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To what extent are the fish compositions of a regulated river related to physico-chemical variables and habitat structure?

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Abstract Habitat structure and physico-chemical variables determine distribution of fish species at local scale. We aimed to determine influences of physicochemical variables and habitat descriptors on fish assemblage structure in a regulated river in Rio de Janeiro State, Southeastern Brazil. The tested hypotheses are that assemblages are determined by these features at the local scale, and that increased flow during the wet season increases fish abundance and richness because increased habitat availability. Samplings were conducted during the dry and wet seasons in four river reaches (upper, middleupper, middle-lower and lower), each one covering an extension of c.a. 1,000 m. Fish assemblage differed among the four river reaches because of different habitat structure. Three physico-chemical variables (turbidity, depth and transparency), four habitat descriptors (type of substrate, riparian cover, shelters and type of mesohabitat), erosion and anthropogenic influences were the most significant factors that determined fish assemblage structure. Seasonal changes in assemblage were less conspicuous irrespective of changes in physico-chemical variables. The hypothesis that habitat structure determines local fish assemblage structure was accepted, but only slight increase in fish abundance was found in the wet season. Overall, physico-chemical variables played a lesser role in

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Laboratório de Ecologia de Peixes, Universidade Federal Rural do Rio de Janeiro, IB/DBA, BR 465, Km 7, 23.890-000 Seropédica, RJ, Brazil e-mail: gerson@ufrrj.br structuring fish assemblages compared to habitat structure at the local scale.

Keywords Regulated rivers · Habitats · Ichthyofauna · Freshwater fishes · Physico-chemical variables

Introduction

Patterns of fish composition and diversity are determined by processes that act at multiple temporal and spatial scales (Heino et al. 2008; Oliveira and Tejerina-Garro 2010). Depending on the focus and the studied scale, several characteristics have been reported as determinants of fish community structure in rivers, including habitat structure (Gorman and Karr 1978; Angermeier and Karr 1983) and physico-chemical variables (Araújo et al. 2009). Overall, it may be difficult to determine patterns, and most studies of the environmental influences on fish assemblages only partially explain such relationships especially when environmental degradation by human activities is present.

Some studies have associated community fish structure with physico-chemical variables. Abes and Agostinho (2001) reported that increases in water temperature and conductivity were directly associated with abundances of *Astyanax bimaculatus*, whereas low pH values were positively associated with occurrence of *Hypostomus* aff. *derbyi* and *Gymnotus carapo* in rivers of the Paraná State, Southern Brazil. Penczak et al. (1994) reported that pH and conductivity influence the fish assemblage structure of two tributaries of

Paraná River, Southern Brazil. Fialho et al. (2008) observed that seasonal changes in flow regulate the fish/habitat relationship via physico-chemical variables, with decreased pH during wet season resulting in fish osmoregulation constraints. Furthermore, seasonal changes in environmental variables and anthropogenic interferences can modify existing physico-chemical characteristics affecting directly fish species (Araújo and Tejerina-Garro 2009).

Like other animals, habitat utilization by fishes is seldom random (Kramer et al. 1997). The type of substratum is a major factor determining fish community structure (Gorman and Karr 1978; Angermeier and Karr 1983). The proportions of different types of substrate are important for fish assemblages, because substrate provides structures for reproduction and feeding. Depending on the substrate composition and depth, nutrients for proliferation of plankton can be provided, thus increasing productivity (Guenther and Spacie 2006). Large boulders provide resting areas for fishes, while small stones and cobbles allow for greater aeration, which favors the embryos developing, buried in the bed (Talmage et al. 2002; Sullivan et al. 2004). Bedrock or large boulders provide more surfaces for concentration of aquatic invertebrates and for the establishment and growth of algae, biofilm and moss (Mueller and Pyron 2010). Clay banks in the riverbed are used for nest construction (Sullivan et al. 2004).

Although some species are able to use a large number of substrate types, some studies have reported preferences for a specific substrate type. For example, *Hypostomus nigromaculatus* prefers rocky substrate (Ferreira and Casatti 2006), while *Brycon behreae* prefers rocky and sandy substrates (Ribeiro and Villalobos 2010). *Cyprinus carpio* was positively associated with sandy substrate and negatively associated with muddy substrate (Crook et al. 2001). Rivers that have diverse types of substrate are associated with increased fish diversity because of the greater availability of niches for reproduction, feeding and other basic functions for the fish community (Gorman and Karr 1978; Mueller and Pyron 2010).

Rivers with marginal vegetation are more resistant to erosion, since riparian cover retains the majority of the sediment brought by runoff. Margins with rich structures such as logs, roots, rocks, vegetation and aquatic macrophytes provide a wide variety of shelters for fish species, increasing density and diversity (Schlosser 1987), reducing pressure from predators, and providing suitable habitats as rearing grounds (Bain et al. 1989; Gore et al. 1989; Flebbe and Dolloff 1995). Moreover, diversity of mesohabitats (pools, runs and riffles) favors fish species richness since many species have preferences for a given mesohabitat. Conversely, loss of habitat quality and quantity can lead susceptible species to drastic reduction of their populations or even to extinction.

