FISH DIVERSITY ALONG SPATIAL GRADIENTS IN THE ITAIPU RESERVOIR, PARANÁ, BRAZIL

OLIVEIRA, E. F.,[1] GOULART, E.[1] and MINTE-VERA, C. V.[2]

[1]Núcleo de Pesquisas em Limnologia, Ictiologia e Aqüicultura, Universidade Estadual de Maringá,
Av. Colombo, 5790, CEP 87020-900, Maringá, Paraná, Brazil

[2]School of Aquatic and Fishery Sciences, University of Washington, P.O. Box 355020,
CEP 98195-5020, Seattle, WA, USA

Correspondence to: Edson Fontes de Oliveira, Núcleo de Pesquisas em Limnologia, Ictiologia e Aqüicultura,
Universidade Estadual de Maringá, Av. Colombo, 5790, Bloco H90,
CEP 87020-900, Maringá, Paraná, Brazil, e-mail: efontes@nupelia.uem.br

Received September 10, 2002 – Accepted March 13, 2003 – Distributed August 31, 2004

(With 4 figures)

ABSTRACT

Local and turnover patterns of fish diversity in the Itaipu Reservoir were evaluated and related to a longitudinal or river-dam gradient (composed of riverine, transitional, and lacustrine zones) and to transversal or upstream-downstream gradients of the tributaries (composed of lotic and lentic stretches of tributaries and reservoir shores). Thirteen stations were sampled quarterly during 2 years. A total of 85 fish species were caught. Local (α) and turnover (β) patterns of fish diversity showed significant differences in reservoir spatial gradients. Along the longitudinal gradient, total and α-diversity were the highest in the riverine and transitional zones of the reservoir and lowest in the lacustrine zone. Along the transversal gradient, total and α-diversity increased from the lotic stretches of the tributaries to the reservoir shores. The lotic and lentic stretches of the tributaries presented the highest β-diversity values, indicating heterogeneity in species compositions among the sub-basins. We conclude with recommendations for reservoir management based on the results of this study.

Key words: fish assemblages, diversity, spatial gradients, neotropical reservoirs.

RESUMO

Diversidade de peixes ao longo de gradientes espaciais no reservatório de Itaipu, Paraná, Brasil

Padrões locais e regionais de diversidade de peixes no reservatório de Itaipu foram avaliados e relacionados aos gradientes longitudinal ou rio–represa (dividido nas zonas fluvial, intermediária e lacustre) e transversal ou cabeceira–foz dos tributários (dividido em trechos lóticos e lênticos dos tributários e margens do reservatório). As coletas foram realizadas trimestralmente durante dois anos. Foram capturadas 85 espécies. Os padrões de diversidade local (α) e *turnover* (β) apresentaram diferenças significativas ao longo dos gradientes espaciais. Ao longo do gradiente longitudinal, as diversidades total e α foram maiores nas zonas fluvial e intermediária. Ao longo do gradiente transversal, as diversidades total e α aumentaram gradualmente do trecho lótico dos tributários às margens do reservatório. Os trechos lóticos e lênticos dos tributários apresentaram os maiores valores de diversidade β, indicando a heterogeneidade na composição de espécies das sub-bacias. Com base nos resultados deste estudo, recomendamos algumas ações de manejo para o reservatório.

Palavras-chave: assembléia de peixes, diversidade, gradientes espaciais, reservatórios neotropicais.

INTRODUCTION

Reservoirs present a good opportunity for studying the effect of scale on the relative importance of factors that determine diversity. On a broad scale, reservoirs are recent and their communities are a combination of species from the former riverine fish fauna as well as introduced species (Fernando & Holčík, 1991; Oliveira & Goulart, 2000). On a regional scale, reservoirs present longitudinal gradients (river-dam) and transversal gradients (upstream-downstream of tributaries).

Longitudinal gradients fall along the main reservoir axis due to changes in basin geomorphology and hydrology and, consequently, in physical, chemical, and biological variables. Along such gradients, fish assemblages may vary widely in composition (Matthews *et al.*, 1989). This gradients may be divided in three zones: riverine, transitional, and lacustrine (Thornton, 1990). The transitional zone is an ecotone between the river upstream and the lacustrine zone of the reservoir downstream. In this ecotone, we expect to find the highest biodiversity, due to the higher availability of microhabitats usable by both lacustrine and riverine species.

Transversal gradients which appear in the secondary axis of a reservoir result from the hydrodynamic and physiographic characteristics of the tributary-reservoir transition. These are the upstream-downstream gradients in tributaries in which three zones may also be characterized: the lotic and lentic stretches of the tributaries and the reservoir shores. The lotic stretch is the portion of the tributary that still retains its riverine characteristics. The lentic stretch, in which the highest fish species diversity is expected and which also constitutes an ecotone, occurs when tributary waters are blocked or slowed down by reservoir waters. The last zone is along the shores of the reservoir itself.

Reservoirs in tropical and subtropical regions have been studied extensively since dam completion (Arcifa & Meschiatti, 1993; Agostinho *et al.*, 1994; Agostinho *et al.*, 1997a; Carvalho *et al.*, 1998). The early years of a new reservoir are marked by high variability in population abundance and patchy distribution of fish due to colonization and adjustment to the new conditions. Studies performed after this period, when populations tend to have stabilized in the new environment, are needed for a full understanding of assemblage structure.

In this study, we analyzed the patterns of fish assemblage diversity as a response to a factorial observational experiment fifteen years after impoundment of the Itaipu Reservoir. Two main factors (longitudinal and transversal gradients) and their interactions were studied. We predicted that, on a regional scale (between-zones), local (α) and turnover (β) diversity would attain the highest values in the transitional zone of the longitudinal gradient and in lentic stretches of tributaries of the transversal gradient because both are ecotones providing a habitat for both riverine and lacustrine species. Also, we predicted that the lacustrine zone of the longitudinal gradient would show the lowest diversity, since this habitat presents conditions least like the original ones. We computed total, local (α), and turnover (β) diversity using several richness indices along longitudinal and transversal gradients of Itaipu Reservoir.

MATERIALS AND METHODS

Study area

Itaipu Reservoir was formed by the impoundment of the Paraná River in October 1982. It lies along the Brazil-Paraguay border between 24°05' and 25°27'S and between 54°05' and 54°48'W (Fig. 1). The Paraná River basin drains about 820,000 km^2. In the impounded area, the Paraná River flows through a narrow tectonic fault, with walls of more than 100 m in height (Maack, 1981) and an average width of 200 m (Andrade, 1941). The Itaipu Reservoir is 151 km long (or 170 km at maximum water level), with surface area of 1,350 km^2 at the average operating level of the dam (220 m). The water level in the reservoir has an annual range of 0.6 m. Average depth is 22 m and average water volume is $29 \times 10^9 m^3$. Average hydraulic retention is 40 days and water speed in the central area may reach 0.6 m/s (Andrade *et al.*, 1988).

