in the Piracicaba-Jaguari River (Fenerich et al., 1975) and Cachoeira Dourada reservoir (Sabinson et al., 2014), where the sex ratio was even. Therefore, the greater disparity in lifespan between females and males of *P. maculatus* from the Uruguay River may explain why females predominate at this site. In this condition, the longer-lived sex can eventually become more abundant (Arendt et al., 2014; Ward et al., 2019).

A hypothesis pending further investigation is the environmental sex reversal. It has been shown that phenotype sex-determining mechanisms can be overpowered by stressful conditions, such as exogenous hormones, extreme temperatures, density, and captivity (Devlin and Nagahama, 2002; McNair Senior et al., 2015). Until recently, sex reversal was unknown within the Neotropical fishes, particularly after a complete gonad differentiation (Fernandino and Hattori, 2019). A novel study on a captive population of *Brycon orbignyanus*, a sympatric species to *P. maculatus*, revealed the gonadal remodeling and sex inversion from females to males with a complete rise to secondary males at ten months of age (1♀:2♂) (Quirino et al., 2022). Like *B. orbignyanus*, *P. maculatus* is a differentiated gonochorist teleost without specific sex chromosomes. Therefore, there is a possibility of being more susceptible to an environmental disturbance in determining the sexual phenotype.

The construction of a cascade of hydroelectric dams altered the course of the Upper Uruguay River. As a consequence of these disturbances, both the bio-geochemistry processes and food webs tend to stabilize through aging, changing the conditions to supplant aquatic populations (Agostinho et al., 2008). The significant number of *P. maculatus* females in the Itá (filled in 1999) and Machadinho (filled in 2001) reservoirs may be related to favorable environmental conditions and food supply that contributes to the growth and maintenance of older individuals (Nikolsky, 1963; Raposo and Gurgel, 2001; Meurer and Zaniboni-Filho, 2012; Murgas et al., 2019). In contrast, the further upstream dam, and the youngest reservoir (HPP Barra Grande, filled in 2005), was the unique site where the female to male ratio did not differ from 1:1.

Deviations from expected sexual proportions can evolve rapidly within the population and do not appear to be necessarily determined by life history or social behavior (Sowersby et al., 2020) and are still a vast unexplored field. However, from an evolutionary view, a female-biased population in which females are larger and live longer than males may carry a potential reproductive advantage. Larger females can also store more oocytes, increasing their potential fertility, and the time of reproductive activity can be extended by the greater female's longevity (Brewis and Bowler, 1985; Gómez-Márquez et al., 2003; Wootton and Smith, 2014). In addition, both characteristics may pass down through generations.

Our study revealed the existence of a wild *P. maculatus* population, biased towards females, providing new data to assist natural populations' management. Despite the importance of sex ratio in population biology, biodiversity conservation, and management of captive populations, sex ratio variation and their origins remain unclear in many taxa (Krackow, 1995; Eberhart-Phillips et al., 2017), this is still a vast unexplored field for freshwater fish.

CONFLICT OF INTERESTS

Nothing to declare.

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AUTHORS' CONTRIBUTIONS

Conceptualization: Ribolli J; **Formal Analysis:** Ribolli J, Bernardes Júnior JJ; **Investigation:** Ribolli J, Bernardes Júnior JJ; **Resources:** Zaniboni-Filho E, Nuñer APO; **Supervision:** Zaniboni-Filho E, Nuñer APO; **Validation:** Zaniboni-Filho E, Nuñer APO; **Data curation:** Guereschi RM; **Methodology:** Guereschi RM; **Funding acquisition:** Zaniboni-Filho E, Nuñer APO; **Project administration:** Zaniboni-Filho E, Guereschi RM, Nuñer APO; **Writing – original draft:** Ribolli J, Bernardes Júnior JJ, Zaniboni-Filho E, Guereschi RM, Nuñer APO; **Writing – review & editing:** Ribolli J, Bernardes Júnior JJ.

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