River damming, impoundments and water withdrawal are among the most common alterations in habitat in rivers (Barthem et al. 1999; Joy and Death 2001; Stanford and Ward 2001) that cause serious impacts on fish communities (Holmquist et al. 1998; Park et al. 2003; Fukushima et al. 2007). Flooding areas upstream of dams results in habitat homogenization because of the decreased flow and drowning of marginal lagoons that are unsuitable for residence and/or spawning of many riverine species (Agostinho et al. 2004). The river reaches downstream from the dams have several habitats unavailable because of the reduction of flow variation caused by operations of the hydroelectric generation plants.

This study describes the fish fauna in a regulated tropical river, comparing fish assemblage structure along four river reaches with different habitats and physico-chemical features. We tested the hypotheses that physico-chemical variables and habitat structure determine composition and structure of fish assemblages at the local scale, and that increased flow during the wet season increases fish abundance and richness because of increased habitat availability. We posed the following questions: (1) Does the ichthyofauna differ in structure and composition among the different river reaches? (2) If so, what are the best predictors of such changes (habitat structure and/or physico-chemical variables)? (3) Is there seasonal (wet versus dry) variation in fish assemblage structure? We predicted that reaches with more structured habitats and more stable environmental variables would have more diverse and richer fauna compared to reaches with less structured habitats and more changes in environmental variables (Question 1). We also predicted that habitat structure would have more influence on fish assemblage than physico-chemical variables because these latter variables in rivers are expected to be stable, varying within the range of tolerance of most fish species whereas habitat structure are species-specific with fishes selecting that type of habitat that they are more adapted (Question 2). Finally, we predicted increased fish richness and abundance during the wet season because of increased habitat availability caused by increased water levels (Question 3).

Materials and methods

Study area and sampling

The Guandu River is 108.5 km long and is one of the most exploited systems in the southeastern Brazil because it supplies water for the Municipality of Rio de Janeiro and several industrial plants in its lower reaches. The headwaters (Lajes Stream) are located in the Sea Mountains at 414 m above sea level (Fig. 1). This river is impounded twice for hydroelectric purpose; firstly near the headwaters forming the Lajes Reservoir, and secondly approximately 10 km below the Lajes dam, forming the Pereira Passos reservoir. After these two hydroelectric plants the river falls c.a. 350 m, and drains floodplain areas until it reaches the estuary in Sepetiba Bay. The river receives about 160 m³s⁻¹ of water from another basin (Paraiba do Sul River basin), which is used upstream in another hydroelectric power plant and discharged into this system upriver of the Pereira Passos Reservoir (Fig. 1). In the middle-lower reaches, the river suffers its third impoundment to accumulate water for supplying 47 m³s⁻¹ to the Rio de Janeiro Municipality. Rainfall in the area can reach 300–400 mm in wet season (January-February) and about 100 mm in dry season (July-August) (Barbiére and Kronemberg 1994).

We sampled four river reaches of approximately 1,000 m long (Table 1): (1) upper reaches, with the



Fig. 1 Study area, Guandu River with indications of the four sampled reaches. 1, upper; 2, middle-upper; 3, middle-lower; 4, lower. WTP, water treatment plant. *Solid arrows*, river flow; *dashed arrows*, water transposition by pumping; *solid dashes*, dams

Reach	Substrate (%)	Shelter	Riparian cover	Anthropogenic influences	Erosion	Mesohabitat
1	Sand (40) Gravel(25) Clay(20) Rock(15)	Floating and submersed macrophytes Polygonacea Twigs	Trees shrubs grasses	Grazing	Moderate	Runs pools
2	Sand (60) Mud(40)	Floating macrophytes cattail	Shrubs grasses	Grazing agriculture	Moderate	Pools
3	Sand(40) Rock(35) Stones(25)	Twigs stones	Grasses pasture shrubs	Urbanized area	High	Riffles runs
4	Mud(70) Sand(30)	Floating macrophytes, grasses	Grasses	Industrial area	High	Pools runs

Table 1 Features of habitat structure for the four river reaches.1, upper; 2, middle-upper; 3, middle-lower; 4, lower

best environmental conditions, highly structured habitat, and different mesohabitat types; (2) middle-upper reaches, located upriver of an impoundment, with reduced flow and enlarged the river course, and substrate predominated by sand and mud; (3) middle-lower reaches, downriver from the impoundment, with turbulent waters, rocky and shingly substrate and eroded margins by human influence; and (4) lower reaches, mostly channelized, next to a large industrial development, with muddy substrate and tidal influence.

