Patterns of dominance and rarity of fish assemblage along spatial gradients in the Itaipu Reservoir, Paraná, Brazil

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ABSTRACT. Patterns of dominance and rarity of fish assemblage in the Itaipu Reservoir were evaluated and related to a longitudinal or river-dam gradient (composed of riverine, transitional and lacustrine zones) and to a transversal or upstream-downstream gradients of the tributaries (composed of lotic and lentic stretches of tributaries and reservoir shores). Thirteen sampling stations were sampled quarterly during 2 years. Patterns of species dominance were investigated using Whittaker plots and patterns of rarity using analysis of variance. A total of 85 fish species were caught. In the reservoir shores of riverine zone, the dominant species was the migratory Prochilodontidae curimba *Prochilodus lineatus* that uses the upstream floodplain as a spawning and nursery area. In the reservoir shores of transitional and lacustrine zones (i.e. close to the dam) the dominant species was the introduced Sciaenidae curvina *Plagioscion squamosissimus*. Loricarids dominated the tributaries. The proportion of rare species presented significant differences along longitudinal gradient. Lowest proportion of rare species was found close to the dam indicating a loss of ecological integrity in this zone.

Key words: fish assemblages, dominance, rarity, spatial gradients, Neotropical reservoirs.

RESUMO. Padrões de dominância e raridade da assembléia de peixes ao longo de gradientes espaciais no reservatório de Itaipu, Estado do Paraná, Brasil. Padrões de dominância e raridade da assembléia de peixes no reservatório de Itaipu foram avaliados e relacionados com os gradientes longitudinal (dividido nas zonas fluvial, intermediária e lacustre) e transversal (dividido em trechos lóticos e lênticos dos tributários e margem do reservatório). As coletas foram realizadas trimestralmente em treze estações durante dois anos. Padrões de dominância e raridade foram investigados utilizando curva de espécie-abundância e análise de variância, respectivamente. Foram capturadas 85 espécies. Na zona fluvial, a espécie dominante na margem do reservatório foi o curimba *Prochilodus lineatus*, que utiliza a planície de inundação a montante como área de reprodução e crescimento. A curvina *Plagioscion squamosissimus*, espécie introduzida, foi dominante nas margens do reservatório das zonas intermediária e lacustre. Loricarídeos dominaram nos tributários. A proporção de espécies raras apresentou diferenças significativas ao longo do gradiente longitudinal. Na zona lacustre, próximo à barragem, foi registrada a menor proporção de espécies raras, indicando perda de integridade ecológica nessa zona.

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

Introduction

Dominance and rarity are of central theoretical and practical importance in conservation biology (Soulé, 1986). Dominant species in an assemblage may exert a powerful control over the occurrence of other species. Also, the concept of dominance has long been ingrained in community ecology. Understanding the causes and consequences of rarity is a problem of profound significance because most species are uncommon or rare, and rare species are generally at greater risk of extinction. Rarity is mainly associated with the requirement of specific habitat, characteristics by the species. In this case, rare species are extremely susceptible to changes in the habitat such as great changes in hydrological conditions and availability of nutrients. Many factors favor the decrease of the number of rare species in continental aquatic environments, as the construction of reservoirs, the introduction of exotic species, the effects of chemical and organic pollution and overfishing (Lowe-McConnell, 1990; Oliveira and Goulart, 2000). The above factors degrade the habitat through loss in spatial heterogeneity that affects distribution of rare species and eventually leads to their local or regional extinction (Gaston, 1994). Thus rarity pattern reflect the degree of integrity of the environment.

Reservoirs are complex systems where both native and introduced species are assembled in an environment that is influenced by the design and operational characteristics of the dam. An unavoidable effect of the impoundment on the aquatic fauna and flora is a shift in species composition and abundance, with extreme proliferation of some species and reduction, or even elimination, of others (Agostinho *et al.*, 1999). Characterizing the dominance and rarity patterns of theses assemblages helps to determine factors that regulate assemblage structure. In this study we analyzed the dominance and rarity patterns in the Itaipu Reservoir (Brazil/Paraguay). On a regional scale, reservoirs present longitudinal gradients (river-dam gradients) and transversal gradients (upstream-downstream gradients in tributaries). Longitudinal gradients fall along the main axis of the reservoir due to changes in basin geomorphology and hydrology and consequently in physical, chemical and biological variables. This gradient may be divided in three zones: riverine, transitional and lacustrine (Thornton, 1990). Transversal gradients appear in the secondary axis of the region of influence of the reservoir and results from the hydrodynamic and physiographic characteristics of the tributary-reservoir transition. Three zones can also be distinguished: the lotic and lentic stretches of the tributaries and the reservoir shores.

