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Article

The influence of a large reservoir on the reproductive activity of the white piranha, *Serrasalmus brandtii* (Lütken, 1875) in Southeast Brazil

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Abstract: In order to assess the influence of the Três Marias dam on the reproduction of the white piranha, *Serrasalmus brandtii*, 1569 specimens captured from June 2011 to May 2012 in three sections of the São Francisco River basin were analyzed: section 1 = Três Marias reservoir (TMR); section 2 = São Francisco River (SFR) segment immediately downstream of TMR; and section 3 = SFR segment at the confluence with the Abaeté River. Total length (TL), body weight (BW), gonadosomatic index (GSI), and gonadal maturation stages were determined for each specimen, while vitellogenic follicle diameter, and absolute (AF) and relative (RF) fecundities were also determined for females. Reproductive activity, including spawned females and spermed males, was recorded throughout the year in the three river segments. Higher frequencies of females and males at the maturing/mature stage were found in the November/December and January/February, which coincided with the period of higher temperature, rainfall, and dissolved oxygen concentration. Mean GSI and vitellogenic follicle diameter were higher in sections 1 and 3 than in section 2 ($P < 0.05$), while AF and RF were higher in section 1 ($P < 0.05$) than in sections 2 and 3. The results of the present study showed that *S. brandtii* had lower reproductive performance in section 2, probably due to thermal disturbances caused by the dam, thus confirming the influence of dams on the reproduction of fish downstream from hydroelectric plant reservoirs.
Keywords: *environmental impact, thermal disturbances, gonadal maturation.*

A influência de um grande reservatório na atividade reprodutiva da piranha branca, *Serrasalmus brandtii* (Lütken, 1875) no sudeste do Brasil

Resumo: Com o objetivo de avaliar a influência da barragem de Três Marias na reprodução da piranha branca, *Serrasalmus brandtii*, foram analisados 1569 exemplares capturados de junho de 2011 a maio de 2012 em três trechos da bacia do rio São Francisco: seção 1 = reservatório de Três Marias (RTM); seção 2 = segmento do rio São Francisco (SRF) imediatamente a jusante do RTM; e seção 3 = segmento RSF na confluência com o rio Abaeté. O comprimento total (CT), peso corpóreo (PC), índice de gonadossomático (IGS) e estágio de maturação gonadal foram determinados para cada amostra, enquanto o diâmetro do folículo vitelogênico, fecundidade absoluta (FA) e relativa (FR) foram determinadas para fêmeas. Nas três seções estudadas, a atividade reprodutiva foi registrada ao longo do ano, incluindo fêmeas desovadas e machos espermiados. Maiores frequências de fêmeas e machos na fase de maturação/maduro foram encontradas nos meses de novembro/dezembro e janeiro/fevereiro, coincidindo com o período de maior temperatura, precipitação e concentração de oxigênio dissolvido. O IGS médio e o diâmetro do folículo vitelogênico foram maiores nas seções 1 e 3 do que na seção 2 ($P < 0,05$), enquanto FA e FR foram maiores na seção 1 ($P < 0,05$) do que nas seções 2 e 3. Os resultados do presente estudo mostraram que *S. brandtii* teve menor desempenho reprodutivo na seção 2, provavelmente devido a perturbações térmicas causadas pela barragem, confirmando a influência das barragens na reprodução de peixes a jusante de reservatórios de usinas hidrelétricas.
Palavras-chave: *impacto ambiental, distúrbios térmicos, maturação gonadal.*

Introduction

Most of the world's major rivers have some kind of damming that causes negative impacts to entire fish communities (Olden & Naiman 2010). Although important for economic development, dams cause serious and irreversible impacts to the natural hydrological regime of rivers including altering the downstream flow (Agostinho et al. 2010, Nunes et al. 2015). Such impacts have been detected downstream of several hydroelectric plants in different parts of the world (Clakson & Childs 2000, Todd et al. 2005, Olden & Naiman 2010). In the São Francisco River in the Southeast Region of Brazil, negative impacts of the Três Marias dam on the reproductive activity of the ichthyofauna have been detected in migratory species, such as *Prochilodus argenteus* (Arantes et al. 2010), *Leporinus reinhardti* (Weber et al. 2013) and *Brycon orthotaenia* (Nunes et al. 2015), and foraging species, such as *Astyanax fasciatus* and *A. bimaculatus* (Normando et al. 2014), but there have been no studies evaluating impacts on typically sedentary species or species pre-adapted to lentic environments such as *Serrasalmus brandtii*.

Among Brazilian carnivorous fish, piranhas and pirambebas exhibit a higher degree of agility in catching prey than other species due to their voracity, especially when they inhabit lentic waters (Braga 1981). The white piranha, *S. brandtii*, is native to Brazil and endemic to the São Francisco River basin. It belongs to the Serrassalmidae family (Mirande 2010), which includes piranhas and pirambebas, which are voracious carnivorous freshwater fish that are restricted to South America and occur in Brazilian reservoirs (Jégu 2003). Males of the species perform uni-parental care and the species is pre-adapted to lentic environments (Braga 1981, Agostinho 2003).

Considering that studies related to the reproduction of *S. brandtii* have only been conducted in lentic environments (Honorato-Sampaio et al. 2015), the objective of the present study was to comparatively analyze the reproduction of *S. brandtii* in three sections of the São Francisco River basin — the Três Marias reservoir, a lentic environment, and two lotic sections of the São Francisco River — and to evaluate the impact of the dam on the reproduction of the species.

Materials and methods

1. *Study area*

A total of 1569 specimens of *S. brandtii* were captured in three sections of the São Francisco River (SFR) basin: section 1 = Três Marias reservoir (TMR) (18º23'27" S, 45º13'12" W); section 2 = SFR in the first 34 km downstream of the TMR (18º07'59" S, 45º14'01" W); and section 3 = 34 to 54 km downstream of the TMR, after the confluence of the SFR with the Abaeté River (18º00'49" S, 45°10'51" W) (Figure 1 and Table 1). Fish were sampled bimonthly from June 2011 to May 2012 using gill nets with meshes ranging from 3.0 to 7.0 cm between opposite knots. The fish, if still alive, were killed by cross-sectioning the cervical cord, following the ethical principles for animal handling established by the Brazilian College of Animal Experimentation - COBEA (www.cobea.org.br).

