

VARIATIONS IN FISH ASSEMBLAGES IN A TRIBUTARY OF THE UPPER PARANÁ RIVER, BRAZIL: A COMPARISON BETWEEN PRE AND POST-CLOSURE PHASES OF DAMS

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ABSTRACT

This paper purposed to evaluate alterations in fish assemblage (structure and species richness) and variations in the abundance of the most abundant species captured in the Piquiri River, due to the closure of Porto Primavera (in 1998; located upstream the Piquiri River mouth) and the Itaipu (in 1982; located downstream) dams in the upper Paraná River. The effects of selected environmental variables were also determined. Fishes were sampled during four distinct periods. Six samplings were conducted in each period, at two different sites (Campina and Apertado). For sampling, gill and trammel nets were used. Species abundances were indexed by catch per unit of effort. Spatial and temporal changes in environmental variables were summarized by a principal components analysis (PCA). To summarize structure of the assemblage, a nonmetric multidimensional scaling (NMS) was used. To test the significance of between-group differences at each periods and sites we used a multiresponse permutation procedure (MRPP). To test the association between fish assemblage and the environmental variables matrices, we used procrustean superimposition approach. A total of 2693 individuals were caught, belonging to 69 species, 4 orders and 19 families. Species richness differed spatially; the Campina site had greater mean richness (13) per sampling than the Apertado site (10). The structure of the fish assemblages showed significant temporal and spatial variations, which were more evident in the last period at the Apertado site (after the closure of Porto Primavera Dam). Spatial and temporal changes in structure of fish assemblages were not associated to environmental variables. Temporal changes in abundance, both in number and in weight, of the most abundant species were verified in both sites. The lack of migratory species was highlighted, which sharply decreased in the last studied period, when they were replaced by sedentary species. These findings appear to be related to regional factors, such as the decrease of floods registered in the upper Paraná basin, exacerbated by the control prompted by dams. Copyright © 2009 John Wiley & Sons, Ltd.

KEY WORDS: fishes; temporal and spatial changes; Paraná River basin; Piquiri River

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INTRODUCTION

Construction of dams, recent in South America (Agostinho *et al.*, 2007) is an old and important human intervention in natural systems. Reservoirs interfere in any river where they are built, altering water flow and terrestrial and aquatic systems in a drastic and permanent way (Tundisi, 1999; Nilsson and Berggren, 2000). Alteration of rivers by damming is a major concern for fish (Ormerod, 2003; Agostinho *et al.*, 2007). Dams can affect fish through alteration in flow patterns (Gehrke *et al.*, 1995; Galat and Lipkin, 2000; Lytle and Poff, 2004); they can also promote changes in connectivity with floodplains (Okada *et al.*, 2003; Petry *et al.*, 2003; Aarts *et al.*, 2004; Hirzinger *et al.*, 2004; Koel, 2004) and may create, in segments immediately below dams, unstable thermal and hydrodynamic conditions (Vanicek *et al.*, 1970; Holden and Stalnaker, 1975; Edwards, 1978). Dams also intercept

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migratory routes of various species, impacting the biogenic capacity of a system and availability of food and shelter for juvenile fish, in addition to promote reduction in fishery harvest (Agostinho *et al.*, 1993, 1994, 2007; Corbacho and Sanchez, 2001; Morita and Yamamoto, 2002).

Impoundment of rivers considerably affects the aquatic fauna by causing changes in the abundance and composition of species, with reduction or even local elimination of some populations (species), and a marked increase of others, which find favourable conditions in the new environment to proliferate (Agostinho *et al.*, 1999, 2007). In this environment, species at higher trophic levels, large body size, high endemism and limited dispersal ability tend to disappear first, whereas persistent species are usually generalists in terms of habitat and food requirements and/or have high abundance, long generation time and inhabit a wide geographic range (Winemiller, 1989; Agostinho *et al.*, 2007).

Various studies in South America analysed impact of dams on fish communities (Agostinho *et al.*, 1993, 1999, 2007; Godinho and Godinho, 1994; Petrere Jr., 1996; Ponton and Vauchel, 1998; Merona and Albert, 1999; Barbosa *et al.*, 1999). However, all these works focused on longitudinal gradient in rivers below dams. Studies evaluating the effects of dams on fish in lateral gradients (tributaries) are practically non-existent, with exception of Hoffman *et al.* (2005) which evaluated the importance of tributaries for the maintenance of fish diversity in Capivara Reservoir, Paranapanema River, Brazil and Oliveira *et al.* (2003, 2004, 2005) which evaluated the fish communities in lentic and lotic stretches of tributaries in the transversal gradient of the Itaipu Reservoir, Brazil. This scarcity of data for most tropical rivers, and especially Neotropical ones, precludes accurate prediction of effects of human-induced perturbations on these systems. For the upper Paraná River and the sets of other rivers and streams that form its basin, which were intensely modified in the last 50 years, the evaluation of spatial and temporal variations in fish assemblage structure due to the construction of dams is highly relevant.

The upper and part of the middle stretches of the Paraná River are located within Brazil, of this area, only a short stretch of approximately 200 km, including the upper Paraná River floodplain, situated between Porto Primavera Dam and the begin of the Itaipu Reservoir near to Guaíra city, Paraná State, does not present dams (Agostinho and Zalewski, 1996). Various studies, developed in this stretch (Vazzoler *et al.*, 1997; Agostinho *et al.*, 2004a; Thomaz *et al.*, 2004), revealed that the floodplain and its tributaries have high biological diversity and they are essential for the maintenance of viable populations of species threatened elsewhere in the basin, especially those of large sized fishes, which migrate long distances for spawning (Agostinho and Zalewski, 1996; Agostinho *et al.*, 2003, 2005; Oliveira *et al.*, 2005). When dams interrupt migratory routes of several fish species, tributaries may act as alternative routes, playing an important role in the maintenance of regional biological diversity and fish stocks (Agostinho *et al.*, 1992; Baumgartner *et al.*, 2004; Sanches *et al.*, 2006).

In this study, we investigated variations in the ichthyofauna of the Piquiri River, a major and unimpounded tributary on the eastern margin of the Paraná River, located in the stretch between Porto Primavera Dam and Itaipu Reservoir. Specifically, we aimed to evaluate the effects of the closure of these dams on fish assemblage structure in this tributary, analysing possible differences between pre and post closure periods. To achieve our objectives, we firstly analysed variations in species richness in the temporal and spatial scales considered. Then, we evaluated changes in the structure of fish assemblages and, finally, we described variations in the abundance of the most important species collected in the area. To overcome any possible confounding effect related to variation in local abiotic (environmental) characteristics, we related them with the structure of fish assemblages. We assumed that the absence of relationship between abiotic variables and assemblage structure indicate more general effect, in the case, the closure of dams in the main channel of the Paraná River.

MATERIALS AND METHODS

Study area

The Piquiri River basin comprises a drainage area of 31 000 km². Its sources are located at the São João Mountains, and it runs 485 km before reaching the Paraná River. The confluence is located above Itaipu Reservoir (dam concluded in 1982) and below Porto Primavera Dam (concluded in 1998), a region that includes the longest undammed stretch of the Paraná River inside Brazil and the remnant of the upper Paraná River floodplain. The most important tributaries of the Piquiri River on the right margin are the Goio-erê, Tricolor and Cantú Rivers, and for the left margin are the Sapucaí and Melissa Rivers (Paiva, 1982) (Figure 1). The Piquiri River show several rapids,

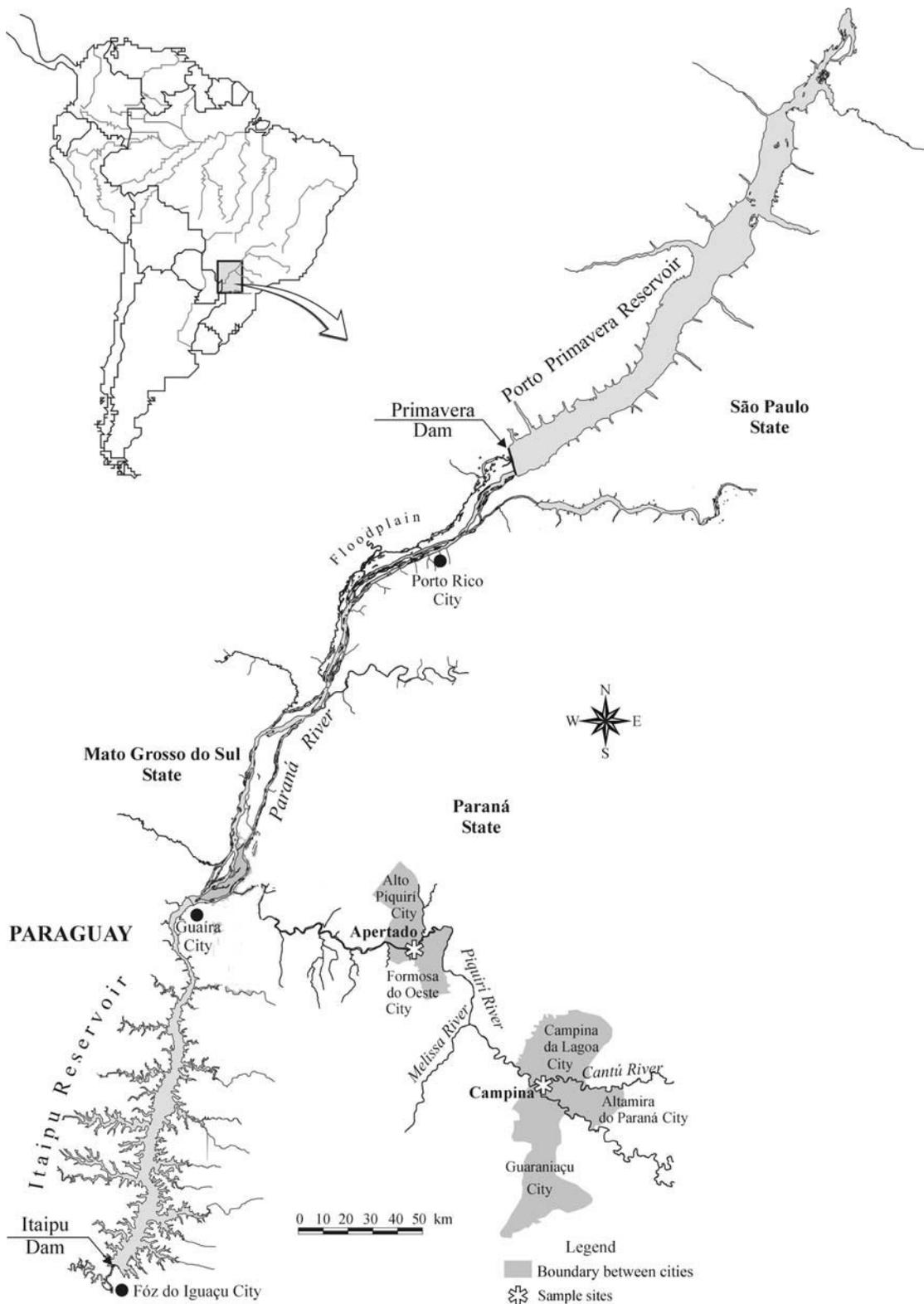


Figure 1. Location of the sampling sites in the Piquiri River basin

small falls and narrow stretches, with difference of more than 1000 m from headwaters to the mouth (Agostinho and Júlio Jr., 1999).