We predicted that opportunistic species would be dominant in impacted areas (such as the lacustrine zone). The proportion of rare species would be higher in the riverine zone and in the lotic stretches of tributaries, because those zones are the closest to the original pristine habitat for which those species are adapted to live. We assessed the patterns of species dominance using Whittaker plots and patterns of rarity using analysis of variance along the longitudinal and transversal gradients of Itaipu Reservoir.

Material and methods

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 (Figure 1). The Paraná River basin drains about 820,000 km^2. The reservoir inundated the former Sete Quedas Falls. 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 200m (Andrade, 1941). The Itaipu Reservoir is 151km long (or 170 km in at maximum water level), and has 1,350 km^2 of surface area of at the average operating level of the dam (220 m). The water level in the reservoir has an annual range of 0.6m. The average depth is 22 m and the average water volume is 29 x 10^9 m^3. The average residence time is 40 days and the water speed in the central area may reach 0.6 m/s. (Andrade *et al.*, 1988).

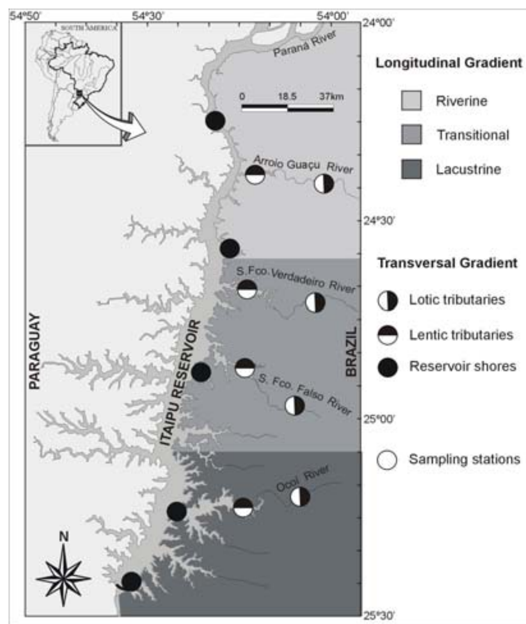

Figure 1. Location of the Itaipu Reservoir and the sampling stations

Sampling was conducted quarterly at 13 stations on the Brazilian side of the reservoir (Eastern margin, Figure 1), from March to December 1997 and from June to December 1998. We sampled the shores of the reservoir and the tributaries using sets of gill nets (2-to-16 cm mesh) and trammel nets (6-to-8 cm mesh). Fishing gears were set for 24-hours periods, checked at early morning, dusk and late evening. Species were identified according to

Britski *et al*. (1999). 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 1,000m^2 of nets per 24 hours.

The effects of longitudinal (river-dam) and transversal (upstream-downstream of tributaries) gradients and their interactions on the structure of fish assemblage 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 levels of nutrient availability. The transitional zone has a 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 concentrations of dissolved nutrients (see Pagioro, 1999, for detailed description of the limnological gradient in the 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 shores of the reservoir are colonized by floating and submersed macrophytes, present slow water speed. This zone is affected by dam operations due to water level variation.

Patterns of species dominance in longitudinal and transversal gradients were compared using species-abundance curves (Whittaker plots, Krebs, 1999). These plots reveal species with the greatest contribution in total abundance, dominance and uniformity patterns for each zone. Species with frequency less than 1% of total CPUE along the spatial gradients were considered to be rare. A Model I factorial analysis of variance (i.e. fixed factors, Zar, 1999) was employed to test the hypothesis that the proportion of rare species is affected by longitudinal and transversal gradients and their interactions. Tests of interactions are important because provide information about the degree of dependence of the effect of one factor on the effects other factors.

