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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

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ABSTRACT

The curimatã-pacu Prochilodus argenteus is an important characiform from the São Francisco River basin that performs longdistance migrations for spawning upstream during the rainy season, when the temperature and photoperiod are elevated. Despite the interruption of the migratory routes by the Três Marias Dam and accentuated decline in fishing, the curimatã-pacu still sustains the fisheries at the Três Marias region in recent decades. The objective of this study was to evaluate the reproductive activity of *P. argenteus* in two sections of the São Francisco River, downstream from the Três Marias Dam, during the rainy season. In the first 34 km of the river, immediately below the dam, most of the females were in gonadal resting. At 34–54 km downstream from the dam, following the confluence with a medium-sized tributary, the Abaeté River, there was a high frequency of males and females in reproductive activity. Follicular atresia was more frequent in the upper section of the river while postovulatory follicles occurred predominantly in the lower section. Fulton's condition factor and gonadosomatic index indicated that the females were in a better physiological and reproductive condition below the confluence with the Abaeté River. In contrast to the females, the males were less affected by damming, and testicular maturation was largely achieved in two river sections. Thus, although the section of the São Francisco River immediately below the Três Marias Dam was found to be unfavourable for the reproduction of the migratory fishes due principally to the hypolimnetic water from the reservoir, reproductive success of P. argenteus was achieved below the Abaeté River. In this section, the species encountered appropriate conditions for maturation and spawning, i.e. warm temperatures above 24°C, high water flow and dissolved oxygen, and low water transparency. These results indicate the importance of a non-regulated tributary to minimize the ecological impact of a dam on the downstream native fish communities. Copyright © 2005 John Wiley & Sons, Ltd.

KEY WORDS: Prochilodus argenteus; São Francisco River; Três Marias dam; Abaeté River; reproduction; follicular atresia; river flow; water temperature

INTRODUCTION

The Três Marias Dam on the São Francisco River, in southeastern Brazil, was constructed in 1961 for the purposes of flow regulation, flood control, and hydroelectric power generation. When full, the Três Marias reservoir has a capacity of 21×10^9 m³ of water, and floods an area of approximately 100 000 ha (Britski *et al.*, 1988). It is warm monomictic, oligotrophic, showing thermal stratification in the summer from November to February, with over 3°C variation between epilimnion and hypolimnion (Esteves *et al.*, 1985). The colder hypolimnetic water characterized by temperatures between 22.5 and 23.5°C, is discharged during hydroelectric generation and is subsequently released into the São Francisco River, downstream from the dam.

The hydrological regime of rivers is substantially altered by hydroelectric power generation; peaks are delayed and attenuated depending on operating requirements. Thermal and hydrodynamic alterations affect reproductive activity, particularly of migratory fishes that depend on flooding and a rise in temperature as a trigger mechanism

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for spawning (Cadwallader, 1978; Parkinson *et al.*, 1999). Several impacts have been reported on fish communities downstream from the reservoirs, such as modification of the composition, and structure of the ichthyofauna, interruption of migratory routes, inhibition of reproduction, interference in feeding and juvenile recruitment areas (Welcomme, 1979; Grizzle, 1981; Hickman and Hevel, 1986; Agostinho *et al.*, 1993). In the Tietê and Paranapanema rivers, Paraná River basin, Brazil, water quality parameters altered by pollution and damming have drastically reduced fish diversity (Barrella and Petrere, 2003).

Follicular atresia is a hormonally controlled degenerative phenomenon that culminates with oocyte resorption prior to ovulation and frequently causes ovary regression (Shanbhag and Saidapur, 1996). It affects oocytes in any phase of development, although most frequently postspawning, when residual vitellogenic oocytes are reabsorbed (Guraya, 1986). Follicular atresia may be induced by endo- and exogenous factors, including stress, fasting, confinement, light, hypoxia, temperature extremes, biocides and inadequate hormone levels, reducing the reproductive capacity of the species and rendering spawning unfeasible (Nagahama, 1983). Postovulatory follicles are remains of ovarian follicles that stay in fish ovaries after ovulation, being reliable indicators of spawning success (McAdam *et al.*, 1999; Drummond *et al.*, 2000). The involution of atretic and postovulatory follicles depends on apoptosis, a process of cell death genetically programmed, which plays a crucial role in development and tissue homeostasis in metazoans (Janz *et al.*, 1997; Miranda *et al.*, 1999; Drummond *et al.*, 2000).

Variations in body length and weight allow us to evaluate how the species obtains food resources from its habitat, indicating the physiological condition of the specimens based on fat accumulation, general well-being, gonadal development, and adaptation to the environment (Nikolski, 1963). The condition factor (K) is an index reflecting interactions between biotic and abiotic variables in the physiological condition of fishes (Lizama and Ambrosio, 2002). Variations in fat content may be related to gonadal maturation or to the hydrological cycle and food availability of the river or reservoir (Bennemann *et al.*, 1996). The gonadosomatic index (GSI) is a good indicator of the reproductive activity of fishes and provides a complementary biological parameter for evaluating gonadal maturation (Maddock and Burton, 1999). Variations in K allow the comparison of two or more populations that live under different conditions of food availability, population density and water temperature (Nikolski, 1963).

