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Effects of extended absence of flooding on the fish assemblages of three floodplain lagoons in the middle São Francisco River, Brazil

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In the Neotropics, a large proportion of fish communities of large rivers use floodplain as habitats for feeding, reproduction, and refuge. An evaluation was made of the effects of extended dry periods on the species richness, abundance and local extinction of fish species in three marginal lagoons in the middle São Francisco River, southeastern Brazil. The studied lagoons fail to receive river floods during the study period (1994-1996). A gradual reduction in richness and abundance was observed in all lagoons. Migratory fish species had the highest probability to become extinct in the two lagoons that remained with large water volume. Species tolerant to low levels of dissolved oxygen had the lowest probability of local extinction in the lagoon showing an abrupt reduction in water volume. Similar changes to those observed in the current study are likely to occur in the floodplains if dams would be constructed in this segment of the river. Adequate water releases from Três Marias reservoir, located upstream, should be considered as a management tool for producing episodic flooding on the marginal lagoons of the region.

Na região neotropical uma grande porção da comunidade de peixes utiliza a planície de inundação como habitat de alimentação, reprodução e refúgio. Neste trabalho, foi avaliado o efeito de um período de seca prolongado sobre a diversidade, abundância e extinção local de peixes de três lagoas marginais do médio curso do rio São Francisco. As lagoas estudadas não receberam água proveniente da cheia do rio durante o período de estudos (1994-1996). Redução gradual na abundância e riqueza de peixes foi abservada em todas as lagoas. Nas lagoas que permaneceram com grande volume de água, espécies migradoras foram as que apresentaram maior probabilidade de extinção. Já na lagoa que apresentou abrupta redução no volume de água, espécies tolerantes a baixos níveis de oxigênio dissolvido apresentaram menor probabilidade de extinção local. Caso barragens venham a ser construídas no médio curso do rio São Francisco, mudanças similares às observadas neste estudo poderão ocorrer com maior freqüência na sua planície de inundação. Vertimentos controlados através do reservatório de Três Marias, localizado a montante, devem ser avaliados como ferramenta de manejo para produzir inundações periódicas nas lagoas marginais da região.

Key words: Floodplain, Migratory fish, Extended drought, Hypoxia.

Introduction

Floodplains are lands periodically covered with water when rivers overflow their banks. In the tropics, a large portion of fish communities uses the floodplains as habitats for feeding, reproduction, and refuge (Agostinho & Zalewski, 1995; Lowe-McConnell, 1999). For this reason, these habitats are priority for fish conservation and management (Costa *et al*., 1998). During the dry season, the flooded areas become isolated from the main channel of the river, forming numerous marginal lagoons and ponds; some of these lagoons persist until the next flood whereas others dry up. Adaptation to this environmental dynamism allows aquatic and floodplain species to persist in the face of seemingly harsh conditions, such as floods and droughts, that regularly destroy and re-create habitat elements (Poff *et al.,* 1997). In response to the adverse conditions of the dry season, some fishes in marginal lagoons opportunistically change their diet according to the availability of food whereas others tolerate low levels of dissolved oxygen (Machado-Allison, 1994).

Five critical components of the flow regime regulate ecological processes in floodplain ecosystems: the magnitude, frequency, duration, timing and rate of change of hydrological conditions (Poff *et al.,* 1997). Life cycles of the biota utilizing floodplain habitats are intrinsically related to all these components (Junk *et al.,* 1989).

Neotropical floodplains have increasingly been altered through river damming and channeling, and stripping of veg-

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etation, with direct consequences to the fish fauna (Agostinho & Zalewski, 1995). Damming directly affects the fish communities, because its changes on the river's flow regimes cause a higher frequency of extended periods without flooding.

This work evaluates the effects of absence of floods on the diversity and abundance (number and biomass) of fish species in three marginal lagoons of the middle São Francisco River, southeastern Brazil. Also, an attempt was made to determine whether the fish species that remained alive during these isolation periods have ecological attributes that distinguish them from those that became locally extinct.

Material and Methods

Study area. The São Francisco River basin is located between parallels 21° and 7° S and corresponds to 7.4 % of the Brazilian territory. The uses of its waters include power generation, irrigation, industrial and urban water supplies, navigation, and fishing. Located downstream Três Marias dam (45°15'50"W; 18° 15'12"S), its floodplain occupies approximately 2,000 km^2 (Welcomme, 1990). Its importance as fish nurseries and role in recruitment of migratory species have been long recognized (Menezes, 1956).