Fish sampling was conducted in two seasons (dry and wet) at seven locations of approximately 145 m long, equally spaced along the longitudinal extent of each river reach, covering different habitats (pools, riffles and runs). At each location, we used three monofilament gillnets (25 m×2.5 m) with mesh sizes of 25, 45 and 65 mm, fishing a total area of c.a. 1.312,5 m² in each river reach (62.5 m²×3 nets×7 locations). The seven sets of three nets were deployed along the river stretch in opposite margins, with three sets in one margin and four sets on the other margin. This procedure aimed to encompass most types of habitats. The nets were deployed during the afternoon and retrieved the following morning, after approximately 12 h. Relative abundance (CPUE) was calculated as the number of fish caught per 100 m² per 12 h. The total sampling design yielded 56 samples (7 locations×4 reaches×2 seasons). All captured fishes were identified to species and measured for total length (mm) and weight (g).

Concurrently with fish sampling, we applied a protocol for assessing habitat structure based on four groups of descriptors (type of substrate, shelters, riparian cover and type of mesohabitat) and three single variables (stones on the banks, anthropogenic influences and erosion) at each sampled location. Visual estimates of the type of substrate (% of rocks, stones, gravel, sand, mud and clay), shelters (% of roots, twigs and logs, slits banks, floating macrophytes and submerged macrophytes) and riparian cover (% of trees, shrubs and grasses) were performed for an area of 500 m² (100 m long×5 m width). Erosion (high, moderate, and absent), stones on the banks (%) and anthropogenic influences (expressed as an index of alteration) were also estimated visually for an area of $5,000 \text{ m}^2$ (100 m along the bank \times 50 m off the margin). Anthropogenic influences were evaluated as an index that was calculated as the sum of a given score multiplied by the estimate percentage of covered area of $5,000 \text{ m}^2$ as follow: pasture (0.3), agriculture (0.4), urban (0.7) and industrial (0.9). The type of mesohabitat (as % of pools and riffles) was estimated for the whole location extension (c.a. 145 m long).

Physico-chemical characteristics of the water were determined by direct measurement using a multiprobe Horiba W-21 (Horiba Trading Co., Shanghai) for the following variables: temperature (°C), pH, redox potential (mV), total dissolved solids (mg L⁻¹), dissolved oxygen (mg L⁻¹) and conductivity (μ S cm⁻¹). Water transparency (cm) was estimated by a Secchi disk, and turbidity was measured using a Policontrol model AP2000 turbidimeter. Water velocity was measured by a digital flow meter FP 211 (Global Waters Flow Probe). Width and depth of the river were obtained at each reach using a digital meter Bushnell Sport 450 laser range finder, and a laser SM-5 digital sounder, respectively.

Data analyses

Physico-chemical environmental variables were compared among the four river reaches for each season using one-way analysis of variance (ANOVA), followed by a posterior Tukey test every time the null hypothesis was rejected at P<0.05. Habitat descriptors expressed as percentages were arcsine transformed and then all data were $\text{Log}_{10}(x+1)$ transformed and compared with two-way ANOVA between the two fixed factors of reach (4 reaches) and season (2 seasons). We used the indicator species analysis (Dufrêne and Legendre 1997) to identify species characterizing each reach or season, i.e. species that tend to occur in a given reach/season, but not in the others.

Two-way analysis of variance (ANOVA) was used to compare the number of individual fish, biomass, richness, Simpson dominance and Shannon-Wiener diversity among the reaches and seasons. Logarithmic transformations [log10(x+1)] of fish abundance (number and biomass) and indices of fish assemblages were performed to meet assumptions of normality and homogeneity of variance, and to reduce the bias of abundant species. Similarly to abiotic data, a post-hoc Tukey test was applied every time the null hypothesis was rejected. ANOVA was performed using STATISTICA 7.1. A direct ordination technique, the Canonical Correspondence Analysis (CCA) was performed with the CANOCO package (ter Braak and Smilauer 2002) to examine relationships between the fish assemblage and habitat/physico-chemical variables. This analysis allows us to represent spatial ordering of samples, species and environmental variables, revealing how multiple species are distributed according to the environmental variation (ter Braak and Smilauer 2002). The significance of the influence environmental variables and habitat descriptors were verified by the Monte Carlo permutation test.

Results

Habitat descriptors

The type of substrate differed significantly (P<0.05) among the four river reaches (Tables 1 and 2). Hard substrate, such as rocks and stones predominated in the middle-lower reaches, while fine substrate, such as gravel and clay predominated in the upper reaches, and mud in the lower reaches. The middle-upper and middle-lower reaches also had more sand substrate compared to the other river reaches. Seasonally, mud was more common in the wet season, while sand in the dry season (Table 2).