Prochilodus argenteus Agassiz 1829, previously classified as *P. marggravii* (Walbaum, 1792) and popularly known as curimatã-pacu, is the most abundant migratory species in the Três Marias region, representing almost 50% of the total catch (Sato and Godinho, 2003). It is an endemic species in the São Francisco basin, and has an illiophagous feeding habit. It is the largest member of the Prochilodontidae family, sometimes reaching a body weight of 15 kg, and is intensively used in hatcheries for restoring fisheries stock. The species performs long-distance migrations upstream for spawning, and has high fecundity. The total spawning and reproductive period extends from November to January in the rainy season, coinciding with the time of occurrence of flooding, higher temperatures, and long photoperiods (Sato *et al.*, 1996; Caldeira *et al.*, 2002). Specimens of *P. argenteus* reach sexual maturation at 27–28 cm total length (Boncompagni, 2002; Bazzoli, 2003). Recently spawned non-adhesive oocytes of *P. argenteus* show delicate fibrils covering a thick zona radiata at the surface, and drift freely downstream in the river after fertilization for dispersion and oxygenation (Rizzo *et al.*, 2002). Ripe oocytes of *P. argenteus* reach increase in deformed larvae, rendering short-term storage unviable (Rizzo *et al.*, 2003). The great migratory capacity of the curimatã-pacu was reported by Pinheiro (1981), who tagged 1012 fishes at the future site of Sobradinho dam and recaptured marked specimens up to 800 and 1100 km upriver after 85 and 168 days, respectively.

Although damming of river basins and impoundments is common in southeastern Brazil, few studies have evaluated their effects on the downstream fish communities (Agostinho *et al.*, 1992, 1993; Barrella and Petrere, 2003), and no study has been recorded for the São Francisco River basin. The purpose of this work was to evaluate the reproductive activity of *P. argenteus* in two sections of the São Francisco River, downstream from the Três Marias Dam.

MATERIAL AND METHODS

Sampling

A total of 1057 adult specimens of *P. argenteus* were captured monthly in the São Francisco River, downstream from the Três Marias Dam, from November 1994 to February 1995 (Figure 1). In the first section, 34 km of the

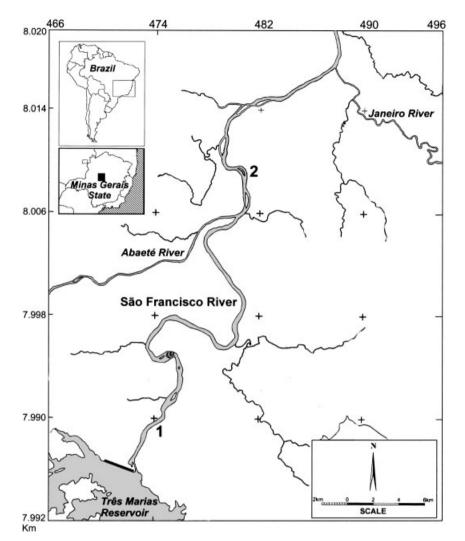


Figure 1. Location of the study sections of the São Francisco River, downstream from the Três Marias dam. 1, Section above the confluence with the Abaeté River, extending from the reservoir until 34 km downstream. 2, Section below the confluence with the Abaeté River, extending from 34 to 54 km downstream from the dam

river immediately downstream from the dam, 209 males and 373 females were captured. In the second section, 34 to 54 km downstream from the dam, after the confluence of the São Francisco River with the Abaeté River, 333 males and 142 females were captured.

Biotic and abiotic variables

Records were made of the total length (TL) and body weight (BW) of all specimens and gonadal weight (GW) of mature females. Fulton's condition factor ($K = BW \times 100/TL^3$) and gonadosomatic index ($GSI = GW \times 100/BW$) were calculated for each specimen and for females in the mature stage, respectively (Le Cren, 1951; Nikolski, 1963).

The water parameters (maximum temperature, concentration of dissolved oxygen, and transparency) were obtained during capture of the specimens from November to February by the limnology team of the Hydrobiology and Hatchery Station of Três Marias—CODEVASF (Company of Development of the São Francisco and Parnaíba Valleys). Temperature (0.1°C) and oxygen (0.01 mg/l) were measured using a Horiba device model U-10 (Horiba,

1991). The water transparency was evaluated through a Secchi disc. The Energy Company of Minas Gerais (CEMIG) supplied rainfall and water discharge data.

Reproductive activity

Fragments of gonads were fixed in Bouin's fluid, embedded in paraffin, sectioned to 5 µm thickness, and stained with hematoxylin-eosine for histological analyses. The stages of gonadal maturation were determined based on previously established criteria for other neotropical freshwater teleosts (Bazzoli, 2003). The follicular atresia was analysed in accordance with previous studies (Rizzo and Bazzoli, 1995; Miranda *et al.*, 1999).

RESULTS

Physiological condition of the specimens

The *P. argenteus* males and females from the section below the Abaeté River confluence showed significantly higher total length and body weight, as compared to those from the section immediately downstream from the dam (Tables I and II). Fulton's condition factor and GSI were also significantly higher for the females sampled below the Abaeté River. In contrast, there was no significant difference in K values for the males from the two sections of the river.

