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Effects of water quantity on connectivity: the case of the upper Paraná River floodplain

Angelo Antonio Agostinho[1,2]*, Cláudia Costa Bonecker[1], Luiz Carlos Gomes[1,2]

[1]Núcleo de Pesquisa em Limnologia, Ictiologia e Aqüicultura, Universidade Estadual de Maringá, Paraná, Brazil. 87020-900.
[2]Departamento de Biologia, Universidade Estadual de Maringá, Paraná, Brazil. 87020-900.
*e-mail: agostinhoaa@gmail.com

Abstract

The hydrological regime is the main force driving processes in river-floodplain systems. The flood pulse concept serves as a base from which to study the processes acting in such a system. However, when the flood pulse is regulated and there is a need to re-establish the hydrography at close to natural conditions, the best way to achieve this is via ecohydrology, a newly emerging paradigm. In this paper, we use principles of ecohydrology to evaluate the effect of water quantity on the limnology, biota and fishery of the upper Paraná River systems, where a UNESCO demonstration site on ecohydrology is located. In addition, we argue that dam operation can be crucial for restoring the hydrography of the Paraná River to near natural conditions. The data used were collected between 1986 and 2006 in several habitats of the floodplain. The limnology, biota (periphyton, phytoplankton, zooplankton, benthic invertebrates, fish, macrophytes and riparian vegetation) and fishery (ecosystems services) were all influenced by the alteration in the hydrography prompted by the functioning of the dams located upstream from the demonstration site area. Moreover, the observed deterioration of the water quality due to the presence of toxic cyanobacteria is another strong argument for adjusting the dam's operation to re-establish the timing of the floods to match critical periods of the biota in order to restore ecosystem biodiversity and services.

Key words: hydrological regime, dam regulation, floodplain, biodiversity, fishery.

1. Introduction

In river floodplain systems, the hydrological regime is the key factor that promotes ecological functioning and determines biodiversity patterns (Neiff 1990; Bunn, Arthington 2002), and this regime is maintained mainly by the flood pulse (Junk *et al.* 1989). The flood pulse regulates the connections and exchange of water among floodplain water bodies and rivers (herein named connectivity, with an emphasis on surface linkage between environments). Flooding also promotes an increase in nutrient inputs from decomposition of detritus accumulated during the low water periods, and these processes are important to maintain the high productivity of aquatic communities over time (Agostinho *et al*. 2004a). Therefore, oscillations in hydrometric levels maintain the river-floodplain connectivity and determine the seasonality of abiotic and biotic structures and processes, which are fundamental for many resident species and those that use the floodplain as a habitat to complete their life cycles (Thomaz *et al.* 2004a). However, the mosaic of environments in a floodplain responds differently to water levels as a function of each one's degree of connectivity with the main river (Pagioro 1992; Ward *et al.* 1999; Tockner *et al.* 2000).

In general, floods are regional driving forces and tend to homogenise the system, and consequently, the between-habitats variability of limnological variables decreases with increasing water levels, suggesting that floods increase the similarity among floodplain habitats and influences the maintenance of biodiversity. Floods also seem to decrease community turnover or beta diversity (Thomaz *et al.* 2007). The higher connectivity observed during this period allows several species to disperse onto the floodplain, making their local extinction less likely. This appears to be very important for maintaining rare species (Thomaz *et al.* 2004a).

On the other hand, during low water periods the floodplain aquatic habitats are isolated from each other and influenced by local forces, such as water inputs, wind and local rains (Thomaz *et al.* 2007). The more pronounced effect of local forcing functions leads to great heterogeneity during this period. Such high habitat heterogeneity may be considered an important feature of the whole system, partially explaining the great diversity found there (Thomaz *et al.* 2004a).

While the flood pulse concept is helpful to understand the ecology of the system, ecohydrology appears to be a better template by which to re-establish ecosystem services (Zalewski *et al.* 1997). Ecohydrology has emerged as a new paradigm that embraces aspects of ecology, hydrology and socio-economics (see Zalewski *et al.* 2009, this issue). It postulates the use of natural processes in order to achieve improved ecosystem functioning. In this paper, we assume that hydrological processes regulate biota.

In the upper Paraná River floodplain, the hydrological regime is regulated by the 26 large reservoirs in its basin and mainly by Porto Primavera Dam, which is located 30 km upstream. The control of the water level exerted by the dams located upstream from this stretch of the floodplain influences nutrient cycling and the structure and composition of several assemblages (phytoplankton, periphyton, aquatic macrophytes, benthos, zooplankton and fishes).

We will argue that water quantity in floodplain rivers is the major feature influencing connectivity, contributing to maintaining ecosystem functioning and, therefore, services. For the upper Paraná River basin, we will show that the construction of dams altered the seasonality of water quantity and especially the timing of the floods, consequently disrupting connectivity during critical periods, with serious alterations in the limnology, biota and fishery. Finally, we conclude that it is possible, using a proper reservoir operation, to re-establish the historically occurring water quantities, (and thus connectivity) at close to their natural levels without a drastic loss of electricity generation.

2. The area

Before 1998, the upper Paraná River had an extensive floodplain between the cities of Três Lagoas, Mato Grosso do Sul State, and Guaira, Paraná State (a 480-km stretch, ≤20 km wide). This section was the only remaining dam-free stretch of the Paraná River in Brazil, except for 30 km downstream from the Itaipu Dam (Agostinho, Zalewski 1996). Above the plain, there are eleven reservoirs with surface areas greater than 200 km^2. Among these, three are in the main channel of the Paraná (Porto Primavera – 2250 km^2, Ilha Solteira – 1195 km^2 and Jupiá – 330 km^2); four are in the Paranapanema River (Capivara – 576 km^2, Jurumirim – 425 km^2, Chavantes – 400 km^2 and Rosana – 220 km^2); and the others are located in the Tiête River (Três Irmãos – 785 km^2, Promissão – 530 km^2 and Barra Bonita – 308 km^2). In addition, there are several reservoirs in the Paranaíba and Grande Rivers, which join and form the Paraná (Grande: Furnas – 1440 km^2, Água Vermelha – 647 km^2, Marimbondo – 438 km^2, Mascarenhas de Moraes – 250 km^2 and Volta Grande – 222 km^2; Paranaíba: Itumbiara – 778 km^2, São Simão – 722 km^2, Emborcação – 485 km^2 and Nova Ponte – 447 km^2). All of these reservoirs were formed to generate electricity, but navigation, flood control, fishery, water supply and recreational uses are common for most of them. However, operation is conducted to maximise the production of electricity along the chain. This is controlled by the "Operador Nacional do Sistema Elétrico" (ONS – Electric System National Operator – a private non-for-profit company), which runs the "Sistema Integrado Nacional (SIN – National Integrated System, which generates 96.5% of Brazil's electricity). For more details on the systems, see Agostinho *et al.* (2008).