Table 2 Comparisons of type of substrate among the river reaches and seasons, according to two-way ANOVA. *F*-values and Tukey comparisons are shown. Reaches: 1, upper; 2, middle-upper; 3, middle-lower; 4, Lower

Type of substrate	Reaches		Seasons		Reaches × Season	
	F	Tukey comparisons	F	Tukey comparisons	F-significance	
Rocks	3.89*	3>2,4	ns	ns	ns	
Stones	7.78**	3>1,2,4	ns	ns	ns	
Gravel	4.54**	1>2,3,4	ns	ns	ns	
Sand	350.8**	2, 3>1>4	9.98**	Dry > Wet	693.7**	
Mud	22.03**	4>2>3,1	8.34**	Wet > Dry	12.76**	
Clay	10.10**	1>2,4	ns	ns	4.94**	

ns non-significant

*P<0.05

**P<0.01

All habitat descriptors, except twigs and logs had significant differences (P < 0.01) among the four reaches (Table 3). Riffles were more frequent in the middle-lower reaches compared to the middle-upper and lower reaches, while pools were more frequent in middle-upper and lower reaches. Riparian cover differed among the river reaches with trees and shrubs predominating in the upper reaches whereas grasses predominated in the middle-lower and lower reaches. The upper and the middle-upper reaches were more sheltered, whereas the middle-lower reaches were less

sheltered. Roots as well as floating and submersed macrophytes were more abundant in the upper and middle-upper reaches compared to the middle-lower reaches. Erosion along the river margins was more frequent in the middle-lower reaches compared with the other reaches, whereas anthropogenic influences were more frequent in the lower reaches and less frequent in the upper and middle-upper reaches. No seasonal difference was found for habitat descriptors except floating macrophytes that were more abundant in wet season compared to dry season (Table 3).

Table 3 Comparisons of habitat descriptors among the river reaches and seasons according to two-way ANOVA. *F*-values and Tukey comparisons are shown. 1, upper; 2, middle-upper; 3, middle-lower; 4, lower

Descriptors	Reaches (R)		Seasons (S	$\mathbf{R} \times \mathbf{Se}$	
	F	Tukey comparisons	F	Tukey comparisons	
Mesohabitat					
Riffles	29.10**	3>1>2,4	ns	ns	ns
Pools	bls 19.72**		ns	ns	4.48**
Riparian cover					
Trees	15.88**	1>2,3>4	ns	ns	ns
Shrubs	12.49**	1>3>2,4	ns	ns	ns
Grasses	12.91**		ns	ns	ns
Shelters					
Roots	6.86**	1,2>3	ns	ns	3.54*
Twigs & logs	ns	ns	ns	ns	ns
Slits banks	9.01**	2,4,1>3	ns	ns	ns
Floating Macrophytes	13.56**	1,2,4>3	4.62*	Wet > Dry	ns
Submersed Macrophytes	39.04**	1,2>4,3	ns	ns	ns
Stones on the banks	14.22**	3>1,2,4	ns	ns	ns
Erosion	83.14**	3>4>1,2	ns	ns	ns
Anthropogenic influence	16.86**	4>3>2,1	ns	ns	4.48**

ns non-significant

*P<0.05

**P<0.01

Physico-chemical variables

Highly significant differences in most physico-chemical variables were found among the river reaches (Table 4). Although water temperature, dissolved oxygen and pH differed significantly among the river reaches, such differences were not biologically significant because the small differences in the units of measurement (<1 unit for each variable). Moreover, the possible effect of

pseudo-replication due to proximity of the locations within each reach could inflate such statistical differences. Turbidity had a trend to be lower in the upper and middle-upper reaches and higher in the middle-lower and lower reaches in both seasons whereas the transparency had the opposite trend. Overall, temperature, pH and turbidity were higher during the wet season whereas dissolved oxygen, redox potential and transparency were higher in the dry season (Table 4).

Table 4 Means \pm standard error for water physico-chemical variables by river reaches during dry and wet seasons. *F* and significance of ANOVA comparisons among river reaches also indicated. Rivers reaches: 1, upper; 2, middle-upper; 3, middle-lower; 4, lower

