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Environmental factors predicting fish community structure in two neotropical rivers in Brazil

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In order to assess the organization patterns of the fish communities in the Jogui and Iguatemi rivers, we collected fish with gill nets tri-monthly from November 1999 to August 2000. *Hypostomus ancistroides* and *Parauchenipterus galeatus* were the most abundant species in the Jogui and Iguatemi rivers, respectively. Longitudinal variation was more important than seasonal in determining the species composition in both rivers, and the difference between seasons was not statistically significant. Altitude was the most important factor determining species distribution.

Com o objetivo de identificar os padrões de organização das comunidades de peixes dos rios Jogui e Iguatemi nós amostramos peixes através de redes de espera trimestralmente entre Novembro/1999 e Agosto/2000. *Hypostomus ancistroides* e *Parauchenipterus galeatus* foram as espécies de peixes mais abundantes nos rios Jogui e Iguatemi, respectivamente. A variação longitudinal foi mais importante que a sazonal na determinação da composição de espécies em ambos os rios e a diferença entre estações não foi significativa. A altitude foi o fator mais importante na determinação da distribuição das espécies.

Key words: Community ecology, Freshwater fish, Environmental factors, Neotropical rivers.

Introduction

Biological communities vary in time and space, as a result of differences in habitat structure (Gorman & Karr, 1978), resource availability (Grenouillet *et al*., 2002), and biogeographical patterns (Jackson & Harvey, 1989; Tonn *et al*., 1990; Matthews & Robison, 1998), among others. Knowledge and prediction of community characteristics in response to different environmental factors is one of the main objectives of community ecology.

The importance of environmental variables to fish communities is dependent on the scale of analysis. On a small scale, biotic factors play an important role in community organization; however in large-scale studies, biogeography and abiotic factors are the main determinants of fish communities (Jackson *et al*., 2001).

The majority of studies attempting to quantify the effects of environmental factors on fish communities in streams and rivers have been conducted in temperate areas (Gorman & Karr, 1978; Poff & Allan, 1995; Martin-Smith, 1998; Pires *et al*., 1999; Oberdorff *et al*., 2001). Among the fewer, comparable studies in tropical regions, especially the Neotropics, are the studies of Garutti (1988), Uieda & Barreto (1999), Mazzoni & Lobón-Cerviá (2000), Abes & Agostinho (2001), Pavanelli & Caramaschi (2003), Chernoff *et al*. (2004), Hoeinghaus *et al*. (2004), Layman & Winemiller (2005), and Arrington & Winemiller (2006).

Studies in the basin of the Upper Paraná River are concentrated in southeastern Brazil (states of São Paulo and Paraná). There have been few studies in the western portion of this basin, although the area is less impacted and contains no large dams. The existing studies were carried out in the lower portion of the Ivinhema basin, with regard to the Paraná River floodplain (Agostinho *et al*., 2000; Petry *et al*., 2003 a, b). For the Iguatemi River basin, studies have examined fish species associations, stream fish communities, and variations in fish diversity (Súarez *et al*., 2003, 2005 and 2006).

The present study investigated the following questions: 1) Which source of variation (longitudinal *vs* temporal) is more important in determining fish composition in the Jogui and Iguatemi rivers? 2) Which environmental factors are most important in determining species distribution?