Sampling

Fishes were collected during four periods: period I (from October 1986 to September 1987), period II (from October 1987 to September 1988), period III (from October 1988 to September 1989) and period IV (from October 2002 to September 2003). The 'Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura (Nupélia)' from 'Universidade Estadual de Maringá' collected data in periods I, II and III (before the closure of Porto Primavera Dam). Period IV (after the closure of Porto Primavera Dam) was sampled by the 'Grupo de Pesquisa em Recursos Pesqueiros e Limnologia (Gerpel)' from 'Universidade Estadual do Oeste do Paraná, Campus de Toledo'.

In each period, six samplings (bimonthly) were performed every year at two different sites (Campina and Apertado) in the Piquiri River. The Campina site (24°45'29"S; 52°53'40"W) is located near the mouth of the Cantú River, in the municipalities of Campina da Lagoa, Guaraniçu and Altamira do Paraná (Figure 1). This site presented steep margins covered by bushes and small trees. The riverbed was rocky and its water flow was moderate. The Apertado site (24°13'40"S; 53°20'05"W) is located downstream from Apertado fall (during high waters fish can swim through); between the municipalities of Formosa do Oeste and Alto Piquiri (Figure 1). Its margins were also steep (canyon shaped), with bushes, grasses and trees. Water speed was slow and riverbed was mostly rocky.

Samplings were conducted with gill (mesh sizes of 3, 4, 6, 8, 10, 12 and 14 cm between opposite knots) and trammel (with inner mesh sizes of 6, 7 and 8 cm between opposite knots) nets, all 20 m long (effort was the same in all periods). Nets remained set for 24 h and checked every 8 h. All fish caught were stored in plastic bags and fixed in formalin (10%) for further laboratory analyses. Each individual was measured (total and standard length in cm) and weighted (g).

Environmental variables

Some environmental data for the Piquiri River were supplied by the 'Instituto Ambiental do Paraná' (IAP—Paraná Environmental Institute). A total of 10 variables were used to describe environmental conditions at each site and period (discharge, $\text{m}^3 \text{s}^{-1}$; conductivity, $\mu\text{S cm}^{-1}$; biochemical oxygen demand, $\text{mg L}^{-1}\text{O}_2$; chemical oxygen demand, $\text{mg L}^{-1}\text{O}_2$; total phosphorus—P, mg L^{-1} ; total nitrogen—N, mg L^{-1} ; dissolved oxygen concentration, mg L^{-1} ; pH; water temperature, °C and turbidity, NTU). These data were used to evaluate the association between possible changes in fish assemblage structure to water quality in the Piquiri River, over the studied periods.

Data analysis

We opted to consider periods I, II, III and IV to evaluate the effects of the closure of Itaipu (in 1982) and Porto Primavera (in 1998) dams. Therefore, we assumed that any changes verified along periods I, II and III may be due to the closure of Itaipu, whereas those in period IV may be due to the closure of Porto Primavera and Itaipu.

Patterns in species richness. Species identification followed the classification proposed by Britski *et al.* (1999), Reis *et al.* (2003) and Graça and Pavanelli (2007). Species abundances were expressed as catch per unit of effort (CPUE) in number (individuals. 1000 m^{-2} of net in 24 h) and weight (kg. 1000 m^{-2} of net in 24 h), as proposed by King (1995). Species richness (number of species) was calculated per sample and site (Magurran, 1988).

To determine whether there were differences between the averages of the species richness, two-way ANOVAs (Factor 1: sites; Factor 2: periods and their interaction) were applied. We tested the assumptions of normality and homoscedasticity using the Shapiro-Wilk and Levene tests, respectively. When the interaction of the two-way ANOVA was not significant, Tukey test was applied to determine which level differed. If assumptions of ANOVA were not met, we used the rank transform method (Quinn and Keough, 2002). We transformed data to ranks and then applied the parametric ANOVA model to ranked data (Conover and Iman, 1981), checking the homoscedasticity in the ranked data. If, nevertheless, assumptions of ANOVA were not met, we used bootstrap methods to test differences between the averages (Quinn and Keough, 2002).

Variations in structure of fish assemblages. To summarize the structure of fish assemblages, we applied a nonmetric multidimensional scaling (NMS) (Kruskal, 1964a, b). Sorensen distances were computed and we followed the general NMS procedure outlined by McCune and Grace (2002). We used random starting configurations, the number of runs with the real data was 100 and the stability criterion was standard deviations ≤ 0.005 in stress over 100 iterations. This analysis was performed on the data matrix of CPUE in number (square root transformed to remove the effect of high values) in different months and sampling sites (by sample).

To test the significance of between-group differences at each periods and sites summarized by NMS we used a multiresponse permutation procedure (MRPP), a nonparametric method for testing multivariate differences among predefined groups (Zimmerman *et al.*, 1985). We tested the significance of the null hypothesis that periods and sites were not different with a Monte Carlo randomization procedure with 10 000 permutations.

Indicator value method (IndVal; Duf re and Legendre, 1997) was used to detect how strongly each species discriminated among periods and sites. The indicator value of a species varies from 0 to 100, and it attains its maximum value when all individuals of a species occur at all sites within a single group. We tested the significance of the indicator value for each species with a Monte Carlo randomization procedure with 1000 permutations.

Variations in environmental variables and relationship with fish assemblages. Environmental variables were summarized by principal components analysis (PCA; Pearson, 1901; Hotelling, 1933). As these variables showed strong linear bivariate relationships, PCA was chosen as the most appropriate ordination technique to summarize variation in n dimensions. To determine which principal components would be retained for interpretation we used as criterion the broken-stick model (Jackson, 1993). According to this model, only the axes with eigenvalues greater than the eigenvalues generated under the randomness of the broken-stick model should be interpreted.

The association between multivariate summaries (environmental variables and structure of fish assemblages) was examined using procrustean superimposition approach (Gower, 1971; Goodall, 1991; Jackson, 1995; Peres-Neto and Jackson, 2001). In this analysis, a pair of data matrices is compared using a rotational-fit algorithm that minimizes the sum-of-the-squared residuals between the two matrices (i.e. m^2 statistic; Gower, 1975; Rohlf and Slice, 1990). The resultant m^2 value is a goodness-of-fit statistic that describes the degree of association between the two matrices. To evaluate the significance of m^2 calculated, a permutation procedure (Jackson, 1995) was applied. To ensure relative stability in the estimated P -values, we used 10 000 random permutations (Jackson and Somers, 1989).

Variations in the abundance of the most important species. The 15 most abundant species (abundance: CPUE in number of individuals and weight per 1000 m^2 of nets for 24 h) captured in Period I were represented graphically to describe variations over time. The degree of variation between years was assessed by rank correlation (Spearman; ρ), and high correlations indicate low alteration in the abundance of the 15 most abundant species over time. We opted for this approach to easily identify changes.

Species richness, NMS, MRPP, IndVal and PCA were computed using the *software* PC-Ord[®] 4.0 (McCune and Mefford, 1999). Analysis of variance and rank correlations were performed using the *software* Statistica[™] 7.0. The procrustes statistic was calculated with the *software* PROTEST[®] (Jackson, 1995). The statistical significance level adopted was $p < 0.05$.

RESULTS

Ichthyofauna survey

During the four periods, a total of 2693 individuals were caught, belonging to 69 species, 4 orders and 19 families. The orders registered were Characiformes (34 species), Siluriformes (26 species), Gymnotiformes (five species) and Perciformes (four species). The most common families were Characidae (12 species), Anostomidae (11 species), Loricariidae (10 species) and Pimelodidae (eight species). The greatest number of species was captured in period IV (51 species) and the smallest in period II (25 species) (Table I).