Physico-chemical variables	Season	River reaches						
		1	2	3	4			
Temperature (°C)	Wet	25.5±0.05 ^a	24.7±0.12 ^b	24.60±0.1 ^b	25.62±0.07 ^a	43.55**		
I man ()	Dry	21.1±0.08 ^a	21.1±0.03 ^a	$20.8{\pm}0.05^{b}$	21.0±0.11 ^a	9.03**		
Dissolved oxygen (mg/l)	Wet	$8.6 \pm 0.09^{\rm b}$	8.7±0.3	9.2±0.02 ^a	8.9±0.03	3.26*		
	Dry	$9.6{\pm}0.05^{b}$	$9.52{\pm}0.05^{b}$	9.9±0.08 ^a	10.1±0.05 ^a	21.86**		
Redox potential (mV)	Wet	197.9±6.9 ^b	228.4±4.9 ^a	197.4±9.5 ^b	211.6±6.4	4.43*		
	Dry	239±5.3 ^b	$241.2{\pm}1.4^{b}$	263.9±3.6 ^a	236.71±1.8 ^b	12.21**		
рН	Wet	7.3±0.08	7.5±0.08	7.5±0.02	7.3±0.2	ns		
-	Dry	6.8±0.03 ^b	6.9±0.06 ^b	$6.6{\pm}0.05^{b}$	7.4±0.13 ^a	15.5**		
Turbidity (NTU)	Wet	62.5 ± 3.4^{d}	83.1±3.9 ^c	266.2±12.2 ^a	$203.9{\pm}25.7^{b}$	112.9**		
• ()	Dry	3.1±0.9 ^c	10.2±0.3 ^b	12.9±0.2 ^b	20.0±0.5 ^a	42.9**		
Transparency (cm)	Wet	30.1±0.02 ^a	28.6±0.2 ^a	12.8±0.1 ^b	10.2 ± 0.04^{c}	120**		
	Dry	125.7±15.2	109.3±0.7	92.1±0.6	87.4±0.4	ns		
Depth (m)	Wet	$1.7{\pm}0.4^{b}$	6.3±0.7 ^a	2.6±0.3 ^b	1.8±0.3 ^b	13.6**		
	Dry	1.3±0.2 °	6.4±0.9 ^a	2.3 ± 0.2^{b}	2.2±0.3 ^b	19.2**		
Velocity (m/s)	Wet	0.5±0.17	0.17±0.04	0.44±0.07	0.24±0.07	ns		
	Dry	0.7±0.16 ^a	0.1 ± 0.04^{b}	0.40±0.07 ^a	0.1±0.02 ^b	8.24**		

Letters indicate significant differences among reaches

ns non-significant

*P<0.05

**P<0.01

Species	Reach				Nº (%)	Biomass (%)	% FO	Size range (mm)	
	1	2	2 3						
Loricariichthys castaneus		Х	Х	Х	151 (23.93)	15450.0 (18.04)	39.28	120–390	
Hoplosternum littorale	Х	Х	Х	Х	74 (11.72)	9464.2 (11.05)	28.57	168–230	
Trachelyopterus striatulus	Х	Х	Х	Х	68 (10.77)	6991.5 (8.16)	33.92	156–198	
Astyanax bimaculatus	Х	Х	Х	Х	63 (9.98)	1389.5 (1.62)	39.28	89–124	
Oligosarcus hepsetus	Х	Х	Х	Х	35 (5.54)	1049.6 (1.22)	28.57	129–179	
Pimelodus maculatus	Х	Х	Х	Х	32 (5.07)	8318.1 (9.71)	17.85	181–361	
Hoplias malabaricus	Х	Х	Х	Х	23 (3.64)	12356.08 (14.43)	25	220-378	
Hypostomus affinis	Х	Х	Х	Х	22 (3.48)	3582.04 (4.18)	28.57	142–335	
Cyphocharax gilbert		Х			22 (3.48)	2017.78 (2.35)	14.28	165–220	
Cichla kelberi	Х	Х		Х	15 (2.37)	1078.35 (1.25)	12.5	92–278	
Centropomus parallelus *			Х	Х	15 (2.37)	2353.7 (2.74)	21.42	122–350	
Genidens genidens *			Х	Х	14 (2.21)	1753.15 (2.04)	19.64	143–296	
Leporinus copelandii		Х	Х		12 (1.90)	5123.14 (5.98)	17.85	194–486	
Crenicichla lacustris	Х		Х	Х	9 (1.42)	826.13 (0.96)	10.71	131–186	
Gymnotus carapo		Х		Х	8 (1.26)	1165.95 (1.36)	8.92	270-401	
Eiguimannia virecens		Х			7 (1.10)	404.44 (0.47)	3.57	219–266	
Rhamdia quelen	Х				7 (1.10)	1582.5 (1.84)	8.92	215-370	
Astyanax parahybae	Х	Х			7 (1.10)	254.87 (0.29)	7.14	83–119	
Mugil liza *			Х	Х	7 (1.10)	1662.02 (1.94)	8.92	260-334	
Leporinus conirostris			Х	Х	6 (0.95)	4580.31 (5.34)	10.71	382–548	
Glanidium albescens	Х		Х		5 (0.79)	351.1 (0.41)	3.57	122–200	
Plagioscion squamosissimus		Х			4 (0.63)	274.8 (0.32)	1.78	236–325	
Rineloricaria sp.		Х			4 (0.63)	47.07 (0.05)	7.14	120–143	
Hoplerythrinus unitaeniatus			х	Х	3 (0.47)	669 (0.78)	5.35	182–230	
Oreochromis niloticus	Х				3 (0.47)	714.3 (0.83)	7.14	156-191	

 Table 5
 The number of individuals, biomass, frequency of occurrence (FO) and size range of fish species in Guandu River. Rivers reaches: 1, upper; 2, middle-upper; 3, middle-lower; 4, lower. * marine species

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Table 5 (continued)