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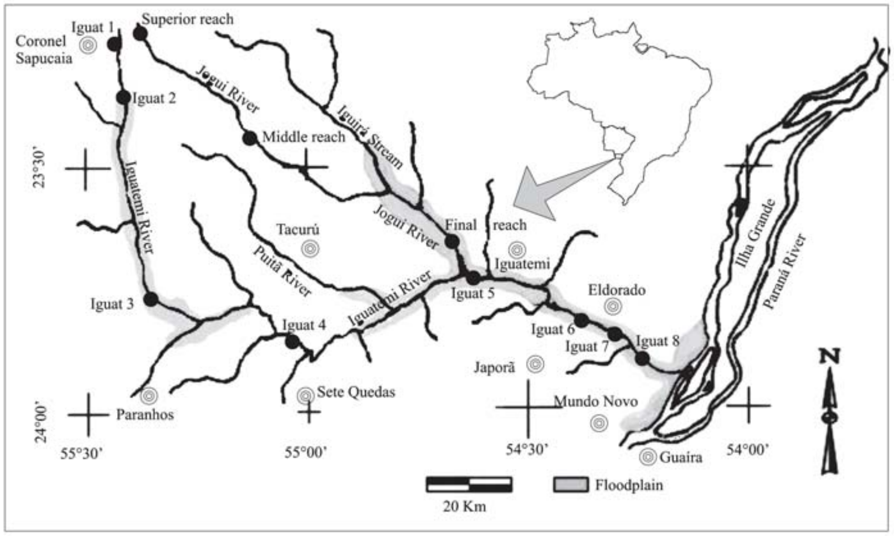


Fig. 1. The Iguatemi River basin, showing the sampling sites in the Jogui and Iguatemi rivers.

Methods

Study Area

The Iguatemi River basin has been strongly impacted by human activities, with extensive deforestation and siltation, mainly due to agriculture.

Eight sampling sites were defined in the Iguatemi River, and three in the Jogui River (Fig. 1). The sites were selected according to their ease of access by land, because both rivers contain several stretches of rapids that prevent the use of boats.

The Iguatemi River is approximately 300 km long and is located in the southern part of the state of Mato Grosso do Sul. It is a floodplain river, with extensive flooded areas and marginal lakes in the lower portions. In the middle portion, the floodplain is much smaller, and includes several marginal lakes with little connection to the river.

The predominant vegetation is savanna (cerrado), alternating with semidecidous seasonal forest. The mouth of the Paraná River is located at 226 m altitude, approximately 20 km from Sete Quedas Falls, an important biogeographic barrier now submerged in the Itaipu Reservoir.

Farming and ranching are the main economic activities. The Brazilian part of the area was logged intensively in the past, and timber extraction is still ongoing in Paraguay. Together, deforestation and agriculture cause siltation in much of the Iguatemi basin.

The sampled sites, in the direction from the headwaters to the mouth, show a reduction in mean water velocity and an increase in turbidity and volume (Table 1). The middle portion of the Jogui River is located between two stretches of riffles. The lower portion has an extensive floodplain area, and is one of the most silted parts of the basin, with many sandbanks in the dry season. In the middle stretch (Iguat-3 to Iguat-5), the Iguatemi River channel is well defined, with practically no flooded areas, and has relatively high banks (± 2.5 m). In many portions there are small riffles with rocks that impede navigation. Both rivers have practically no aquatic macrophytes; there are stands of grasses along their banks in the lower portion of each basin.

Table 1. Mean values and standard deviations for environmental characteristics of sampling points in the Jogui and Iguatemi rivers from November, 1999 to August, 2000. Conduct. = Water conductivity; DO = Dissolved oxygen; Turb. = Turbidity; Temp. = Water temperature; Veloc. = Water velocity; Alt. = Altitude.