Patterns in species richness

Species richness by sample differed significantly between sites (ANOVA; $F = 6.30$; $p = 0.02$), and there was no significant temporal differences for this descriptor ($F = 2.00$; $p = 0.13$), interaction was not significant ($F = 1.22$;

Table I. List of species registered during the studied periods (period I = from October 1986 to September 1987; period II = from October 1987 to September 1988; period III = from October 1988 to September 1989 and period IV = from October 2002 to September 2003)

	Period			
	I	II	III	IV
Class Actinopterygii				
Superorder Ostariophysi				
Order Characiformes				
Family Acestorhynchidae				
<i>Acestorhynchus lacustris</i> (Lütken, 1875)	x	x	x	x
Family Characidae				
<i>INCERTAE SEDIS</i>				
<i>Astyanax altiparanae</i> Garutti and Britski, 2000	x	x	x	x
<i>Astyanax fasciatus</i> (Cuvier, 1819)	x	x	x	
<i>Astyanax schubarti</i> Britski, 1964			x	
<i>Astyanax</i> sp.	x		x	x
<i>Oligosarcus paranensis</i> Menezes and Géry, 1983		x		
<i>Salminus brasiliensis</i> (Cuvier, 1816)			x	x
Subfamily Bryconinae				
<i>Brycon orbignyana</i> (Valenciennes, 1850)			x	
Subfamily Characinae				
<i>Galeocharax knerii</i> (Steindachner, 1879)	x	x	x	x
<i>Roeboides descavadensis</i> Fowler, 1932				x
Subfamily Serrasalminae				
<i>Myleus tiete</i> (Eigenmann and Noris, 1900)	x	x	x	x
<i>Serrasalmus maculatus</i> (Kner, 1858)	x	x	x	x
<i>Serrasalmus marginatus</i> Valenciennes, 1837				x
Family Anostomidae				
<i>Leporellus vittatus</i> Valenciennes, 1850	x			x
<i>Leporinus amblyrhynchus</i> Garavella and Britski, 1987	x	x	x	
<i>Leporinus elongatus</i> Valenciennes, 1850	x			
<i>Leporinus friderici</i> (Bloch, 1794)		x	x	x
<i>Leporinus obtusidens</i> (Valenciennes, 1836)	x		x	x
<i>Leporinus octofasciatus</i> Steindachner, 1915	x	x	x	x
<i>Leporinus striatus</i> Kner, 1858	x		x	x
<i>Leporinus</i> sp.				x
<i>Schizodon altoparanae</i> Garavella and Britski, 1990				x
<i>Schizodon borellii</i> (Boulenger, 1890)				x
<i>Schizodon nasutus</i> Kner, 1858	x	x	x	
Family Curimatidae				
<i>Cyphocharax modestus</i> (Fernández-Yépez, 1948)	x	x	x	x
<i>Cyphocharax nagelii</i> (Steindachner, 1881)	x	x	x	
<i>Steindachmerina insculpta</i> (Fernández-Yépez, 1948)	x	x	x	x
Family Prochilodontidae				
<i>Prochilodus lineatus</i> (Valenciennes, 1836)	x	x	x	x
Family Erythrinidae				
<i>Hoplias</i> aff. <i>lacerdae</i> Miranda Ribeiro, 1908			x	x
<i>Hoplias</i> aff. <i>malabaricus</i> (Bloch, 1794)	x	x	x	x
Family Parodontidae				
<i>Apareiodon affinis</i> (Steindachner, 1879)	x	x	x	x
<i>Apareiodon piracicabae</i> (Eigenmann, 1907)			x	x
<i>Parodon nasus</i> Kner, 1859			x	x
Family Cynodontidae				
<i>Rhaphiodon vulpinus</i> Spix and Agassiz, 1829				x

(Continues)

Table I. (Continued)

	Period			
	I	II	III	IV
Order Gymnotiformes				
Family Gymnotidae				
<i>Gymnotus</i> aff. <i>inaequilabiatus</i> (Valenciennes, 1839)	x		x	
Family Sternopygidae				
<i>Eigenmannia trilineata</i> López and Castello, 1966			x	
<i>Eigenmannia virescens</i> (Valenciennes, 1836)	x	x		
<i>Sternopygus macrurus</i> (Bloch and Schneider, 1801)	x		x	
Family Apterontidae				
<i>Apterontus</i> aff. <i>albifrons</i> (Linnaeus, 1766)				x
Order Siluriformes				
Family Auchenipteridae				
<i>Ageneiosus inermis</i> (Linnaeus, 1766)				x
<i>Auchenipterus osteomystax</i> (Miranda Ribeiro, 1908)			x	
<i>Parauchenipterus galeatus</i> (Linnaeus, 1766)				x
Family Callichthyidae				
<i>Hoplosternum littorale</i> (Hancock, 1828)				x
Family Cetopsidae				
<i>Cetopsis gobioides</i> Kner, 1858				x
Family Heptapteridae				
<i>Pimelodella</i> sp.				x
<i>Rhamdia quelen</i> (Quoy and Gaimard, 1824)	x	x		x
Family Pimelodidae				
<i>Hypophthalmus edentatus</i> Spix and Agassiz, 1829				x
<i>Iheringichthys labrosus</i> (Lütken, 1874)	x	x	x	x
<i>Pimelodus heraldoi</i> Azpelicueta, 2001	x	x	x	
<i>Pimelodus maculatus</i> La Cèpède, 1803	x	x	x	x
<i>Pimelodus ornatus</i> Kner, 1858				x
<i>Pimelodus</i> sp.				x
<i>Pseudopimelodus mangurus</i> (Valenciennes, 1835)	x			
<i>Pseudoplatystoma corruscans</i> (Spix and Agassiz, 1829)	x		x	
Family Doradidae				
<i>Pterodoras granulatus</i> (Valenciennes, 1821)				x
Family Loricariidae				
Subfamily Ancistrinae				
<i>Megalancistrus parananus</i> (Peters, 1881)		x	x	x
Subfamily Hypostominae				
<i>Hypostomus albopunctatus</i> (Regan, 1908)				x
<i>Hypostomus ancistroides</i> (Ihering, 1911)				x
<i>Hypostomus margaritifer</i> (Regan, 1908)				x
<i>Hypostomus regani</i> (Ihering, 1905)				x
<i>Hypostomus</i> spp.	x	x	x	x
Subfamily Loricariinae				
<i>Loricaria</i> sp.				x
<i>Loricariichthys platymetopon</i> Isbrücker and Nijssen, 1979				x
<i>Loricariichthys rostratus</i> Reis and Pereira, 2000				x
<i>Hisonotus</i> sp.				x
Order Perciformes				
Family Cichlidae				
<i>Crenicichla haroldoi</i> Luengo and Britski, 1974	x		x	
<i>Crenicichla britskii</i> Kullander, 1982	x	x	x	
<i>Crenicichla</i> sp.				x
<i>Oreochromis niloticus</i> (Linnaeus, 1758)				x
Total number of species	32	25	37	51

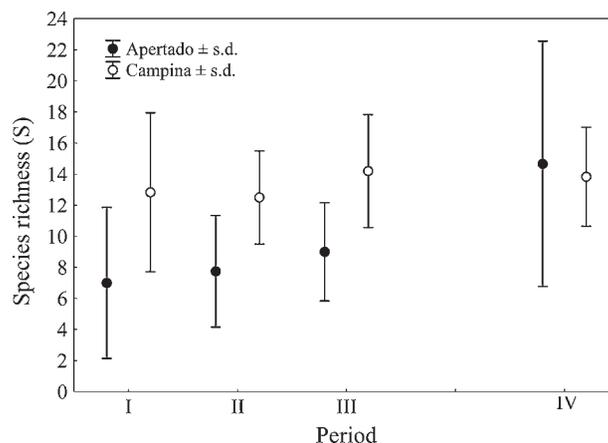


Figure 2. Variations in mean species richness per sampling for Apertado and Campina sites in the Piquiri River, during the four studied periods (I = from October 1986 to September 1987; II = from October 1987 to September 1988; III = from October 1988 to September 1989 and IV = from October 2002 to September 2003) (s.d. = standard deviation)

$p = 0.32$) (Figure 2). Assumptions of ANOVA were met (Shapiro Wilk: $p < 0.05$; Levene: $p < 0.05$). In period IV, the maximum value of species richness by sample was registered in Apertado (26 species) and the average number of species (15) was similar to Campina (14). However, for all periods, species richness was significantly higher in Campina (mean = 13; s.d. = 3.7) than Apertado (mean = 10; s.d. = 6).

Variations in structure of fish assemblages

Nonmetric multidimensional scaling (NMS) summarized structure of the fish assemblages and separated the sites and periods considered in this study (Figures 3A–C). After 44 iterations, the stability criterion was met with a final stress of 14.61 (Monte Carlo test: $p = 0.004$) for 3-dimensional solution. The proportion of variance represented by each axis, based on the r^2 between distance in the ordination space and distance in the original space was 0.43 for axis 1, 0.20 for axis 2 and 0.07 for axis 3, all totalling 0.70.

The location of the points along axis 1 (Figure 3A) identified periods (temporal scale) as the main pattern in the structure of the ichthyofauna and period IV, especially for Apertado (open triangles), differed the most. The spatial and temporal variability were also shown along axis 2. Axis 3 evidenced the spatial variability. Thus, groups were separated by the spatial and temporal scales considered. Campina and Apertado sites were separated along NMS axes 1, 2 or 3 (Figures 3A–C), as well as, period I, II, III and IV were also separated. There were significant differences in the structure of the fish assemblage between sites and periods (MRPP; $p < 0.001$).

For the spatial scale, Campina and Apertado sites were characterized by different sets of indicator species (Table II). Four species, including *Loricariichthys platymetopon* Isbrücker and Nijssen, 1979 and *Loricariichthys rostratus* Reis and Pereira, 2000, were significant indicators for Apertado and 10 species were significant indicators for Campina. For the temporal scale, the IndVal method, only found significant species in period IV, such as, *Apareiodon piracicabae* (Eigenmann, 1907), *Crenicichla* sp., *Hypostomus albopunctatus* (Regan, 1908), *Hoplias* aff. *malabaricus* (Bloch, 1794), *L. platymetopon*, *L. rostratus*, *Leporellus vittatus* (Valenciennes, 1850), *Pimelodus ornatus* Kner, 1858, *Pimelodella* sp., *Roeboides descalvadensis* Fowler, 1932, *Rhaphiodon vulpinus* Spix and Agassiz, 1829, *Schizodon altoparanae* Garavella and Britski, 1990 and *Schizodon borellii* (Boulenger, 1890).