Sampling

Sampling was conducted quarterly at 13 stations on the Brazilian side of the reservoir (eastern margin, Fig. 1), from March to December 1997 and from June to December 1998. We used sets of gill nets (2-to-16 cm mesh) and trammel nets (6-to-8 cm mesh) with 20 m in length on the shores of the reservoir and 10 m in the tributaries. Fishing gear was set for 24-hour periods, checked at early morning, dusk, and late evening. Species were identified according to CETESB (1981) and Britski *et al.* (1999), and for the loricarids (armored catfishes), according to Zawadzki (2001). The response variables used in the analysis were species relative abundances indexed as catch per unit of effort (CPUE) standardized to number of individuals per 1,000 m^2 of nets per 24 hours.

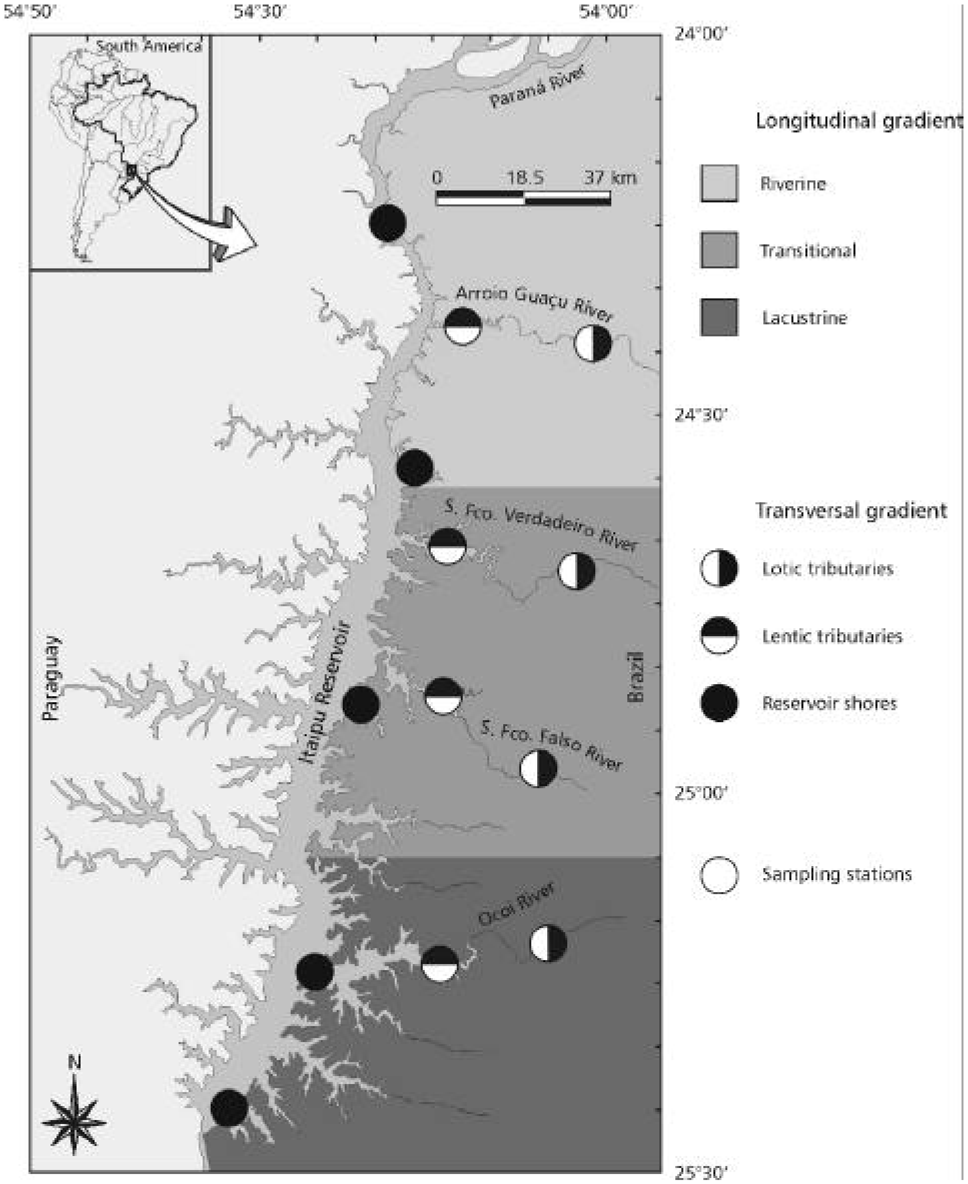

Fig. 1 — Location of Itaipu Reservoir and the sampling stations.

Longitudinal and transversal gradients

The effects of longitudinal (river-dam) and transversal (upstream-downstream of tributaries) gradients and their interactions on fish assemblage structure were studied. The longitudinal gradient was sectioned into riverine, transitional, and lacustrine zones, according to Thornton (1990). The riverine zone is a typical lotic environment, with intense flow and high nutrient availability levels. The transitional zone has relatively higher light penetration, primary productivity, and fish density than the other zones. The lacustrine zone, close to the dam, presents long water permanence and low dissolved nutrient concentrations (see Pagioro, 1999, for detailed description of the limnological gradient in Itaipu Reservoir). The transversal gradient was sectioned into lotic and lentic stretches of tributaries and reservoir shores. The lotic stretches present the highest water speed with alternation of rapids and pools. The lentic stretches have large pool areas formed when the tributary waters reach the reservoir and are slowed down. The reservoir shores present slow water speed and are colonized by aquatic plants such as the submerged *Egeria najas* and *Chara* spp. and the floating *Eichhornia crassipes* and *Salvinia auriculata* (Thomaz *et al.*, 1999). This zone is affected by dam operations due to water level variations.

Data analysis

We used rarefaction curves to estimate species richness in each location based on the number of species actually sampled. Rarefaction (R) was based on the equation (Hurlbert, 1971):

$$R = \sum_{i-1}^{s} = \left[1 - \left(\frac{N - m_i}{n} \right) \Big/ \left(\frac{N}{n} \right) \right],$$

in which N is the total number of individuals, S is the total number of species, m_i is the number of individuals of species i, and n is the number of individuals in the subsample. We compared the rarefaction curves with species accumulation curves (cumulative number of species richness as a function of cumulative number of samples). The further the rarefaction curve lies above the accumulation curve, the more heterogeneous is the sample (Colwell, 1997). Estimate of total richness (collected and non-collected species) of fish assemblages in each zone was done by an incidence-based coverage estimator (ICE). The ICE was based on the equation (Lee & Chao, 1994): $ICE = S_{freq.} + S_{rare}/C_{ice} + Q_i/C_{ice} \, . \, \gamma_{ice}^2$, in which $S_{freq.}$ = number of frequent species (each found in more than 10 samples), S_{rare} = number of rare species (each found in 10 or fewer samples), C_{ice} = sample incidence coverage estimator, Q_i = number of species that occur in exactly i samples; and γ_{ice}^2 = estimated coefficient of variation of the Q_i's for rare species. We used EstimateS v.5.0 to compute rarefaction and species accumulation curves and ICE (Colwell, 1997).