Sites	pH	Conduct.	DO	Turb.	Temp.	Veloc.	Alt.
Jogui River							
Upper reach	6.1±0.2	23.3±4.8	8.0±1.2	11±11.5	20.7±1.0	0.35±0.1	468
Middle reach	6.4±0.3	19.3±0.7	7.7±0.6	33.3±12.0	23.0±0.5	0.52±0.4	324
Lower reach	6.3±0.8	8.3±1.3	7.3±1.3	113.5±41.5	22.9±3.9	0.28±0.1	250
Iguatemi River							
Iguat-1	5.6±0.4	34.2±3.9	8.3±1.3	14.3±5.6	20.3±1.9	0.51±0.1	482
Iguat-2	6.0±0.5	24.2±3.0	7.5±1.5	151.8±257.6	21.5±1.2	0.40±0.1	400
Iguat-3	6.0±0.4	8.8±1.5	7.0±0.9	86±20.6	22.6±2.1	0.47±0.2	352
Iguat-4	6.2±0.6	9.3±0.7	7.6±1.3	112±24.0	20.7±4.0	0.44±0.1	295
Iguat-5	6.2±0.6	9.8±1.7	7.4±0.9	128.8±53.6	22.8±4.1	0.39±0.2	247
Iguat-6	6.0±0.6	9.3±2.3	7.6±1.5	122.3±55.1	21.4±2.6	0.44±0.3	235
Iguat-7	6.3±0.6	26.5±1.4	7.0±2.0	137.8±76.4	23.4±2.8	0.37±0.3	230
Iguat-8	6.9±0.8	9.7±35.2	7.5±1.7	123.3±29.8	21.3±4.5	0.36±0.1	226

Data Collection

We carried out four sampling excursions: in November 1999, February 2000, May 2000, and August 2000. Samples were collected using a set of nylon gillnets with different mesh sizes (20, 30, 40, 50, 60, 70, 80, 110 mm) between adjacent knots, 10 m long and 1.5 m high. The gillnets were placed in the afternoon and lifted the next morning (approximately 15h). At each sampling site, a set of environmental factors was recorded (pH, conductivity, dissolved O_2, water velocity, water temperature, turbidity, and altitude).

Specimens were fixed in 10% formalin and preserved in 70% ethanol. Counting and identification were done using the identification key of Britski *et al*. (1999) and by comparison with specimens at the Museu de Zoologia of the Universidade de São Paulo (MZUSP).

Data Analyses

We performed a cluster analysis with the Morisita-Horn index and unweighted pair group method average (UPGMA) as the clustering method to describe the spatial and temporal pattern of similarity in species absolute abundance among samples. The similarity matrices were compared with the cophenetic matrix using a Mantel test aimed at determining data distortion in the clustering process. The value of rc = 0.80 for the cophenetic coefficient of correlation was adopted as a fidelity criterion (Romesburg, 1985).

To complement the cluster analysis results, we utilized analysis of similarity (ANOSIM), a non-parametric tool proposed by Clarke (1993) in order to see if there is a significant difference in fish species composition among the river sites and the seasons. We did not perform a two-way ANOSIM because of the absence of some species from some samples, which did not permit us to calculate interactions between factors. We used a Bray-Curtis distance to obtain a dissimilarity matrix, and this analysis was performed using an R package (R Development Core Team, 2005).

The abundance data for species that occurred in two or more samples and environmental factors were used in a canonical correspondence analysis (CCA; Ter Braak, 1986). This is one of the best methods for direct gradient analysis in community ecology (Ter Braak, 1986; Rodriguez & Lewis, 1997), for describing the major trends in species distribution and environmental factor correlates. The environmental variables were transformed to log2+0.1. This procedure was carried out with an R package, using a CCA function in the Vegan package. The significance of environmental factors was assessed using the "envfit" function, which after determining r^2 for environmental variables, uses a permutation procedure to define the significance of each environmental variable (999 permutations) on all axes conjointly. If one variable shows moderate correlation with axis 1 but not with axis 2, its general importance may be non-significant.

Table 2. List of species, number of individuals, and frequency of occurrence of fish collected in the Jogui and Iguatemi rivers, in the period of November, 1999 to August, 2000.