Variations in environmental variables and relationship with fish assemblages

Mean values (\pm standard deviation) of the environmental variables for sites and periods sampled are shown in Table III. Principal components analysis summarized the matrix of environmental variables. Three axes were retained for interpretation (cumulative explained variance = 53.76%; Table IV). These axes (ordinations) were compared with NMS axis (ordinations) that summarized the structure of fish assemblages. The spatial and temporal

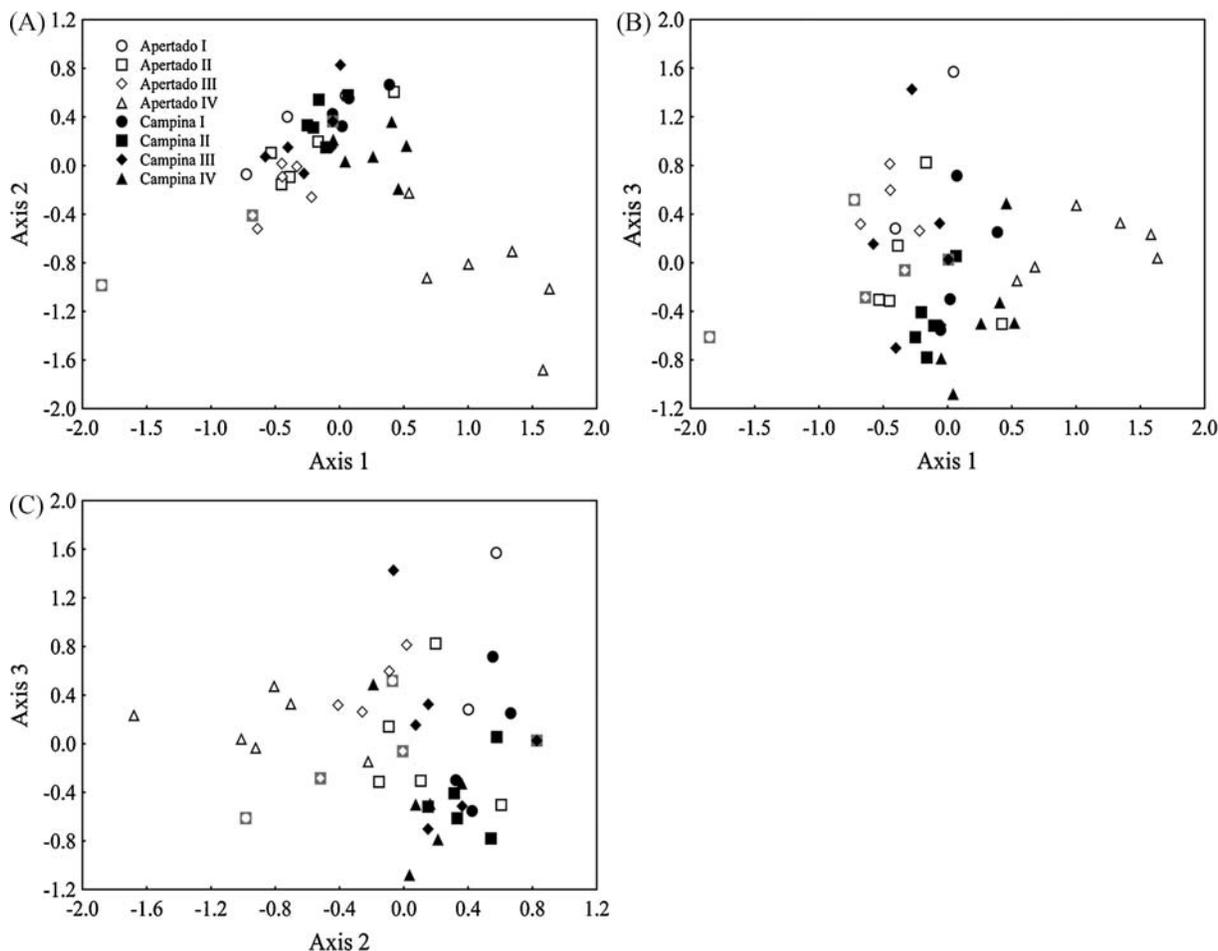


Figure 3. Nonmetric multidimensional scaling (NMS) ordination of fish assemblage at sites Apertado and Campina and periods (I = from October 1986 to September 1987; II = from October 1987 to September 1988; III = from October 1988 to September 1989 and IV = from October 2002 to September 2003). (A) Axis 1 versus Axis 2, (B) Axis 1 versus Axis 3 and (C) Axis 2 versus Axis 3

arrangement of the two sites and four periods on the first three axes, in both ordinations, showed no similarities. The fit of the three spatial and temporal arrangements using PROTEST was smaller than expected at random ($m^2 = 0.931$; $p = 0.218$), confirming, statistically, the lack of correlations between environmental variables and the spatial and temporal arrangements of the structure of fish assemblages for the Piquiri River basin.

Variation in abundance of the most abundant species

For the Apertado, there was a wide variation among periods. In periods I, II and III, small sized species such as *Astyanax altiparanae* Garutti and Britski, 2000, and *Steindachnerina insculpta* (Fernández-Yépez, 1948), presented high abundance. In weight, *Prochilodus lineatus* (Valenciennes, 1836) dominated (Figures 4A–C). However, during period IV, there was a clear change in species abundance. The dominant species in number of individuals and weight was *L. rostratus*, followed by *Leporinus friderici* (Bloch, 1794) (Figure 4D). For this site, relevant changes in abundance were found. The initially abundant species were replaced by species that were absent before. The correlation analyses (Spearman ρ) of the abundance for the 15 most abundant species between the periods, in number as well as in weight, confirmed these results; high positive correlations were found between periods I, II and III (Table V). However, correlations were negative between period IV and I, II and III (Table V), showing high temporal changes in species abundance.

Table II. Summary of the indicator species analysis showing the relative abundances, relative frequencies and indicator values for the sites sampled (Campina and Apertado; only species with significant values). Bold font indicates significant indicator values ($p < 0.05$, Monte Carlo permutation test)

Species	Relative abundances		Relative frequencies		Indicator values	
	Apertado	Campina	Apertado	Campina	Apertado	Campina
<i>A. fasciatus</i>	83	17	52	14	44	2
<i>A. lacustris</i>	6	94	5	90	0	85
<i>Hypostomus</i> sp.	27	73	57	95	16	69
<i>I. labrosus</i>	9	91	38	71	4	65
<i>L. amblyrhynchus</i>	0	100	0	48	0	48
<i>L. friderici</i>	100	0	48	0	48	0
<i>L. osctofasciatus</i>	8	92	5	33	0	31
<i>L. platymetopon</i>	100	0	29	0	29	0
<i>L. rostratus</i>	100	0	29	0	29	0
<i>M. tiete</i>	0	100	0	48	0	48
<i>P. heraldoi</i>	7	93	5	29	0	27
<i>S. insculpta</i>	11	89	57	86	6	76
<i>S. marginatus</i>	5	95	5	52	0	50
<i>S. nasutus</i>	9	91	29	52	3	48

For Campina, *S. insculpta* was the most abundant species in all periods (Figure 5). However, in periods I, II and III, it was followed by *Galeocharax knerii* (Steindachner, 1879), *Acestrorhynchus lacustris* (Lütken, 1875) and *A. altiparanae* (Figures 5A–C), whereas in period IV it was followed by *Iheringichthys labrosus* (Lütken, 1874) (Figure 5D). There were significant correlations for CPUE in number among periods for the 15 most abundant species (Table V), but correlations decreased overtime, mainly in relation to the first period. The abundance in weight for Campina in periods I, II and III followed the same tendency shown in Apertado, with high catch of *P. lineatus* (Figure 5B). However, in period IV, changes in weight of the fish assemblage in Campina were relevant. *Iheringichthys labrosus* was the most abundant species. The correlation analysis corroborated these results; high significant correlations were found between periods I, II and III. However, we found weak correlation between these periods and period IV (Table V).

DISCUSSION

The species number registered in the two sampled stations at the Piquiri River (69) was higher than that found in previous studies. Gubiani *et al.* (2006) registered 62 species in three sampling sites in this river. Agostinho *et al.* (1997, 2004b) reported 57 species and these authors highlighted the absence, in the Piquiri River, of some widely distributed species in the upper Paraná River basin, such as *Parauchenipterus galeatus* (Linnaeus, 1766), *Plagioscion squamosissimus* (Heckel, 1840), *R. vulpinus*, the genera *Loricaria*, *Loricariichthys* and *Roeboides* and the families Doradidae and Ageneiosidae (nowadays Auchenipteridae). Now, with the exception of *P. squamosissimus*, all the above species and groups were caught in the Piquiri River, which might lead to similarities in species richness between the sites in period IV. When compared to other rivers from the Paraná River basin, the identified number of species is similar to the Iguatemi River (77 species), lower than the Ivinheima River (91) (Agostinho *et al.*, 1997, 2004b) and the Tibagi River (110) (Shibatta *et al.*, 2002) but higher than the Iguacu River (52) (Garavello *et al.*, 1997). Some of the species registered in the Piquiri River reached the upper Paraná after the filling of Itaipu Reservoir, which inundated the barrier (Sete Quedas waterfalls) that separated the Lower and the High Paraná River (Bonetto, 1986). These species are *Roeboides descavadensis*, *Serrasalmus marginatus* Valenciennes, 1837, *Schizodon borellii*, *Eigenmannia trilineata* López and Castello, 1966, *Ageneiosus inermis* (Linnaeus, 1766), *Parauchenipterus galeatus*, *Hypophthalmus edentatus* Spix and Agassiz, 1829, *Pimelodus*

Table III. Summary of the environmental variables (Mean \pm SD) for sites during the study period in the Piquiri River (BOD: biochemical oxygen demand; COD: chemical oxygen demand) (I—from October 1986 to September 1987; II—from October 1987 to September 1988; III—from October 1988 to September 1989 and IV—from October 2002 to September 2003)