Environmental parameters

Temperature and dissolved oxygen values were higher and transparency was lower in the section below the Abaeté River (Table III). Rainfall was more abundant in the months of November and December (Figure 2). Discharge was higher below the confluence with the Abaeté River (Table III).

Gonadal maturation and reproductive activity

The gonadal maturation of *P. argenteus* was classified into four stages (Figures 3A–D and 4A–D). The relative frequencies of the gonadal maturation stages (Figure 5) indicated that mature females and males were predominant

Table I. Total length (TL), body weight (BW), Fulton condition factor (K) and gonadosomatic index (GSI) of females of *P. argenteus* in two sections of the São Francisco River, downstream from the Três Marias Dam, from November 1994 to February 1995

	Below the Abaeté River		Above the Abaeté River		t
	Mean \pm SD	Range	Mean ± SD	Range	
TL (cm)	47.1 ± 8.0	34.0-73.0	35.9 ± 4.1	28.0-48.0	20.86
BW (kg)	1.58 ± 0.95	0.40-6.25	0.60 ± 0.23	0.25-1.75	18.55
K	1.38 ± 0.14	1.04-1.82	1.25 ± 0.12	0.84-1.83	10.50
GSI*	14.30 ± 3.43	7.27-22.90	6.36 ± 1.63	3.60-10.56	16.81

Differences are significant with p < 0.05; t = Student's *t*-test. *GSI of mature females.

Table II. Total length (TL), body weight (BW) and Fulton condition factor (K) of males of *P. argenteus* in two sections of the São Francisco River, downstream from the Três Marias dam, from November 1994 to February 1995

	Below the Abaeté River		Above the Abaeté River		t
	Mean \pm SD	Range	Mean ± SD	Range	
TL (cm)	41.8 ± 4.3	33.0-64.0	34.3 ± 3.5	29.0-49.0	21.23
BW (kg) K	$0.95 \pm 0.36 \\ 1.25 \pm 0.10^{a}$	0.45-3.45	0.52 ± 0.18 1.25 ± 0.11^{a}	0.30–1.40 0.93–1.68	16.11 - 0.05

Differences are significant with p < 0.05, except values marked with superscript 'a'; t = Students' t-test.

	Below the Abaeté River		Above the Abaeté River		t
	Mean \pm SD	Amplitude	$Mean \pm SD$	Amplitude	
Temperature (°C)	25.4 ± 1.0	24.0-27.0	23.4 ± 0.5	22.5-24.0	12.98
Oxygen (mg/l)	6.85 ± 0.83	5.78-7.80	3.32 ± 0.85	2.73-4.58	4.28
Oxygen (mg/l) Flow (m ³ /s)	632.8 ± 73.4	626.0-870.0	584.8 ± 73.2	381.0-850.0	5.66
Transparency (cm)	$7.8\pm5.0^{\rm a}$	4.0-15.0	$17.5\pm8.7^{\rm a}$	10.0-30.0	-1.81

Table III. Temperature, concentration of dissolved oxygen, transparency and flow of the water in two sections of the São Francisco River, downstream from the Três Marias Dam, from November 1994 to February 1995

Differences are significant with p < 0.05, except values marked with superscript 'a'; t = Student's t-test.

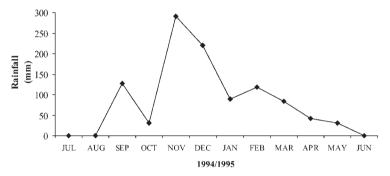


Figure 2. Rainfall in the Três Marias region from July 1994 to June 1995, with its peak in November and December

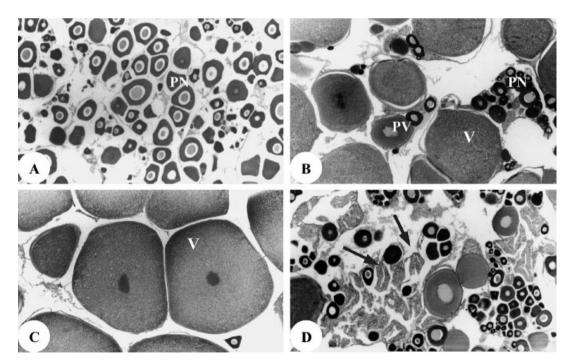


Figure 3. Sections of ovaries of adult *P. argenteus* in different stages of maturation: (A) resting; (B) maturation; (C) mature; (D) spawned (all × 42). PN, Perinucleolar oocyte; PV, previtellogenic oocyte; V, vitellogenic oocyte; arrow indicate postovulatory follicle

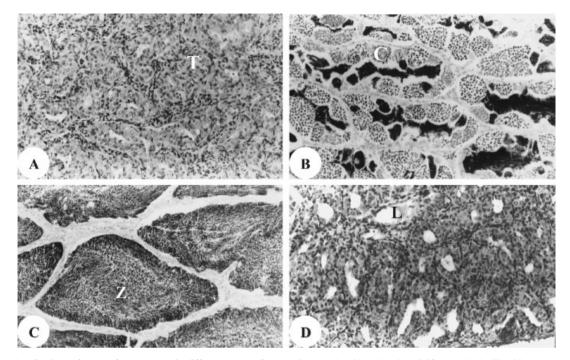


Figure 4. Sections of testes of *P. argenteus* in different stages of maturation. (A) Resting, closed seminiferous tubule (T) with spermatogonia only (×186). (B) Maturation, abundant cysts of spermatogenic cells (×180). (C) Mature, abundant spermatozoa (Z) into the seminiferous tubule lumen (×166). (D) Spent seminiferous tubules with spent lumes (L) (×182)