Despite being one of the most regulated river stretches in the world (more than 46 large dams, according to WCD, 2000), the flood regime in the study area did not change drastically because of several important tributaries in this stretch. In 1998, Porto Primavera Dam, located in the middle of the last dam-free stretch of the river, was closed, which reduced the floodplain's length to 230 km between the Itaipu Reservoir and the Porto Primavera Dam (Fig. 1).

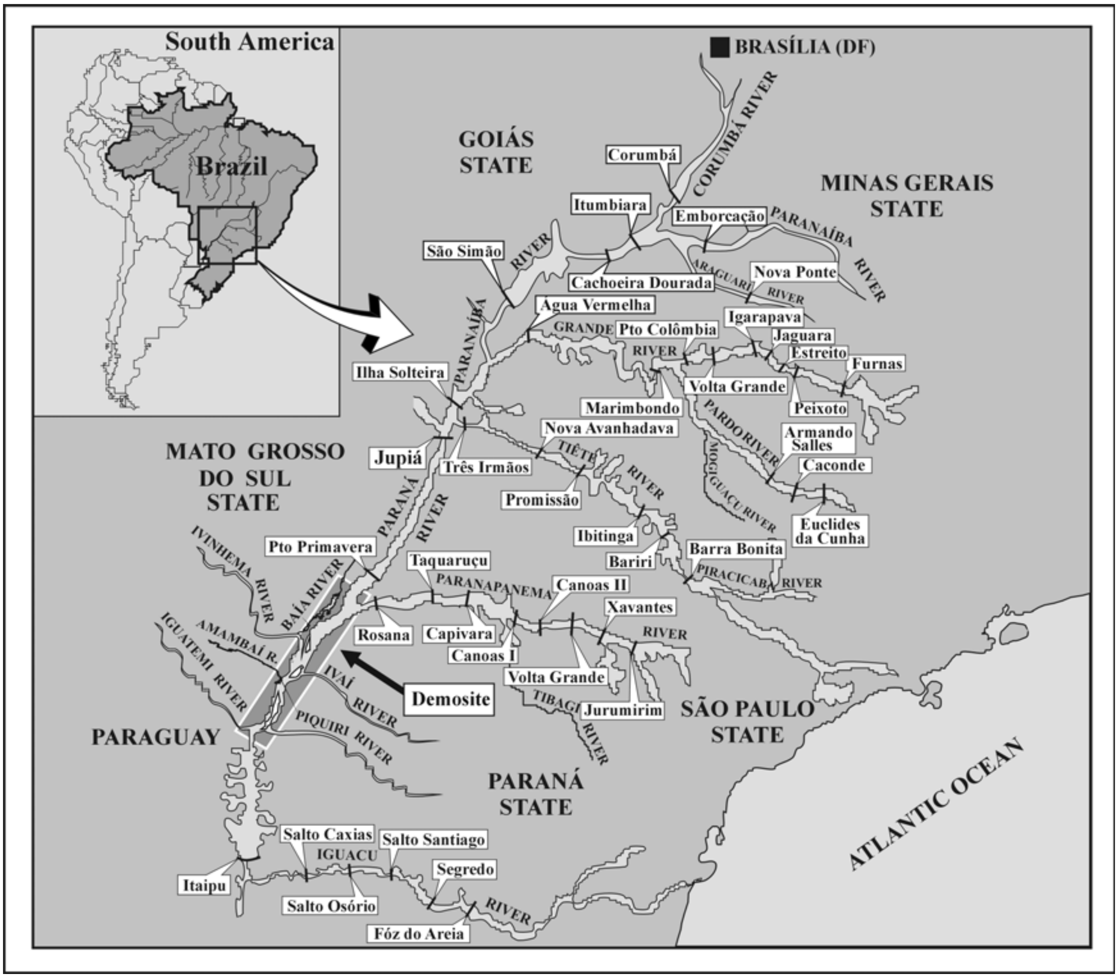

Fig. 1. Map of the upper Paraná River showing major dams and the floodplain where most of the activities of the demonstration site (Demosite) are conducted (Modified from Agostinho *et al.* 2007).

In this segment, the river has a wide-braided channel with a low slope (0.09 m km^{-1}) and heavy accumulation of sediments on its bed, creating sandbanks and small islands. Secondary channels, the Baía River, and the lower courses of rivers entering on the west bank (e.g., Ivinheima, Amambai, and Iguatemi rivers) form complex anastomoses in this section. The east margin of the river is higher, and its tributaries have larger slopes (Paranapanema, 0.6 m km^{-1}; Ivai, 1.30 m km^{-1}; Piquiri, 2.2 m km^{-1}) with smaller floodplains (Agostinho *et al.* 1995).

The area of the demonstration site is located along the lower third of the upper Paraná River between the mouths of the Paranapanema and Ivinheima Rivers. At this point, the Paraná River channel is 3.4 km to 4.0 km wide, with an extensive alluvial plain on its west margin. Annual water temperatures fluctuate between 10.3°C and 33.6°C, with an average of 22.0°C (Stevaux, 1994). The pluvial regime in the region is marked by a wet season from October to February during which monthly rainfall averages more than 125 mm and a dry season from June to September, when rainfall is less than 80 mm. Average annual rainfall reaches 1500 mm, characterising the climate of the region as tropical-subtropical (IBGE 1990).