Results

We captured 8,675 individuals belonging to 24 families and 85 species in the Itaipu Reservoir (Table 1). Patterns of dominance along the longitudinal gradient and their interaction with the transversal gradient are shown in Figure 2. In the riverine zone, the highest total relative abundance was estimated for reservoir shores, whereas lotic stretches of the tributaries had the lowest values. In lotic and lentic stretches of the tributaries *P. granulosus* was the dominant species. Along the reservoir shores, *P. lineatus* was on average the dominant species. The introduced piscivore *C. monoculus* had the highest variability in relative abundance, indicating that its rank, on average 5th, may change in time.

In the lotic stretches of the tributaries of transitional zone, *H. auroguttatus*, *P. granulosus* and *L. rostratus* showed moderate dominance (Figure 2). The lentic stretches of the tributaries showed the highest total relative abundance, with strong dominance of *L. rostratus*. The second-ranking species, *Loricaria sp.*, had the highest variability. The introduced piscivore *P. squamosissimus* was on average the dominant species in the reservoir shores. The species *P. granulosus* and *A. affinis* (ranked 3rd and 5th) had the highest range in relative abundance, indicating that their ranks may not be stable over time. In the lotic and lentic stretches of the tributaries of lacustrine zone, the curimatid *S. insculpta* dominated, followed by the cichlid *C. niederleinii* and the doradid *T. paraguayensis*. The highest relative abundance of lacustrine zone was recorded along the reservoir shores. The dominant species on average was the introduced piscivore *P. squamosissimus*, followed by *A. affinis*, which had highest range in relative abundances.

Only the longitudinal gradient had significant effect on the proportion of rare species (ANOVA; $F=6.02$; $P<0.01$; Table 2). The effects of longitudinal and transversal gradients were independent as indicated by the non-significant interaction between them. The highest average proportion of rare species along the longitudinal gradient occurred in the transitional zone, followed by the riverine zone (Figure 3a and 3b). In that gradient, the reservoir shores had the highest average proportion of rare species in the transitional zone, while the lentic stretches of tributaries had the highest average in the riverine zone. In the lacustrine zone, the reservoir shores and lotic stretches of tributaries had the highest average proportion of rare species (Figure 3c). The lotic stretches of tributaries of the lacustrine zone had the highest variability in the proportion of rare species along of the study period. Emphasis should be given to the fact that the average proportion of rare species decreases in the proximity of the dam, showing the deleterious effects of impoundment.

Table 1. Systematic position of species collected during the period of study 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* (Gosline, 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)