	Jogui River		Iguatemi River	
	No. Indiv.	Freq. Occ. %	No. Indiv.	Freq. Occ. %
Characiformes				
Anostomidae				
Leporinus friderici	5	30.0	21	34.5
Leporinus obtusidens	-	-	5	13.8
Leporinus sp.	-	-	2	6.9
Schizodon borellii	1	10.0	10	20.7
Schizodon intermedius	-	-	1	3.4
Schizodon nasutus	2	10.0	5	10.3
Characidae				
Acestrorhynchus lacustris	2	20.0	1	3.4
Astyanax altiparanae	7	30.0	9	20.7
Astyanax eigenmanniorum	18	40.0	4	3.4
Myleus levis	-	-	1	3.4
Oligosarcus paranensis	2	20.0	9	3.4
Roeboides paranensis	1	10.0	-	-
Salminus brasiliensis	2	20.0	1	3.4
Serrasalmus marginatus	-	-	11	13.8
Serrasalmus maculatus	2	20.0	-	-
Curimatidae				
Steindachnerina insculpta	3	20.0	2	6.9
Cynodontidae				
Rhaphiodon vulpinus	-	-	3	10.3
Erythrinidae				
Hoplias malabaricus	5	40.0	6	13.8
Prochilodontidae				
Prochilodus lineatus	4	20.0	2	6.9
Siluriformes				
Auchenipteridae				
Auchenipterus nuchalis	-	-	2	6.9
Parauchenipterus galeatus	2	10.0	33	20.7
Parauchenipterus striatulus	-	-	5	10.3
Ageneiosidae				
Ageneiosus brevifilis	-	-	1	3.4
Ageneiosus valenciennesi	-	-	1	3.4
Callichthyidae				
Hoplosternum littorale	3	20.0	-	-
Doradidae				
Doras eigenmanni	-	-	2	6.9
Pterodoras granulosus	1	10.0	5	6.9
Hepapteridae				
Pimelodella gracilis	4	20.0	-	-
Rhamdia cf. *quelen*	4	30.0	2	3.4
Loricariidae				
Hypostomus ancistroides	24	40.0	15	20.7
Hypostomus strigaticeps	17	30.0	20	13.8
Hypostomus sp.	-	-	17	10.3
Loricariichthys platymetopon	8	20.0	1	3.4
Pimelodidae				
Hemisorubim platyrhynchos	2	20.0	10	20.7
Iheringichthys labrosus	1	10.0	-	-
Pimelodus fur	-	-	1	3.4
Pimelodus maculatus	1	10.0	-	-
Pimelodus ornatus	1	10.0	-	-
Pseudoplatystoma corruscans	1	10.0	1	3.4
Gymnotiformes				
Apteronotidae				
Apteronotus brasiliensis	1	10.0	-	-
Gymnotidae				
Gymnotus sp.	2	20.0	-	-
Sternopygidae				
Eigenmannia trilineata	1	10.0	1	3.4
Perciformes				
Sciaenidae				
Plagioscion squamosissimus	-	-	2	6.9

Table 3. Results of canonical correspondence analysis (CCA) for the fish communities in the Jogui and Iguatemi rivers. ns = non significant; *= significant to 0.05; **= significant to 0.01; ***= significant to 0.001.

	Jogui River			Iguatemi River		
Total "inertia"	2.869			5.746		
Water Characteristics	Axis 1	Axis 2	r^2	Axis 1	Axis 2	r^2
pH	0.15	-0.08	0.02 ns	-0.52	-0.22	0.31 ns
Conductivity	-0.88	-0.25	**0.83** **	0.20	0.80	**0.57** **
Dissolved oxygen	-0.36	-0.35	0.24 ns	0.57	-0.36	**0.40** *
Turbidity	0.87	0.18	**0.79** **	-0.82	-0.27	**0.72** ***
Water temperature	0.51	0.35	0.37 ns	-0.59	0.13	0.33 ns
Water velocity	-0.14	-0.21	0.06 ns	0.33	0.26	0.16 ns
Altitude	-0.98	-0.19	**0.99** ***	0.97	0.01	**0.89** ***
Explained variation (%)	33.9	22.6		15.0	9.2	

Results

In the Jogui River, we obtained 134 individuals belonging to 31 species. In the Iguatemi River, we obtained 212 individuals belonging to 34 species. *Hypostomus ancistroides* was the most abundant species (24 ind.) in the Jogui River, followed by *Astyanax eigenmanniorum* (18); both occurred exclusively in the upper reaches (Fig. 1). In the Iguatemi River, the most abundant fish species was *Parauchenipterus galeatus* (33), followed by *Leporinus friderici* (21) and *Hypostomus strigaticeps* (20). Table 2 lists the species and their total abundances in each river.