The three lagoons under study, 'Curral-de-Vara', 'Cajueiro' and 'Juazeiro', are located in the medium São Francisco River region, 600 km downstream Três Marias dam, in a stretch rich in marginal lagoons (Fig. 1). The lagoons were connected to the river during the previous rainy season (January 1994) and remained isolated throughout the study period. Curral-de-Vara and Cajueiro retained a large volume of water during this period, and their oxygen concentrations were always greater than 5 $mg \times l^{-1}$ (Pompeu, 1997). However, Juazeiro showed a significant loss in water volume; in September 1995, it had a very small water surface and low oxygen concentration (2 $mg \times l^{-1}$) (Pompeu, 1997) and subsequently dried up.

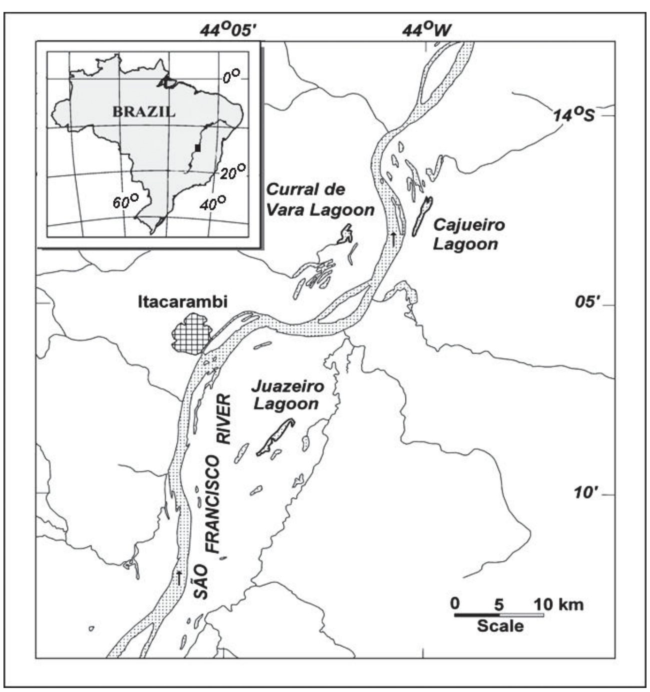

Fig. 1. Study area showing the location of the marginal lagoons.

Sampling and analyses. Four field trips for collecting fishes were made over a period of two years (1994-1996), comprising dry (September/1994 and September/1995) and wet seasons (March/1995 and March/1996). In each trip (three days), gill nets (mesh sizes 3, 4, 5, 6, 7, 8, 10, 12, 14 and 16 cm opposite knots) were set between 10:00 and 14:00h and between 17:00 and 21:00h. For capturing smaller fishes, dragnets of 1mm mesh size were used during the morning and afternoon. Drag netting was the only capture method used in the Juazeiro lagoon in September 1995. Since no recolonization by flooding occurred during the period of study, the fish richness of each lagoon was represented by all species captured along the period of study.

After being captured, the fishes were immediately fixed in 10% formaldehyde solution and subsequently preserved in 70% ethanol solution. In the laboratory, each fish was weighed, measured for standard length and identified. Catch per unit of effort (CPUE) in number (CPUEn) and in biomass (CPUEb) was used to express data on numerical abundance (number of individuals per 10 m^2 of net in 8 h; CPUEn) and biomass (grams per 10 m^2 of net in 8 h; CPUEb).

To determine whether fish abundance decreased over the dry period, differences in total CPUE were tested using ANOVA (SAS, 1985), and Tukey test was used as a *post hoc* procedure. Since an abrupt reduction in the water volume occurred in the Juazeiro lagoon between March/1995 and September/1995, it was impossible to use gillnets in the September/1995 field trip. Thus, the tests of CPUE differences were conducted only on data from the Curral-de-Vara and Cajueiro lagoons.