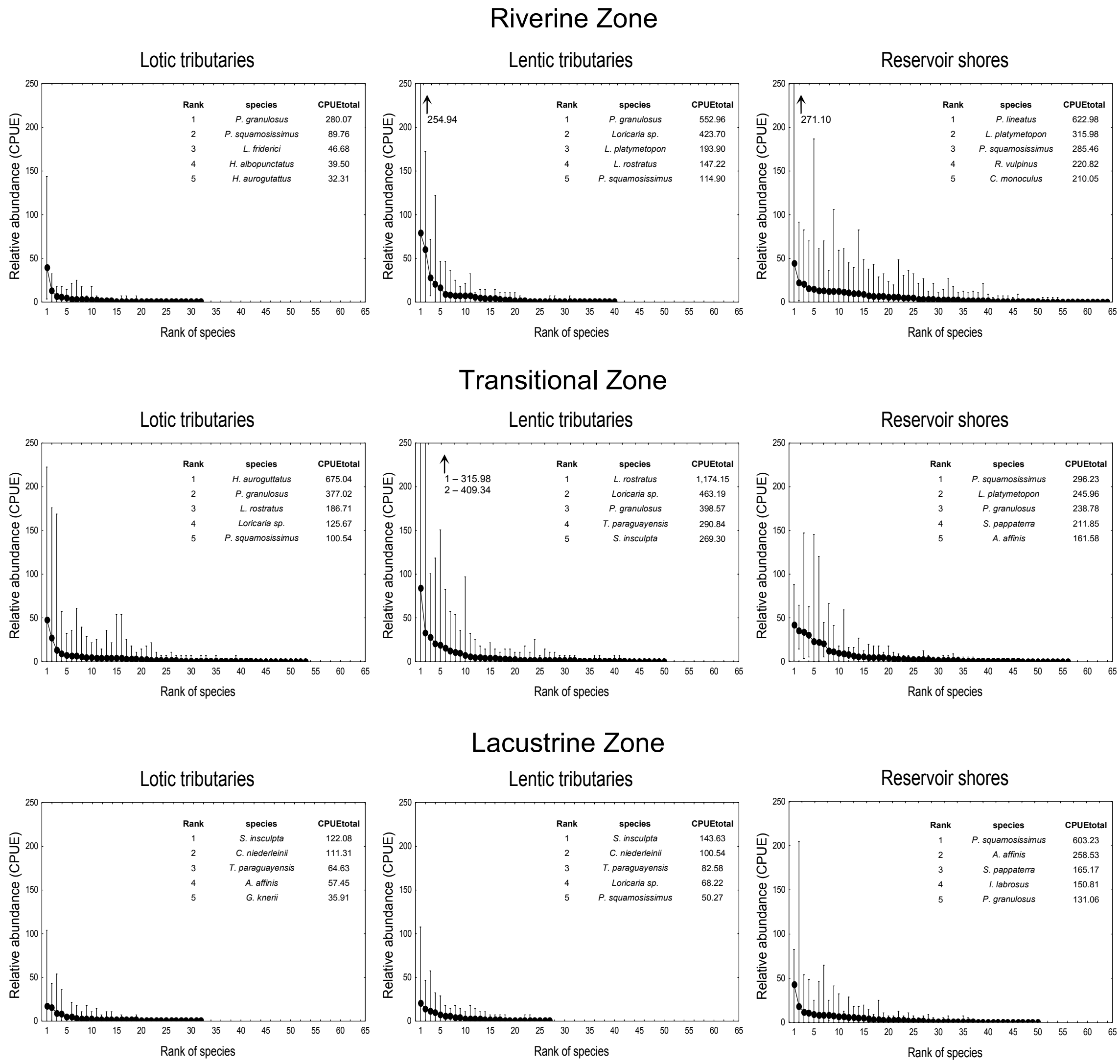

Figure 2. Species-abundance curve along the longitudinal and transversal gradients of the Itaipu Reservoir (vertical bars represents the maximum and minimum values)

Table 2. Factorial analysis of variance for proportion of rare species in spatial gradients of the Itaipu Reservoir (DF = degrees of freedom)

	DF	Proportion of rare species	
	(effect; error)	F	P
Longitudinal gradient (1)	2; 82	6.02	0.00
Transversal gradient (2)	2; 82	0.55	0.58
(1)*(2)	4; 82	0.48	0.75

Discussion

Dominant species varied along the spatial gradients. The riverine zone along the longitudinal gradient showed the dominance of *P. granulosus* and *P. lineatus*. These are migratory species whose spawning habitat lies in the floodplain and tributaries (Vazzoler *et al.*, 1997). *P. granulosus*, dominant in the lotic and lentic stretches of the tributaries of the riverine zone, used to occur only downstream Sete Quedas Falls, which constituted a geographical barrier to its dispersion (Zawadzki *et al.*, 1996). This species reached the upper stretches of the Paraná River after of the impoundment flooded the falls, eliminating the barrier. The migratory *P. lineatus*, dominant in the reservoir shores of the riverine zone, was moderately abundant in the first years after the impoundment (Benedito-Cecílio *et al.*, 1997). In that phase, the feeding conditions were exceptionally good because of the drowning of abundant tree vegetation, where its food (periphyton) develops (Benedito-Cecílio and Agostinho, 2000). This species uses the big rivers of the upper stretch of the floodplain upstream for reproduction; juveniles develop in the floodplain of the Upper Paraná River during the first two years (Agostinho *et al*., 1993).