The cluster of species abundance in the Jogui River (Morisita-Horn) clearly separates the upper reach from the middle and lower reaches (Fig. 2). For the Iguatemi River, the samples were also segregated according to their position in the drainage basin (Fig. 2); however, this relationship was not as evident as in the Jogui River. Headwater sites showed low seasonal variation compared to lowland sites.

We detected significant differences in the species compositions in the Jogui and Iguatemi lotic gradients (Jogui ANOSIM R = 0.952; P = 0.02; Iguatemi ANOSIM R = 0.352; P = 0.01). However, there were no differences between seasons (Jogui ANOSIM R = -0.385; P = 0.984; Iguatemi ANOSIM R = -0.047; P = 0.799).

The CCA results showed that altitude is the most important factor determining fish distribution in both rivers (Table 3 and Fig. 3), followed by turbidity and conductivity in the Jogui River, and by water temperature and dissolved oxygen in the Iguatemi River. A larger portion of the variation was explained by environmental factors in the Jogui River (56.4%) than in the Iguatemi River (23.4%).

The importance of altitude in fish communities also can be seen in the altitudinal species distribution (Fig. 4): *H. ancistroides*, *H. strigaticeps*, and *A. eigenmanniorum*, among others, occurred only in high-altitude reaches in both rivers; whereas *P. galeatus*, *S. marginatus*, and *L. platymetopon*, among others, occurred only in the lower reaches.

Discussion

The numerical prevalence of *H. ancistroides* and *A. eigenmanniorum* in the Jogui River, which occurred mainly in headwaters, to the detriment of species with wide distributions or characteristic of the lower reaches, was the main factor that led to the separation among the sampled points in the cluster analysis, separating the upper reaches of the Jogui River from the lower ones.

In the Iguatemi River, *P. galeatus* was most prevalent, followed by *L. friderici* and *H. strigaticeps*. The first species occurred predominantly in the lower reaches, the second was widely distributed in the basin, and *H. strigaticeps* occurred predominantly in the upper reaches, also leading to separation of the initial and final portions of the river.