To determine whether the species that survived during the period of lagoon isolation had biological characteristics that distinguished them from the extinct ones, the following ecological attributes were compared:

a) Standard length - the fish species were grouped into the following categories, according to the standard length of the largest individual captured: class 1 = SL< 5cm; class 2 = 5cm $\leq$ SL < 15cm; class 3 = 15cm $\leq$ SL < 30cm; and class 4 = SL $\geq$30cm;

b) Reproductive migratory trait - 1 was attributed to the migratory species and 0 to the non-migratory species;

c) Trophic category - numerical values were attributed to each category according to Angermeier (1995). Thus, 1 = detritivore and herbivore, 3 = invertivore and 5 = piscivore. For the species classified in more than one trophic category, the value corresponded to the average between them (*e.g.*, 4 = invertivore-piscivore).

d) Hypoxia tolerance - 0 was attributed to tolerant species and 1 to non-tolerant species.

Associations between the ecological attributes and local extinction were examined using Fisher´s exact test (Fleiss, 1981). Biological segregation between groups of non-extinct and extinct species was made through multiple logistic regression, which was also used for calculating the odds ratio. For this analysis, the standard length was considered as a continuous variable. The odds ratio is equal to the extinction probability ratio between two groups of species (*e.g.*, migratory and non-migratory), calculated according to Hosmer & Lemeshow (1989):

$OR = e^{\beta i}$, where:
OR = odds ratio for variable i,
β_i = regression coefficient for variable i.

Statistical significance was indicated by P-values of 0.05 or less.

Since the lagoons were connected to the river during 1993/1994 and 1996/1997 rainy seasons, the minimal São Francisco River flow enough to flood the study area was estimated from the maximum monthly discharge during that period. The minimal flow frequency was evaluated for a period of 20 years before and after the construction of Três Marias Dam, closed in 1961. The data were obtained from the meteorological station of Manga Municipality, State of Minas Gerais, the nearest city to the study area.

Results

A total of 11,072 fishes belonging to 48 species were captured; of those, 1,511 were captured by gill nets and 9,561 by dragnets. Their ecological attributes are indicated in Table 1. The Curral-de-Vara lagoon showed greater number of species (44) than Cajueiro and Juazeiro lagoons (34). A gradual reduction in species richness was observed in all lagoons along the period of study (Fig. 2). Curral-de-Vara and Cajueiro also showed a gradual decrease in CPUEn (Fig. 3) and CPUEb values during the same period (Fig. 4), the latter being significant ($P < 0.05$).

Standard length and trophic category of the non-extinct species were not significantly different from those of the extinct ones (Table 2). At Cajueiro, the migratory species became extinct at a significantly higher rate ($P < 0.05$) than the non-migratory species. In the other lagoons, although a relation between migration and local extinction was also observed, the differences in the extinction rates between these two groups were not significant ($P > 0.05$) (Table 2). In the Juazeiro lagoon, species tolerant to hypoxia had significantly greater chance of survival than the non-tolerant ones (Table 2).

Although the logistic regression model was significant only for the Juazeiro, the analyses indicated that in all lagoons, the migratory species had at least 10 times more chances of becoming extinct. In the Juazeiro lagoon, in addition, the probability of extinction of the species with no tolerance to low dissolved oxygen levels was approximately 10^9 times higher (Table 3).

Considering that the lagoons were connected to the river during the rainy seasons of 1993/1994 and 1996/1997 and not in 1994/1995 and 1995/1996, the minimal river flow enough to flood the study area was calculated to be approximately 5,000 $m^3 \times s^{-1}$. After Três Marias dam closure (1959), the frequency

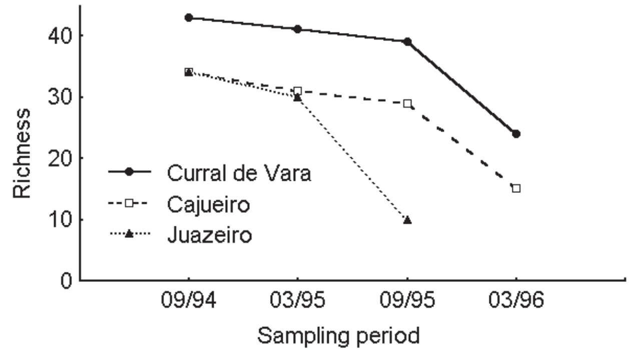

Fig. 2. Fish richness in the marginal lagoons of the middle São Francisco River, Brazil, from September 1994 to March 1996.