2. *Sampling, biological indices, and biometry*

All fish were dissected and measured for total length (TL), body weight (BW), and gonad weight (GW). These biometric data were used to calculate the gonadosomatic index (GSI = GWx100/BW) and the Fulton condition factor (K = BWx100/TL^3) for each of the three river sections.

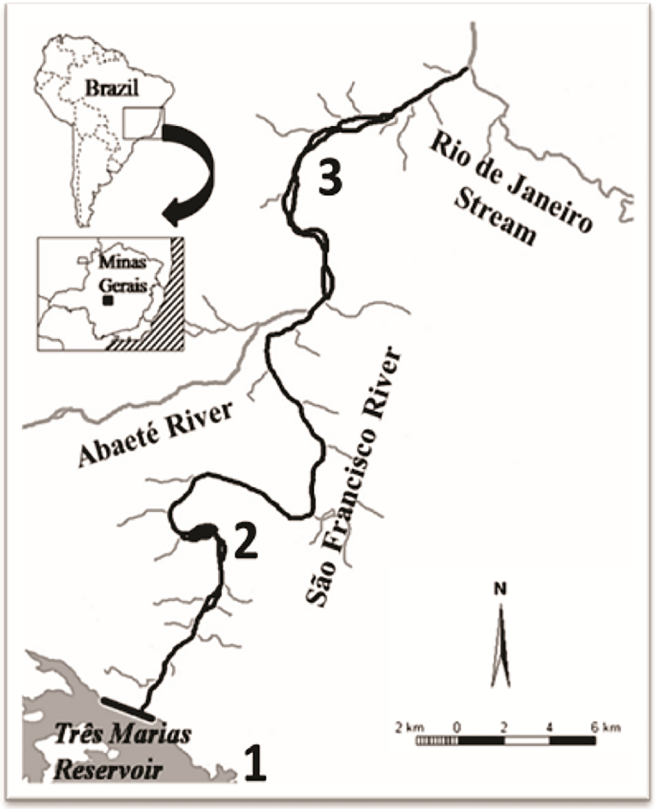

Figure 1. Study area in the São Francisco River (SFR) basin, showing the locations of the studied sections: section 1 = Três Marias Reservoir; section 2 = section of the SFR above the confluence with the Abaeté River, extending from the dam 34 km downstream to the confluence with the Abaeté River; and section 3 = section below the confluence with the Abaete River, extending from 34 to 54 km downstream from the dam.

3. *Histology, gonadal maturation stage and spawning type*

For histological analysis, fragments from the middle region of the ovaries and testes were fixed in Bouin's fluid for 24 hr, embedded in paraffin, sectioned at 5 µm thickness, and stained with haematoxylin-eosin (HE). Stages of gonadal maturation, spawning type, and the frequency distribution were established based on the macro- and microscopic characteristics of the gonads and on variation in the gonadosomatic index (Honorato-Sampaio et al. 2009, Weber et al. 2013, Normando et al. 2014, Nunes et al. 2015, Brandao et al. 2017).

Size at first gonadal maturation was determined as the smallest total length of females and males with gonads in the maturing/mature stage from each section (Boncompagni-Júnior et al. 2013, Brandão et al. 2017).

4. *Histometry, fecundity and sex ratio*

The diameter of 50 vitellogenic follicles, with little shrinkage and intact spherical shape, at the maturating/mature stage of development was measured from histological slides using an Olympus BX 50 light microscope with Olympus CellSens Standard 1.9 software.

Table 1. Water temperature, dissolved oxygen concentration and pH for the three studied sections of the São Francisco River Basin (SFR) from June 2011 to May 2012: section 1 = Três Marias dam; section 2 = SFR immediately downstream of the Três Marias dam; and section 3 = confluence between SFR and Abaeté River.

	Section 1	Section 2	Section 3
	Mean ± SD	Mean ± SD	Mean ± SD
Temperature (ºC)	28.83 ± 0.01	23.21 ± 0.57	24.31 ± 0.71
Oxygen (mg L^{-1})	9.65 ± 0.01	5.55 ± 1.67	7.97 ± 0.55
pH	6.58 ± 0.06	5.83 ± 0.46	6.35 ± 0.51
Flow (m^3 s)	-	570.2 ± 61.2	630.8 ± 60.4

In order to determine fecundity, sub-samples of mature ovaries (n = 10 from for each section) were collected. Samples from the middle region of the ovaries were fixed in a modified Gilson solution (100 ml of 60% ethanol, 880 ml of distilled water, 15 ml of 80% nitric acid, 18 ml of glacial acetic acid, and 20 g of mercuric chloride). Dissociated vitellogenic follicles were separated and counted under a stereoscopic microscope. The number obtained in the sub-sample was extrapolated for the total weight of the ovaries through the simple rule of three. Absolute fecundity (AF) was calculated using the equation: AF = OVA × GW, where OVA is the number of follicles per gram of ovary. Relative fecundity (RF) was calculated using the equations TL (AF/TL) and GW (AF/GW).

The sex ratio in the three sections of the basin was determined as the ratio of the absolute frequency of females to that of males. The chi-square test (x^2; $p < 0.05$) was applied to detect possible differences in the proportions between the sexes.

5. *Statistical analysis*

The variables of the three sections were tested for normality (Shapiro-Wilk) and subjected to an analysis of variance to test for significant differences in mean values of TL, BW, GSI, K, DF, AF, AF/TL and AF/GW. The parametric Duncan test was used to compare mean values. When the assumption of normality was not met, even after appropriate transformations, the data were subjected to the nonparametric Kruskal-Wallis test. A significance level of $P < 0.05$ was employed for all tests.

Results

A total of 992 specimens was collected in section 1 (522 females, 470 males), 349 in section 2 (216 females, 133 males), and 228 in section 3 (118 females, 110 males). There were slightly more females than males in sections 1 and 3, but not significantly so (section 1 = 2.72, section 3 = 0.28), whereas females predominated in section 2 (section 2 = 19.74).