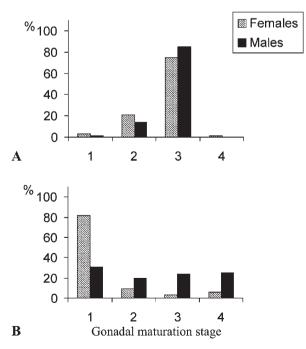


Figure 5. Frequency of the reproductive cycle stages of adult *P. argenteus* in two sections of the São Francisco River, downstream from the Três Marias Dam: (A) below the Abaeté River; (B) above the Abaeté River. Stages: 1, resting; 2, maturation 3, mature 4, and spawned/spent

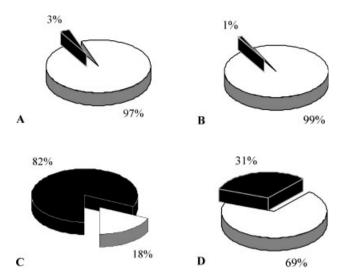


Figure 6. Frequency of adult *P. argenteus* in resting (■) and reproductive activity (□) in two sections of the São Francisco River, downstream the Três Marias Dam. (A) Females and (B) males below the confluence with the Abaeté River. (C) Females and (D) males above the confluence with the Abaeté River

in the section below the Abaeté River. Females in the resting phase were abundant in the section of the river above the Abaeté River. Specimens in reproductive activity including maturation, mature and spawned/spent stages were more frequent below the Abaeté River as compared with the section immediately downstream from the dam (Figure 6).

Ovaries exhibiting signs of recent spawning, with numerous postovulatory follicles, were only observed in specimens captured below the Abaeté River (Figure 3D). In contrast, testes with spent seminiferous tubules were observed in both sections of the river (Figure 4D). In the section immediately downstream from the dam, postovulatory follicles were eventually observed in some females.

Follicular atresia

In the section immediately downstream from the dam, the females showed atretic follicles in all months of study (Figure 7). About 20–33% of the maturing females showed ovarian regression with a high proportion of vitellogenic atretic follicles in each month (Figure 7A). In the section below the Abaeté River, the frequency of vitellogenic atretic follicles was lower and these were only observed in January and February (Figure 7B). During involution of the atretic follicles, follicular cells exhibited condensed chromatin in aggregates underlying the nuclear envelope, cell retraction, and cell fragments, resembling programmed cell death by apoptosis (Figures 7C, D).

DISCUSSION

In neotropical fish populations, 'piracema', upstream migration for spawning, is triggered by the onset of rain and elevated temperature and the reproductive success of a species has been associated with increased temperatures and water levels (Lowe-McConnell, 1987; Parkinson *et al.*, 1999). Although the Três Marias Dam impounded in the upper São Francisco River has interrupted the migratory routes of several fish species, the present study has showed that 34-54 km downstream from the dam, *P. argenteus* encountered adequate environmental conditions for reproduction, i.e. water flow above 600 m³/s, water temperature over 24°C, water transparency up to 15 cm depth, and concentrations of dissolved oxygen above 5 mg/l. In contrast, lower temperature and oxygen content, higher transparency, and regulated water flow had a harmful effect on the reproductive dynamics of *P. argenteus* immediately downstream from the dam.

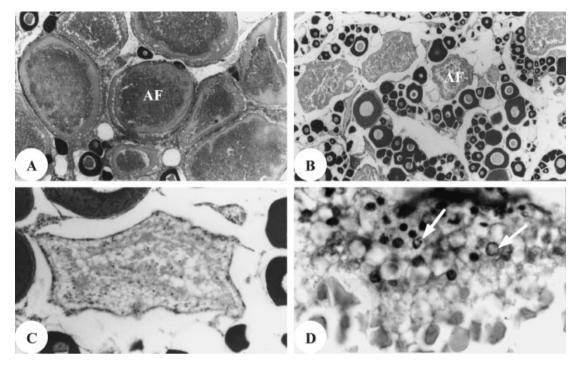


Figure 7. Regression of *P. argenteus* ovaries in the São Francisco River, downstream from the Três Marias Dam. (A) Ovarian regression at the section above confluence with the Abaeté River (\times 43). (B) Ovarian regression postspawning at the section below the confluence with the Abaeté River (\times 43). (C) Vitellogenic atretic follicle in advanced regression (\times 164). (D) Detail of the follicular cells in apoptosis (arrows) during advanced regression of vitellogenic atretic follicles (\times 744)

The reproductive dynamics is regulated by the hypothalamo-pituitary axis, especially through the gonadotrophins (Redding and Patiño, 1993). In addition to the well-known effects of growth hormone on somatic growth, it has also been shown to modulate gonadal steroidogenesis in several species (Blázquez *et al.*, 1998). In the present study, males and females presented higher total length and body weight and better reproductive condition below the confluence with the Abaeté River, indicating that the ecological conditions were favourable to the physiology of the neuroendocrine system. Variations of K values are related to reproductive activity, with higher values coinciding with the increased GSI, and a higher frequency of ripe females (Barbieri and Verani, 1987), such as those observed in the section of the river below the confluence with the Abaeté River. Lower K and GSI were observed in the section immediately downstream from the dam, since most females were in gonadal resting or showed ovarian regression. The variations of K values may also reflect different feeding resources; however, as an illiophagous fish, based on the ecological chain, *P. argenteus* encounters nourishment in the two sections of study.