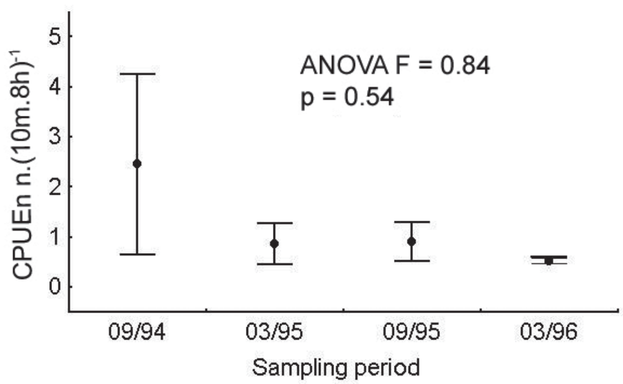

Fig. 3. Catch per unit of effort in number of individuals (CPUEn) in the 'Curral-de-Vara' and 'Cajueiro' lagoons of the middle São Francisco River, Brazil, from September 1994 to March 1996 (dot = mean; whiskers = maximum and minimum).

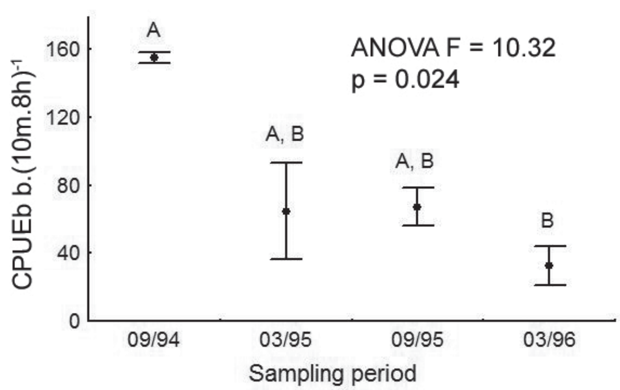

Fig. 4. Catch per unit of effort in biomass (CPUEb) in the 'Curral-de-Vara' and 'Cajueiro' lagoons of the middle São Francisco River, Brazil, from September 1994 to March 1996 (dot = mean; whiskers = maximum and minimum). Different letters above columns indicate significant differences.

Table 1. Ecological attributes of the fishes captured in the 'Curral-de-Vara', 'Cajueiro' and 'Juazeiro' lagoons, São Francisco River, from September, 1994 to March, 1996. Species denomination followed Reis *et al.*, 2003; 1: Sato *et al.* (1987), Lamas (1993); 2: Pompeu & Godinho (2003); 3: Carter & Beadle (1931), Bastos (1956), Driedzic *et al.* (1978), Hochachka *et al.* (1978), Kramer *et al.* (1978), Acuña & Sanz (1992), Rantin *et al.* (1992), Machado-Allison (1994); N = non-migratory, Y = migratory, U = migratory trait unknown; herb = herbivore, invert = invertivore, detri = detritivore; N = hypoxia intolerant, Y = hypoxia tolerant.