Alpha diversity was assessed using some assemblage attributes such as species richness (S), Shannon-Wiener diversity index (H'), and equitability (E). Species richness was defined as the number of species caught at a sampling station on each sampling date. The Shannon-Wiener diversity index (H') was estimated using the equation: $H' = -\Sigma \, (n_i/N) * \log(n_i/N)$, in which n_i = relative abundance (CPUE) of species i and N = relative abundance for all species. Equitability in the distribution of individuals captured among species was based on the equation $E = H'/\log S$. Alpha diversity variables were computed using PC-ORD v. 3.2 (McCune & Mefford, 1997). A Model I factorial analysis of variance (fixed factors, Zar, 1999) was employed as an exploratory analysis to assess whether the variability of α-diversity (S, E, and H') was affected by longitudinal and transversal gradients, sampling month, and their interactions. Tests of interactions are important because they provide information about the degree of dependence of the effect of one factor on the effects of others.

Beta diversity indices were applied to quantify turnover in species composition along longitudinal and transversal gradients (Wilson & Shmida, 1984; Blackburn & Gaston, 1996). Two spatial scales were studied: one, within each zone and the other, among the zones of each gradient. Two indices were used: $\beta_1 = [(S_R/ \alpha_{mean}) - 1]/[N - 1] * 100$, and $\beta_2 = [(S_R/\alpha_{max}) - 1]/[N - 1] * 100$ (Harrison *et al.*, 1992). For the within-zone analysis, we used S_R = total richness in each zone, α_{mean} = mean richness of stations within each zone, α_{max} = maximum richness of stations within each zone, and N = number of stations in each zone. For between-zones analysis was used differentiation between pairs of stations of all the zones along spatial gradients, with S_R = total number of species in the pair, α_{mean} = mean richness in the two stations, α_{max} = maximum richness among stations, and N = number of stations.

While β_1 is a direct comparison among stations of each zone of the spatial gradients, β_2 measures the value by which regional diversity exceeds maximum diversity of each station. β_1 and β_2 converge closely when variation in α-diversity is small.

The Mantel test (Fortin & Gurevitch, 1993) was employed to assess the null hypothesis that β-diversity patterns are random and, therefore, not affected by spatial gradients. The Mantel test is a correlation matrix between the matrix of pairwise β-diversity indices and a model matrix, with value 0 for pairs of sampling stations in the same zone, and value 1 in different zones for either the longitudinal or the transversal gradient. Significance was assessed by comparing the actual value with a set of values generated using 20,000 permutations of the β-diversity matrix. The computations were performed using NTSYS-pc v.1.8 (Rohlf, 1994).

RESULTS

A total of 8,675 individuals belonging to 24 families and 85 species were caught in the overall sampling (Table 1). Along the longitudinal gradient, the transitional zone presented the highest number of species (ICE = 82 species, Fig. 2), and the lacustrine zone presented the lowest (ICE = 61). Along the transversal gradient, the reservoir shores presented the highest number of species (ICE = 78 species) and the lotic stretch of the tributaries presented the lowest (ICE = 65). The lacustrine zone of the longitudinal gradient and the reservoir shores of the transversal gradient were the two zones with the smallest differences between species accumulation and rarefaction curves (Fig. 2).

The longitudinal and transversal gradients had significant but independent effects on α-diversity (species richness and H', Table 2), as indicated by the non-significant interaction between them. The temporal effect was also significant as well as the interaction between transversal gradient and time, i.e., α-diversity differences among the zones of the transversal gradient depended on the sampling period. The highest effect was that of the transversal gradient (F for richness = 134.13, F for H' = 67.93; Table 2). Neither the main factors nor their interactions had significant effects on equitability estimates (E, Table 2).

Along the longitudinal gradient, the riverine and transitional zones had the highest average richness and diversity index (Figs. 3a and 3c). Independently of the zone of the longitudinal gradient, the reservoir shores of the transversal gradient had throughout the year a greater richness and diversity index than that of the tributaries (Figs. 3a and 3c). In general, the highest richness and diversity indices were recorded during the summer (December and March), and the lowest during the winter (June). Reduction in richness and diversity index during the winter may be related to changes in gear efficiency. We used passive gear that depends on fish activity and since at low winter temperatures fish are not as active as in the summer due to reduced metabolism, they are, therefore, less vulnerable. Equitability showed no significant variability, and thus α-diversity changes (measured by the H' Shannon-Wiener diversity) resulted from richness changes (Fig. 3b).

In the within-zone assessment of the β-diversity (i.e., one value computed for indexing in each zone), we observed that along the longitudinal gradient the two indices were slightly higher for the riverine and lacustrine zones than for the transitional zone (Fig. 4). Along the transversal gradient, the lotic and lentic stretches of tributaries presented higher β-diversity indices (both β_1 and β_2, Fig. 4) than the reservoir shores, revealing a homogenization effect of the reservoir and the highest turnover in species of the lotic and lentic stretches of tributaries.

For between-zones β-diversity assessment, we computed both β_1 and β_2, for each pair of stations from both within and between zones of either the longitudinal or the transversal gradient. There was a positive correlation between β-diversity matrices and that of the longitudinal gradient (Mantel test; β_1: r = 0.19, p = 0.05; β_2: r = 0.22, p = 0.03), indicating significant differences in the species composition pattern among the gradient zones. For the transversal gradient, the correlation matrix was only significant for β_1 (r = 0.32, p = 0.01), while for there was no significant correlation (r = 0.062, p = 0.32).

TABLE 1
Systematic position of species collected during study period in the Itaipu Reservoir.