Follicular atresia is characterized by structural disorganization of the oocyte, fragmentation of the zona pellucida, yolk liquefaction, hypertrophy of the follicular cells and thickening of the connective theca, being a physiological process postspawning (Rizzo and Bazzoli, 1995; Miranda *et al.*, 1999). In thermal effluent areas of Sweden and Lithuania, high temperature negatively influences the oogenesis of temperate climate fishes, inducing follicular atresia during vitelogenesis, gonadal anomalies such as multi-nucleus oocytes, hermaphroditism and asynchronous oocyte development, seriously reducing the reproductive potential of the species (Luksiene *et al.*, 2000). In the present study, high rates of follicular atresia and low GSI were observed in all months of sampling in the section immediately below the dam, indicating that the environmental conditions are inadequate for oocyte development and gonadal maturation. Physiological follicular atresia during ovarian regression postspawning was observed in the section above the Abaeté River, coinciding with a period of reduced rainfall and water flow.

Apoptosis is related to the involution of atretic and postovulatory follicles postspawning (Miranda *et al.*, 1999; Drummond *et al.*, 2000); yet it may also occur during gonadal maturation (Janz and Van Der Kraak, 1997).

Exposure of wild fish populations to bleached kraft pulp mill effluent results in elevated apoptosis in ovarian follicles associated with a variety of negative impacts on reproductive fitness including reduced ovarian development and alterations in endocrine homeostasis (Janz *et al.*, 1997). In the present study, apoptosis was frequently observed during follicular atresia, immediately downstream from the dam. According to Piechotta *et al.* (1999), this cell death process may be a sensitive biomarker for monitoring impacted habitats.

Temperature and photoperiod are the two major environmental regulators of reproductive seasonality in teleosts, and the extent to which each fish species depends on temperature and photoperiod varies considerably, and may reflect the varied habitats and reproductive strategies (Blázquez *et al.*, 1998). Experimental studies determined an optimum temperature of 22.1°C for development of vitellogenic oocytes in indian catfish *Heteropneustes fossilis*; lower or higher temperatures may inhibit oocyte development or induce follicular atresia (Saxena and Sandhu, 1994). In the section immediately downstream from the dam in the present study, the water temperature was between 22.5 and 24°C and may have inhibited ovarian maturation in most females, and increased follicular atresia in others. In medaka *Oryzias latipes*, the number of mature oocytes decreases and follicular atresia increases, while spermatogenesis remains active under reduced temperature conditions (Koger *et al.*, 1999). In contrast to the females, 69% of the males in the present study were reproductively active immediately below the dam, indicating that testicular maturation of *P. argenteus* is apparently less susceptible to environmental conditions, as has also been reported for medaka.

The influence of the temperature on final oocyte maturation and spawning is also well known. Previous studies have showed that females of *P. argenteus* fail to respond to hormone-induced spawning when the hypolimnetic water from the Três Marias reservoir is used, with the response to hormonal treatment gradually improving as the water temperature increases above 23°C (Sato *et al.*, 1996). In the Murray–Darling basin, Australia, a decline in the abundance of several native fish species has been attributed to disruption of thermal spawning cues by the release of unseasonably cold water from deep-release reservoirs during spring and summer (Preece and Jones, 2002). These authors encountered maximum daily temperature approximately 5°C lower in the Namoi River immediately downstream from the Keepit Dam, Australia; however the magnitude of the thermal disturbance progressively diminished with distance from the dam and the annual temperature was 3°C lower immediately downstream from the Três Marias Dam and adequate environmental conditions for reproduction were restored only after the confluence with the Abaeté River. Since few small-sized tributaries occur in the first section of the river, the temperature is practically unaltered until 34 km downstream. According to Preece and Jones (2002), the relative contribution of flow from the tributaries is important in determining the pattern of recovery downstream from a dam.