Species	Maximum standard length (cm)	Migratory Behavior[1]	Trophic category[2]	Hypoxia tolerance[3]
Acestrorhynchus britskii Menezes, 1969	17.3	N	piscivore	N
Acestrorhynchus lacustris (Lütken, 1875)	23.4	N	piscivore	N
Anchoviella vaillanti (Steindachner, 1908)	3.6	N	invertivore	N
Astyanax sp.	3.8	N	herb-invert	N
Astyanax fasciatus (Cuvier, 1819)	4.4	N	invertivore	N
Astyanax bimaculatus (Linnaeus, 1758)	7.0	N	herb-invert	N
Brycon orthotaenia Günther, 1864	24.0	Y	herbivore	N
Bryconamericus stramineus Eigenmann, 1908	4.2	N	herb-invert	N
Characidium sp.	2.9	N	invertivore	N
Cichla temensis Humboldt, 1821	34.4	N	piscivore	N
Cichlasoma sanctifranciscense Kullander, 1983	4.6	N	invertivore	N
Crenicichla lepidoda Heckel, 1840	8	N	invertivore	N
Curimatella lepidura Eigenmann & Eigenmann, 1889	11.0	N	detritivore	N
Eigenmannia virescens (Valenciennes, 1842)	25.5	N	invertivore	N
Gymnotus carapo Linnaeus, 1758	26.2	N	invertivore	Y
Hemigrammus marginatus Ellis, 1911	3.1	N	invertivore	N
Hoplerythrinus unitaeniatus (Agassiz, 1829)	24.6	U	detri-herb	Y
Hoplias malabaricus (Block, 1794)	31.3	N	piscivore	Y
Hoplosternum littorale (Hancock, 1828)	18.8	N	detri-invert	Y
Hyphessobrycon santae (Eigenmann, 1907)	2.2	U	invertivore	N
Leporinus piau Fowler, 1941	20.5	N	herb-pisci	N
Leporinus renhardti Lütken, 1875	17.0	Y	invertivore	N
Leporinus taeniatus Lütken, 1875	10.8	Y	herbivore	N
Hyphessobrycon micropterus Eigenmann, 1915	2.60	U	invertivore	N
Moenkhausia costae (Steindachner, 1907)	5.7	N	invertivore	N
Myleus micans (Lütken, 1875)	15.0	U	invertivore	N
Orthospinus franciscensis (Eigenmann, 1914)	9.0	N	invertivore	N
Phenacogaster franciscoensis Eigenmann, 1911	3.4	U	invertivore	N
Pimelodella cf. *vittata* (Lütken, 1874)	5.6	N	invertivore	N
Pimelodus maculatus La Cepède, 1803	23.0	N	invertivore	N
Pimelodus pohli Ribeiro & Lucena, 2006	16.0	N	invertivore	N
Pamphorichthys hollandi (Henn, 1916)	2.8	U	herb-invert	N
Prochilodus costatus Valencienes, 1850	23.3	Y	detritivore	N
Prochilodus argenteus Agassiz, 1829	36.6	Y	detritivore	N
Psellogrammus kennedyi (Eigenmann, 1903)	4	U	herb-invert	N
Pseudoplatystoma corruscans (Spix & Agassiz, 1829)	68.0	Y	piscivore	N
Pterygoplichthys etentaculatus (Spix & Agassiz, 1829)	23.4	U	herbivore	Y
Pygocentrus piraya (Cuvier, 1819)	31.0	N	piscivore	N
Roeboides xenodon (Reinhardt, 1851)	9.4	N	invertivore	N
Salminus sp.	58.0	Y	piscivore	N
Schizodon knerii (Steindachner, 1875)	27.3	N	herbivore	N
Serrapinnus piaba (Lütken, 1875)	3.3	N	herb-invert	N
Serrapinnus heterodon (Eigenmann, 1915)	3.1	U	herb-invert	N
Serrasalmus brandtii Lütken, 1875	18.0	N	invert-pisc	N
Synbranchus marmoratus Bloch, 1795	17	U	piscivore	Y
Tetragonopterus chalceus Spix & Agassiz, 1829	9.0	N	invertivore	N
Trachelyopterus galeatus (Linnaeus, 1766)	16.5	N	invertivore	Y
Triportheus guentheri (Garman, 1890)	12.4	N	invertivore	N

of occurrence of such flow was notably lower due to its regulatory influence (Figs. 5 and 6).

Discussion

The fish richness of a lake is limited by the species capacity to persist and coexist and it results from the equilibrium between colonization and losses through local extinction (Barbour & Brown, 1974). Fish colonization in marginal lagoons generally occurs during the rainy (flooding) season and extinction during the dry season (Halyc & Balon, 1983). During the dry season, there are high levels of predation, reduction in food availability and quality, and, in some cases, decreased oxygen availability and dryness (Junk *et al.*, 1989). All these factors may have influenced the probability of species extinction and played a significant role in fish richness and abundance decrease in the analyzed lagoons during the period of isolation. Richness was also strongly correlated with the lagoon's isolation time from the main river in Pantanal (Súarez *et. al.*, 2004), and differences in frequency and inten-

Table 2. Number of extinct species (maximum number of species) by ecological attribute and the respective extinction probability for three marginal lagoons of the middle São Francisco River during the dry periods of 1994 to 1996.