- CLASS CHONDRICHTHYES
  - Order MYLIOBATIFORMES
    - Family POTAMOTRYGONIDAE
      - *Potamotrygon motoro* (Natterer, 1841)
- CLASS OSTEICHTHYES
  - Order CHARACIFORMES
    - Family CHARACIDAE
      - Subfamily BRYCONINAE
        - *Brycon orbignyanus* (Valenciennes, 1849)
      - Subfamily TETRAGONOPTERINAE
        - *Astyanax altiparanae* Garutti & Britski, 2000
        - *Astyanax fasciatus* (Cuvier, 1819)
        - *Moenkhausia intermedia* (Eigenmann, 1908)
      - Subfamily SALMININAE
        - *Salminus maxillosus* Valenciennes, 1849
      - Subfamily CYNOPOTAMINAE
        - *Galeocharax knerii* (Steindachner, 1875)
      - Subfamily CHARACINAE
        - *Roeboides paranensis* Pignalberi, 1975
      - Subfamily ACESTRORHYNCHINAE
        - *Acestrorhynchus lacustris* (Reinhardt, 1874)
      - Subfamily MYLEINAE
        - *Metynnis* sp.
        - *Piaractus mesopotamicus* (Holmberg, 1887)
      - Subfamily SERRASALMINAE
        - *Serrasalmus marginatus* Valenciennes, 1847
        - *Serrasalmus spilopleura* Kner, 1860
    - Family CYNODONTIDAE
      - *Rhaphiodon vulpinus* Agassiz, 1829
    - Family PARODONTIDAE
      - *Apareiodon affinis* (Steindachner, 1879)
    - Family PROCHILODONTIDAE
      - *Prochilodus lineatus* (Valenciennes, 1847)
    - Family CURIMATIDAE
      - *Steindachnerina insculpta* (Fernández-Yépez, 1948)
    - Family ANOSTOMIDAE
      - *Leporellus vittatus* (Valenciennes, 1849)
      - *Leporinus lacustris* Campos, 1945
      - *Leporinus friderici* (Bloch, 1794)
      - *Leporinus obtusidens* (Valenciennes, 1847)
      - *Leporinus octofasciatus* Steindachner, 1815
      - *Leporinus macrocephalus* Garavello & Britski, 1988
      - *Leporinus* sp.
      - *Schizodon altoparanae* Garavello & Britski, 1990
      - *Schizodon borellii* (Boulenger, 1900)
      - *Schizodon nasutus* Kner, 1858
    - Family ERYTHRINIDAE
      - *Hoplias* aff. *malabaricus* (Bloch, 1794)
      - *Hoplerythrinus unitaeniatus* (Spix, 1829)
  - Order GYMNOTIFORMES
    - Family RHAMPHICHTHYIDAE
      - *Rhamphichthys rostratus* (Linnaeus, 1766)
    - Family GYMNOTIDAE
      - *Gymnotus carapo* (Linnaeus, 1758)
    - Family STERNOPYGIDAE
      - *Eigenmannia trilineata* Lopez & Castello, 1966
      - *Eigenmannia* sp.
      - *Sternopygus macrurus* (Schneider, 1801)
    - Family APTERONOTIDAE
      - *Apteronotus albifrons* (Linnaeus, 1766)
      - *Porotergus ellisi* Aramburu, 1957
  - Order SILURIFORMES
    - Family AGENEIOSIDAE
      - *Ageneiosus brevifilis* Valenciennes, 1840
      - *Ageneiosus valenciennesi* Bleeker, 1864
      - *Ageneiosus ucayalensis* Castelnau, 1855
    - Family PIMELODIDAE
      - *Hypophthalmus edentatus* Spix, 1829
      - *Rhamdia quelen* (Quoy & Gaimard, 1824)
      - *Pimelodella gracilis* (Valenciennes, 1840)
      - *Pimelodus ornatus* Kner, 1857
      - *Pimelodus maculatus* Lacépède, 1803
      - *Pimelodus blochii* Valenciennes, 1840
      - *Iheringichthys labrosus* Kröyer, 1874
      - *Pinirampus pirinampu* (Spix, 1829)
      - *Megalonema platanus* (Günther, 1880)
      - *Hemisorubim platyrhynchos* (Valenciennes, 1840)
      - *Paulicea luetkeni* (Steindachner, 1875)
      - *Sorubim lima* (Schneider, 1801)
      - *Pseudoplatystoma corruscans* (Agassiz, 1829)
    - Family AUCHENIPTERIDAE
      - *Auchenipterus osteomystax* (Ribeiro, 1918)
      - *Parauchenipterus galeatus* (Linnaeus, 1766)
    - Family DORADIDAE
      - *Pterodoras granulosus* (Valenciennes, 1833)
      - *Trachydoras paraguayensis* (Eigenmann & Ward, 1907)
      - *Rhinodoras dorbignyi* (Kröyer, 1855)
    - Family CALLICHTHYIDAE
      - *Hoplosternum littorale* (Hancock, 1828)
    - Family LORICARIIDAE
      - Subfamily ANCISTRINAE
        - *Megalancistrus aculeatus* (Perugia, 1891)
        - *Ancistrus cirrhosus* Valenciennes, 1840
        - *Ancistrus* sp.
      - Subfamily LORICARIINAE
        - *Loricariichthys platymetopon* Isbrücker & Nijssen, 1979
        - *Loricariichthys rostratus* Reis & Pereira, 2000
        - *Loricaria* sp.
      - Subfamily HYPOSTOMINAE
        - *Hypostomus albopunctatus* (Regan, 1907)
        - *Hypostomus commersonii* Valenciennes, 1840
        - *Hypostomus* aff. *derbyi* (Haseman, 1911)
        - *Hypostomus regani* (Iheringi, 1905)
        - *Hypostomus* aff. *myersi* (Gouline, 1974)
        - *Hypostomus auroguttatus* Natterer & Heckel, 1853
        - *Hypostomus ancistroides* (Iheringi, 1911)
        - *Hypostomus* sp.
        - *Liposarcus anisitsi* (Eigenmann & Kennedy, 1903)
    - Family CLARIIDAE
      - *Clarias gariepinus* (Burchell, 1822)
  - Order PERCIFORMES
    - Family SCIAENIDAE
      - *Plagioscion squamosissimus* (Heckel, 1840)
    - Family CICHLIDAE
      - *Satanoperca pappaterra* (Heckel, 1840)
      - *Cichlasoma paranaense* Kullander, 1983
      - *Cichla monoculus* Spix & Agassiz, 1831
      - *Cichla* sp.
      - *Crenicichla britskii* Kullander, 1982
      - *Crenicichla niederleinii* (Holmberg, 1891)
      - *Tilapia rendalli* (Boulenger, 1897)
  - Order CYPRINIFORMES
    - Family CYPRINIDAE
      - *Cyprinus carpio* Linnaeus, 1758
  - Order SYNBRANCHIFORMES
    - Family SYNBRANCHIDAE
      - *Synbranchus marmoratus* Bloch, 1795
  - Order PLEURONECTIFORMES
    - Family ACHIRIDAE
      - *Catathyridium jenynsii* (Günther, 1862)