Sites variables/periods	Apertado				Campina			
	I	II	III	IV	I	II	III	IV
Discharge ($\text{m}^3 \text{s}^{-1}$)	262.25 \pm 86.79	310.46 \pm 148.00	359.41 \pm 255.79	399.34 \pm 296.08	85.71 \pm 104.19	61.08 \pm 47.35	50.38 \pm 46.18	46.84 \pm 23.20
Conductivity ($\mu\text{S cm}^{-1}$)	75.92 \pm 75.51	45.87 \pm 4.13	42.70 \pm 1.20	46.75 \pm 2.52	51.86 \pm 3.87	60.19 \pm 16.38	47.96 \pm 4.33	60.95 \pm 2.08
BOD ($\text{mg L}^{-1} \text{O}_2$)	0.97 \pm 0.04	0.95 \pm 0.06	1.17 \pm 0.47	1.60 \pm 0.46	0.97 \pm 0.03	1.07 \pm 0.22	1.20 \pm 0.45	1.04 \pm 0.64
COD ($\text{mg L}^{-1} \text{O}_2$)	3.34 \pm 3.27	6.12 \pm 0.63	5.50 \pm 4.64	8.20 \pm 5.83	2.82 \pm 2.23	4.38 \pm 2.29	3.90 \pm 2.61	3.55 \pm 2.82
Total phosphorus ($\text{mg L}^{-1} \text{P}$)	0.14 \pm 0.14	0.15 \pm 0.20	0.03 \pm 0.01	0.04 \pm 0.04	0.07 \pm 0.10	0.03 \pm 0.02	0.03 \pm 0.02	0.04 \pm 0.04
Total nitrogen ($\text{mg L}^{-1} \text{N}$)	0.47 \pm 0.24	0.44 \pm 0.15	0.35 \pm 0.11	0.20 \pm 0.11	0.21 \pm 0.19	0.41 \pm 0.33	0.45 \pm 0.23	0.36 \pm 0.27
Dissolved oxygen (mg L^{-1})	8.32 \pm 0.86	8.72 \pm 0.98	10.17 \pm 1.13	8.84 \pm 1.43	7.50 \pm 0.29	7.88 \pm 2.78	9.84 \pm 2.56	7.45 \pm 3.74
pH	7.18 \pm 0.21	7.30 \pm 0.22	7.14 \pm 0.55	7.11 \pm 0.27	7.77 \pm 0.31	7.39 \pm 3.05	7.34 \pm 0.36	7.14 \pm 0.35
Water temperature ($^{\circ}\text{C}$)	24.25 \pm 2.72	19.50 \pm 5.45	19.10 \pm 3.97	22.78 \pm 3.60	24.17 \pm 1.33	26.66 \pm 7.06	19.50 \pm 4.45	22.24 \pm 3.92
Turbidity (NTU)	39.83 \pm 6.40	35.63 \pm 4.53	18.75 \pm 13.19	19.38 \pm 14.90	29.96 \pm 11.50	43.56 \pm 29.78	30.31 \pm 25.48	24.59 \pm 23.33

Table IV. Results of principal component analysis (PCA). It is given, for each axis, the eigenvalues, the percent of variance explained and the broken-stick eigenvalues. For each variable is listed the eigenvector (loading or correlation) (BOD: biochemical oxygen demand; COD: chemical oxygen demand)

	Axis 1	Axis 2	Axis 3
Eigenvalues	2.285	1.681	1.410
Broken-stick eigenvalues	2.929	1.929	1.429
% of variance	22.847	16.808	14.104
Discharge	0.004	-0.380	0.131
Conductivity	-0.471	0.076	-0.087
BOD	-0.098	-0.487	-0.302
COD	-0.218	-0.523	-0.267
Total phosphorus	-0.300	-0.131	0.004
Total nitrogen	-0.456	0.042	-0.040
Dissolved oxygen	-0.041	-0.351	0.685
pH	-0.318	0.143	0.562
Water temperature	-0.339	0.417	-0.165
Turbidity	-0.454	-0.061	-0.011

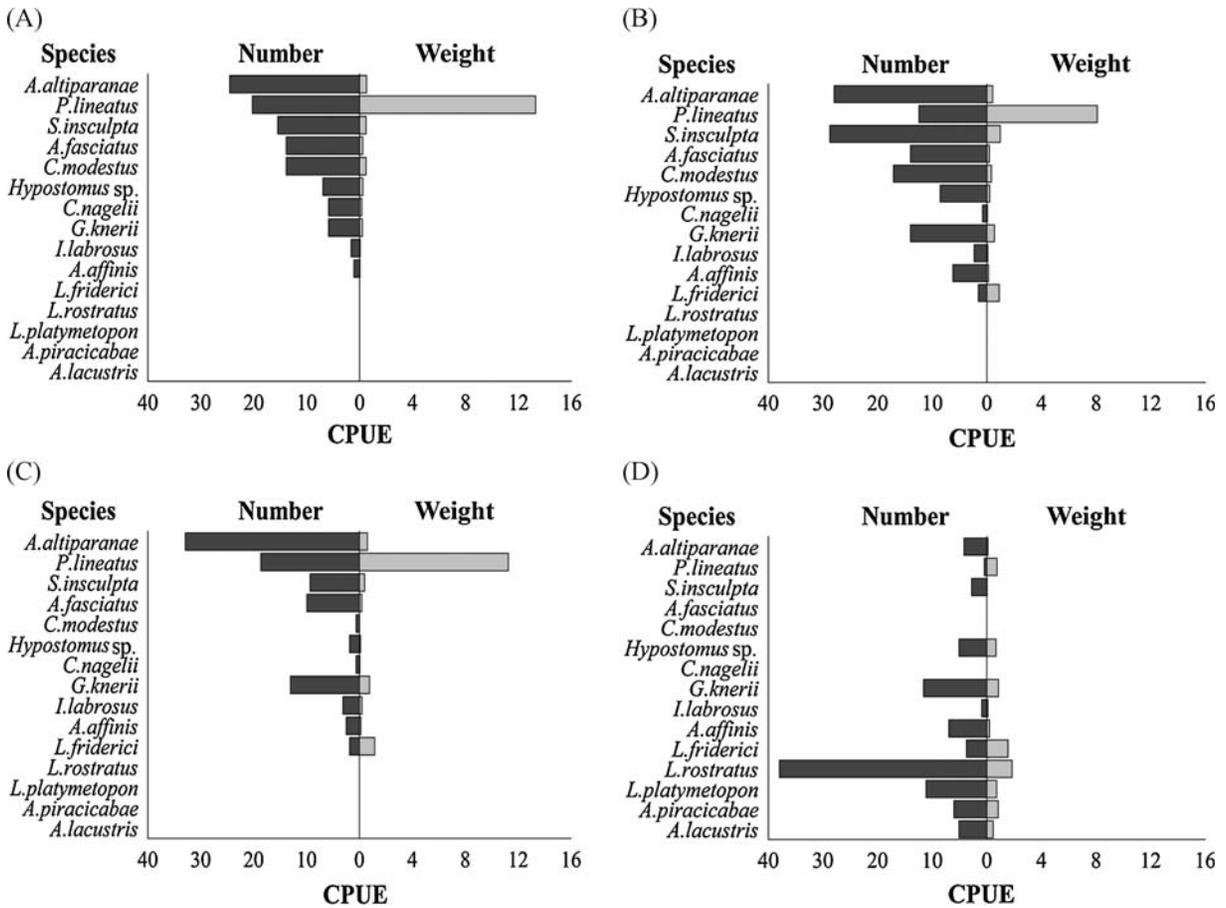


Figure 4. Catch per unit of effort (CPUE) in number (individuals. 1000 m⁻² nets in 24 h) and weight (kg. 1000 m⁻² nets in 24 h) for the 15 most abundant species captured in Period I (A; from October 1986 to September 1987) in Apertado. The same species are shown for period II (B; from October 1987 to September 1988), period III (C; from October 1988 to September 1989) and period IV (D; from October 2002 to September 2003) in the Piquiri River

Table V. Spearman rank correlations between abundances (CPUE in number—individuals. 1000 m⁻² of nets in 24 h—in bold; and CPUE in weight—kg. 1000 m⁻² of nets in 24 h—in italic) of the 15 most abundant species in each sampling site in the different periods (period I—from October 1986 to September 1987; period II—from October 1987 to September 1988; period III—from October 1988 to September 1989; and period IV—from October 2002 to September 2003)

Sites	Periods				
Apertado	I		II	III	IV
			0.89*	0.76*	-0.60*
	II	<i>0.74*</i>		0.81*	-0.47
	III	<i>0.56*</i>	<i>0.90*</i>		-0.32
	IV	<i>-0.66*</i>	<i>-0.29</i>	<i>-0.18</i>	
Campina	I		II	III	IV
			0.89*	0.81*	0.59*
	II	<i>0.95*</i>		0.85*	0.56*
	III	<i>0.85*</i>	<i>0.83*</i>		0.63*
	IV	<i>0.08</i>	<i>0.09</i>	<i>-0.01</i>	

*Significant correlations.