3. Water quantity and connectivity

The flood period in the Paraná River usually occurs from November/December to April/May. High water levels characterise this phase, and some pulses occur with amplitudes of up to 2-3 m. The occurrence of two or three annual flood pulses is quite common during periods of high water levels. Smaller pulses (<0.5 m) occur weekly during the dry season (Thomaz *et al.* 1992), resulting from the operation of upstream dams. Therefore, the seasonal water level fluctuation in the upper Paraná River floodplain is not

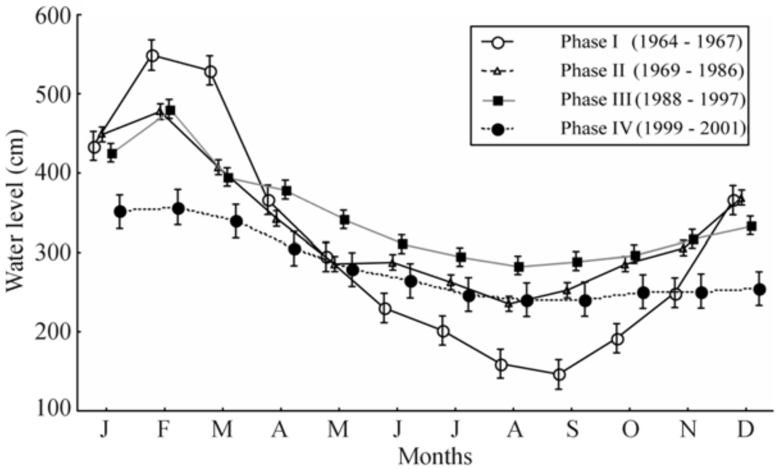

Fig. 2. Changes in water level in the upper Paraná River. Each phase corresponds to a period immediately after a closure of a large dam above the studied area, except phase I (natural discharge).

continuously sinusoidal (i.e., it presents several pulses) like those of other large rivers such as the Amazon (Rai, Hill 1982), and uninterrupted periods of falling and rising water are rarely observed (Agostinho *et al.* 2000). On average, the water level of the Paraná River fluctuates about 2.5 m during each seasonal cycle, but considerable interannual variation may be observed. The flood amplitude may reach up to 7.5 m, but years with almost no flooding have been recorded.

Dam construction in the Paraná River altered water levels in the studied region, as exemplified in Figure 2. During phase I there were few reservoirs above the floodplain and none in the main channel of the Paraná River. For every large reservoir filled just above the studied area (Jupiá before phase II; Rosana before phase III and Porto Primavera before phase IV), the hydrography was altered. Then, after the closure of Porto Primavera Dam, mean water levels during the flood period decreased about 40% when compared to those registered in phase I. These changes, therefore, altered the timing of the high and low water periods, which led to decreased connectivity in critical periods and severely impacted the limnology and biota in the region. The data sets used throughout this paper were collected from 1987 to 2005.

4. Influence on limnology

The seasonal dynamics of the limnological variables are determined mainly by the hydrometric level of the Paraná River and its main tributaries. Patterns of stratification and water circulation (diel mixing), chlorophyll-*a* and nutrient concentrations are clearly affected by hydrological fluctuations. However, seasonal variation seems to represent a secondary effect upon limnological variables (Thomaz *et al.* 2004a).

The aquatic environments connected to the Paraná River have, in general, low turbidity and low phosphorus concentrations. On the other hand, the environments connected to the Ivinheima River have high turbidity, and those connected to the Baía River have high nitrate concentrations and lower pH values (Rocha 2003). The limnological characterisations of the floodplain lakes certainly differ according to the river to which each is connected. A large geographic scale can explain those differences, and the reservoirs upstream in the basin also influence these patterns. However, in environments far from the river, there are time lags between hydrological variation and its effects upon limnological features.

Some limnological variables (pH, electrical conductivity and total alkalinity) in the Paraná River remained relatively constant and independent of the oscillations in hydrometric levels. The highest values of dissolved oxygen occurred during the low water period. On the other hand, total nitrogen and phosphorus concentrations tended to increase with rising mean hydrometric levels of the Paraná River, which is the opposite of what was observed in the floodplain environments. The maximum values of the Secchi depth were associated with the lowest mean hydrometric levels (Thomaz *et al.* 2004a).

Before the construction of Porto Primavera Dam, it was possible to observe a slight seasonality in some limnological features related to hydrometric level fluctuations. However, this dam, along with the others upstream, caused conspicuous changes in Secchi depth and total phosphorus concentrations in the Paraná River channel, where it was possible to register the highest values and a sharp decrease in the concentration of this nutrient (Thomaz *et al.* 2004a).

5. Influence on the biota

In this section, we described the structure and dynamic of the communities before and after the construction of Porto Primavera Dam. Species diversity and abundance variations of the different communities in both phases were presented and results were obtained in different studies.

Periphyton

Studies on the periphytic algal community in the floodplain were developed by Rodrigues and Bicudo (2001, 2004) and Rodrigues *et al.* (2004). In three habitats with different hydrodynamic regimes (a lagoon, a backwater and a Paraná River side channel) sampled before the construction of Porto Primavera Dam (1994), 228 species were registered (Rodrigues, Bicudo 2004). The community was represented mainly by Bacillariophyceae and Zygnemaphyceae (74 and 62 species, respectively). After Porto Primavera (2000-2004), 503 species were recorded in this algae community, and these classes were important to the periphyton composition (172 and 90 species, respectively) (Rodrigues *et al.* 2004). This large difference may be related to the number of sites studied (10 before the dam; 32 in 2000; 10 in 2001 and 2002).

Greater species richness was observed in the lakes in both phases, and it was related to the development of aquatic macrophytes, which favours greater habitat heterogeneity, and to the growth of the dominant classes, which usually benefit from the lentic hydrodynamic and the morphometry of these environments.

Greater species richness, number of life forms and biomass accrual rate were observed during the high water periods. On the other hand, the lowest species richness was recorded in the lotic habitat and was associated with water velocity. Changes in the community composition among the lotic, the lagoon and the backwater environments were also observed. In addition, the high water period promoted greater community similarity among these habitats.

The abrupt changes in the fluviometric level of the Paraná River, caused by the absence of flood pulses or by the operation of dams located upstream, can be considered a physical disturbance, which also controls the community dynamics. During the high water period, in which the disturbance related to flow is more intense, there was a typical dominance of opportunistic species in lentic environments. In the lotic environment, the community was characterised by species adapted to disturbances.

Therefore, the response of periphytic algae to disturbances depends on the magnitude and duration of the flood period. Community proprieties, such as development stage and taxonomic aspects (e.g., species pool in the environment), were conditioned on type of habitat and hydrological period. The biomass losses of the community in the different environments of the floodplain were also associated with the greatest disturbance regime during the high water period. The species succession was also influenced by the hydrological period and decreased from lentic to lotic environments, in which flow was probably the main forcing function.

Phytoplankton

The phytoplankton community was represented by high species richness before and after the dam's construction (from 436 taxa to 552 taxa, respectively; but more sites were sampled after). Before the dam (until 1998), Chlorophyceae and Euglenophyceae were the most specious classes (105 taxa and 87 taxa, respectively). After its completion (2000-2006), Chlorophyceae was also dominant (147 taxa), followed by Cyanobacteria (89 taxa). In both phases, greater numbers of species were recorded in lakes and in the Baía River. Greater species richness was observed during the low water period (Train, Rodrigues 2004; Train *et al.* 2004).