Migratory fishes frequently exhibit total spawning and group-synchronous oocyte development (Sato, 1999; Rizzo *et al.*, 2002; Bazzoli, 2003; Sato *et al.*, 2003) as was also observed for *P. argenteus* in the section below the Abaeté River. Alterations of the pattern of oocyte development were reported in cold-water fish exposed to thermal effluent from a nuclear power plant (Luksiene and Sandström, 1994; Luksiene *et al.*, 2000). In Malaysia, the reproductive seasonality of a tropical freshwater cyprinid was altered to an aseasonal pattern, probably as an effect of river flow regulation by dams, which eliminated the dominant flood period, and most seasonal variations of river flow (McAdam *et al.*, 1999). In the present study, some females, immediately downstream from the dam, showed incomplete maturation and rare postovulatory follicles, which might be indicative of disturbance of the gonadal maturation in this river section. Recently, Hatanaka and Galetti (2003), studying the population genetics of *P. argenteus* using RAPD (Random Amplified Polymorphic DNA) technique, suggested the occurrence of a structured population downstream from the Três Marias Dam, with competition between the specimens for greater resources; then, a minor fraction of this population (the weaker specimens) completes its migration towards the dam during the reproductive period, while the majority possibly migrate to locations with environmental conditions more favourable for reproduction. However, radio-tracking studies are necessary in order to evaluate the movements of the migratory fish in the São Francisco River.

One of the main effects downstream of a reservoir has been a reduction in the flow peaks of the river, preventing water from entering marginal lagoons that are essential to the ecology of many fish species that use them as spawning and growth sites (Ligon *et al.*, 1995). The São Francisco River is rich in floodplains and marginal lagoons, particularly in the stretch between the town of Pirapora (*c.* 140 km downstream of the Três Marias Dam) and

Sobradinho Reservoir (c. 1200 km from Pirapora). After adults reproduce in the mainstream of the river and in its tributaries downstream of the Três Marias Dam, eggs and larvae of the migratory species, including *P. argenteus*, are carried downstream reaching the marginal lagoons, which are the nursery habitats for growth of the young, acting as recruitment areas of the migratory species (Sato and Godinho, 2003). In the Upper Paraná, as in other tropical floodplain rivers, the flood pulse is the primary factor acting as a synchronizing cue for spawning, and lotic water is fundamental to oocyte fertilization, fluctuation and drifting (Godoy, 1975).

The effects of regulated flow on remaining stream fish communities are most severe immediately below the dam, with effects becoming less severe as tributary inflow and other physical processes such as water temperature ameliorate the dam's effects (Brown and Ford, 2002). Reduction in water flow during the summer may also affect reproductive migration (Geen, 1975). In this study, ovulating females were captured only in the high flow period of the Abaeté River, coinciding with the temperature and rainfall peaks. Similarly, in the Mogi-Guaçu River, Upper Paraná River basin, Brazil, spawning during the reproductive period is reported to coincide with rising water levels, turbidity and water temperatures above 23°C (Schubart, 1954; Godoy, 1954). Therefore, the flow regime of the Abaeté River may be an important determinant of the reproductive success of native fish species in the São Francisco River, downstream from the Três Marias Dam. Similar observations were also registered for the fish communities of a regulated river in California (Brown and Ford, 2002).

A historical analysis of the flow regime of the São Francisco River showed that there was no diverted water discharge from the Três Marias reservoir during the reproductive period of fishes in most of the years. In contrast, the Paraná River, southeastern Brazil, receives diverted water every year from the Itaipú reservoir, in addition to the water passing through the turbines. Yet, even though they showed gonadal development, the large size migratory species living downstream were unable to carry out spawning activities and developed extensive ovarian atresia (Agostinho *et al.*, 1993). Therefore, our results in the São Francisco River, immediately downstream from the Três Marias Dam, are similar to those obtained in the Paraná River, downstream from the Itaipú reservoir.

Other migratory fishes captured downstream from the Três Marias Dam, such as *Salminus brasiliensis*, *Brycon* orthotaenia, Conorhynchos conirostris, Pseudoplatystoma corruscans and Prochilodus costatus, showed the same tendency as observed for *P. argenteus*, with the resting stage predominating immediately downstream from the dam and reproductive activity predominating below the Abaeté River. Reports from fishermen, as well as observations made over the past 20 years, also indicate the spawning of migratory fishes in the São Francisco River, after its confluence with the Abaeté River, and also in the Abaeté River. Spermiating males were constantly collected, and 'snoring' sounds emitted by *Prochilodus* spp. males at the time of reproduction are frequently heard. Similarly, the spawning areas of large migratory fishes of the Paraná River basin are located in the upper portion of the non-regulated larger tributaries and the nursery areas are located in the adjacent floodplains (Petrere *et al.*, 2002). Thus, the results of the present study emphasize the importance of non-regulated tributaries in minimizing the ecological impact of dams on native fish communities downstream.

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REFERENCES

Agostinho AA, Júlio Jr HF, Borghetii JR. 1992. Considerações sobre os impactos dos represamentos sobre a ictiofauna e medidas para sua manutenção. Um estudo de caso: reservatório de Itaipu. *Revista Unimar* 14: 89–107.

Barrella W, Petrere Jr M. 2003. Fish community alterations due to pollution and damming in Tietê and Paranapanema rivers (Brazil). *River Research and Applications* **19**: 59–76.

Agostinho AA, Mendes VP, Suzuki HI, Canzi C. 1993. Avaliação da atividade reprodutiva da comunidade de peixes dos primeiros quilômetros a jusante do reservatório de Itaipu. *Revista Unimar* **15**: 175–189.

Barbieri G, Verani, JR. 1987. O fator de condição como indicador do período de desova em *Hypostomus* aff. *plecostomus* (Linnaeus, 1758) (Osteichthyes, Loricaridae), na represa do Monjolinho (São Carlos, SP). *Ciência e Cultura* **39**: 655–658.