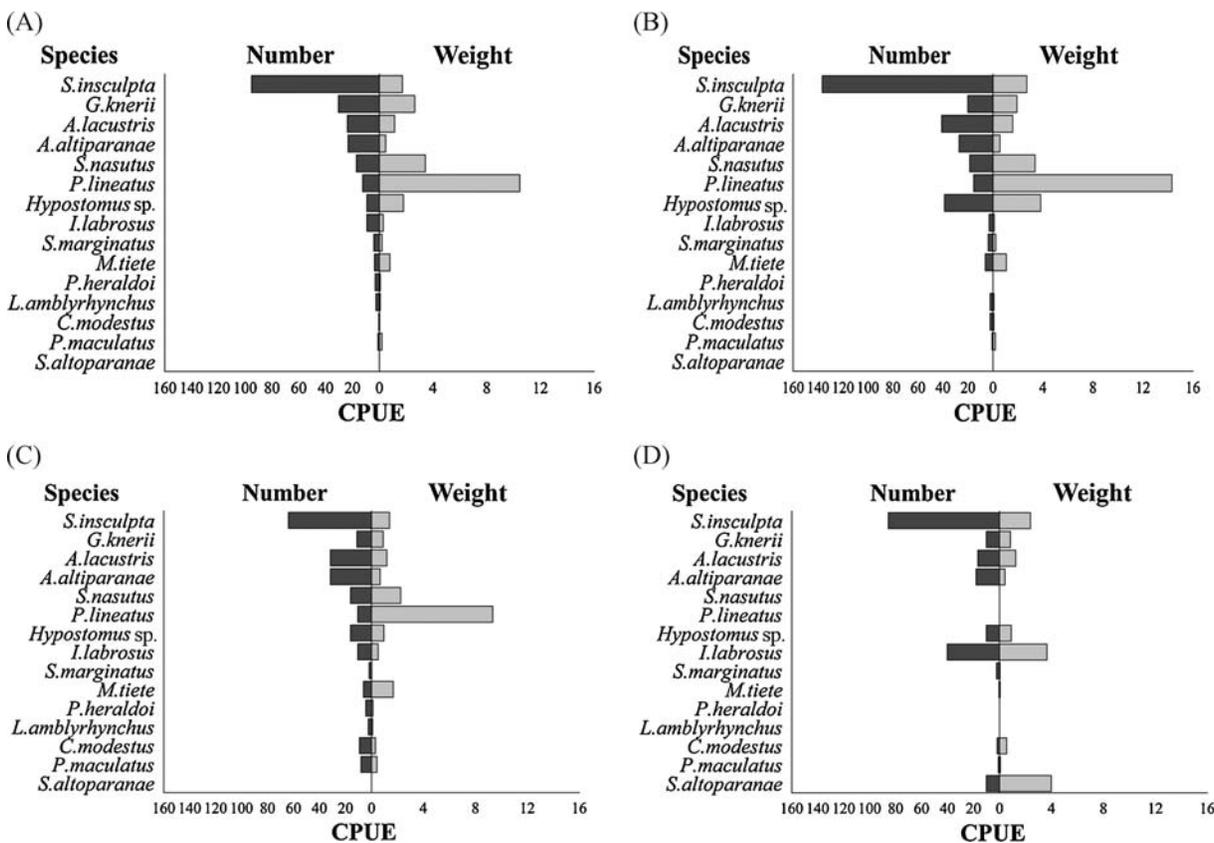


Figure 5. Catch per unit of effort (CPUE) in number (individuals. 1000 m⁻² nets in 24 h) and weight (kg. 1000 m⁻² nets in 24 h) for the 15 most abundant species captured in Period I (A; from October 1986 to September 1987) in Campina. The same species are shown for period II (B; from October 1987 to September 1988), period III (C; from October 1988 to September 1989) and period IV (D; from October 2002 to September 2003) in the Piquiri River

ornatus, *Pterodoras granulosus* (Valenciennes, 1821), *Loricariichthys platymetopon*, *Loricariichthys rostratus* and *Oreochromis niloticus* (Linnaeus, 1758) (Agostinho *et al.*, 1994).

The role of biogeographic barriers, such as waterfalls, in isolating freshwater fish fauna is thoroughly recognized (Rahel, 2007; Han *et al.*, 2008). Human activities, as construction of dams, have provided the invasion of non-native fish species and have led to decline of native fish populations, and the understood biotic homogenization, that refers to the increased similarity of biota over time (Mckinney and Lockwood, 1999; Rahel, 2007; Han *et al.*, 2008). This is corroborated in this study. Fish species introduced in the upper Paraná River are colonizing tributaries and are replacing native fish.

The Paraná River basin presents several dams, especially in main river channels, which affect in several ways the structure of the ichthyofauna (locally and regionally). Reservoirs lead to complex environmental responses in the aquatic environment, physical, chemical and biological, and these alterations can drastically affect structure of assemblages (Agostinho *et al.*, 1992; Benedito-Cecilio *et al.*, 1997; Agostinho *et al.*, 2004c,d). In general, within the reservoir, it is verified decrease in species numbers, especially large sized migratory species, which are replaced by small sized and opportunist species (Winemiller, 1989; Agostinho *et al.*, 2003, 2004c,d, 2007). For example, Agostinho *et al.* (1994) described that large sized migratory species, such as pacu (*Piaractus mesopotamicus* (Holmberg, 1887)) and piracanjuba (*Brycon orbignyanus* (Valenciennes, 1850)), formerly abundant upstream from the Itaipu Dam, apparently disappeared from the Itaipu Reservoir few years after its formation. In addition, Gomes and Agostinho (1997) report that anthropogenic actions that interfere on water level, such as operation of dams, in the case located downstream from Porto Primavera, may determine failures in recruitment, altering abundance in later years. These affirmations are conspicuous in rivers that present dams. However, in the upper Paraná River dams seemed to affect the ichthyofauna regionally, especially long distance migratory species. For example, in the Piquiri River there are no reservoirs, but the ichthyofauna changed drastically over time and this may be due to the regional effect of dam construction in the Paraná basin, especially for *P. lineatus* (long distance migratory species) and Loricariids which became abundant after the drowning of Sete Quedas waterfalls by the Itaipu Reservoir.

The abundance of *P. lineatus* in the Piquiri River seriously decreased in recent years. It is no longer among the 15 most abundant species, as observed in other areas of the upper Paraná River (Gomes and Agostinho, 1997; Agostinho *et al.*, 2000), and this is apparently due to the construction of dams, as noted by Agostinho *et al.* (2004a). Benedito-Cecilio *et al.* (1997) affirm that *P. lineatus* was moderately abundant in the first years after the formation of the Itaipu Reservoir. Gubiani *et al.* (2007) demonstrated that the absence of floods may reduce the persistence of this species to dangerous levels. These authors studied the upper Paraná River floodplain, considered a nursery area for migratory species. Then, the absence of floods in several years (needed to trigger *P. lineatus* spawning) leads to failure in recruitment, which, along time, reflected on the abundance of the species over the entire area, including the Piquiri River. Moreover, Sanches *et al.* (2006), studying flow regulation by dams affecting ichthyoplankton in the Paraná River, showed that after the closure of the Porto Primavera Dam, larvae of commercially important migratory species were absent in the main channel of the Paraná River and some tributaries, except the Ivinheima River.

In the Piquiri River, to evaluate the temporal patterns in fish species abundance, two sites (Campina and Apertado) were analysed separately. Spearman correlations, for the Campina site, between the I period and the other consecutive periods, shown that the most recent fish assemblage structure differed from the earliest sampled periods. This pattern was clear for Apertado. Thus, the remarkable changes in the assemblage in the Apertado may be related to the hydrologic alterations caused by the dam constructed in the Paraná River main channel, as demonstrated by Agostinho *et al.* (2000, 2003). These authors report that the hydrometric level regulation by dams upstream and downstream of the Paraná River floodplain has led to changes in the fish fauna of this river, but not in the tributaries.

Longitudinal gradients in large and un-dammed rivers are expected to show some variation in fauna and functioning, but they can be thought as a continuum (Vannote *et al.*, 1980) with increase in species richness and abundance from upstream to downstream (Matthews, 1998). Oliveira *et al.* (2003, 2005), studying spatial gradients in fish assemblages in the Itaipu Reservoir and its tributaries, showed that in lotic stretches of the tributaries was found the lowest values for total relative abundance. Moreover, in the lentic stretches, they verified the highest total relative abundance, with strong dominance of *Loricariichthys rostratus*.

Loricariichthys rostratus and *L. platymetopon* used occurring only downstream Sete Quedas Falls, as cited above. According to Agostinho *et al.* (1997), these species prefer lotic and semilotic environments, directly associated

with their feeding habits, thus, in this study, this species was dominant in the Apertado site (rapids near to Paraná River) in period IV. This scenario, also observed by Oliveira *et al.* (2003, 2005) for tributaries of the Itaipu Reservoir, associated with changes in abundance of *P. lineatus* in recent years, were the main factors explaining the alterations in abundance of the 15 most abundant species in this study.

According to Petry *et al.* (2003), the upper Paraná River floodplain failed to experience a continuous flood in 2000 because the lack of rain and the severe flow regulation promoted by dams upstream. Gubiani *et al.* (2007) showed that during 1999–2002, pronounced floods were absent in the upper Paraná River floodplain. Alterations in the hydrologic regime may have influenced the Piquiri River local fish assemblage dynamics, mainly migratory species, that need environmental stimuli (rain and floods) to trigger migration and spawning (Vazzoler, 1996). This hypothesis is strengthened due to the absence of relation between fish assemblage and selected environmental variables of the Piquiri River. The role of abiotic factors in structuring fish assemblages is thoroughly recognized (Sheldon, 1968; Gorman and Karr, 1978; Schlosser, 1982; Balon *et al.*, 1986; Rahel and Hubert, 1991; Belliard *et al.*, 1997; Matthews, 1998; Jackson *et al.*, 2001; Oberdorff *et al.*, 2001). In addition to the abiotic factors, several other factors may influence in the structuring of fish assemblages, but it is clear that regional processes (construction of dams) played an important role promoting spatial and temporal variations in fish assemblages. Therefore, it is difficult to affirm that only the dams constructed in the Paraná River affected the composition and structure of the Piquiri River fish assemblage. But, as reported herein, it is a factor that should be evaluated in detail in this river and in other tributaries as well. In addition, large rivers pose many logistic challenges to study fish assemblages, as well as, their responses to both natural and human induced changes. Long-term data, such as those that have been presented here, can provide insights on changes in fish assemblage and are adequate to subsidize management actions.

In conclusion, it appears that dam construction, besides modifying the hydrograph, causes strong impacts over the ichthyofauna when fish assemblages are merged, such as the case of the Itaipu Reservoir, that connected the Lower to the High Paraná, introducing species previously restricted to downstream of Sete Quedas waterfalls. In addition, migratory species, which need to migrate to complete their spawning, were the most affected by dams. The occurrence of free stretches upstream reservoirs could minimize the impact over the migratory species. However, it seems that this failed to happen at the free stretch between the Itaipu Reservoir and the Porto Primavera Dam in the upper Paraná River, mainly due to the flow regulation promoted by them, as asserted by Gubiani *et al.* (2007) and by the results of this study. The abundance and persistence of migratory species, mainly *P. lineatus*, has strongly decreased during recent years in this area. Thus, impacts caused by reservoirs located downstream and upstream of spawning and nursery areas and tributaries, exacerbated by weather variations appear to be stronger than previously reported and need to be better evaluated.