Species	Reach				Nº (%)		Biomass (%)		% FO Size range (n	
	1	2	3	4						
Metynnis maculatus		Х			2 (0.31)		72.1 (0.08)		3.57	82–93
Geophagus brasiliensis			Х	2 (0.31)		318.94 (0.37)		3.57	150–183	
Centropomus undecimalis *			Х	2 (0.31)		227.51(0.26)		3.57	142–156	
Callichthys callichthys			Х	2 (0.31)		34.62 (0.04)		1.78	153	
Pimelodus fur		Х		1 (0.15)		281.1 (0.32)		1.78	170	
Trichogaster trichopterus			Х	1 (0.15)		7.2 (0.01)		1.78	90	
Gymnotus pantherinus			Х		1 (0.15)		172.5 (0.20)		1.78	351
Tilapia rendalli			Х		1(0.15)		128.2 (0.14)		1.78	265
Astronotus ocellatus			Х	1 (0.15)		35.3 (0.04)		1.78	125	
Centropomus sp. *			Х	1 (0.15)		38.8 (0.04)		1.78	154	
Genidens barbus *		Х		1 (0.15)		851.2 (0.99)		1.78	372	
Total				631	100	85627.12	100			

Fish composition

A total of 631 fishes, weighting 85627.12 g and representing 5 orders, 18 families, 29 genera and 36 species were recorded. Siluriformes had the highest richness with 12 species, followed by Perciformes with 11 species, 5 of which were marine. Characiformes had 9 species followed by Gymnotiformes with 3 species and Mugiliformes with only one marine species (Table 5).

Nineteen species accounted for more than 1 % of the total number of fishes, comprising 92.6 % of the numerical abundance (Table 5). Seventeen species accounted for more than 1 % of the total biomass, comprising 87.8 % of the total weight. The four most numerous species (*L. castaneus, H. littorale, T. striatulus* and *A. bimaculatus*) accounted for more than 50 % of the total numbers and had frequencies of occurrence higher than 25 %. The species that most contributed to biomass were *L. castaneus, H. malabaricus, H. littorale, P. maculatus* and *T. striatulus* accounting for more than 50 % of the total weight.

Twelve species were indicators of either river reaches or seasons (Table 6) according to Species Indicator Analysis (P<0.05). Four species were indicator of the upper (H. malabaricus, O. hepsetus, P. maculatus and R. quelen) and of the middle-upper (A. bimaculatus, C. gilbert, L. castaneus and P. squamosissimus) reaches, whereas two species were indicators of the middle-lower reaches (L. copelandii and C. parallelus), and only one of the lower reaches (H. littorale) (Table 6). Only two species were indicators of wet season (H. littorale and T. striatulus).

The number of individuals differed significantly among the river reaches, with the highest values in the middle-upper reaches, and lowest in the middlelower reaches (F=3.57; P<0.05) in both seasons. Seasonally, the highest numerical abundances (F=7.19; P<0.01) and biomass (F=4.74; P<0.05) were recorded in wet season compared to dry season. The other examined parameters of community structure (D-Margalef richness, Simpson dominance and H-Shannon diversity) did not change significantly between reaches and seasons (Fig. 2).
 Table 6 Indicator values and significance for species by river reaches and seasons according to Species Indicator Analysis. 1, upper; 2, middle-upper; 3, middle-lower; 4, Lower

Species	Indicator values (%)	Reach	Season
Hoplias malabaricus	33	1*	ns
Oligosarcus hepsetus	28	1*	ns
Pimelodus maculatus	43	1**	ns
Rhamdia quelen	50	1**	ns
Astyanax bimaculatus	32	2*	ns
Cyphocharax gilbert	67	2**	ns
Loricariichthys castaneus	47	2**	ns
Plagioscion	33	2**	ns
squamosissimus Leporinus copelandii	29	3*	ns
Centropomus parallelus	33	3*	ns
Hoplosternum littorale	27	4*	Wet *
Trachelyopterus striatulus	26	ns	Wet **

ns non-significant

*P<0.05

**P<0.01

Habitat influences on fish assemblages

The amount of the total variation explained by the type of substrate, that is, the sum of all canonical (or constrained) eigenvalues was 0.826, which accounts for 18.5 % of the overall inertia (4.46), or variance in species dispersion in the data set. Clay and gravel predominated in the upper reaches that was directly associated with occurrence of O. hepsetus, P. maculatus, R. quelen, P. fur, C. kelberi and H. malabaricus. The middleupper reaches were also characterized by soft substrate and was directly associated with occurrence of M. maculatus, L. castaneus, P. squamosissimus, C. gilbert, E. virescens and Rineloricaria sp. In contrast, the middle-lower reaches had hard substrate with a predominance of cobble, sand and rock and was directly associated to H. affinis, L. copelandii, C. parallelus and G. barbus, while the lower reaches had mud substrate and was directly associated with



Fig. 2 Mean and standard error (*vertical lines*) for fish community parameters in the four river reaches and two seasons. Rivers reaches: 1, upper; 2, middle-upper; 3, middle-lower; 4, lower