Marginal lagoon	Ecological Atribute					Probability (Fisher's exact test)
	Maximum standard length (cm)					
	>5	5-15	15-30	> 30		
Curral-de-Vara	9 (13)	2 (10)	6 (15)	2 (5)		0.114
Cajueiro	5 (10)	5 (5)	6 (13)	3 (6)		0.191
Juazeiro	7 (9)	6 (7)	9 (15)	2 (3)		0.712
	Trophic category					
	Detritivore/herbivore	Detritivore/invertivore	Invertivore	Invertivore/piscivore	Piscivore	
Curral-de-Vara	5 (8)	5 (8)	7 (19)	0 (0)	2 (8)	0.355
Cajueiro	3 (5)	2 (5)	11 (16)	0 (1)	4 (7)	0.159
Juazeiro	5 (6)	2 (6)	12 (15)	0 (0)	3 (7)	0.348
	Reproductive trait					
	Migratory		Non-migratory			
Curral-de-Vara	5 (7)		14 (36)			0.121
Cajueiro	5 (6)		9 (28)			0.032
Juazeiro	4 (4)		20 (30)			0.229
	Tolerance to hypoxia					
	Tolerant		Non-tolerant			
Curral-de-Vara	2(4)		18(39)			0.641
Cajueiro	3(5)		15(28)			0.591
Juazeiro	0 (7)		24 (27)			< 0.001

sity of communication between the lagoons and the river were determinant for the species richness in an isolated lagoon of the Upper Paraná River floodplain (Cunico *et. al.*, 2004). Smaller fish catches during the dry season were also observed in marginal lagoons of the Paraná River (Bonetto *et al.*, 1969; Cordiviola de Yuan, 1992).

Regarding the probability of maintenance in the lagoon during the period of isolation, the extinction rate was higher among the migratory species, than the non-migratory ones. In addition to being unable to reproduce in the lagoons, migratory fish are target fisheries species due to their large size and commercial value. In the Upper Paraná River floodplain lagoon, the density of migratory fish was also lower in a year characterized by low water levels, short inundation period and interrupted floods (Cunico *et. al.*, 2004).

Some fishes can tolerate low dissolved oxygen levels that frequently occur in floodplains during the dry season (Machado-Allison, 1994). In Lake Camaleão (Amazon River basin), which shows oxygen deficits during long periods, at least a quarter of its species can live in waters with very low dissolved oxygen concentrations (Junk *et al.*, 1983). In Pantanal, species that remain in isolated lagoons are represented by: (1) individuals that fail to return (or fail to have the opportunity) to the river before isolation, and (2) species that would exhibit some adaptation to the pool characteristics (*e.g.* hypoxia, presence/absence of sheltering macrophytes, desiccation), and therefore may be able to survive until the next flood (Catella, 1992).

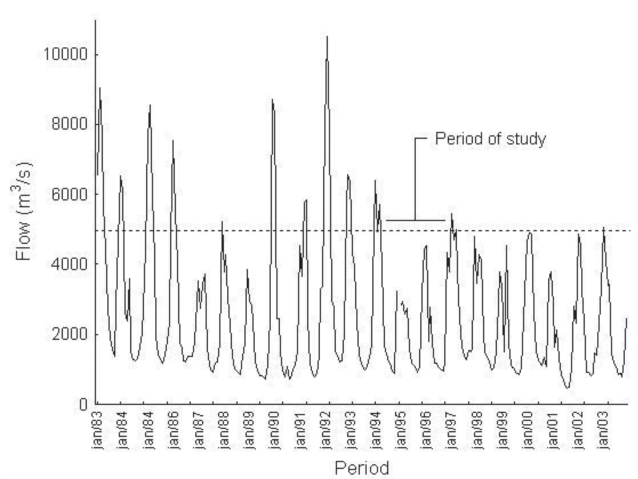

Fig. 5. São Francisco River flow at the town of Manga, State of Minas Gerais, during the last 20 years before 2003, including the period of study.

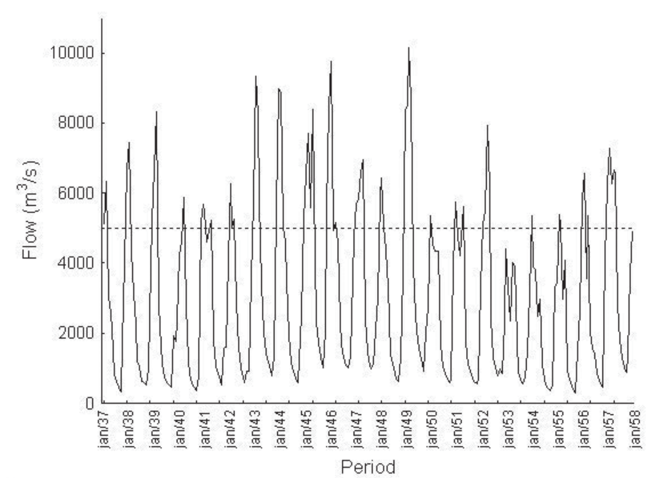

Fig. 6. São Francisco River flow at the town of Manga, State of Minas Gerais, during 20 years before the closure of Três Marias Dam.