Females and males had statistically higher values for TL, BW, and GSI in the section immediately downstream from the Três Marias reservoir (section 1), than in sections 2 and 3 (Table 2).

Three stages of gonadal maturation were established for adult females (F) and males (M): F1 (16.87 ± 2.80)/M1 (16.43 ± 5.23 cm) = resting; F2 (22.75 ± 8.80 cm)/M2 (18.19± 6.60 cm) = maturing/mature; and F3 (20.79 ± 6.23 cm)/M3 (19.90 ± 6.80 cm) = spawned for females and spent for males (Figures 2 and 3).

Fish in reproductive activity, including spawned females and spermed males, were recorded throughout the year in all three sections. The peak for spawned females and spermed males in the three sections occurred in the bimonthly periods of November/December and January/February. A long reproductive period (Figure 4) and the occurrence of spawning females with follicles in all stages of development, including post-ovulatory folicles, confirm that *S. Brandtii* is a partial spawner.

Sections 1 and 3 had greater vitellogenic follicle diameters ($p < 0.05$) than section 2 (Table 2).

The size at first gonadal maturation for each section was: section 1 = females 14.2 cm and males 12.5 cm; section 2 = females 12.1 cm and males 11.8 cm; and section 3 = females 12.8 cm and males 11.6 cm. Absolute fecundity (AF) and relative fecundity (RF), calculated using TL and GW, were greater in section 1 ($P < 0.05$) than in sections 2 and 3 (Table 2).

Discussion

The results of the present study showed that *S. brandtii* reproduces in all three of the analyzed sections of the São Francisco River basin, although with lower performance in section 2 immediately downstream of the Três Marias dam. The physical and chemical conditions of the water in this section are known to be unfavourable for the reproduction of several fish species (Sato et al. 2005). The lower reproductive performance of *S. brandtii* in this section may be related to the low dissolved oxygen and temperature of the water due to thermal stratification of the reservoir during the summer and to water of the hypolimnion entering the turbines, as well as the anthropic impact of flow control (Santos et al. 2012). Impacts caused by the release of cooler water with low dissolved oxygen have been detected downstream of several other dams in different locations throughout the world (Clarkson & Childs 2000, Donaldson et al. 2008).

Fish from sections 2 and 3 had significantly lower lengths and weights than those from section 1, which may also be due to the negative environmental impacts (Nikolsky 1963) immediately downstream of the dam, as was also observed for *Schizodon knerii* (Brandão et al. 2016). Larger size at first gonadal maturation was observed for females in section 1, which may be related to differences in environmental conditions and food availability (Nikolsky 1963, Pawson et al. 2000). It could also be related to the production of sex hormones, such as 17-β oestradiol, which is responsible for both the somatic growth and gonadal development (Blázquez et al. 1998, Arantes et al. 2010).

The morphological characteristics of the ovaries and testes of *S. brandtii* we found to be similar to those of other species of the family Serrassalmidae (Honorato-Samapio et al. 2009). As has been reported for other piranhas, the mature ovaries of *S. brandtii* exhibited asynchronous development with follicles in different growth stages (i.e. perinucleolar, cortical alveolar and vitellogenic follicles; Honorato-Samapio et al. 2009, Marcon et al. 2017). Three gonadal maturation stages for females and males were established in the present study, which are similar

Table 2. Biological variables for females and males of *S.brandtii* captured in three sections of the São Francisco River basin (SFR) from June 2011 to May 2012. Section 1 = Três Marias dam; section 2 = SFR immediately downstream of the Três Marias dam; and section 3 = confluence of the SFR with the Abaeté River. N = number of fish caught; TL = total length; BW = body weight; GSI = gonadosomatic index at maturing/mature stage; K = Fulton condition factor; DF = diameter of the vitellogenic follicle; AF = absolute fecundity; relative fecundity RF = AF/TL and AF/gonadal weight (GW).

	Females					
	Section 1 (n=522)		Section 2 (n=216)		Section 3 (n=118)	
	Range	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD
TL	10.2 - 34.7	18.7 ± 4.9[a]	14.0 - 22.5	15.4 ± 2.6[b]	13.8 -29.0	15.4 ± 4.2[b]
BW	30.0 - 480.0	143.0 ± 104.0[a]	23.0 - 219.7	83.7 ± 42.5[b]	26.0 - 432.0	85.0 ± 70.8[b]
GSI	0.7 - 3.6	2.1 ± 0.9[a]	0.6 - 2.6	1.40 ± 0.6[b]	0.5 - 1.6	1.42 ± 0.3[b]
K	1,2 - 3,2	1.90 ± 0.3[a]	0.3 - 2.3	1.70 ± 0.4[b]	0.3 - 4.6	1.90 ± 0.6[ab]
DF	622.9 - 1124.7	866.7 ± 156.3[a]	544.6 - 1031.3	729.2 ± 112.4[b]	619.3 - 984.4	859.9 ± 112.5[a]
AF	6011.0 - 8700.0	7041.6 ± 1105.5[a]	3277.0 - 4436.0	3856.5 ± 579.5[b]	5393.0 - 5822.0	5607.5 ± 303.3[ab]
AF/TL	248.3 - 330.6	302.4 ± 46.9[a]	192.7 - 208.2	200.4 ± 10.9[b]	190.8 - 199.0	194.9 ± 5.8[b]
AF/GW	464.7 - 542.0	503.3 ± 54.6[a]	272.3 - 360.6	316.4 ± 62.4[b]	373.3 - 377.2	375.2 ± 2.7[ab]
	Males					
	Section 1 (n=470)		Section 2 (n=133)		Section 3 (n=110)	
TL	10.0 - 31.5	17.4 ± 4.2[a]	13.0 - 22.0	14.9 ± 2.8[b]	13.0 - 26.0	15.5 ± 2.7[b]
BW	25.1 – 312.0	103.2 ± 66.3[a]	22.4 - 216.0	77.2 ± 42.7[b]	25.0 - 182.0	85.0 ± 40.8[b]
GSI	0.4 - 2.9	1.3 ± 0.9[a]	0.3 - 0.9	0.4 ± 2[b]	0.3 - 1.0	0.5 ± 0.2[b]
K	0.4 - 2.9	2.0 ± 0.4[a]	0.4 - 3.2	1.8 ± 0.6[a]	1.0 - 3.5	1.9 ± 0.3[a]

Data expressed as mean ± standard deviation (SD); different letters in the same row indicate statistically significant differences between sections ($p < 0.05$).