In general, the algae communities in the different environments were dominated by large numbers of sporadic species (more than 50%) and nanoplanktonic species. The smaller size class species (20 µm - 40 µm) were registered during both high and low water period, and a larger size class species (>100µm) in the low water period. Flooding led to decreased phytoplankton biomass and favoured the development of nanoplanktonic species, which present adaptations to thrive in high flow (C-strategists; Reynolds 1994) (Train, Rodrigues 2004).

After damming, phytoplankton community composition changed, Cyanobacteria abundance increased and this group dominated algae biomass. Recently, *Radiocystis fernandoi* was registered in the Paraná River, although it is not a potamoplankton species. This inoculate probably came from floodplain lakes and/or upstream reservoirs (Train *et al.* 2004).

The variations in the structure of phytoplankton among the seven studied years (2000–2006) were strongly influenced by the Paraná River's level and the sediment suspended in it as a result of climatic changes and anthropogenic activities (Train *et al.* 2004). Operation of upstream dams appears to favour the development of Cyanobacteria, and this group represents a risk to human health due to the toxicity of several species (loss of water quality). Cyanotoxin can also be accumulated in fish flesh and be consumed by humans. Cyanobacteria blooms have been observed in different environments of the Paraná River, and cyanotoxin (microcystin) has already been detected in the Itaipu Reservoir, below the floodplain area. Therefore, the increased biomass of cyanobacteria in the floodplain might promote decreased local and regional phytoplankton species richness. In addition, it may influence fishing (either recreational or professional) activities, and it can deteriorate water quality, affecting human consumption and recreation.

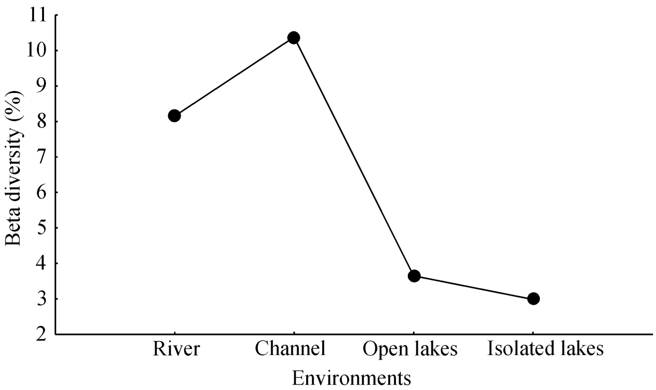

Fig. 3. The β-diversities of the rotifer community recorded in the different environments (open lakes = floodplain lakes and backwater) and systems formed by the main rivers (rainy and dry periods).

Zooplankton

The zooplankton communities before the construction of Porto Primavera Dam were composed of 385 species of rotifers (230), testate amoebae (74), cladocerans (64) and copepods (17) in the different environments of the floodplain, including lakes (permanent and temporary environments), channels and rivers. After the dam's construction (2000-2006), 435 species were registered (242 rotifer species, 99 testate amoeba species, 71 cladoceran species and 23 copepod species) in the same types of environments and lakes disconnected from the rivers (not temporary environments). These results were related to the higher number of sites sampled after the dam was constructed and to dam operation, which exerted a flow variation in the floodplain (Lansac-Tôha *et al.* 2004a and b).

Rotifers presented the greatest species richness in the two periods due to their opportunistic characteristics, including reproductive strategies and different feeding preferences (e.g., algae and bacteria). Surveys of the floodplain showed the importance of the connectivity among the environments to rotifer species richness and β diversity (Fig. 3), which was lower in isolated lakes than in the river and channel. Rotifer abundance was also highest in connected lakes (Aoyagui, Bonecker 2004; Bonecker *et al.* 2005).

The high densities of rotifers in isolated floodplain lakes during the rainy period reflect the rapid development of planktonic populations in lentic environments, probably due to the absence of pronounced flooding and the consequent overflow. In contrast, we recorded the lowest abundance values in the channels and rivers during the dry period. This finding could be the result of the lower connectivity and faunal exchange between lotic and lentic environments during this period (Fig. 4) (Bonecker *et al.* 2005).

In the first period (before the dam's construction), the highest number of zooplankton species was found, in general, during the high water period, showing the influence of the hydrological cycle on zooplankton composition. Flooding of the shores increased the number of habitats in the different environments and connected the habitats that were isolated during the low water periods. Moreover, the connectivity among the habitats (rivers, channels and lakes) was more intensive, and it promoted changes in fauna composition. Testate amoebae and rotifers were more specious in the river and microcrustaceans in the lakes, showing the heterogeneity of the environment.

The operation of the dam promoted spatial and temporal variations in zooplankton composition. In general, high species richness was registered during high water periods, but some groups of species were more prevalent in the low water period, mainly in the rivers and channels, such as cladocerans and copepods. For instance, testate amoebae contributed to zooplankton richness mainly in the rivers and channels and rotifers in the lakes (Velho *et al.* 1999).

It was not possible to observe a single pattern of temporal fluctuation in the abundance of zooplanktonic groups before the closure of Porto Primavera. Rotifers and cladocerans were abundant during low water periods, and copepods reached high densities during high water periods due to the high abundance of nauplii and copepodids. Testate amoebae showed no clear seasonal abundance patterns, and their abundance does not appear to be synchronously related to the hydrological cycle (Bini *et al.* 2003).

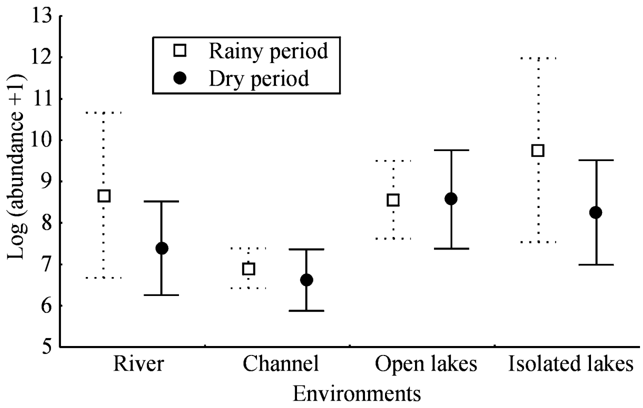

Fig. 4. Rotifer abundance (ind m^{-3}) recorded in the different environments (open lakes = floodplain lakes and backwater) during the rainy and dry periods (symbol = average, bar = standard deviation).