Table 3. Summary of multiple logistic regression models for each lagoon of the middle São Francisco River.

Lagoon/variable	Estimator	- 2 log L	Probability	Odds ratio
Curral-de-Vara				
length	-0.046		0.223	0.956
migration	2.551		0.089	12.82
feeding	-0.028		0.933	0.973
hypoxia	-0.976		0.395	0.377
model		5.056	0.282	
Cajueiro				
length	-0.044		0.288	0.957
migration	2.343		0.179	10.41
feeding	-0.035		0.924	0.965
hypoxia	-1.079		0.329	0.340
model		3.064	0.547	
Juazeiro				
length	0.178		0.323	1.195
migration	12.01		<0.001	1.6×10^5
feeding	0.616		0.565	1.852
hypoxia	22.00		<0.001	3.5×10^9
model		26.25	<0.001	

Tolerance to hypoxic conditions was apparently a determinant for the survival of the species in the Juazeiro lagoon, following the marked reduction of its water volume. Of the seven species that survived, four are capable of breathing atmospheric oxygen (*H. unitaeniatus*: Driedzic *et al*., 1978; *M. etentaculatus*: Carter & Beadle, 1931, Kramer *et al*., 1978; *H. littorale*: Carter & Beadle, 1931; and *S. marmoratus*: Kramer *et al*., 1978). *Hoplosternum littorale*, in addition to breathing atmospheric oxygen, shows blood cell modifications that ensure greater efficiency during hypoxia (Acuña & Sanz, 1992). Although not breathing atmospheric oxygen, *Hoplias malabaricus* tolerates very low oxygen levels, it needs little water convection to breathe (Rantin *et al*., 1992) and it has a large respiratory gill surface area (Driedzic *et al*., 1978; Hochachka *et al*., 1978). Since the trophic position and maximum size of the species are unrelated to their chances of local extinction, the number of locally extinct species in each size class or trophic category may have reflected an inherent characteristic of the fish fauna rather than a predisposition to extinction.

Losses of fish biomass resulting from dryness are estimated for the middle Paraná River to be 40,000 t of fish×year^{-1} (Bonetto *et al*., 1969), and to be related to flow intensity (Cunico *et al.,* 2004). Although drought is a natural phenomenon, additional impacts due to long periods of flood absence caused by anthropic actions cannot be discarded. The flood regime differentially affects reproduction and recruitment of species of different life histories. Dependence of flooding seems to be lower for sedentary species with parental care when compared with migratory species that spawn in upper basin stretches and whose young inhabit flood areas during their initial development (Agostinho *et al.,* 2004). As a consequence, river regulation by dams may impose drastic constraints on migratory fish and on those that spawn in floodplains with important consequences for commercial fishing (Sato & Godinho, 2003; Agostinho *et al.,* 2003; 2004).

If the flooding that preceded the period covered by the current work was an unusual event, it would have filled the lagoons with an unusually large number of species and biomass. Then, the subsequent decline would be merely the relaxation of the system back to a natural level. However, the 1993/1994 flooding was not exceptional, but a very common one (see Fig. 5). The reduction in the water level fluctuation in the middle São Francisco River resulting from Três Marias dam may be causing an important impact on the natural functioning of its floodplains. Considering new dam constructions in the main river and tributaries, a possibility that appears in different governmental proposals, similar changes to those observed in the marginal lagoons of the current work would likely become permanent conditions. Taking into account the current observations, water releases from Três Marias reservoir during the rainy season should be assessed as a management tool for periodic flooding of the marginal lagoons in the region (Godinho *et al*., 2003), with potential to improve recruitment of migratory species. In addition, mitigatory water releases from new dams should be taken as part of the adopted measures to reduce impacts on downstream flow.

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