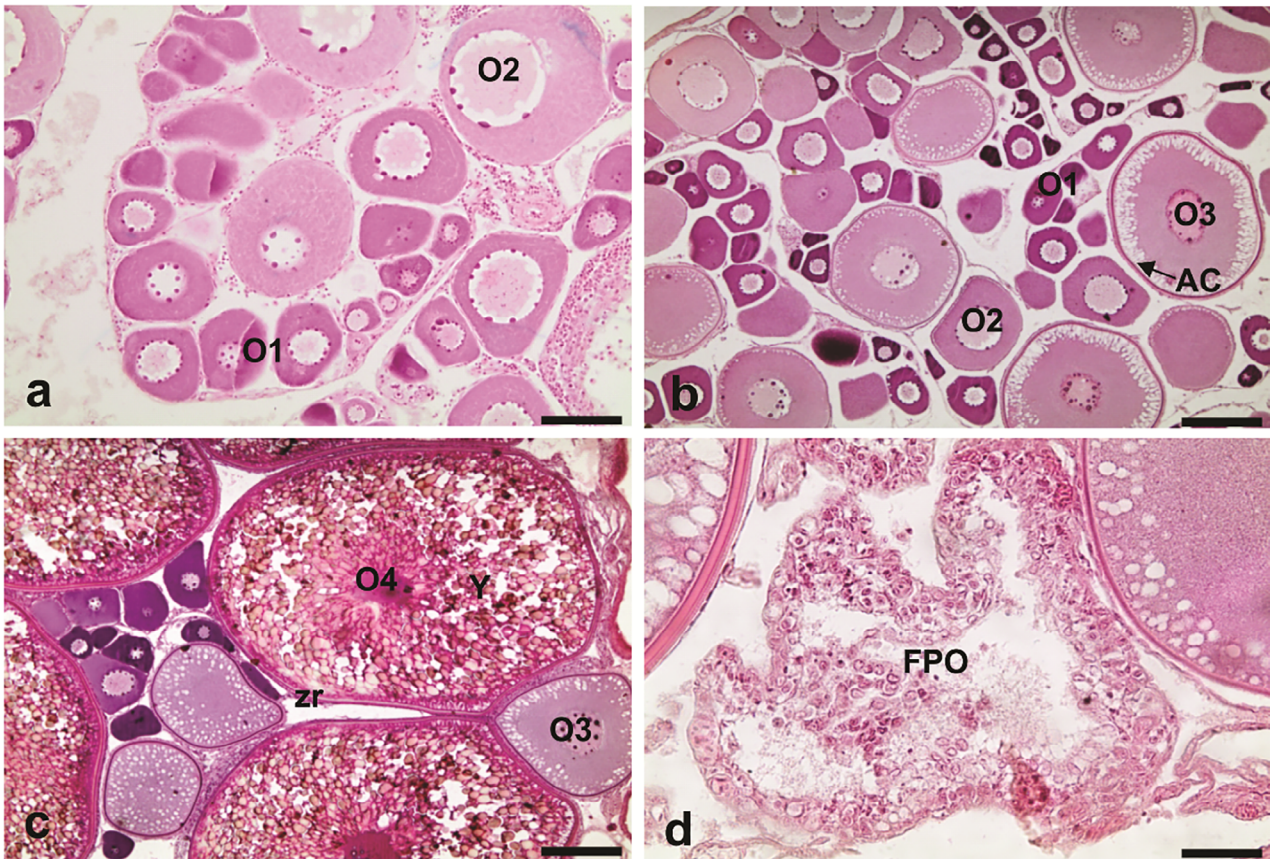

Figure 2. Histological sections of ovaries of *S. brandtii* in different gonadal maturation stages and stained with HE. **a** F1 = resting stage: ovary containing initial (O1) and advanced (O2) perinucleolar follicles. **b** presence of pre-vitellogenic follicles (O3) with cortical alveoli (CA) in a moment of rapid development, which is rare to find in ovarian tissue prior to F2. **c** F2 = maturing/mature stage: ovaries with pre-vitellogenic (O3) and vitellogenic (O4) follicles. **d** F3 = spawned stage: with post-ovulatory follicles (POF). Legend: Vitellogenic follicles (O4) filled with yolk globules (Y), and zona radiata (ZR). **d** F3 = spawned stage: with post-ovulatory follicles (POF). Bars: a, b and c = 200 µm; d = 50 µm.