On the other hand, we observed a general and clear spatial pattern in the abundance of zooplankton. The highest zooplankton abundance was recorded in lakes and the lowest in channels and rivers. Rotifers dominated in the lakes and channels, followed by testate amoebae and copepods. The first two groups were also abundant in rivers. Cladocerans were more abundant in lakes and channels. Although these microcrustaceans were not dominant in the plankton community, there was a tendency for greater densities to be observed in lakes with a high degree of connectivity (Alves *et al.* 2005).

After the construction of Porto Primavera Dam, the spatial distribution of the zooplankton abundance was also remarkable. More individuals were recorded in lakes (open and isolated environments), especially in those isolated from the river. The degree of connectivity among the environments was also important to the testate amoebae community structure in the floodplain. Regional species richness was positively correlated with local species richness in a lagoon that is well-connected to the associated river.

Benthic invertebrates

The structure and dynamic of the benthic community studied before the dam's construction (1987-1999) showed that the species-habitat type association occurred according to the physical and chemical characteristics of each environment. For example, small vermiform animals (Nematoda, Oligochaeta, Chironomidae and Harpacticoida) were found in the interstitial spaces of sandy sediments in the main channel of the Paraná River. In muddy bottoms, mainly in lakes, larger sized fauna were registered. *Corbicula fluminae* (Bivalvia), an invasive species, dominated in the main and secondary channels in the floodplain (Takeda, Fujita 2004).

Faunistic surveys in the different environments, including main and secondary channels and lakes, have demonstrated the occurrence of 82 taxa (not including Chironomidae). The greatest species richness was observed in secondary channels and the least in isolated lakes (not connected to the river).

The benthic chironomid fauna observed came from 44 taxa. This community showed high species richness and abundance in the channels and rivers, mainly during the low water period. Hydrodynamics and the flood pulse seem to function as controlling factors in the processes determining the spatial and temporal variation of this community. Moreover, particle size and the organic make up of the sediment were also important (Higuti 2004).

In general, the surface available for colonisation by benthic invertebrates increases with the river level, along with the amount of allochthonous matter that may serve as an energy source. Substrate heterogeneity generally creates more microhabitats, favouring an increase in faunal diversity.

After the dam's construction (2000-2001), the benthic macro-invertebrate community was represented by 23 taxa in different environments of the floodplain, including rivers, channels, lakes and backwaters. A greater abundance of individuals was verified in channels. In general, the hydrological cycle influenced the community structure since the abundance decreased during the low water period (Takeda *et al.* 2004b).

In this phase, *Corbicula fluminae* proliferated considerably in the region to the detriment of native species such as *Cyanocyclas limosa*. Greater abundance of *Corbicula fluminae* was recorded in secondary channels, followed by the Paraná River. The adaptability of this species to lotic environments was related to the relatively constant flow, the absence of sudden differences in the hydrological cycle, and the relatively constant physical and chemical characteristics as compared to the lakes, where water fluctuation is more pronounced. The results also suggest that the native species are better adapted to the water level fluctuations dictated by the main river. In general, the construction of the dam affected all benthic populations of the floodplain, especially Bilvavia.

Another invasive bivalve species, *Limnoperna fortunei*, is rapidly colonising the Paraná River upstream from the Plata River (Argentina). This species may cause substantial interference in the hydro-electrical turbines, obstructing water supply systems and consequently causing economic impacts. Moreover, the colonisation of this species in the Paraná River reservoirs above the area may cause serious ecological disasters downstream (Takeda *et al.* 2004a).

The Chironomidae community was composed of 29 genera. Water level fluctuations before the dam's construction influenced changes in this community by a substitution of grazers/scratchers for omnivorous and detritivorous/herbivorous species (Takeda *et al.* 2004b).

Fish spawning and recruitment

The environmental factors in the upper Paraná River basin are similar to those of other South American basins in that their flood regimes have great relevance in the reproductive and recruitment success of fish (Welcomme 1979; Lowe-McConnell 1987; Machado-Allison 1990; Vazzoler, Menezes 1992). This is evident by the high degree of synchrony between floods and the principal events of the reproductive cycle (maturation of oocytes, migration, spawning and initial development of juveniles) and because of the relationship between recruitment success and the

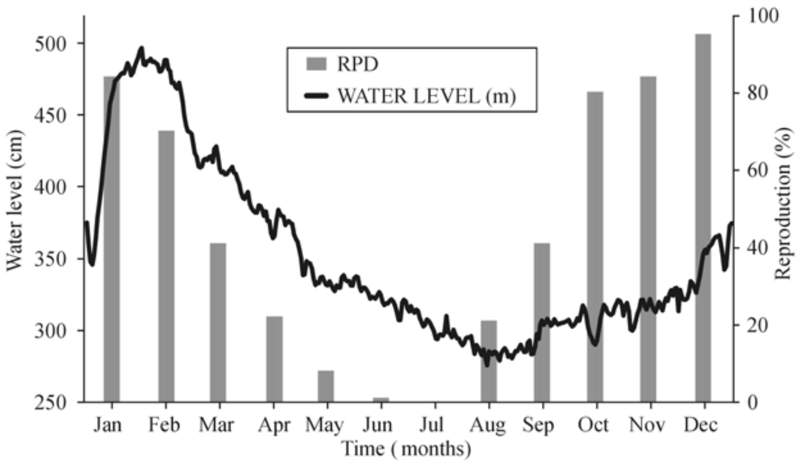

Fig. 5. Daily average water level from 1978 to 2000 (line) and monthly frequency of reproductive female fish (ripe+semi-spent; bars) in the upper Paraná River floodplain during an annual cycle (modified from Vazzoler *et al.* 1997 and Agostinho *et al.* 2001, 2004b).

timing, duration and amplitude of floods (Gomes, Agostinho 1997; Agostinho *et al.* 2004b).

The frequencies of individuals with ripe or semi-spent gonads, indicative of recent spawning, were higher during a period of increasing water level (Fig. 5). When water levels are rising, hydrated eggs drift along the river and spill over onto the floodplain, where they complete their development (Godoy 1975; Agostinho *et al.* 2004b).

Agostinho *et al*. (2004b) conducted a seven-year survey of the biomass of species with different reproductive strategies in three lakes of the floodplain of the upper Paraná River. Young-of-the-year of large migratory fishes and adults and juveniles of species with other life history strategies occupy these habitats. Flood duration (number of days from September to March in which the water level was higher than the 3.5-m floodplain inundation height; 221.5 m s.l. in Porto São José Hydrometric Station; Verissimo 1999) the main factor affecting recruitment (Gomes, Agostinho 1997) was correlated (Spearman ρ) with fish biomass, separated by reproductive strategy (Fig. 6).