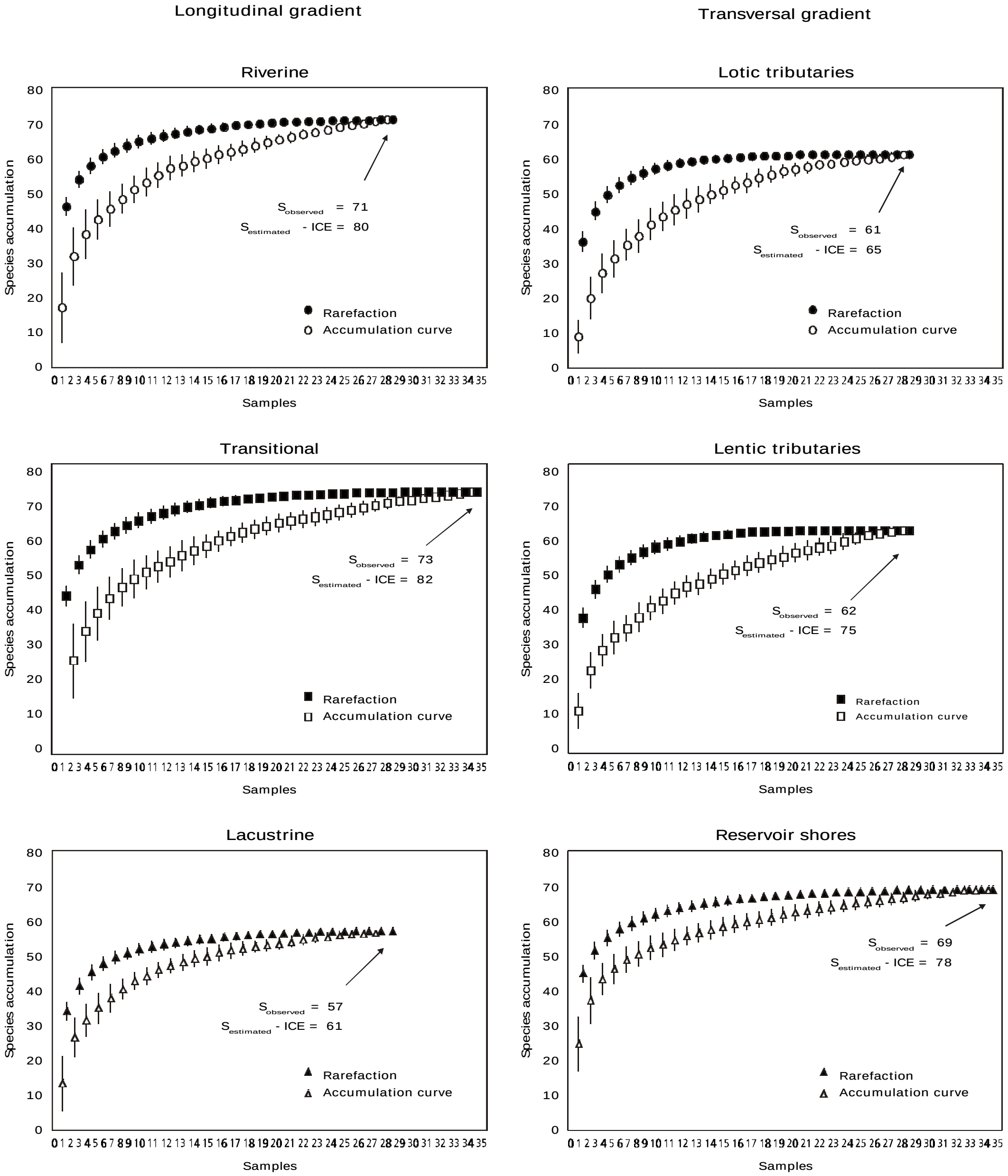

Fig. 2 — Rarefaction and species accumulation curves, total diversity (number of species observed S and estimated ICE) along longitudinal and transversal gradients in Itaipu Reservoir (vertical bars represents the standard deviation calculated by resampling).

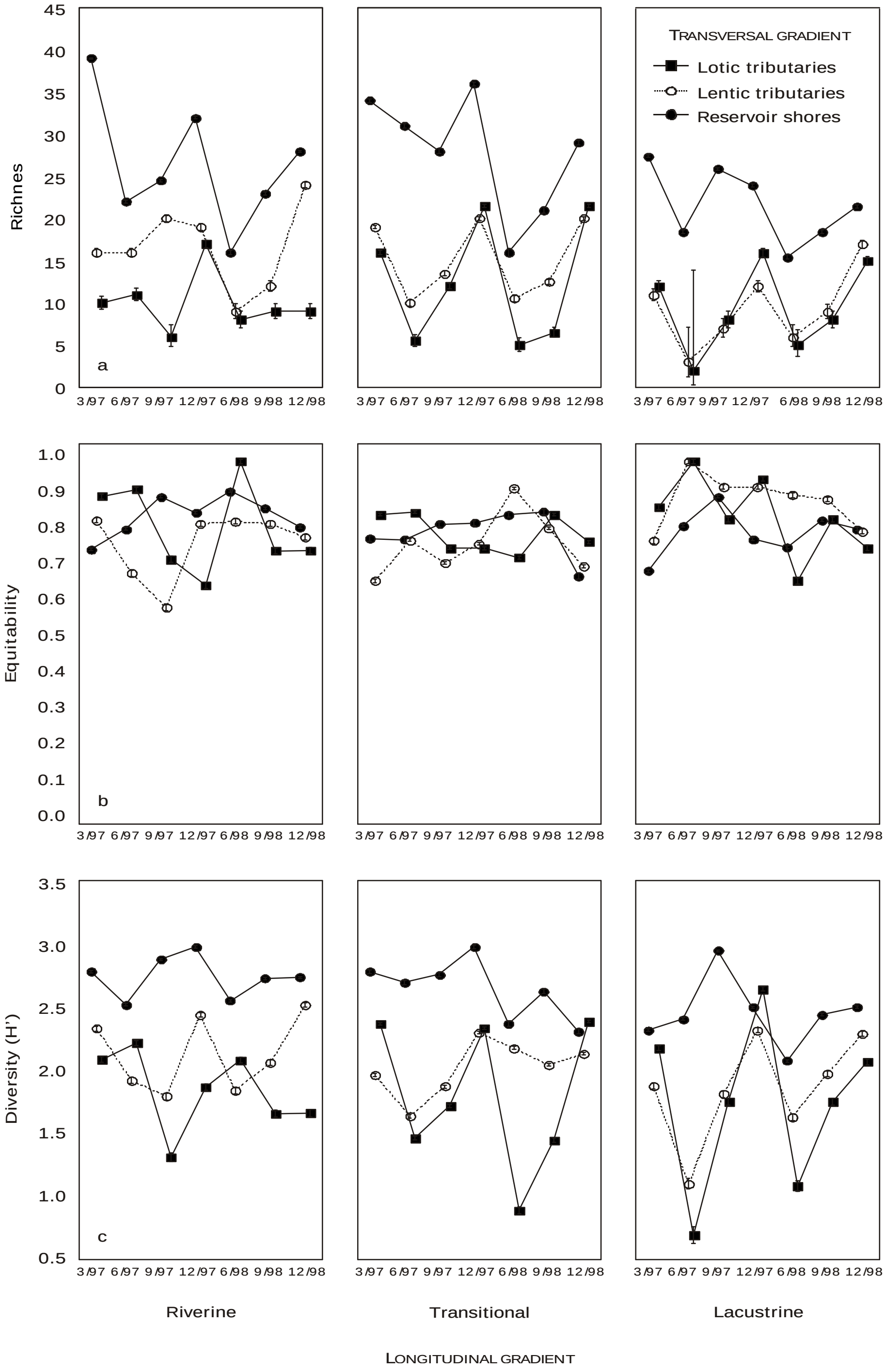

Fig. 3 — Richness (a), equitability (b) and Shannon-Wiener diversity index (c) in Itaipu Reservoir for the longitudinal gradient (riverine, transitional, and lacustrine zones), the transversal gradient (lotic and lentic stretches of tributaries and reservoir shores), and the months of sampling (vertical bars represents the standard error).