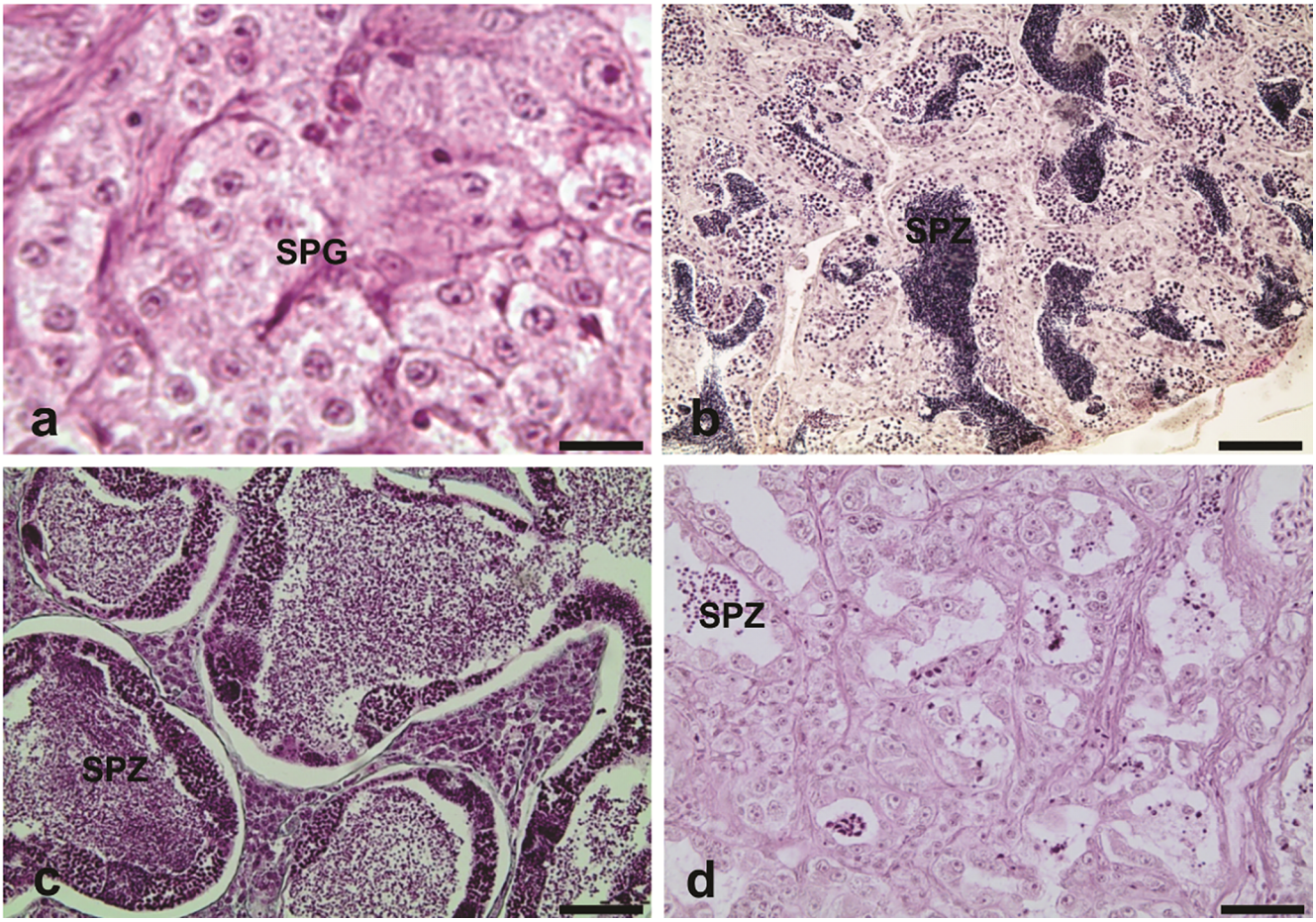

Figure 3. Histological sections of testes of *S. brandtii* in different gonadal maturation stages and stained with HE. **a** M1 = resting stage: containing only spermatogonia (SPG). **b** small amount of spermatozoa (SPZ) in the lumen of the seminiferous tubules in a moment of rapid development, which is rare to find in testis tissue prior to M2. **c** M2 = maturing/mature stage: with seminiferous tubules filled with spermatozoa (SPZ). **d** M3 = spent stage: empty lumen of the seminiferous tubules or with a small amount of residual spermatozoa. Bars: a = 20 µm; b and c = 80 µm; d = 40 µm.

to those that have been reported for other species of Serrassalmidae (Honorato-Samapio et al. 2009) and for fish of other groups (Weber et al., 2013, Normando et al. 2014, Nunes et al. 2015, Brandao et al. 2017).

The GSI can reflect environmental quality since it is directly linked to energy reserves available for breeding (Le Cren, 1951, Yoda & Yoneda 2009, Thomé et al. 2012). The GSI for three sections followed gonad development, with higher values in section 1, thus confirming that *S. brandtii* preferentially favors lentic environments (Braga 1981). The higher GSI values for females caught above the Três Marias dam may be a consequence of the greater number of vitellogenic follicles produced (fecundity) and/or the larger vitellogenic follicles (diameter) for the females of this section.

The highest frequency of spawned females and spent males for the three sections occurred in the bimonthly periods of November/December and January/February, which coincide with high temperatures and rainfall, and longer photoperiods. Indeed, high values for these environmental factors are known to favor the reproductive activity of fish in the Neotropical Region (Lowe McConnel 1987).

The Fulton condition factor (K) provides important information on the physiological state of fish, assuming that individuals with higher K values are in better health (Nikolsky 1963, Vazzoler 1996, Froese 2006). In the present study, the highest K values for females and males were recorded in section 1 where water temperature, and oxygen quality were more favorable.

Histometric analysis of maturing/mature ovaries showed four classes of vitellogenic follicle diameter, indicating asynchronous folliculogenesis with distinct populations of vitellogenic follicles that will be spawned in batches. These findings are consistent with that observed for other teleosts that have fractioned spawning and batch fecundity (Melo et al. 2011, Armstrong & Witthames 2012). Asynchronous folliculogenesis is characteristic of species with long reproductive periods, multiple or fractioned spawning or batch fecundity. As are histological characteristics of spawned females, frequency of maturation stages and variation in the gonadosomatic index (Nikolsky 1963, Núñez & Duponchelle 2009; Lubzens et al. 2010), as is the case for *S. brandtii* of the present study.

The present study found batch fecundity and statistically higher fecundity relative to total length and gonadal weight in section 1, followed by section 3, showing that, as with GSI and vitellogenic follicle diameter, fecundity may be influenced by more favorable reproductive conditions for *S. brandtii*, particularly in section 1. Physical and chemical conditions of water are known to be the main factors influencing reproductive potential, as evidenced by vitellogenic follicle number and diameter (Yoda & Yoneda 2009, Armstrong & Witthames