A significant correlation was found for large migratory fishes (ML in Fig. 6). For the other reproductive strategies, correlations were not significant. Migratory fishes were favoured by annual periods of flooding longer than 75 days, such as in 1998 (Fig. 6). The closure of Porto Primavera Dam in December 1998 resulted in diminished water discharge during the flood period to a level similar to those observed in the dry season. This event explained the low numbers of migratory fish captured in 1999 (Fig. 6), despite a flood

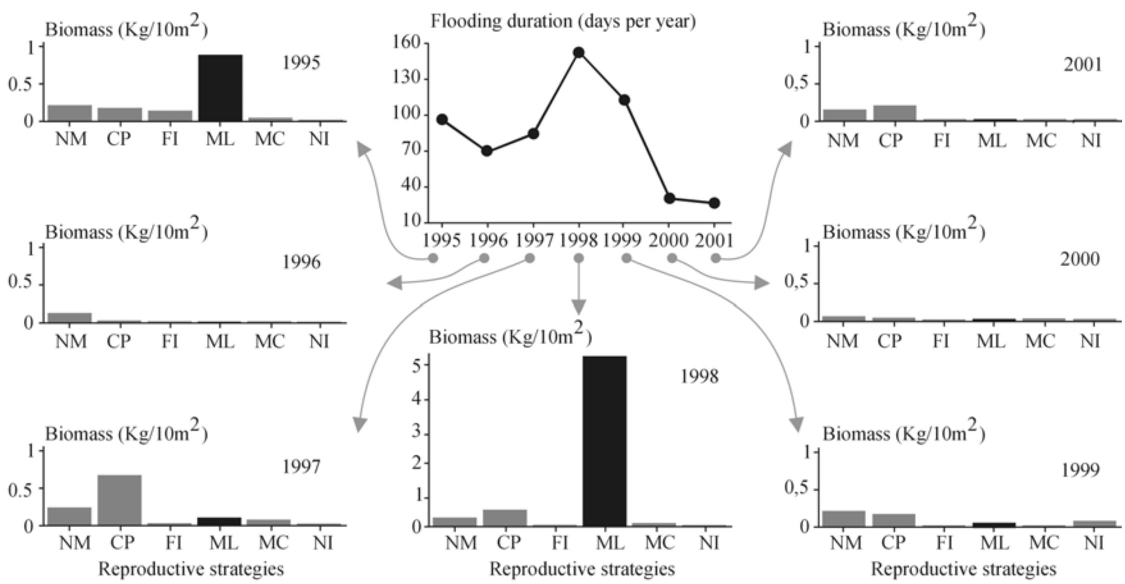

Fig. 6. Average biomass estimate (kg wet mass 10 m^{-2}) of juvenile fishes in three lakes of the upper Paraná River floodplain, according to reproductive strategy obtained six months after the peak of reproduction (NM=sedentary; CP=parental care; FI=internal fertilisation; ML=long-distance migratory; MC=short-distance migratory; NI=not identified). Number of inundation days per year is represented in the upper middle graph (modified from Agostinho *et al.* 2004b).

duration exceeding 100 days. According to Sanches *et al*. (2006), the larval density of large migratory species during this period was high. It appears that larvae were not able to access the floodplain habitats, thus affecting the biomass of the cohort. After the Porto Primavera Dam's closure, flooding was extremely rare. In 2000, the absence of floods was associated with a regional drought; and in 2001, the Porto Primavera Reservoir filled completely, retaining more water. During years when the water levels in the Paraná River are held artificially low, recruitment in fish species with sedentary and parental care strategies may be associated with lateral tributary sources not directly affected by the dams. However, when flooding is absent because of regional drought, all strategies are affected.

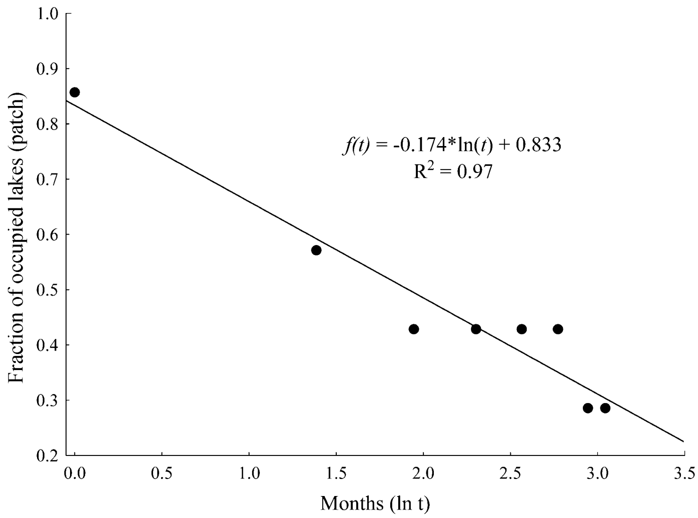

Fig. 7. Fit of a non-linear regression model for the fraction of floodplain lakes occupied by *Prochilodus lineatus* over time for data from Group 2 (January 1999 to December 2002; modified from Gubiani *et al.* 2007).

Gubiani *et al*. (2007) conducted another study that demonstrated the importance of the connectivity. These authors studied the persistence of the populations of the long-distance migratory species *Prochilodus lineatus*. The flood pulse influenced the persistence of this species. When floods inundated the plain (1992-1993), the fraction of occupied lakes reached 100%, indicating that all sampled lakes were occupied and the plain was saturated by *P. lineatus*. In the absence of floods (1999-2001), a clear exponential decrease was observed in the fraction of occupied lakes. This allowed the fitting of a linear model: $f = pe * \ln(t) + a$ (R^2=0.97; Fig. 7), which the authors called the drought-dependent model, where *pe* is the velocity of persistence decrease (extinction rate) and *a* is defined by the initial condition of the model. In this period, there were no relevant flood pulses. Thus, the species was not dispersed onto the plain, and migration was not possible due to the reduced water level.

Apparently, the decay in the fraction of occupied lakes is dependent on the time between flood events. The longer the time between floods, the more intense the decrease in the fraction of occupied floodplain lakes will be, with effects on the persistence of *P. lineatus*.

Again, a factor that may seriously affect this dynamic is the existence of several reservoirs because they have substantially altered the seasonality of the flood pulse. In this floodplain, juveniles of *P. lineatus* may represent more than 70% of the fish biomass in lakes after a long flood. However, if a flood is short, the species may be completely absent in the region (Agostinho, Zalewski 1995). In lakes of the same studied area, Agostinho *et al.* (2004b) observed that *P. lineatus* accounted for 65% of the total fish biomass.