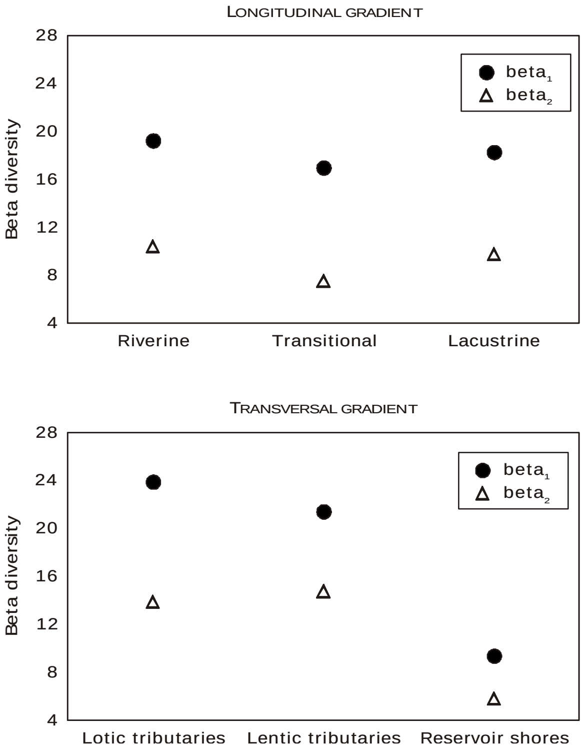

Fig. 4 — Beta diversity (β_1 and β_2) in different zones of the longitudinal and transversal gradients in Itaipu Reservoir.

TABLE 2
Factorial analysis of variance for some fish assemblage attributes according to spatial gradients (longitudinal and transversal) and time (months) of Itaipu Reservoir (DF = Degrees of Freedom; S = species richness; E = equitability; H' = Shannon-Wiener diversity index).

	DF	**S**		**E**		**H'**	
	(effect; error)	**F**	**P**	**F**	**P**	**F**	**P**
Longitudinal gradient (1)	2; 28	**15.15**	0.00	2.29	0.12	**4.04**	0.03
Transversal gradient (2)	2; 28	**134.13**	0.00	0.06	0.94	**67.93**	0.00
Months (3)	6; 28	**18.60**	0.00	1.10	0.39	**8.41**	0.00
(1)*(2)	4; 28	1.75	0.17	1.78	0.16	0.28	0.89
(1)*(3)	12; 28	0.80	0.64	1.09	0.40	1.61	0.15
(2)*(3)	12; 28	**2.07**	0.05	1.09	0.40	**2.21**	0.04
(1)*(2)*(3)	24; 28	1.09	0.40	0.61	0.88	1.63	0.11

DISCUSSION

Total, regional, and local diversity varied with spatial gradients. Along the longitudinal gradient, local (α) total diversity presented a peak in the transitional zone, followed closely by the riverine zone. The transitional zone of Itaipu Reservoir is commonly characterized by a high abundance of submerged and floating macrophytes in the margin areas. Nevertheless, these aquatic plants are restricted to shallow areas no deeper than two meters, near the mouths of the tributaries (Thomaz *et al.*, 1999). Aquatic plants are important habitats for fish because they increase spatial heterogeneity and feeding resource availability (Thomaz & Bini, 1999). For example, the São Francisco Verdadeiro and São Francisco Falso rivers are large tributaries having their mouths in this zone, and foraging potential in the lotic and lentic stretches of such tributaries may be sufficient to support more biomass and diversity than is the case in other sites. Also, in this intermediate or ecotone environment, both lotic and lentic species may co-exist, using the habitat temporally; hence the species richness tends to increase. As is known, ecotones play an important role in fish diversity (Kolasa & Zalewski, 1995) and community structure (Willis & Magnuson, 2000) in aquatic ecosystems.

The riverine zone of the longitudinal gradient is directly influenced by Paraná River upstream, wich dictates the limnological characteristics along this gradient, e.g., part of the organic and suspended material carried to Itaipu Reservoir originates in this environment (Pagioro & Thomaz, 2002) and constitutes temporary habitats for initial life stages of some migratory species such as *Prochilodus lineatus* (Agostinho *et al.*, 1993), *Salminus maxillosus*, *Pimelodus maculatus*, *Rhaphiodon vulpinus*, and *Leporinus obtusidens* (Oliveira *et al.*, 2001). The riverine zone is the main habitat for several species that are adapted to the formerly pristine stream habitat. Those species may also spend some of their life cycle in both the transitional and lacustrine zones. Ultimately, the riverine zone accounts for the high number of species of the transitional and lacustrine zones and of the upstream floodplain (Agostinho *et al.*, 1999).

The lacustrine zone had the smallest richness and the highest homogeneity (smallest difference between the rarefaction and species accumulation curves) along the gradient. This pattern was similar to that formerly verified in Itaipu Reservoir (Benedito-Cecílio *et al.*, 1997) as well as in other reservoirs of the Paraná River basin (Foz de Areia, Iguaçu River, Agostinho *et al.*, 1997a; in Jurumirim, Paranapanema River, Carvalho *et al.*, 1998; four reservoirs of the Grande and Paranaíba Rivers, Upper Paraná River basin, Santos, 1999). The reduced richness of the lacustrine zone may be the result of local and historical processes. For example, sites in the lacustrine zone are highly affected by operational procedures of the hydroelectric plant and absence of natural lakes in the basin, in addition to which the Upper Paraná River lacked species adapted to lentic environments that could have colonized this zone (see Gomes & Miranda, 2001). The lacustrine zone is an environment that can severely restrict occupation by fishes, because of thermal and chemical stratification and decreased range of suitable microhabitats.

Along the transversal gradient, local (α) total diversity presented a true gradient with lower diversity in the lotic zone and higher diversity on the reservoir shores. Aquatic macrophytes and woody debris in the littoral areas of Itaipu Reservoir make it possible the colonization for a diversified associated fauna, especially crustaceans and insects, to colonize. These organisms increase fish diversity in the habitat, since they are potential food sources for a great number of species, such as characids (*Astyanax altiparanae*, *Moenkhausia intermedia*, and *Roeboides paranensis*), cichlids (*Crenicichla britskii*), and gymnotiforms (*Gymnotus carapo* and *Eigenmannia trilineata*) (Agostinho *et al.*, 1997b). Macrophytes are consumed by some species (for example, *Schizodon borellii*, *S. nasutus*, *S. altoparanae*, and *Leporinus lacustris*; Agostinho *et al.*, 1997b) and constitute reproduction sites and refuge against predators. The lentic stretches of tributaries presented total richness similar to that of the reservoir shores, since this zone is an ecotone between the reservoir itself and the lotic stretches of the tributaries. Thus, they offer a wide range of exploitable microhabitats not only by species typical of lentic environments but also by those of lotic ones.

The highest heterogeneity (difference between rarefaction and accumulation curves) occurred in the lotic and lentic stretches of the tributaries. Decreased species richness in the reservoir towards the lotic stretches of the tributaries may be related to: flow regulation; reduction of aquatic vegetation, mainly floating macrophytes; changes in substratum type and to limnological conditions of this gradient (Oliveira, 2000). The low diversity of tributaries may also be due to the relatively reduced area of these sub-basins.