G. carapo, G. brasiliensis, H. littorale and *H. unitaeniatus* (Fig. 3).

The amount of the total variation explained by habitat descriptors was 1.457, which accounts for 32.7 % of the overall inertia. Trees, shrubs and submersed macrophytes occurred mainly in the upper river reaches, and were directly associated with *R. quelen*, *G. albescens*, *H. malabaricus*, *P. maculatus*, *C. kelberi* and *O. hepsetus*. Samples from the middle-upper reaches were characterized by the presence of pools,



Fig. 3 Ordination diagram (triplot) from canonical correspondence analysis, including fish species, type of substrate and seasons. Samples coded by the number of the river reaches (1, 2, 3, 4) and seasons (D, dry; W, wet). Species codes: Abi, A. *bimaculatus*; Apa, A. *parahybae*; Cgi, C. *gilbert*; Cke, C. *kelberi*; Cla, C. *lacustris*; Cpa, C. *parallelus*; Cun, C. *undesimailis*; Evi, E. *virensces*; Gal, G. *albescens*; Gba, G. *barbus*; Gbr, G. *brasiliensis*; Gca, G. *carapo*; Gge, G. *genidens*; Haf, H. *affinis*; Hli, H. *littorale*; Hma, H. *malabaricus*; Hun, H. *unitaeniatus*; Lca, L. *castaneus*; Lcn, L. *conirostris*; Lco, L. *copelandii*; Mli, M *Liza*; Mma, M. *maculatus*; Ohe, O. *hepsetus*; Oni, O. *niloticus*; Pfu, P. *fur*; Pma, P. *maculatus*; Psq, P. *squamosissimus*; Rqu, R. *quelen*; Rsp, R. sp; Tst, T. *striatulus*

silt banks, and floating macrophytes that were directly associated with occurrences of *M. maculatus, L. castaneus, Rineloricaria sp., E. virescens, C. gilbert* and *P. squamosissimus*. In contrast, fish species associated with the middle-lower reaches included *L. copelandii, H. affinis, G. genidens, G. brasiliensis* and *G. barbus* and were associated with the presence of riffles and large stones in the margins. The lower reaches had grasses in the margins and significant anthropogenic influences, because of channelization of the river and the proximity of an emergent industrial development and were associated with presence of species such as *H. littorale, M. liza, H. unitaeniatus, G. carapo* and *C. undecimalis* (Fig. 4).

Physico-chemical influences on fish community

The amount of the total variation explained by physicchemical variables was 1.157, which accounts for 25.9 % of the overall inertia. Monte Carlo analysis



Fig. 4 Ordination diagram (triplot) from canonical correspondence analysis, including fish species, habitat descriptors and seasons. Samples coded by the number of the river reaches (1, 2, 3, 4) and seasons (D, dry; W, wet). Species codes: Abi, A. *bimaculatus*; Apa, A. *parahybae*; Cgi, C. *gilbert*; Cke, C. *kelberi*; Cla, C. *lacustris*; Cpa, C. *parallelus*; Cun, C. *undesimailis*; Evi, E. *virensces*; Gal, G. *albescens*; Gba, G. *barbus*; Gbr, G. *brasiliensis*; Gca, G. *carapo*; Gge, G. *genidens*; Haf, H. *affinis*; Hli, H. *littorale*; Hma, H. *malabaricus*; Hun, H. *unitaeniatus*; Lca, L. *castaneus*; Lcn, L. *conirostris*; Lco, L. *copelandii*; Mli, M *Liza*; Mma, M. *maculatus*; Ohe, O. *hepsetus*; Oni, O. *niloticus*; Pfu, P. *fur*; Pma, P. *maculatus*; Psq, P. *squamosissimus*; Rqu, R. *quelen*; Rsp, R. sp; Tst, T. *striatulus*

revealed that turbidity, transparency, depth and velocity of the water contributed most to species distribution. Transparency was directly associated with species from the upper and middle-upper reaches during dry season, such as *A. parahybae*, *A. bimaculatus*, *T. striatulus* and *O. hepsetus*. In contrast, species from the middle-lower and lower reaches were associated with high turbidity, such as *G. barbus*, *C. parallelus* and *L. copelandii*. The middle-upper reaches were characterized by the highest depth and directly related to *M. maculatus*, *L. castaneus and C. gilbert* while the upper and middle-lower estuary had the highest water velocity and was associated with occurrences of *H. malabaricus* and *C. lacustris* (Fig. 5).