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REFERENCES

- Aarts BGW, Van Den Brink FWB, Nienhuis PH. 2004. Habitat loss as the main cause of the slow recovery of fish faunas of regulated large rivers in Europe: the transversal floodplain gradient. *River Research and Applications* **20**: 3–21. DOI: 10.1002/rra.720
- Agostinho AA, Júlio HF Jr. 1999. Peixes da bacia do alto rio Paraná. In *Ecologia de comunidades de peixes tropicais*, Lowe-McConnell RH (ed.). EDUSP: São Paulo; 374–400.
- Agostinho AA, Zalewski M. 1996. *A planície alagável do alto rio Paraná: Importância e preservação*. EDUEM: Maringá.
- Agostinho AA, Júlio HF Jr, Borghetti JR. 1992. Considerações sobre os impactos dos represamentos na ictiofauna e medidas para sua atenuação. Um estudo de caso: Reservatório de Itaipu. *Revista Unimar* **14**: 89–107.

- Agostinho AA, Vazzoler AEA, de M, Gomes LC, Okada EK. 1993. Estratificación espacial y comportamiento de *Prochilodus scrofa* em distintas fases del ciclo de vida, en la planicie de inundación del alto rio Paraná y embalse de Itaipu, Paraná, Brasil. *Revue D'Hydrobiologie Tropicale* **26**: 79–90.
- Agostinho AA, Borghetti JR, Vazzoler AEAdEM, Gomes LC. 1994. Itaipu reservoir: impacts on the ichthyofauna and biological bases for its management. *Annual International Workshop on Regional Approaches to Reservoir Development and Management in the La Plata River Basin: Focus on Environmental Aspects*, pp. 1–2, 08/05–16/1991. UNCRD/ILEC/UNEP: São Carlos, Foz do Iguaçu/Brazil and Iacretá/Argentina.
- Agostinho AA, Júlio HF Jr, Gomes LC, Bini LM, Agostinho CS. 1997. Composição, abundância e distribuição espaço-temporal da ictiofauna. In *A Planície de Inundação do Alto Rio Paraná*, Vazzoler AEA de M, Agostinho AA, Hahn NS (eds). EDUEM: Maring; 179–208.
- Agostinho AA, Miranda LE, Bini LM, Gomes LC, Thomaz SM, Suzuki HI. 1999. Patterns of colonization in neotropical reservoirs, and prognoses on aging. In *Theoretical Reservoir Ecology and its Applications*, Tundisi JG, Straskraba M (eds). International Institute of Ecology: São Carlos; The Netherlands Backhuys Publishers: Leiden; Brazilian Academy of Sciences: Rio de Janeiro; 227–265.
- Agostinho AA, Thomaz SM, Minte-Vera CV, Winemiller KO. 2000. Biodiversity in the high Paraná River floodplain. In *Biodiversity in Wetlands: Assessment, Function and Conservation*, Gopal B, Junk WJ, Davis JA (eds). The Netherlands Backhuys Publishers: Leiden; 89–118.
- Agostinho AA, Gomes LC, Suzuki HI, Júlio HF Jr. 2003. Migratory fish from the upper Paraná River basin, Brazil. In *Migratory Fishes of South America: Biology, Social Importance and Conservation Status*, Carolsfeld J, Harvey B, Ross C, Baer A, Ross C (eds). World Fisheries Trust, the World Bank and the International Development Research Centre: Victoria; 19–99.
- Agostinho AA, Rodrigues L, Gomes LC, Thomaz SM, Miranda LE. 2004a. *Structure and Functioning of the Paraná River and Its floodplain: LTER—Site 6—(PELD—Sítio 6)*. EDUEM: Maring.
- Agostinho AA, Bini LM, Gomes LC, Júlio HF Jr, Pavanelli CS, Agostinho CS. 2004b. Fish assemblages. In *The Upper Paraná River and its Floodplain: Physical Aspects, Ecology and Conservation*, Thomaz SM, Agostinho AA, Hahn NS (eds). The Netherlands Backhuys Publishers: Leiden; 223–246.
- Agostinho AA, Thomaz SM, Gomes LC. 2004c. Threats for biodiversity in the floodplain of the Upper Paraná River: effects of hydrological regulation by dams. *Ecohydrology & Hydrobiology* **4**: 267–280.
- Agostinho AA, Gomes LC, Veríssimo S, Okada EK. 2004d. Flood regime, dam regulation and fish in the Upper Paraná River: effects on assemblage attributes, reproduction and recruitment. *Reviews in Fish Biology and Fisheries* **14**: 11–19. DOI: 10.1007/s11160-004-3551-y
- Agostinho AA, Thomaz SM, Gomes LC. 2005. Conservation of the biodiversity of Brazil's inland waters. *Conservation Biology* **19**: 1–7. DOI: 10.1111/j.1523-1739.2005.00701.x
- Agostinho AA, Gomes LC, Pelicice FM. 2007. *Ecologia e manejo de recursos pesqueiros em reservatórios do Brasil*. EDUEM: Maring.
- Balon EK, Crawford SS, Lelek A. 1986. Fish communities of the upper Danube River (Germany, Austria) prior to the new Rhein-Main-Donau connection. *Environmental Biology of Fishes* **15**: 243–271.
- Barbosa FAR, Padišák J, Espíndola ELG, Borics G, Rocha O. 1999. The cascading reservoir continuum concept (CRCC) and its application to the River Tiête basin, São Paulo State, Brazil. In *Theoretical Reservoir Ecology and Its Applications*, Tundisi JG, Straskraba M (eds). International Institute of Ecology: São Carlos; C Brazilian Academy of Sciences: Rio de Janeiro, Backhuys Publishers: Leiden; 425–437.
- Baumgartner G, Nakatani K, Gomes LC, Bialetzki A, Sanches PV, Makrakis MC. 2004. Identification of spawning sites and natural nurseries of fishes in the upper Paraná River, Brazil. *Environmental Biology of Fishes* **71**: 115–125. DOI: 10.1007/s10641-004-0098-z
- Belliard J, Boët P, Tales E. 1997. Regional and longitudinal patterns of fish community structure in the Seine River basin, France. *Environmental Biology of Fishes* **50**: 133–147. DOI: 10.1023/A:1007353527126
- Benedito-Cecilio E, Agostinho AA, Júlio HF Jr, Pavanelli CS. 1997. Colonização ictiofaunística do reservatório de Itaipu e áreas adjacentes. *Revista Brasileira de Zoologia* **14**: 1–14.
- Bonetto AA. 1986. The Paraná river system. In *The Ecology of River Systems*, Davies BR, Walker KF (eds). W. Junk Publishers: Dordrecht; 541–555.
- Britski HA, Silimon KS, Lopes BS. 1999. *Peixes do Pantanal: Manual de identificação*. Embrapa: Brasília.
- Conover WJ, Iman RL. 1981. Rank transform as a bridge between parametric and nonparametric statistics. *American Statistics* **35**: 124–133.
- Corbacho C, Sanchez JM. 2001. Patterns of species richness and introduced species in native freshwater fish faunas of a mediterranean-type basin: the Guadiana River (southwest Iberian Peninsula). *Regulated Rivers: Research and Management* **17**: 699–707. DOI: 10.1002/rrr.631
- Dufrêne M, Legendre P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* **67**: 345–366.
- Edwards RJ. 1978. The effect of hypolimnion reservoir releases on fish distribution and species diversity. *Transactions of the American Fisheries Society* **107**: 71–77.
- Galat DL, Lipkin R. 2000. Restoring ecological integrity of great rivers: historical hydrographs aid in defining reference conditions for the Missouri River. *Hydrobiologia* **422/423**: 29–48. DOI: 10.1023/A:1017052319056
- Garavello JC, Pavanelli CS, Suzuki HI. 1997. Caracterização da ictiofauna do rio Iguaçu. In *Reservatório de Segredo: bases ecológicas para o manejo*, Agostinho AA, Gomes LC (eds). EDUEM: Maringá. 61–84.
- Gehrke PC, Brown P, Schiller CB, Moffatt DB, Bruce AM. 1995. River regulation and fish communities in the Murray-Darling River System, Australia. *Regulated Rivers: Research and Management* **11**: 363–375.