Species turnover analysis is important because: (1) it shows the degree to which habitats have been partitioned by species; (2) β-diversity values may be used to compare habitat diversity between different systems; (3) α- and β-diversity measure total diversity, or the biotic heterogeneity of a specific area (Wilson & Shmida, 1984). Sampling stations along longitudinal gradient presented similar β-diversity within each zone, with slightly higher values for the riverine and lacustrine zones. This indicates the same amount of species turnover within each longitudinal gradient zone. In contrast, between zones there is a significant turnover of species, as indicated by the results of the Mantel test. Longitudinal gradient is, therefore, a good β-diversity predictor in Itaipu Reservoir. If the same zone is repeatedly sampled, a higher probability exists of capturing the same species than when sampling in different zones. Such pattern denotes a longitudinal gradient in fish assemblage distribution in Itaipu Reservoir, i.e., the β-diversity pattern is not random in this gradient.

Along the transversal gradient, the sampling stations on the reservoir shores presented lower species composition turnover (i.e., higher similarity) than the sampling stations in the tributaries. This homogeneity in composition among the reservoir shore stations may result from higher connectivity between stations, since they are contiguous and the fish may swim more easily between them than between stations in the tributaries. In contrast, the sampling station within the lotic and lentic stretches of the tributaries presented the highest β-diversity, higher even than the values obtained along the longitudinal gradient. The highest species composition heterogeneity within the lotic and lentic stretches of the tributaries suggests that the different sub-basins of the tributaries present partially distinct fauna. For the between-zones comparison, the Mantel test was significant only for the β_1 index. The α-diversity for the transversal gradient zones had a wider variability than for the longitudinal gradient zones, so that may explain why significant changes in species composition were detected only by the β_1 index which, since it is estimated according to local mean richness (Harrison *et al.*, 1992), is more sensitive to α-diversity variations.

Higher species composition heterogeneity was found within transversal gradient zones rather than longitudinal ones. In the literature, longitudinal gradients have long been recognized as important in reservoirs (Thornton, 1990; Carvalho *et al.*, 1998; Agostinho *et al.*, 1999). In this study, we showed that transversal gradients are more influential than longitudinal gradients; we suggest, therefore, that special attention should be given them in studies of ichthyofauna diversity in particular, and of aquatic fauna and flora in general.

As a result of this study of ichthyofauna diversity patterns along spatial gradients, we suggest the following reservoir management policy: (1) conservation of habitat quality in the floodplain upstream and reservoir tributaries to maintain high richness patterns in the riverine and transitional zones (longitudinal gradient) and in the reservoir shores and the lentic stretches of tributaries (transversal gradient); (2) increase of protected bank area and marginal vegetation restoration in the lacustrine zone (longitudinal gradient) and in the lotic stretches of tributaries (transversal gradient) in order to enhance habitat complexity and diversity and, consequently, species diversity in those zones that presented the lowest diversity; (3) maintenance of a constant reservoir operation level, with necessary variations introduced cautiously since these will mostly affect the littoral areas of the reservoir shores, i.e., the highest diversity zones; (4) adequate fishery activity management, taking into account the non-random spatial structure and fish diversity compartmentalization in the reservoir along the longitudinal and transversal gradients; and (5) maintenance of a monitoring program allowing the study of fish diversity pattern dynamics.

Acknowledgements — We are grateful to the Postgraduate Program in Ecology of Continental Aquatic Environments and the Nucleus of Research in Limnology, Ichthyology, and Aquaculture of the State University of Maringá for logistic support. We would like to acknowledge field and laboratory assistance of Vitor de S. Ferreira, Fabiane Abujanra, Edson K. Okada, Vanderlei P. da Silva, Angela M. Ambrósio, Cláudio H. Zawadzki, Carla S. Pavanelli, Sebastião Rodrigues, Francisco A. Teixeira, and Gilmar Baumgartner. We also thank Angelo A. Agostinho, Luiz C. Gomes, Luis M. Bini, and Suzan Speckman for valuable comments on the manuscript and Maria S. R. Arita for reference normalization. Itaipu Binacional and CAPES provided funding for this project.

REFERENCES

AGOSTINHO, A. A., VAZZOLER, A. E. A. de M., GOMES, L. C. & OKADA, E. K., 1993, Estratificación espacial y comportamiento de *Prochilodus scrofa* en distintas fases del ciclo de vida, en la planicie de inundación del alto río Paraná y embalse de Itaipu, Paraná, Brasil. *Rev. Hydrobiol.* trop., *26*(1): 79-90.

AGOSTINHO, A. A., JÚLIO Jr., H. F. & PETRERE Jr., M., 1994, Itaipu reservoir (Brazil): impacts of the impoundment on the fish fauna and fisheries, pp. 171-184. *In*: I. G. Cowx (ed.), *Rehabilitation of freshwater fisheries*. Blackwell Scientific Publications, Oxford.

AGOSTINHO, A. A., FERRETTI, C. M. L., GOMES, L. C., HAHN, N. S., SUZUKI, H. I., FUGI, R. & ABUJANRA, F., 1997a, Ictiofauna de dois reservatórios do rio Iguaçu em diferentes fases de colonização: Segredo e Foz do Areia, pp. 275-292. *In*: A. A. Agostinho & L. C. Gomes (eds.), *Reservatório de Segredo: bases ecológicas para o manejo*. EDUEM: Nupélia, Maringá.

AGOSTINHO, A. A., HAHN, N. S., GOMES, L. C. & BINI, L. M., 1997b, Estrutura trófica, pp. 229-248. *In*: A. E. A. de M. Vazzoler, A. A. Agostinho & N. S. Hahn (eds.), *A planície de inundação do alto rio Paraná: aspectos físicos, biológicos e socioeconômicos*. EDUEM: Nupélia, Maringá.

AGOSTINHO, A. A., MIRANDA, L. E., BINI, L. M., GOMES, L. C., THOMAZ, S. M. & SUZUKI, H. I., 1999, Patterns of colonization in neotropical reservoirs, and prognoses on aging, pp. 227-265. *In*: J. G. Tundisi & M. Straškraba (eds.), *Theoretical reservoir ecology and its applications*. International Institute of Ecology, São Carlos.

ANDRADE, T., 1941, *O rio Paraná: no roteiro da marcha para o oeste*. Irmãos Pongetti – Zelio Valverde Editores, Rio de Janeiro, 165p.

ANDRADE, L. F., BRUNKOW, R. F., XAVIER, C. F. & DOMINGUES, L. L., 1988, Fitoplâncton e características físico-químicas do reservatório de Itaipu, Paraná-Br. *In*: J. G. Tundisi (ed.), *Limnologia e manejo de represas*, pp. 205-268. USP-EESC/CRHEA/ACIESP, São Carlos, v.1, t.1. (Série: Monografias em Limnologia).

ARCIFA, M. S. & MESCHIATTI, A. J., 1993, Distribution and feeding ecology of fishes in a brazilian reservoir: Lake Monte Alegre. *Interciencia*, *18*(6): 302-313.