During flood events, the higher connectivity among floodplain habitats (including the main river channel) allows movement of several fish species. Fish disperse throughout the area, and after water retraction, the landscape again becomes a mosaic of fragmented habitats, similar to what occurs in the mainland-island metapopulation model (Gotelli 2001). In this case, the river works as the "mainland" and the lakes as the "islands", and the flood pulse is the dispersal mechanism that intensifies colonisation since reproduction of migratory fish species occurs during high water periods, as in the case of *P. lineatus* (Gubiani *et al.* 2007).

Fisheries

The artisanal fishery conducted in the Paraná River's main channel immediately below the demosite area was studied from 1987 to 2005 by Costa (2007). This temporal series was grouped, a priori, according to the main events related to the hydrological cycle of the region, with floods in 1990 and 1997 and the closure of Porto Primavera Dam in 1998 (Fig. 8). This grouping resulted in three distinct periods: **per-A -** 1987 to 1990; **per-B -** 1991 to 1997 and **per-C** - 1998 to 2005.

Considering the objectives of this paper, we selected four long distance migratory species with high market value in the fisheries. All of them (*Pseudoplatystoma corruscans*, *Zungaro zungaro*, *Salminus brasiliensis* and *P. lineatus*) presented large declines in the catch per effort (CPUE; kg $fisher^{-1}$ day^{-1}) in periods B and C (Fig. 9). The low catch in per-B, besides the high mean water level, may be explained by the lack of seasonality in the fish stocks in the area, imposed by the

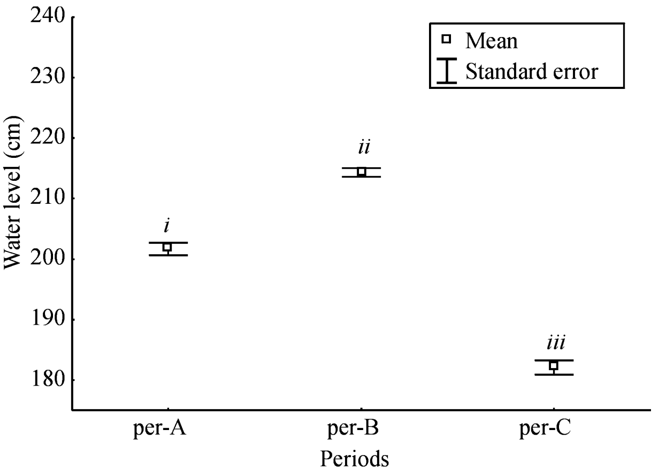

Fig. 8. Mean water level (±standard error) in the Paraná River channel for the three distinct periods grouped a priori. Letters above bars indicate the differences according to the Tukey test (ANOVA: $F_{[1,2]}$=284.2; p<0.0001) (modified from Costa *et al.* in prep).

operation of dams upstream, that forced fishers to change their target species, fishing on these large migratory fish sporadically.

Therefore, there are further indications that the longitudinal migration of fish to spawning sites was altered in the upper Paraná River, especially for *S. brasiliensis*, *P. corruscans* and *P. lineatus*, which are fully dependent on the habitats and resources made available by the flood pulse (Welcomme 1985; Lowe-McConnell 1987; Junk *et al.* 1989; Winemiller 2003).

These changes are implicated in alterations of the fishing techniques employed by fishers. They started to capture a greater quantity of less commercially valuable species, similar to what happened after the construction of Itaipu Dam (Hoeinghaus *et al.* 2009). As a result, the number of landed species increased in an attempt to improve profits reduced by the low number of large fish caught. Before, fishers used to fish in the main channel of the Paraná River to catch the large sized migratory species. Fishery in floodplain lakes was conducted only to capture bait. Today, due to the absence of flooding and the related absence of recruitment of commercially important species (as presented before), fishery is common in several habitats of the floodplain. As a result, a new variety of species are now landed, like *Hoplias aff. malabaricus*. This is a sedentary species common in floodplain lakes of the upper Paraná River floodplain, along with *H. unitaeniatus* and *Hoplosternum littorale* (Luiz *et al.* 2004). This last species, along with *Gymnotus inaequilabiatus* and *Parauchenipterus galeatus,* presented increased landings over the periods considered. This increase may be a result of the fact that they can be sold to recreational fishers, complementing the commercial fishers' income.

Aquatic macrophytes

Surveys of aquatic macrophytes increased after the dam's construction, and 60 species were registered in the different environments of the floodplain, including rivers, channels, backwaters and permanent and temporary lakes. Emergent species were the dominant life forms in the environments (27 species), followed by free-floating species and submerged-rooted (10 species), free-submerged (2 species) and rooted with floating leaves (1 species) (Thomaz *et al.* 2004b).

The increase in submerged species richness and frequency is probably related to the environmental changes in the basin due to the cascades of reservoirs upstream, including an increase in Secchi depth, decrease of water level fluctuations (water level control), and continuous inputs of propagules carried by the river from reservoirs densely colonised by these aquatic macrophyte species.

The transport of propagules by the Paraná River from source populations in upstream reservoirs, along with differences in hydrological and limnological characteristics of the main tributaries in the ecosystem, were important to determine the diversity patterns identified in the lakes connected to a river channel. In addition, the high alpha and beta diversities verified in these environments connected to the Paraná River suggest that despite their shallow depths and small areas, they should receive high priority for managing plants in the floodplain.

Another study carried out after the dam's construction (2000-2002) showed that the degree of connectivity among lakes (permanent and not connected) and rivers was also important to the aquatic plant community structure. Community composition was more heterogeneous during the low water period, when floodplain lakes were less connected among themselves and with the main river. A species richness decrease was also recorded in this period, and it may be attributed to low habitat availability for colonisation due to the exposure of the marginal areas of lakes (Santos, Thomaz 2004).

The significant relationship between species richness and depth emphasises the important role of the fluviometric level to the community structure. Floods were also important to disrupt succession, to reduce the dominance of a few species, and/or for dispersal of propagules among environments. The increased exchanges of organisms and inorganic and organic matter among habitats permitted by higher connectivity are the probable explanation for the homogenisation effects of floods (Thomaz *et al.* 2004b; Thomaz *et al.* 2007).