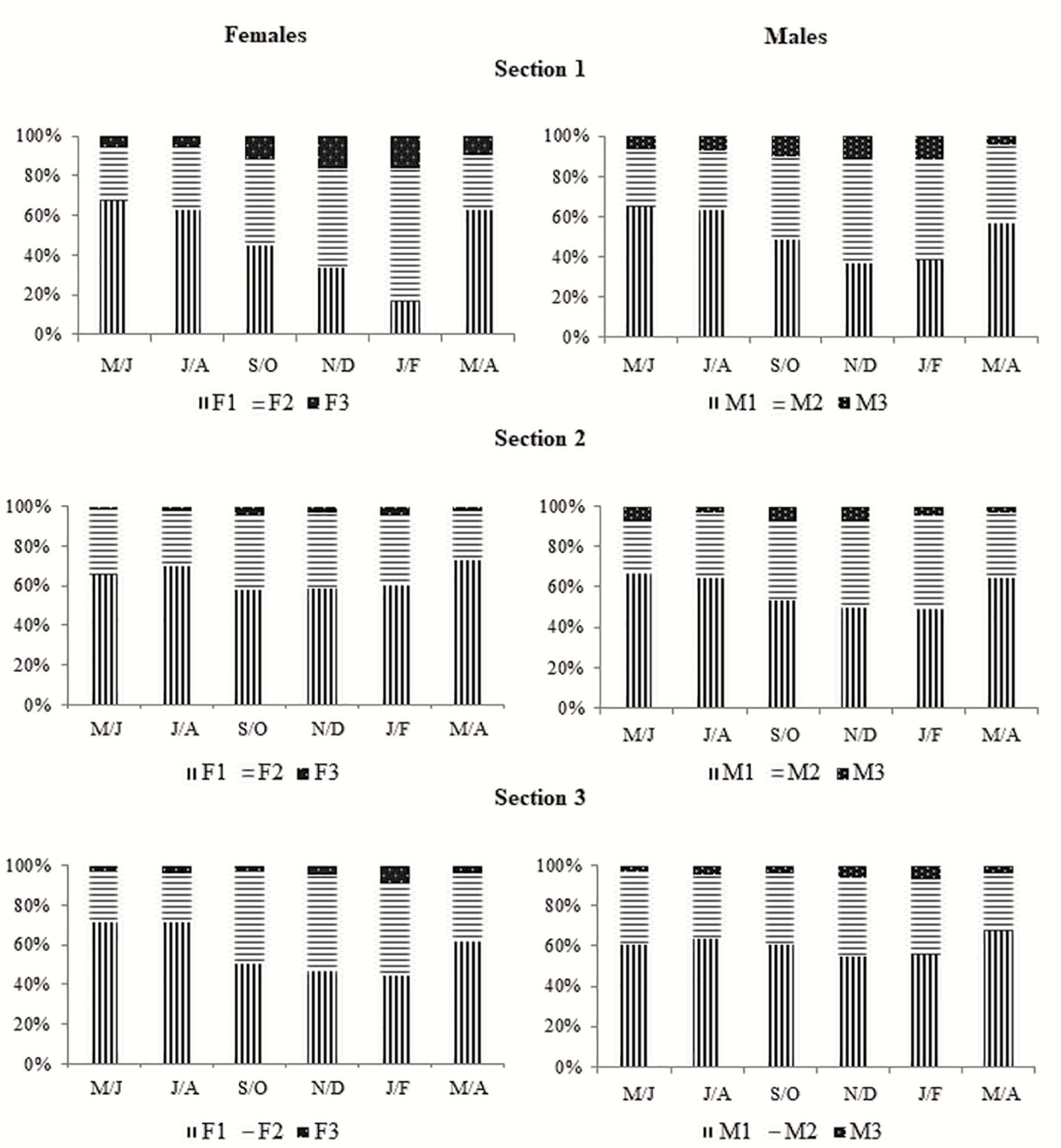

Figure 4. Bimonthly (May-June = M/J; July-August = J/A; September-October = S/O; November-December = N/D; January-February = J/F; March-April = M/A) relative frequency of gonadal maturation stages of female and male *S. brandtii* captured June 2011 to May 2012 in the Três Marias reservoir (section 1), São Francisco River immediately downstream of the Três Marias reservoir (section 2), and after the confluence of the São Francisco River with the Abaeté River (section 3). F1 = resting, F2 = maturation/mature, F3 = spawned, M1 = resting, M2 = maturing/mature, and M3 = spermiated.

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2012). In addition to the known effects of the hypothalamic-pituitary axis on reproduction, Jensen et al. (2004), Chakrabarty et al. (2012), and Marcon et al. (2017) found differences in the concentrations of vitellogenin, estradiol and aromatase, and in vitellogenic follicle diameter, in impacted environments, indicating impairment of follicular development. The present results showed that fish in section 2 may be experiencing endocrine alteration in the advanced secondary follicles; however, further investigation into the pathways leading to this change are needed.

Sex ratio may be related to differences between the sexes, selectivity of the sampling apparatus, food availability, and/or population stratification (Carvalho et al. 2009). Furthermore, male parental care of eggs and larvae, a behavior peculiar to piranhas and pirambebas (Braga 1981, Agostinho 2003), make them less readily captured by gill nets. On the other hand, a 1:1 sex ratio has been reported for the piranha *Pygocentrus piraya* in the Três Marias Reservoir (Cruz et al., 1996, Ferreira et al., 1996). In general, the present study sampled slightly more females than males in the three studied sections of the São Francisco River Basin.

The results of the present study showed that *S. brandtii*, a sedentary species, reproduces in all three of the studied sections of the São Francisco River basin, although with lower reproductive performance in section 2, which is immediately downstream of the Três Marias dam and where fish had lower values for TL, BW, GSI, K, FD, AF, and RF. These findings are probably related to the thermal disturbances caused by the release of cooler water from the hypolimnion of the reservoir since tropical fish decrease their feeding activity under low temperatures, which negatively affects their health (Lowe McConnel 1987). Indeed fish are able to find favorable conditions for reproduction by moving away from dams, such as in section 3, thus confirming the negative impact of dams on fish reproduction downstream of reservoirs of hydroelectric power plants.

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Author Contributions

Nilo Bazzoli: Substantial contribution in the concept and design of the study. Contribution to data collection. Contribution to data analysis and interpretation. Contribution to manuscript preparation.

Viviane Elizabeth de Souza Silva: Substantial contribution in the concept and design of the study. Contribution to data collection. Contribution to data analysis and interpretation. Contribution to manuscript preparation.

Lucas Marcon: Substantial contribution in the concept and design of the study. Contribution to data analysis and interpretation. Contribution to manuscript preparation.