- Godinho HP, Godinho AL. 1994. Ecology and conservation of fish in southeastern Brazilian river basins submitted to hydroelectric impoundments. *Acta Limnologica Brasiliensia* **5**: 187–197.
- Gomes LC, Agostinho AA. 1997. Influence of the flooding regime on the nutritional state and juvenile recruitment of the curimba, *Prochilodus scrofa*, Steindachner, in upper Paraná River, Brazil. *Fisheries Management and Ecology* **4**: 263–274.
- Goodall C. 1991. Procrustes methods in the statistical analysis of shape. *Journal of the Royal Statistical Society B* **53**: 285–339.
- Gorman OT, Karr JR. 1978. Habitat structure and stream fish communities. *Ecology* **59**: 507–515.
- Gower JC. 1971. A general coefficient of similarity and some of its properties. *Biometrics* **27**: 857–871.
- Gower JC. 1975. Generalized procrustes analysis. *Psychometrika* **40**: 33–51.
- Graça WJ, Pavanelli CS. 2007. *Peixes da planície de inundação do alto Rio Paraná e áreas adjacentes*. EDUEM: Maringá.
- Gubiani EA, Holzbach AJ, Baumgartner G, Rezende Neto LB, Bergmann F. 2006. Fish, Piquiri River, Upper Paraná River basin, Paraná state, Brazil. *Check List* **2**: 9–14.
- Gubiani EA, Gomes LC, Agostinho AA, Okada EK. 2007. Persistence of fish populations in the upper Paraná River: effects of water regulation by dams. *Ecology of Freshwater Fish* **16**: 191–197. DOI: 10.1111/j.1600-0633.2006.00211.x
- Han M, Fukushima M, Fukushima T. 2008. A spatial linkage between dams and non-native fish species in Hokkaido, Japan. *Ecology of Freshwater Fish* **17**: 416–424. DOI: 10.1111/j.1600-0633.2008.00294.x
- Hirzinger V, Keckeis H, Nemeschkal HL, Schiemer F. 2004. The importance of inshore areas for adult fish distribution along a free-flowing section of the Danube, Austria. *River Research and Applications* **20**: 137–149. DOI: 10.1002/rra.739
- Hoffmann AC, Orsi ML, Shibatta OA. 2005. Diversidade de peixes do reservatório da UHE Escola Engenharia Mackenzie (Capivara), Rio Paranapanema, bacia do alto rio Paraná, Brasil, e a importância dos grandes tributários na sua manutenção. *Iheringia Serie Zoologia* **95**: 319–325.
- Holden PB, Stalnaker CB. 1975. Distribution and abundance of mainstream fishes of the middle and upper Colorado River basins, 1967–1973. *Transactions of the American Fisheries Society* **104**: 217–231.
- Hotelling H. 1933. Analysis of a complex of statistical variables into principal components. *Journal of Experimental Psychology* **24**: 417–441.
- Jackson DA. 1993. Stopping rules in principal components analyses: a comparison of heuristic and statistical approaches. *Ecology* **74**: 2204–2214.
- Jackson DA. 1995. Protest: a procrustean randomization test of community environment concordance. *Ecoscience* **2**: 297–303.
- Jackson DA, Somers KM. 1989. Are probability estimates from the permutation model of Mantel's test stable? *Canadian Journal of Zoology* **67**: 766–769.
- Jackson DA, Peres-Neto PR, Olden JD. 2001. What controls who is where in freshwater fish communities—the roles of biotic, abiotic, and spatial factors. *Canadian Journal of Fisheries and Aquatic Sciences* **58**: 157–170. DOI: 10.1139-cjfas-58-1-157
- King M. 1995. *Fisheries Biology, Assessment and Management*. Fishing News Books: Oxford.
- Koel TM. 2004. Spatial variation in fish species richness of the Upper Mississippi River System. *Transactions of the American Fisheries Society* **133**: 984–1003.
- Kruskal JB. 1964a. Multidimensional scaling by optimizing goodness of fit to a nonmetric hypotheses. *Psychometrika* **29**: 1–27.
- Kruskal JB. 1964b. Nonmetric multidimensional scaling: a numerical method. *Psychometrika* **29**: 115–129.
- Lytle DA, Poff NL. 2004. Adaptation to natural flow regimes. *Trends in Ecology and Evolution* **19**: 94–100. DOI:10.1016/j.tree.2003.10.002
- Magurran AE. 1988. *Ecological Diversity and Its Measurement*. Croom Helm: London.
- Matthews WJ. 1998. *Patterns in Freshwater Fish Ecology*. Chapman and Hall: New York.
- McCune B, Grace JB. 2002. *Analysis of Ecological Communities*. Glenden Beach, Oregon.
- McCune B, Mefford MJ. 1999. *PC-ORD: Multivariate Analysis of Ecological Data (Version 4)*. MJM Software Design, Glenden Beach, Oregon.
- McKinney ML, Lockwood JL. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology and Evolution* **14**: 450–453.
- Merona B, Albert P. 1999. Ecological monitoring of fish assemblages downstream of a hydroelectric dam in French Guiana (South America). *Regulated Rivers: Research and Management* **15**: 339–351.
- Morita K, Yamamoto S. 2002. Effects of habitat fragmentation by damming on the persistence of stream-dwelling char populations. *Conservation Biology* **16**: 1318–1323. DOI: 10.1046/j.1523-1739.2002.01476.x
- Nilsson C, Berggren K. 2000. Alterations of riparian ecosystems caused by river regulation. *Bioscience* **50**: 783–792.
- Oberdorff T, Pont D, Hugueny B, Chessel D. 2001. A probabilistic model characterizing riverine fish communities of French rivers: a framework for environmental assessment. *Freshwater Biology* **46**: 399–415.
- Okada EK, Agostinho AA, Petrere M Jr, Penczak T. 2003. Factors affecting fish diversity and abundance in drying ponds and lagoons in the upper Paraná River basin, Brazil. *Ecology & Hydrobiology* **3**: 97–110.
- Oliveira EF de, Goulart E, Minte-Vera CV. 2003. Patterns of dominance and rarity of fish assemblage along spatial gradients in the Itaipu Reservoir, Paraná, Brazil. *Acta Scientiarum: Biological Sciences* **25**: 71–78.
- Oliveira EF de, Goulart E, Minte-Vera CV. 2004. Fish diversity along spatial gradients in the Itaipu Reservoir, Paraná, Brazil. *Brazilian Journal of Biology* **64**: 447–458.
- Oliveira EF de, Minte-Vera CV, Goulart E. 2005. Structure of fish assemblages along spatial gradients in a deep subtropical reservoir (Itaipu Reservoir, Brazil-Paraguay border). *Environmental Biology of Fishes* **72**: 283–304.
- Ormerod SJ. 2003. Current issues with fish and fisheries: editor's overview and introduction. *Journal of Applied Ecology* **40**: 204–213.
- Paiva GV. 1982. *Grandes represas do Brasil*. Editerra: Brasília.
- Pearson K. 1901. On lines and places of closest fit to systems of points in space. *Philosophical Magazine* **2**: 559–572.

- Peres-Neto PR, Jackson DA. 2001. How well do multivariate data sets match? The advantages of a Procrustean superimposition approach over the Mantel test. *Oecologia* **129**: 169–178. DOI: 10.1007/s004420100720
- Pettrere M Jr. 1996. Fisheries in large tropical reservoirs in South America. *Lakes & Reservoirs: Research and Management* **2**: 1–23.
- Petry AC, Agostinho AA, Gomes LC. 2003. Fish assemblages of tropical floodplain lagoons: exploring the role of connectivity in a dry year. *Neotropical Ichthyology* **1**: 111–119.
- Ponton D, Vauchel P. 1998. Immediate downstream effects of the Petit Saut dam on young neotropical fish in a large tributary of the Sinnamary river (French Guiana, South America). *Regulated Rivers: Research and Management* **14**: 227–243.
- Quinn GP, Keough MJ. 2002. *Experimental Design and Data Analysis for Biologists*. Cambridge University Press: Cambridge.
- Rahel FJ. 2007. Biogeographic barriers, connectivity and homogenization of freshwater faunas: it's a small world after all. *Freshwater Biology* **52**: 696–710. DOI: 10.1111/j.1365-2427.2006.01708.x
- Rahel FJ, Hubert WA. 1991. Fish assemblages and habitat gradients in a Rocky Mountain—Great Plains stream: biotic zonation and additive patterns of community change. *Transactions of the American Fisheries Society* **120**: 319–332.
- Reis RE, Kullander SO, Ferraris CJ Jr. 2003. *Check List of the Freshwater Fishes of South and Central America*. EDIPUCRS: Porto Alegre.
- Rohlf FJ, Slice D. 1990. Extensions of the Procrustes method for the optimal superimposition of landmarks. *Systematic Zoology* **39**: 40–59.
- Sanches PV, Nakatani K, Bialetzki A, Baumgartner G, Gomes LC, Luiz EA. 2006. Flow regulation by dams affecting ichthyoplankton: the case of the Porto Primavera Dam, Paraná River, Brazil. *River Research and Applications* **22**: 555–565. DOI: 10.1002/rra.922
- Schlösser IJ. 1982. Trophic structure, reproductive success, and growth rate of fishes in a natural and modified headwater stream. *Canadian Journal of Fisheries and Aquatic Sciences* **39**: 968–978.
- Sheldon AL. 1968. Species diversity and longitudinal succession in stream fishes. *Ecology* **49**: 193–198.
- Shibatta OA, Orsi ML, Bennemann ST, Silva-Souza AT. 2002. Diversidade e distribuição de peixes na bacia do rio Tibagi. In *A bacia do Rio Tibagi*, Medri ME, Bianchini E, Shibatta OA, Pimenta JA (eds). EDUEL: Londrina; 403–423.
- Thomaz SM, Agostinho AA, Hahn NS. 2004. *The Upper Paraná River and Its Floodplain: Physical Aspects, Ecology and Conservation*. The Netherlands Backhuys Publishers: Leiden.
- Tundisi JG. 1999. Reservatórios como sistemas complexos: teoria, aplicações e perspectivas para usos múltiplos. In *Ecologia de Reservatórios: Estrutura, Função e Aspectos Sociais*, Henry R (ed.). FUNDIBIO: Botucatu; FAPESP, [São Paulo]; 19–38.
- Vaníček CD, Kramer RH, Franklin DR. 1970. Distribution of Green River fishes in Utah and Colorado following closure of Flaming Gorge Dam. *Southwestern Naturalist* **15**: 297–315.
- Vannote RL, Minshall GW, Cummings KW, Sedell JR, Cushing CE. 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* **37**: 130–137.
- Vazzoler AEAdM. 1996. *Biologia da reprodução de peixes teleósteos: Teoria e prática*. EDUEM: Maringá.
- Vazzoler AEAdM, Agostinho AA, Hahn NS. 1997. *A planície de inundação do alto rio Paraná: Aspectos físicos, biológicos e socioeconômicos*. EDUEM: Maringá.
- Winemiller KO. 1989. Patterns of variation in life history among South American fishes in seasonal environments. *Oecologia* **81**: 225–241. DOI: 10.1007/BF00379810
- Zimmerman GM, Goetz H, Mielke PW. 1985. Use of an improved statistical method for group comparisons to study effects of prairie fire. *Ecology* **66**: 606–611.