This clear longitudinal differentiation in interaction, with

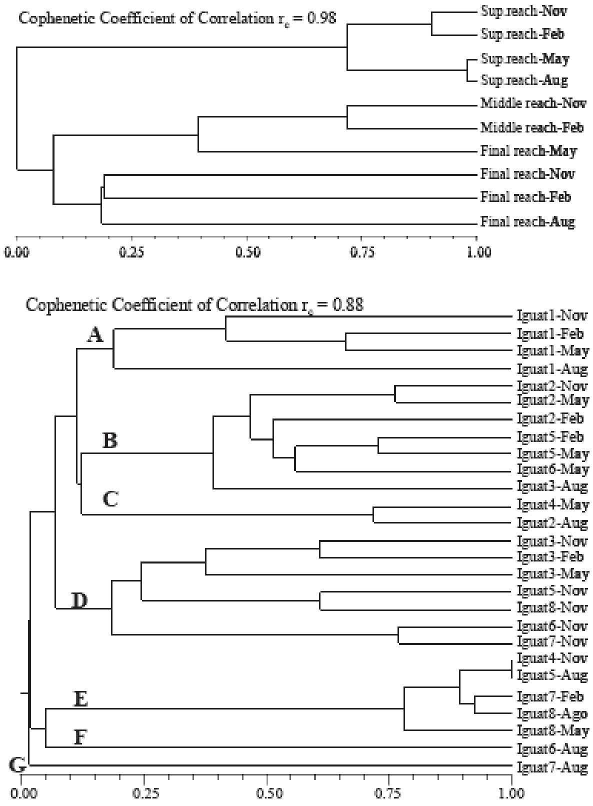
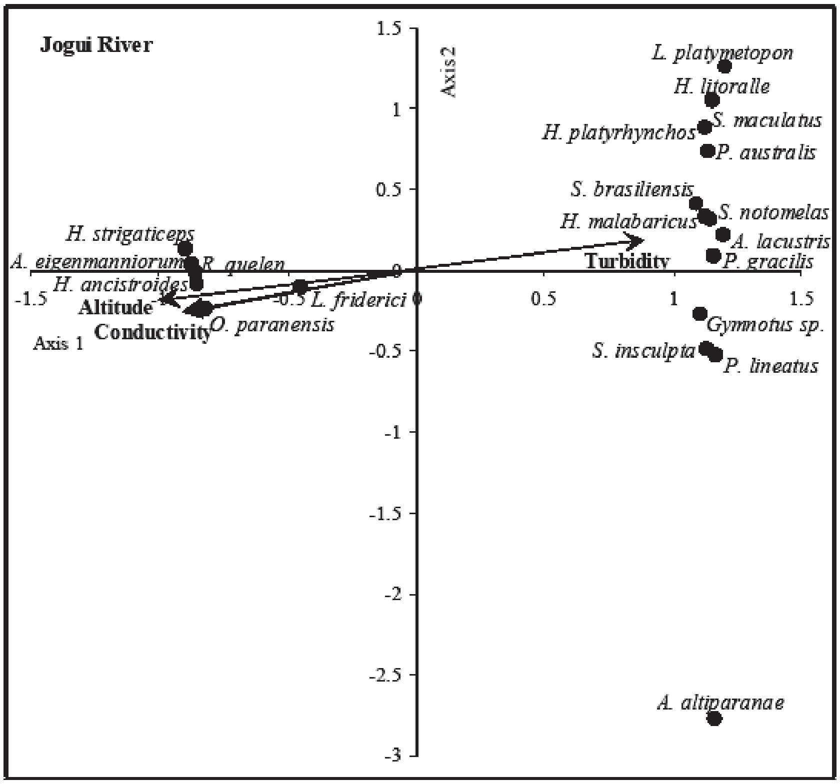


Fig. 2. Similarity dendrogram of fish communities in Jogui River (above) and Iguatemi Rivers (below).



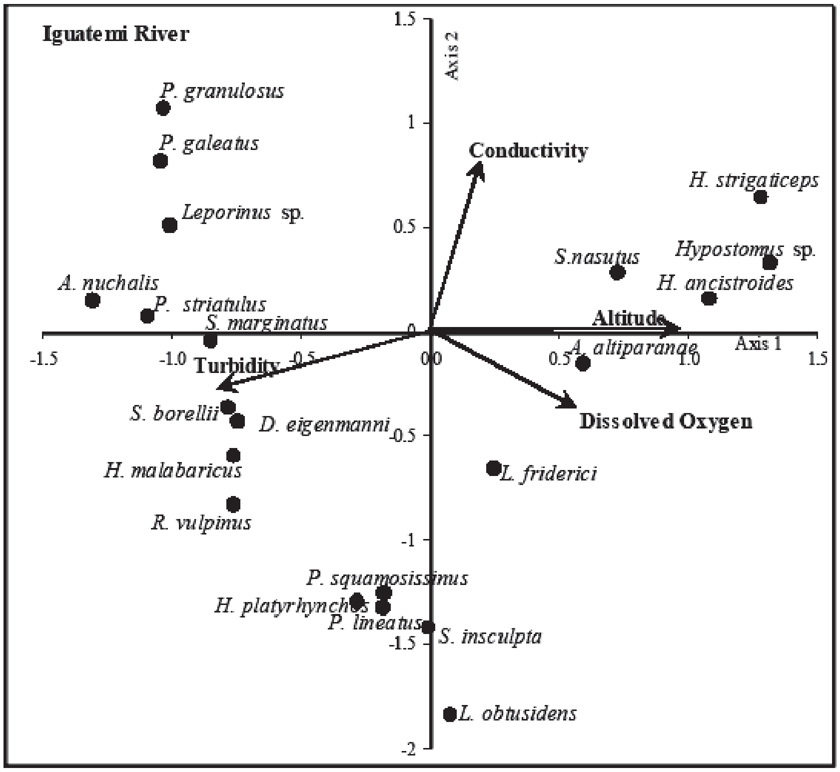


Fig. 3. Scatterplot of canonical correspondence analysis (CCA) for the fish communities of the Jogui and Iguatemi Rivers.