Kleber Biana Santiago: contribution to fishes collection in the three sections.

José Enemir dos Santos: Contribution to data collection.

Elizete Rizzo: Contribution to critical revision, adding intelectual content.

Conflicts of interest

The authors declare that they have no conflict of interest related to the publication of this manuscript.

References

AGOSTINHO, C.S. 2003. Reproductive aspects of piranhas *Serrasalmus spilopeura* and *Serrasalmus marginatus* into the upper Paraná River. Braz. J. Biol. 63: 1-6. http://dx.doi.org/10.1590/S1519-69842003000100002.

AGOSTINHO, A.A., PELICICE, F.M. & GOMES, L.C. 2008. Dams and the fish fauna of the Neotropical region: impacts and management related to diversity and fisheries. Braz. J. Biol. 68: 1119-1132. http://dx.doi.org/10.1590/S1519-69842008000500019.

ARANTES, F.P., SANTOS H.B., RIZZO, E., SATO, Y. & BAZZOLI, N. 2010. Profiles of sex steroids, fecundity, and spawning of the curimatã-pacu *Prochilodus argenteus* in the São Francisco River, downstream from the Três Marias Dam, Southeastern Brazil. Anim. Reprod. Sci. 118: 330-336. doi: 10.1016/j.anireprosci.2009.07.004.

ARMSTRONG, M.J. & WITTHAMES, P.R. 2012. Developments in understanding of fecundity of fish stocks in relation to egg production methods for estimating spawning stock biomass. Fish. Res. 118: 35-47. https://doi.org/10.1016/j.fishres.2010.12.028.

BLÁZQUEZ, M., BOSMA, P.T., FRASER, E.J., VAN LOOK, K.J. & TRUDEAU, V.L. 1998. Fish as models for the neuroendocrine regulation of reproduction and growth. Comp. Biochem. Physiol. C Pharmacol. Toxicol. Endocrinol.119: 345-364. https://doi.org/10.1016/S0742-8413(98)00023-1.

BONCOMPAGNI-JÚNIOR, O., NORMANDO, F.T., BRITO, M.F.G. & BAZZOLI, N. 2013. Reproductive biology of *Prochilodus argenteus* Agassiz., 1829 (Pisces: Prochilodontidae) in São Francisco River, Brazil. J. Appl. Ichthyol. 29: 132-138. https://doi.org/10.1111/jai.12018.

BRAGA, A. R. 1981. Ecologia e etologia das piranhas do nordeste do Brasil (Pisces – Serrasalmus Lacépede, 1803). Fortaleza, p. 268.

BRANDÃO, D.E.L., VIRTUDE, A.N., MARCON, L., SANTOS, J.E., SANTIAGO, K.B., RIZZO, E. & BAZZOLI, N. 2017. Comparative analyses of reproductive activity in *Schizodon knerii* (Steindachner, 1875) (Characiformes: Anostomidae) in three sections of the São Francisco River basin. J. Appl. Ichthyol. 33: 1118-1124. https://doi.org/10.1111/jai.13457.

CHAKRABARTY, S., RAJAKUMAR, A., RAGHUVEER, K., SRIDEVI, P., MOHANACHARY, A., PRATHIBHA, Y., BASHYAM, L., DUTTA-GUPTA, A. & SENTHILKUMARAN, B. 2012. Endosulfan and flutamide, alone and in combination, target ovarian growth in juvenile catfish, *Clarias batrachus*. Comp. Biochem. Physiol. C Pharmacol. Toxicol. Endocrinol. 155: 491-497. doi: 10.1016/j.cbpc.2011.12.007.

CLARKSON, R.W. & CHILDS, M.R. 2000. Temperature Effects of Hypolimnial-Release Dams on Early Life Stages of Colorado River Basin Big-River Fishes. Copeia. 2000: 402-412. http://www.jstor.org/stable/1448187.

CRUZ, A.M.G., SATO, Y., RIZZO, E., SANTOS, G.B. & BAZZOLI, N. 1996. Sexual maturation of piranha *Pygocentrus piraya* (Pisces, Characidae) from Três Marias Reservoir, Minas Gerais. Bios 4: 17-21.

DONALDSON, M.R., COOKE, S.J., PATTERSON, D.A. & MACDONALD, J.S. 2008. Cold shock and fish. J. Fish Biol. 73: 1491-1530. https://doi.org/10.1111/j.1095-8649.2008.02061.x.

FERREIRA, R.M.A., BAZZOLI, N., RIZZO, E. & SATO, Y. 1996. Aspectos reprodutivos da piranha, *Pygocentrus piraya* (Teleostei, Characiformes), espécie nativa da bacia do Rio São Francisco. Arq. Bras. Med. Vet. Zoo. 48: 71-76.

FROESE, B.R. 2006. Cube law, condition factor and weight – length relationships: history, meta-analysis and recommendations. J. Appl. Ichthyol. 22: 241-253. https://doi.org/10.1111/j.1439-0426.2006.00805.x.

JÉGU, M. 2003. Subfamilia Serrasalmidae. In: Reis, R.E., Kullander, S.V., Ferraris Jr, C.J. (Eds). Check list of the freshwater fishes of South and Central America. Porto Alegre: EDIPUCRS.

JENSEN, K.M., KAHL, M.D., MAKYNEN, E.A., KORTE, J.J., LEINO, R.L., BUTTERWORTH, B.C. & ANKLEY, G.T. 2004. Characterization of responses to the antiandrogen flutamide in a short-term reproduction assay with the fathead minnow. Aquat. Toxicol. 70: 99-110. https://doi: 10.1016/j.aquatox.2004.06.012.

HONORATO-SAMPAIO, K., PRADO, P.S., SATO, Y. & BAZZOLI, N. 2015. Comparative morphology of the oocyte surface and early development in four characiformes from the São Francisco River, Brazil. J. Morphol. 276: 1258-1278. doi: 10.1002/jmor.20416.