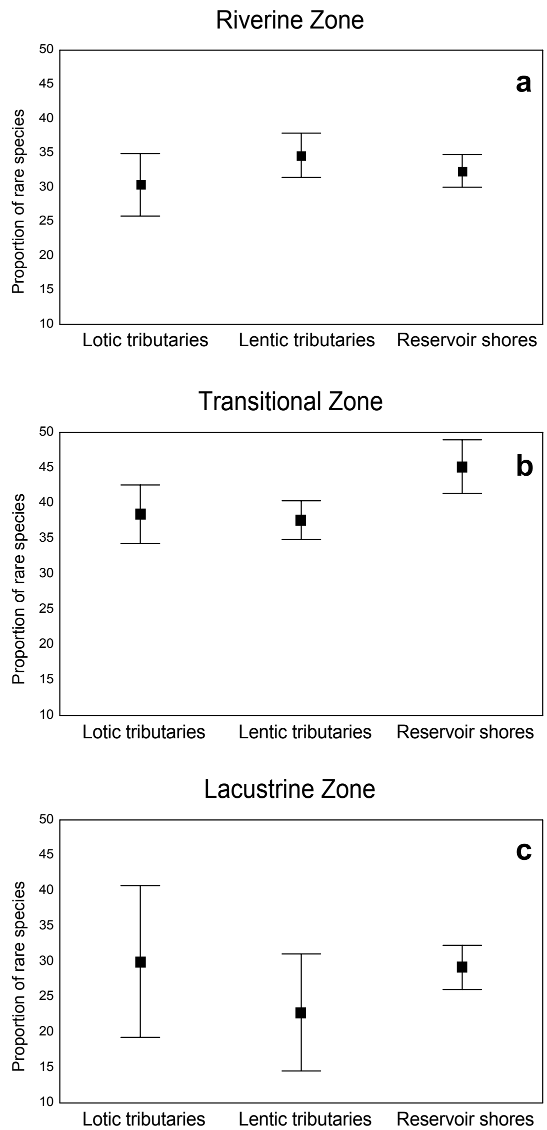

Figure 3. Mean and standard error for the proportion of rare species in the combinations of the longitudinal and transversal gradients of the Itaipu Reservoir

The high spatial heterogeneity and productivity of the floodplain upstream influence the high variability in the species abundance in the reservoir shores of the riverine zone. The non-native species *C. monoculus* was the 5th most abundant species in the reservoir shores. This is a predatory species, native from the Amazon Basin, and is widely appreciated by recreational fishermen due to its more aggressive behavior (it will "fight" when hooked). The successful colonization by *C. monoculus* depends on the presence of vast littoral zones, because this species use shallow and near-shore areas for spawning (Williams *et al*., 1998).

In the transitional zone the high relative abundance of *L. rostratus*, *H. auroguttatus* and *P. granulosus* may be related to the presence of the large tributaries São Francisco Verdadeiro and São Francisco Falso. These species prefer lotic and semi-lotic environments, directly associated with their feeding habits (*L. rostratus* and *H. auroguttatus* are detritivores; *P. granulosus* is an omnivore; see Agostinho *et al*., 1997). The estuaries of these tributaries in the reservoir form wide semi-lotic environments in this zone with high diversity of habitats. This diversity of habitats in the transitional zone may be related to the high variability in the species abundance in the lentic stretches of tributaries and reservoir shores. Agostinho *et al.* (1997) state that *L. rostratus* is rare and sporadic in some environments upstream of the reservoir, in our study it was dominant in the lentic stretches of the tributaries of the transitional zone. How this species prefer semi-lotic environments, it was rare in the pre-impoundment phase and became abundant in the Ocoí, São Francisco Verdadeiro and Falso Rivers after dam closure (Benedito-Cecílio *et al*., 1997). The piscivore *P. squamosissimus* was dominant in the reservoir shores of the transitional zone. This species is typically found in littoral areas that have high spatial heterogeneity and high prey availability.