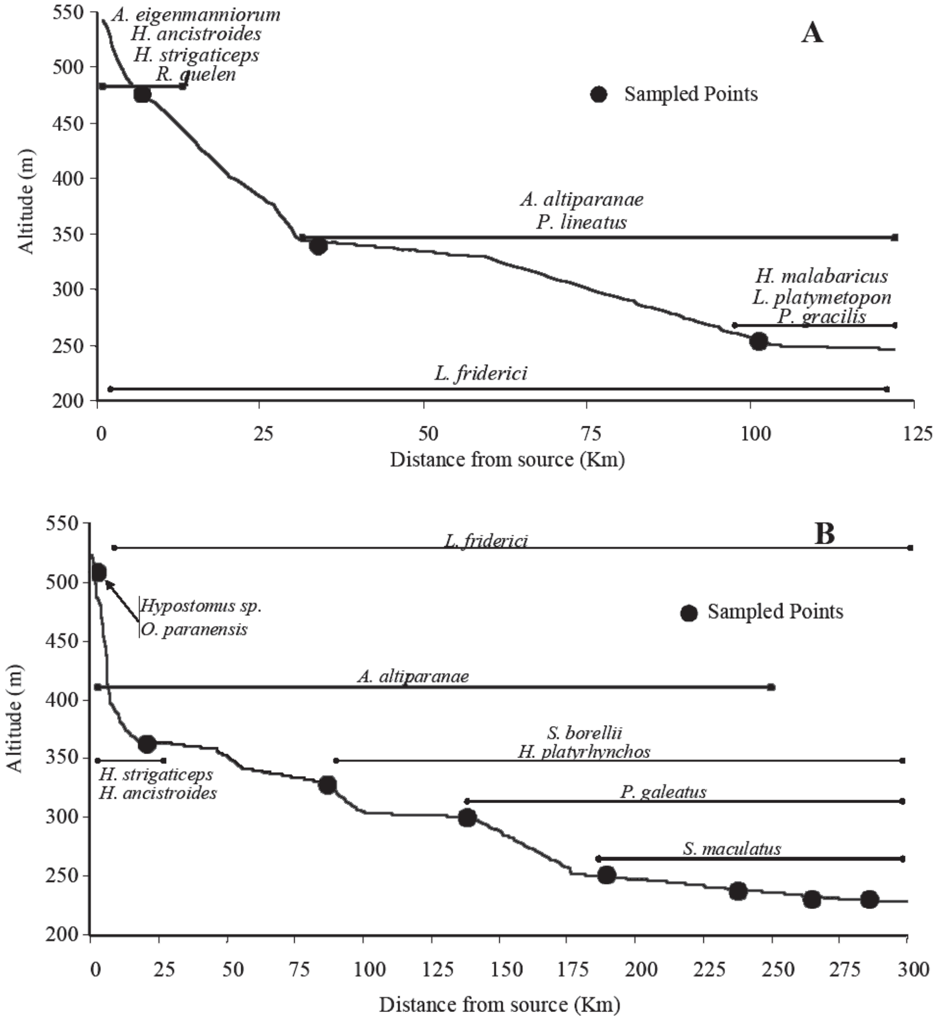


Fig. 4. Altitudinal distributions of the main fish species in the Jogui (A) and Iguatemi (B) rivers. Black dots represent sampling sites. Horizontal black lines represent species distribution range.

no temporal variation in species composition, suggests that spatial differences among sites are more important than temporal differences in environmental characteristics in to determining species occurrence.