HONORATO-SAMPAIO, K., SANTOS, G.B., BAZZOLI, N. & RIZZO, E. 2009. Observations on the seasonal breeding biology and fine structure of the egg surface in the white piranha *Serrasalmus brandtii* from the São Francisco River basin, Brazil. J. Fish Biol. 75(7): 1874-1882. doi: 10.1111/j.1095-8649.2009.02422.x.

LE CREN, E.D. 1951: The length–weight relationship and seasonal cycle in gonad weight and condition in the perch (*Perca fluviatilis*). J. Anim. Ecol. 20:201-219.

LOWE-MCCONNELL, R.H. 1987. Respostas dos Peixes às Condições em Águas Tropicais. In: Lowe-McConnell RH. Ecological Studies in Tropical. Cambridge University Press, London.

LUBZENS, E., YOUNG, G., BOBE, J., & CERDÀ, J. 2010. Oogenesis in teleosts: how eggs are formed. Gen. Comp. Endocrinol. 165: 367-89. doi: 10.1016/j.ygcen.2009.05.022.

MARCON, L., THOMÉ, R.G., MOUNTEER, A.H., BAZZOLI, N., RIZZO, E. & BENJAMIN, L.A. 2017. Immunohistochemical, morphological and histometrical analyses of follicular development in *Astyanax bimaculatus* (Teleostei: Characidae) exposed to an organochlorine insecticide. Ecotoxicol. Environ. Saf. 143: 249-258. doi: 10.1016/j.ecoenv.2017.05.029.

MELO, R.M.C., FERREIRA, C.M., LUZ, R.K., SATO, Y., RIZZO, E. & BAZZOLI, N. 2011. Comparative oocyte morphology and fecundity of five characid species from São Francisco River basin, Brazil. J. Appl. Ichthyol. 27: 1332-1336. https://doi.org/10.1111/j.1439-0426.2011.01876.x.

MIRANDE, J.M. 2010. Phylogeny of the family characidae (Teleostei: Characiformes): from characters to taxonomy. Neotrop. Ichthyol. 8: 385-568. http://dx.doi.org/10.1590/S1679-62252010000300001.

NIKOLSKY, G.V. 1963. The Ecology of Fishes. Academic Press, London, 352 pp.

NORMANDO, F.T., SANTIAGO, K.B., GOMES, M. V. T., RIZZO, E. & BAZZOLI, N. 2014. Impact of the Três Marias dam on the reproduction of the forage fish *Astyanax bimaculatu* and *A. fasciatus* from the São Francisco River, downstream from the dam, southeastern Brazil. Environ. Biol. Fish. 97: 309-319. https://doi.org/10.1007/s10641-013-0153-3.

NUNES, D.M.F., MAGALHÃES, A.L.B., WEBER, A.A., GOMES, R.Z., NORMANDO, F.T., SANTIAGO, K.B., RIZZO, E. & BAZZOLI, N. 2015. Influence of a large dam and importance of an undammed tributary on the reproductive ecology of the threatened fish matrinxã *Brycon orthotaenia* Günther, 1864 (Characiformes: Bryconidae) in southeastern Brazil. Neotrop. Ichthyol. 13: 317-324. doi: 10.1590/1982-0224-20140084.

NÚÑEZ, J. & DUPONCHELLE, F. 2009. Towards a universal scale to assess sexual maturation and related life history traits in oviparous teleost fishes. Fish Physiol. Biochem. 35: 167-80. doi: 10.1007/s10695-008-9241-2.

OLDEN, J.D. & NAIMAN, R.J. 2010. Incorporating thermal regimes into environmental flows assessments: modifying dam operations to restore freshwater ecosystem integrity. Freshw. Biol. 55: 86-107. https://doi.org/10.1111/j.1365-2427.2009.02179.x.

PAWSON, M.G., PICKETT, G.D. & WITTHAMES, P.R. 2000. The influence of temperature onset of first maturity in sea bass. J. Fish Biol. 56: 319-327. https://doi.org/10.1111/j.1095-8649.2000.tb02109.x.

SANTOS, H.A., POMPEU, P.S. & KENJI, D.O.L. 2012. Changes in the flood regime of São Francisco River (Brazil) from 1940 to 2006. Eg. Environ. Change. 12: 123-132. https://doi.org/10.1007/s10113-011-0240-y.

SATO, Y., BAZZOLI, N., RIZZO, E., BOSCHI, M.B. & MIRANDA, M.O.T. 2005. Influence of the Abaeté River on the reproductive success of the neotropical migratory teleost *Prochilodus argenteus* in the São Francisco River, downstream from the Três Marias Dam, southeastern Brazil. River Res. Appl. 21: 939-950. https://doi.org/10.1002/rra.859.

THOMÉ, R.G., DOMINGOS, F.F.T., SANTOS, H.B., MARTINELLI, P.M., SATO, Y., RIZZO, E. & BAZZOLI, N. 2012. Apoptosis, cell proliferation and vitellogenesis during the folliculogenesis and follicular growth in teleost fish. Tissue Cell. 44: 54-62. doi: 10.1016/j.tice.2011.11.002.

TODD, C. R., RYAN, T., NICOL, S. J. & BEARLIN, R. A. 2005. The impact of cold water releases on the critical period of post-spawning survival and its implications for Murray cod (*Maccullochella peelii peelii*): a case study of the Mitta River, southeastern Australia. River Res. Appl. 21: 1035-1052. https://doi.org/10.1002/rra.873.

VAZZOLER, A.E. 1996. Biologia da reprodução de peixes teleósteos: teoria e prática. EDUEM, Maringá, 169 pp. (in Portuguese).

WEBER, A.A., NUNES, D.M.F., GOMES, R.Z., RIZZO, E., SANTIAGO, K.B. & BAZZOLI, N. 2013. Downstream impacts of a dam and influence of a tributary on the reproductive success of *Leporinus reinhardti* in São Francisco River. Aquat. Biol. 19: 195-200. https://doi.org/10.3354/ab00531.

YODA, M. & YONEDA, M. 2009. Assessment of reproductive potential in multiple-spawning fish with indeterminate fecundity: a case study of yellow sea bream *Dentex hypselosomus* in the East China Sea. J. Fish Biol. 74: 2338-2354. doi: 10.1111/j.1095-8649.2009.02246.x.

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