BENEDITO-CECÍLIO, E., AGOSTINHO, A. A., JÚLIO Jr., H. F. & PAVANELLI, C. S., 1997, Colonização ictiofaunística do reservatório de Itaipu e áreas adjacentes. *Rev. Bras. Zool.*, *14*(1): 1-14.

BLACKBURN, T. M. & GASTON, K. J., 1996, The distribution of bird species in the New World: patterns in species turnover. *Oikos*, *77*(1): 146-152.

BRITSKI, H. A., SILIMON, K. Z. de S. & LOPES, B. S., 1999, *Peixes do Pantanal: manual de identificação*. EMBRAPA, Brasília, 184p.

CARVALHO, E. D., SILVA, V. F. B., FUJIHARA, C. Y., HENRY, R. & FORESTI, F., 1998, Diversity of fish species in the River Paranapanema–Jurumirim Reservoir transition region (São Paulo, Brazil). *Ital. J. Zool.*, *65*: 325-330.

COLWELL, R. K., 1997, *User's guide to EstimateS 5: statistical estimation of species richness and shared species from samples.* Version 5.0.1. University of Connecticut, Storrs. Available in: <http://viceroy.eeb.uconn.edu/estimates>.

COMPANHIA DE TECNOLOGIA DE SANEAMENTO AMBIENTAL – CETESB, 1981, *Itaipu Binacional – Ictiofauna: complementação do inventário ictiofaunístico*. CETESB, São Paulo, 3v.

FERNANDO, C. H. & HOLČÍK, J., 1991, Fish in reservoirs. *Int. Revue Ges. Hydrobiol.*, *76*: 149-167.

FORTIN, M. -J. & GUREVITCH, J., 1993, Mantel tests: spatial structure in field experiments, pp. 342-359. *In*: S. M. Scheiner & J. Gurevitch (eds.), *Design and analysis of ecological experiments.* Chapman & Hall, New York.

GOMES, L. C. & MIRANDA, L. E., 2001, Riverine characteristics dictate composition of fish assemblages and limit fisheries in reservoirs of the Upper Paraná River Basin. *Regul. Rivers: Res. Mgmt.*, *17*: 67-76.

HARRISON, S., ROSS, S. J. & LAWTON, J. H., 1992, Beta diversity on geographic gradients in Britain. *J. Anim. Ecol.*, *61*: 151-158.

HURLBERT, S. H., 1971, The nonconcept of species diversity: a critique and alternative parameters. *Ecology*, *52*(4): 577-585.

KOLASA, J. & ZALEWSKI, M., 1995, Notes on ecotone attributes and functions. *In*: F. Schiemer, M. Zalewski & J. E. Thorpe (eds.), *The importance of aquatic-terrestrial ecotones for freshwater fish*, pp. 1-7. Kluwer Academic Publishers, Dordrecht. (Developments in Hydrobiology; 105).

LEE, S.-M. & CHAO, A., 1994, Estimating population size via sample coverage for closed capture-recapture models. *Biometrics*, *50*: 88-97.

MAACK, R., 1981, *Geografia física do Estado do Paraná.* J. Olympio, Rio de Janeiro, 450p.

MATTHEWS, W. J., HILL, L. G., EDDS, D. R. & GELWICK, F. P., 1989, Influence of water quality and season on habitat use by striped bass in a large southwestern reservoir. *Trans. Am. Fish. Soc.*, *118*: 243-250.

McCUNE, B. & MEFFORD, M. J., 1997, *PC-ORD: Multivariate analysis of ecological data*. Version 3.0. MjM Software Design, Oregon, 47p.

OLIVEIRA, E. F., 2000, *Padrões de distribuição espacial da assembléia de peixes após 15 anos da formação do reservatório de Itaipu, Paraná, Brasil.* Master Thesis, Universidade Estadual de Maringá, Maringá, Brasil, 49p.

OLIVEIRA, E. F. & GOULART, E., 2000, Distribuição espacial de peixes em ambientes lênticos: interação de fatores. *Acta Scientiarum*, *22*(2): 445-453.

OLIVEIRA, E. F., LUIZ, E. A., AGOSTINHO, A. A. & BENEDITO-CECÍLIO, E., 2001, Fish assemblages in littoral areas of the upper Paraná river floodplain, Brazil. *Acta Scientiarum*, *23*(2): 369-376.

PAGIORO, T. A., 1999, *Variações espaço-temporais das características físicas e químicas da água, material em sedimentação e produtividade primária fitoplanctônica no reservatório de Itaipu, PR, Brasil.* Doctoral Thesis, Universidade Estadual de Maringá, Maringá, Brasil, 59p.

PAGIORO, T. A. & THOMAZ, S. M., 2002, Longitudinal patterns of sedimentation in a deep, monomictic subtropical reservoir (Itaipu, Brazil-Paraguay). *Arch. Hydrobiol.*, *154*(3): 515-528.

ROHLF, F. J., 1994, *NTSYS-pc: numerical taxonomy and multivariate analysis system*. Version 1.80. Exeter Publishing, New York.

SANTOS, G. B., 1999, *Estrutura das comunidades de peixes de reservatórios do Sudeste do Brasil, localizados nos rios Grande e Paranaíba, bacia do alto Paraná*. Doctoral Thesis, Universidade Federal de São Carlos, São Carlos, Brasil, 166p.

THOMAZ, S. M. & BINI, L. M., 1999, A expansão das macrófitas aquáticas e implicações para o manejo de reservatórios: um estudo na represa de Itaipu, pp. 597-625. *In*: R. Henry (ed.), *Ecologia de reservatórios: estrutura, função e aspectos sociais.* FAPESP: FUNDIBIO, Botucatu.

THOMAZ, S. M., BINI, L. M., SOUZA, M. C., KITA, K. K. & CAMARGO, A. F. M., 1999, Aquatic macrophytes of Itaipu Reservoir, Brazil: survey of species and ecological considerations. *Braz. Arch. Biol. Technol.*, *42*(1): 15-22.

THORNTON, K. W., 1990, Perspectives on reservoir limnology, pp. 1-13. *In*: K. W. Thornton, B. L. Kimmel & F. E. Payne (eds.), *Reservoir limnology: ecological perspectives*. John Wiley & Sons, New York.

WILLIS, T. V. & MAGNUSON, J. J., 2000, Patterns in fish species composition across the interface between streams and lakes. *Can. J. Fish. Aquat. Sci.*, *57*: 1042-1052.

WILSON, M. V. & SHMIDA, A., 1984, Measuring beta diversity with presence-absence data. *J. Ecol.*, *72*: 1055-1064.

ZAR, J. H., 1999, *Biostatistical analysis*. 4th ed. Prentice Hall, New Jersey, 663p.

ZAWADZKI, C. H., 2001, *Sistemática e variação aloenzimática da família Loricariidae (Teleostei: Siluriformes) dos reservatórios de Corumbá e Itaipu, bacia do alto rio Paraná, Brasil.* Doctoral Thesis, Universidade Estadual de Maringá, Maringá, Brasil, 59p.