- Bazzoli N. 2003. Parâmetros reprodutivos de peixes de interesse comercial na região de Pirapora. In Águas, peixes e pescadores do São Francisco das Minas Gerais, Godinho HP, Godinho AL (eds). PUC-Minas: Belo Horizonte; 291–306.
- Bennemann ST, Orsi ML, Shibatta O. 1996. Atividade alimentar de espécies de peixes do rio Tibagi, relacionada com o desenvolvimento de gordura e gônadas. *Revista Brasileira de Zoologia* 13: 501–512.
- Blázquez M, Bosma PT, Fraser EJ, Van Look KJW, Trudeau, VL. 1998. Fish as models for the neuroendocrine regulation of reproduction and growth (review). *Comparative Biochemistry and Physiology Part C* **119**: 345–364.
- Boncompagni Jr, O. 2002. Biologia reprodutiva do curimatá-pacu, Prochilodus marggravii (Walbaum, 1792) (Characiformes: Prochilodontidae) do rio São Francisco, região de Pirapora, Minas Gerais PUC-Minas: Belo Horizonte.
- Britiski HA, Sato Y, Rosa ABS. 1988. Manual de identificação de peixes da região de Três Marias, com chaves de identificação para os peixes da Bacia do São Francisco. CODEVASF: Brasília.
- Brown LR, Ford T. 2002. Effects of flow on the fish communities of a regulated California river: implications for managing native fishes. *River Research and Applications* **18**: 331–342.
- Cadwallader PL. 1978. Some causes of the decline in range and abundance of native fish in the Murray Darling River system. *Proceedings of the Royal Society of Victoria*: **90**: 211–224.
- Caldeira FC, Sato Y, Rizzo E, Bazzoli N. 2002. Atividade reprodutiva de *Prochilodus marggravii* (Pisces: Prochilodontidae) no rio São Francisco, à jusante do reservatório de Três Marias, MG. *Bios* 10: 81.
- Drummond CD, Bazzoli N, Rizzo E, Sato Y. 2000. Postovulatory follicle: a model for experimental studies of programmed cell death or apoptosis in teleosts. *Journal of Experimental Zoology* 287: 176–182.
- Esteves FA, Amorim JC, Cardoso EL, Barbosa FAR. 1985. Caracterização limnológica preliminar da represa de Três Marias (MG) com base em alguns parâmetros ambientais básicos. *Ciência e Cultura* **37**: 608–617.
- Geen GH. 1975. Ecological consequences of the proposed Moran Dam on the Fraser River. *Journal of the Fisheries Research Board of Canada* **32**: 126–135.
- Godoy MP. 1954. Locais de desovas de peixes num trecho do rio Mogi Guaçu, estado de São Paulo, Brasil. *Revista Brasileira de Biologia* 14: 375–396.
- Godoy MP. 1975. Peixes do Brasil, subordem Characoidei. Bacia do rio Mogi Guassu. Editora Franciscana: Piracicaba.
- Grizzle JM. 1981. Effects of hypolimnetic discharge on fish health below a reservoir. *Transactions of the American Fisheries Society* **110**: 29–43.
- Guraya SS. 1986. The Cell and Molecular Biology of Fish Oogenesis. Karger: Basel.
- Hatanaka T, Galetti Jr PM. 2003. RAPD markers indicate the occurrence of structured populations in a migratory freshwater fish species. *Genetics and Molecular Biology* 26: 19–25.
- Hickman GD, Hevel KW. 1986. Effect of a hypolimnetic discharge on reproductive sucess and growth of warmwater fish in a downstream impoundment. In *Reservoir Fisheries Management: Strategies for the 80's*, Hall GE, Avyle M JVD (eds). American Fisheries Society: Bethesda; 286–293.
- Horiba. 1991. Water Quality Checker U-10: Instruction Manual. Horiba: Kioto.
- Janz DM, McMaster ME, Munkittrick KR, Van Der Kraak G. 1997. Elevated ovarian follicular apoptosis and heat shock protein-70 expression in white sucker exposed to bleached kraft pulp mill effluent. *Toxicology and Applied Pharmacology* **147**: 391–398.
- Janz DM, Van Der Kraak G. 1997. Supression of apoptosis by gonadotropin, 17B-estradiol, and epidermal growth factor in rainbow trout preovulatory ovarian follicles. *General Comparative Endocrinology* 105: 186–193.
- Koger CS, Teh SJ, Hinton DE. 1999. Variations of light and temperature regimes and resulting effects on reproductive parameters in medaka (*Oryzias latipes*). *Biology of Reproduction* **61**: 1287–1293.
- Le Cren ED. 1951. The length-weight relationship and seasonal cycle in gonad weight and condition in the perch (*Perca fluviatilis*). Journal of Animal Ecology 20: 201–219.
- Ligon FK, Dietrich WE, Trush WJ. 1995. Downstream ecological effects of dams. BioScience 45: 183-192.
- Lizama MAP, Ambrosio AM. 2002. Condition factor in nine species of fish of the Characidae family in the Upper Paraná River floodplain, Brazil. *Brazilian Journal of Biology* **62**: 113–124.
- Lowe-McConnell RH. 1987. Ecological Studies in Tropical Fish Communities. Cambridge University Press: London.
- Luksiene D, Sandström O. 1994. Reproductive disturbance in a roach (*Rutilus rutilus*) population affected by cooling water discharge. *Journal* of Fish Biology 45: 613–625.
- Luksiene D, Sandström O, Lounasheimo L, Andersson J. 2000. The effects of thermal effluent exposure on the gametogenesis of female fish. *Journal of Fish Biology* **56**: 37–50.
- Maddock DM, Burton MPM. 1999. Gross and histological observations of ovarian development and related condition changes in American Plaice. *Journal of Fish Biology* **58**: 928–944.
- McAdam DSO, Liley NR, Tan ESP. 1999. Comparison of reproductive indicators and analysis of the reproductive seasonality of the tinfoil barb, *Puntius schwanenfeldii*, in the Perak River, Malaysia. *Environmental Biology of Fishes* **55**: 369–380.
- Miranda ACL, Bazzoli N, Rizzo E, Sato Y. 1999. Ovarian follicular atresia in two teleost species: a histological and ultrastructural study. *Tissue and Cell* **31**: 480–488.
- Nagahama Y. 1983. The functional morphology of teleost gonads. In *Fish Physiology*, Hoar WS, Randall DJ (eds). Academic Press: New York; 233–275.
- Nikolski GV. 1963. The Ecology of Fishes. Academic Press: London.
- Parkinson D, Philipport JC, Baras E. 1999. A preliminary investigation of spawning migration of grayling in a small stream a determined by radio-tracking. *Journal of Fish Biology* 55: 172–182.