In the Cinaruco River (Venezuela), Arrington & Winemiller (2006) suggested a strong habitat influence on fish and macroinvertebrate species composition, with nonrandom associations of species among habitats. Although this study covered only a flooded portion of the river, similar results were found in other studies (*e.g.*, Bhat, 2003; Pavanelli & Caramaschi, 2003; Hoeinghaus *et al*., 2004) where habitat characteristics and migration dynamics determined species distribution.

According to the neutral theory, local communities are composed in accordance with combined stochastic and deterministic processes, where local composition can result from random combinations of the regional species pool (Hubbel, 2001). On the other hand, Peres-Neto (2004) found that biotic interactions may not play an important role in determining local species composition, and environmental constraints act to select those species from the regional species pool which respond similarly to environmental factors.

Discussing the excess of rare species in natural communities, Magurran & Henderson (2003) suggested that communities possess two groups of species, one composed of persistent species that show strong associations with local environmental characteristics, and a second composed of occasional species for which their occurrence is generally stochastic and regulated by migration rates.

In our study, we observed that headwater sites showed smaller temporal variation compared to lower sites. This result may corroborate the hypothesis about the role of stochastics in species composition, as a result of high migration rates at sites with larger volume and smaller hydrological variation compared to headwaters (Taylor & Warren, 2001). Similar results were found by Langeani *et al*. (2005), comparing riffle and pool communities in the Tietê River basin (Upper Paraná River).

Analyzing assemblage organization in stream fishes, Grossmann *et al*. (1998) suggested that species composition changes seasonally, although habitat use by the resident species does not change. Therefore, the importance of seasonality is dependent on the migration rate. In the Iguatemi River basin, the existence of many rapids from the headwaters to the middle portion may reduce migration and consequently its importance for species composition. This pattern corroborates the observations of Súarez & Petrere Júnior (2003) who found that migration influenced species co-occurrence only slightly. However, these studies do not eliminate the importance of biotic influences on fish communities, and a recent study by Gravel *et al*. (2006) suggested that competition and stochastic exclusion can both simultaneously drive community dynamics and structure species assemblages.

Poff (1997) suggested that hydrological variables limit species distributions, leading to different assemblages according to habitat characteristics. In our study, there was a clear differentiation between the initial and final portions of the rivers, which may result from differences in migration ability of fish species.

In the Jogui River, three variables explained 56.4% of the variation in species composition. This result and a stronger correlation between altitude and conductivity may be due to the small number of sample sites, which simplified the longitudinal gradient and increased the apparent difference in species composition. For the Iguatemi River, the existence of rapids along the river and the smaller floodplain area along most of the river make this gradient more complex, and therefore it is difficult to explain most of the species distributions. Associated with this, intense rains during the sampling period altered the environmental characteristics, increasing the conductivity and turbidity of sites Iguat-2 and Iguat-7 in February.

The settling and occupation of a certain geographical area by a given species, is based on the criterion of physical continuity. Thus, a certain species would tend to occupy a continuous area in a homogeneous way and without any differentiation, in the absence of ecological obstacles to its dispersion (Vanzolini, 1970). On the other hand, Arrington & Winemiller (2006) found in the Cinaruco River (Venezuela) that although many species were forced to traverse extensive, inadequate habitats to colonize structured habitat patches, in their samples, the fish never occurred in habitats other than those for which they are specialized.

Some fish species occurred exclusively in the initial reaches, while others occurred exclusively in the final ones. Therefore, only a unified analysis of the entire river could demonstrate this segregation in the fish species distribution. We conclude that the differences between the headwater habitats and the floodplain act to reduce the migration rate of some fish species, leading to their segregation. This is corroborated by the CCA results which showed that longitudinal factors most affected the species distribution, according to River Continuum Concept (Vannote *et al*., 1980).

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