The distribution of two dominant mud-eater species in the lotic and lentic stretches of the tributaries in the lacustrine zone, *S. insculpta* and *A. affinis*, may be related to enrichment in bottom deposits in the littoral areas and with a larger periphytic surface available, mainly over inundated terrestrial vegetation close to the dam. These two species have an insignificant role in professional fishing (Agostinho *et al*., 1994), but they are important links in the food web, since they transform slime, detritus and benthos in energetic components available to upper trophic levels (Benedito-Cecílio and Agostinho, 2000). *P. squamosissimus* also dominated in the reservoir shores of the lacustrine zone, which is an environment that can be severely restrictive to the occupation by fishes, because of thermal and chemical stratification and decrease of the range of exploitable microhabitats. The low variability in the relative abundance of species in the lacustrine zone may be directly related to these restricting conditions. *P. squamosissimus* was introduced from the Amazon basin into the upper stretches of the basin in 1968

(Cruz *et al.*, 1990) and lately has been the main species in the commercial fisheries in the reservoirs of the Paraná River (Torloni *et al.*, 1993). Its success in reservoirs may be attributed to its reproductive strategy. This species produces small, pelagic and buoyant eggs spawned in several batches during the reproductive period (Agostinho *et al*., 1999).

Patterns of rarity of fish assemblage in the reservoir were significantly affected by longitudinal gradient. The riverine zone of the longitudinal gradient has direct influence of the Paraná River, that dictate the limnological characteristics along this gradient (e.g. most of the organic and suspended material that reach at the Itaipu Reservoir has its origin in the Paraná River main channel, Pagioro and Thomaz, 2002) and constitutes temporary habitats for initial life stages of some species (Oliveira *et al*., 2001). The riverine zone is the main habitat for several species that are adapted to the former pristine stream habitat. Those species may also spend some of his 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). This tendency for higher species diversity in the riverine zone may be an explanation for the high number and proportion of the rare species.

The higher proportion of rare species in the transitional zone may be related to the higher abundance of floating and submerged aquatic macrophytes in the margin areas (Oliveira, 2000). Aquatic plants are important habitats for fish because they increase spatial heterogeneity and availability of feeding resources (Thomaz and Bini, 1999). Also, in this intermediate or ecotone environment, both lentic and lotic species may co-exist, using the habitat temporally; hence the proportion of rare species tends to increase. The lacustrine zone of the Itaipu Reservoir presented the lowest average proportion of rare species. Our results corroborated those of Vaughn and Taylor (1999), according to whom one of the deleterious effects of impoundment is the decrease in the proportion of rare species with the proximity of dam. The lacustrine zone is directly influenced by operational procedures of the hydroelectric plant, while depth, physical and chemical characteristics make the occupation of the environment difficult.

From the understanding of the patterns of dominance and rarity along spatial gradients, we suggest the following management actions for reservoirs: (i) protection and restoration of critical habitats, in special conservation of the habitat quality in the floodplain upstream and in the tributaries of the reservoir to maintain the patterns of high relative abundance and high proportion of rare species in the riverine and transitional zones (longitudinal gradient) and their interactions with the transversal gradient; (ii) increase of protected bank area and restoration of marginal vegetation in the lacustrine zone (longitudinal gradient), in order to the enhance shelter availability, habitat complexity and diversity and, consequently, promote the maintenance of populations of rare species. Habitats structurally more complex have a large variety of microhabitats which supporting more species than do simple habitats; (iii) implement case studies about the effect of species introductions, for example with *P. squamosissimus*, to provide advice to managers; and (iv) maintenance of a monitoring program that will allow to study the dynamics of the patterns of dominance and rarity.

Acknowledgements

We are grateful to the Postgraduate Program in Ecology of Continental Aquatic Environments and the Center of Research in Limnology, Ichthyology and Aquaculture of the State University of Maringá for logistic support. We would like to acknowledge the assistance in the field and laboratory of Vitor de S. Ferreira, Fabiane Abujanra, Edson K. Okada, Vanderlei P. da Silva, Angela M. Ambrósio, Carla S. Pavanelli, Sebastião Rodrigues, Francisco A. Teixeira and Gilmar Baumgartner. We also thank Horácio F. Júlio Jr. and José R. Verani for valuable comments on the manuscript and Maria S. R. Arita for reference normalization. Itaipu Binacional and Capes provided funding for this project.

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Received on August 29, 2002.
Accepted on October 24, 2002.