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- Petrere Jr M, Agostinho AA, Okada, EK, Júlio Jr HF. 2002. Review of the fisheries in the Brazilian portion of the Paraná/Pantanal basin. In *Management and Ecology of Lake and Reservoir Fisheries*, Cowx IG (ed.). Blackwell Science: London; 123–143.
- Piechotta G, Lacorn M, Lang T, Kammann U, Simat T, Jenke HS, Steinhart H. 1999. Apoptosis in Dab (*Limanda limanda*) as possible new biomarker for anthropogenic stress. *Ecotoxicology and Environmental Safety* 42: 50–56.

Pinheiro CVL. 1981. Relatório de pesca no lago de Sobradinho para o ano de 1980. SUDEPE: Juazeiro, Brazil.

- Preece RM, Jones HA. 2002. The effect of Keepit dam on the temperature regime of the Namoi River, Australia. *River Research and Applications* 18: 397–414.
- Redding M, Patiño R. 1993. Reproductive physiology. In The Physiology of Fishes, Evans DH (ed.). CRC Press: Boca Raton; 503-534.
- Rizzo E, Bazzoli N. 1995. Follicular atresia in curimatá-pioa *Prochilodus affinis* Reinhardt, 1874 (Pisces, Characiformes). *Revista Brasileira de Biologia*. **55**: 697–703.
- Rizzo E, Sato Y, Barreto BP, Godinho HP. 2002. Adhesiveness and surface patterns of eggs in neotropical freshwater teleosts. *Journal of Fish Biology* **61**: 615–632.
- Rizzo E, Godinho HP, Sato Y. 2003. Short-term storage of oocytes from the neotropical teleost fish *Prochilodus marggravii*. *Theriogenology* **60**: 1059–1070.
- Sato Y. 1999. Reprodução de peixes da bacia do rio São Francisco: indução e caracterização de padrões. Doctoral thesis, Universidade Federal de São Carlos: São Carlos, SP.
- Sato Y, Godinho HP. 2003. Migratory fishes of the São Francisco River. In *Migratory Fishes of South America: Biology, Fisheries and Conservation Status*, Carolsfelds J, Harvey B, Ross C, Baer A (eds). IDRC and World Bank: Victoria; 195–232.
- Sato Y, Cardoso EL, Godinho AL, Godinho HP.1996. Hypophysation parameters of the fish *Prochilodus marggravvi* obtained in routine hatchery station conditions. *Revista Brasileira de Biologia* **56**: 59–64.
- Sato Y, Fenerich-Verani N, Nuñer APO, Godinho HP, Verani JR. 2003. Padrões reprodutivos de peixes da Bacia do Rio São Francisco. In Águas, peixes e pescadores do São Francisco das Minas Gerais, Godinho HP, Godinho AL (eds). PUC-Minas: Belo Horizonte; 229–274.
- Saxena PK, Shandu R. 1994. Influence of temperature on ovarian recrudescense Indian catfish, *Heteropneustes fossilis. Journal of Fish Biology* **44**: 168–171.

Schubart O. 1954. A piracema no rio Mogi Guassú (Estado de São Paulo). Dusênia 5: 49-59.

- Shanbhag B, Saidapur SK. 1996. Attetic follicles and corpora lutea in the ovaries of fishes: structure-function correlations and significance. In *Fish Morphology–Horizons of New Research*, Datta Munshi JS, Dutta MHM (eds). AA Balkema: Brookfield; 147–168.
- Welcomme RL. 1979. Fisheries Ecology of Foodplain Rivers. Longman: London.