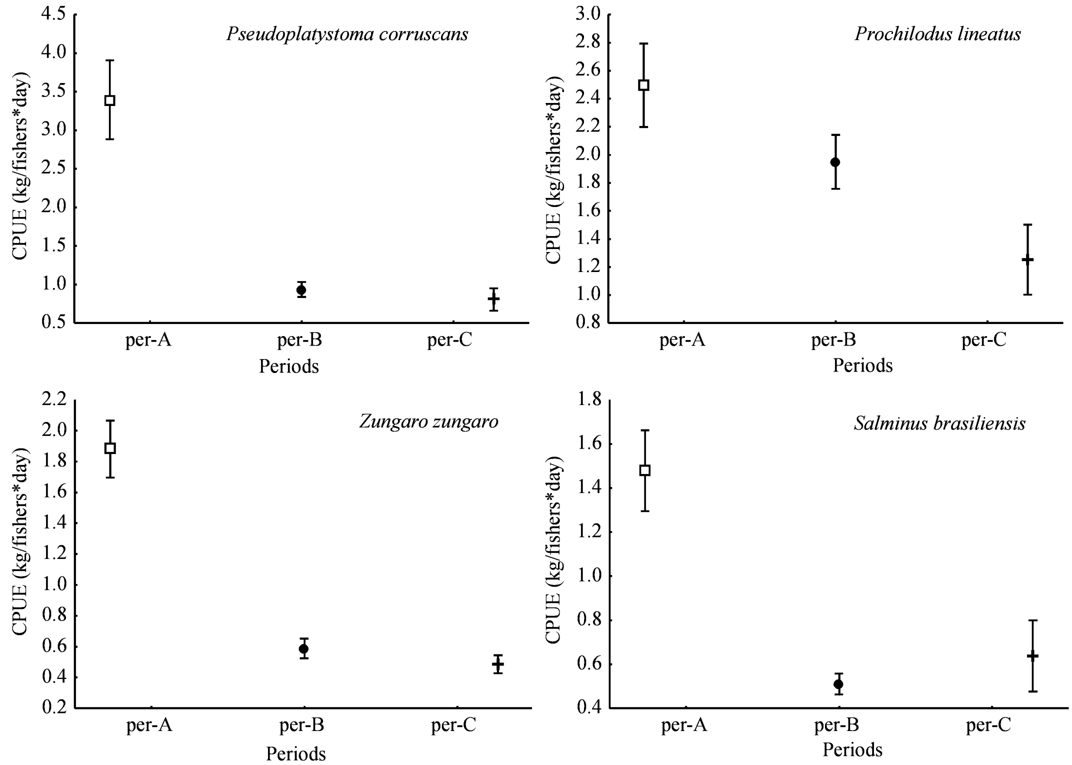

Fig. 9. Variations in mean catch per unit of effort (CPUE; kg $fisher^{-1}$ day^{-1}) for four long-distance migratory species exploited in the artisanal fisheries conducted in the main channel of the Paraná River (bars indicate one standard error).

Riparian vegetation

Surveys of vegetation in the demosite area registered 742 species belonging to 409 genera and 119 families (Souza *et al.* 2004). Studies conducted by Kita and Souza (2003) show the importance of the water level to riparian vegetation in the Figueira Lagoon. These authors described the dominance (50.6%) of terrestrial biological forms in the region, followed by amphibious ones (37.1%), in the period from 1997 to 2001. After that period, surveys were continued in this lagoon, and the authors registered a clear trend in the biological forms: terrestrial forms increased, whereas amphibious forms decreased. In 2002, the figures were 65.0% for terrestrial and 29.0% for amphibious. However, in 2005, terrestrial forms contributed 73.0% and amphibious only 21.0%. The increase in terrestrial forms was attributed to the absence of floods in these years, which led to diminished connectivity, allowing terrestrial forms to develop.

6. Re-establishing connectivity and ecosystem services

The spatial scale determines the structure and dynamics of the aquatic communities in the floodplain to the detriment of temporal scale, although the fluviometric level of the Paraná River was influenced by the dam's construction. However, the spatial variations of species richness and abundance of the communities were related to the degree of connectivity among lotic and lentic environments, water level variation and the intensities of floods in the floodplain. Thus, the results suggest that the structure and dynamics of aquatic communities were also influenced by the flood regime, mainly controlled by the Porto Primavera Dam. After the construction of this dam, the discharge of the Paraná River was redistributed, altering the hydrological regime, which apparently favoured the increased species richness and abundance of the plankton community. The increase in the abundance of cyanobacteria with potentially toxic species (already registered in the area) is notable and might be related to the absence of the dilution effect promoted by the flood regime (Thomaz *et al.* 2007). Moreover, the structure of the benthic invertebrate community changed due to the altered hydrography and to changes in the type of sediment suspended, reflecting the influence of the dam retention.

Fish were also strongly affected by the flood regime, with alterations in spawning, recruitment and persistence, especially for those species that endure long-distance migratory movements to spawn. All species with this strategy are commercially important in the fisheries conducted in the upper Paraná. The alteration in the water level led to alterations of the landed species and fishing techniques employed to catch fish.

The temporal variation was also important, and it was associated with the reservoir's operation; however, other temporal factors masked the results, such as dry and wet years (El Niño and La Niña - climatic events). It is clear that the changes in the communities in the floodplain environments influenced the changes in the production of this ecosystem. Thus, the energy transference among the trophic levels and the detritus pool of the system was also affected, and these processes have a considerable importance in the river-floodplain system dynamic.

In conclusion, it is clear that the alteration in water quantity led to poor functioning of the floodplain, which resulted in drastic changes in the services provided by the ecosystem it represents. Apparently, the principles of ecohydrology are adequate to induce the re-establishment of the functioning of this ecosystem, which depends on returning the hydrography to close to natural conditions. This can be achieved by coupling water releases from the dams upstream to the biological cycles of the species and maintaining high degrees of connectivity; generation capacity would not be lost because the dam can be operated to achieve this objective. In addition, the release of water from the reservoirs to augment flow in critical periods may also promote better water quality in the region due to the increased abundance of potentially toxic algae (Cyanobacteria). However, because of the way the dams are operated, it is difficult to couple water releases with ecosystem functioning. In the ONS (Electric System National Operator) there are no representatives from environmental agencies or non-government organisations. The sole environmental goal considered by ONS is to avoid catastrophic floods. Therefore, any alteration in the dam's operation must be established with the ONS (Agostinho *et al.* 2004c, 2008). The proposed measure must be undertaken very soon, before some species became locally extinct in the floodplain, which is located in the last undammed stretch of the Paraná River inside Brazilian territory.

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