Discussion

The four examined reaches of the Guandu River had different fish composition and structure that were



Fig. 5 Ordination diagram (triplot) from canonical correspondence analysis, including fish species, physico-chemical variables and seasons. Samples coded by the number of the river reaches (1, 2, 3, 4) and seasons (D, dry; W, wet). Species codes: Abi, A. *bimaculatus*; Apa, A. *parahybae*; Cgi, C. *gilbert*; Cke, C. *kelberi*; Cla, C. *lacustris*; Cpa, C. *parallelus*; Cun, C. *undesimailis*; Evi, E. *virensces*; Gal, G. *albescens*; Gba, G. *barbus*; Gbr, G. *brasiliensis*; Gca, G. *carapo*; Gge, G. *genidens*; Haf, H. *affinis*; Hli, H. *littorale*; Hma, H. *malabaricus*; Hun, H. *unitaeniatus*; Lca, L. *castaneus*; Lcn, L. *conirostris*; Lco, L. *copelandii*; Mli, M *Liza*; Mma, M. *maculatus*; Ohe, O. *hepsetus*; Oni, O. *niloticus*; Pfu, P. *fur*; Pma, P. *maculatus*; Psq, P. *squamosissimus*; Rqu, R. *quelen*; Rsp, R. sp; Tst, T. *striatulus*

closely associated to habitat structure descriptors, and to a lesser extent to the type of substrate and physicochemical variables. The upper reaches seems to be the most preserved segment of the river because of better margin conditions, presence of shelters, and the most diversity of substrate. Moreover, low turbidity and high transparency are other characteristics of this reach that favor the occurrence of the three carnivorous indicator species, namely, *O. hepsetus, R. quelen* and *H. malabaricus.* The presence of native carnivorous is an indication of a health lotic environment since those fishes depend on a complex trophic structure to support top carnivorous species. In systems with decreased water quality, the native carnivorous species tend to decrease or even to disappear (Pinto and Araújo 2007).

The middle-upper reaches had the most fish abundance, and *C. gilbert, A. bimaculatus, L. castaneus* and *P. squamosissimus* are the indicator species. *Cyphocharax gilbert* was recorded solely in this river reach, which has decreased flow due to the proximity of the dam. According to Smith et al. (2009), areas predominantly lentic exhibit high abundances of Chyphocharax spp. and this is in accordance with our findings. In this river reach, the flooded margins favor abundant floating macrophytes, pools and shelters availability to species adapted to low current velocity. Astyanax bimaculatus is a very abundant small-sized species, which prey on insects and organic matter accumulated in flooded river margins (Esteves 1996), while L. castaneus uses preferably sand and mud substrate of pools. Plagioscion squamosissimus is a non-native species that was introduced from Amazonian rivers and succeed in colonizing rivers and reservoirs in Southeastern Brazil (Agostinho et al. 2004). This species was recorded only in this reach and seems to be using unoccupied niches formed by the proximity of the impoundment. Some concern should be raised because this is a non-native top carnivorous with potentiality to change fish assemblage structure (Pinto and Araújo 2007).

The middle-lower reaches had the lowest number of individuals and two indicator species, *Leporinus copelandii* and *Centropomus parallelus*, with the former being a rheophilic species, and the latter, an estuarine upriver migrant. Both species had their upriver distribution limited by the river impoundment. Marine migratory species such as *G. genidens*, *G. barbus*, *C. parallelus* and *M. liza* were also recorded at this river reach, as their distribution upriver are also limited by the dam. Migrant species agglomerations down from dams have been reported by Taylor and Warren (2001) and Gehrke et al. (2002) as an interfering factor on fish community structure.

The lower reaches correspond to the estuarine part of the river. The riparian cover is composed mainly by grass and there is a high anthropogenic influence due to the proximity of an industrial development which discharges effluent into the river main channel. *Hoplosternum littorale* was the only fish species indicator of this reach. This species has been associated to harsh environmental conditions of the Paraiba do Sul River and can tolerate very polluted areas where others species cannot occur (Araújo et al. 2009).

Only slight seasonal changes were observed in fish community structure, on spite of major changes in physico-chemical variables. As expected for regulated rivers, habitats descriptors did not change seasonally, and this lack of seasonal changes can explain the lack of seasonal difference in fish community structure. Moreover, the constant introduction of approximately flow of 160 m³sec⁻¹ pumped from the Paraíba do Sul

River for hydroelectric purpose corresponds to most of water volume in the system contributing to reduction in flows peaks caused by seasonal rainfall changes. Only four of the eight examined physico-chemical variables were significant to explain fish distribution according to CCA (turbidity, transparency, depth and velocity). High water transparency favors species that use vision to detect and hunt preys, which explain of carnivorous species in the wet and dry seasons. Contrarily to Melo et al. (2009) that did not found significant seasonal differences in transparency and turbidity, we found high transparency in dry season is associated to low rainfall, and high turbidity in wet season associated to lack of marginal vegetation and deforested areas that favor the runoff of sediment into the river.

Diversity of substrate and mesohabitat, associated with hydraulic variables such as depth and water velocity can influence species distribution and act as "filter of species" (Poff 1997) allowing a selected number of species from a universe of possible colonizers to use the available habitat (Súarez and Petrere-Júnior 2007; Valério et al. 2007). Therefore, differences in habitat structure among the four river reaches may act as primary factors structuring fish community irrespective of seasonal variation in physico-chemical variables. This suggests a determinist pattern of species occurrence and re-enforce the relationship between species versus habitat structure. Preference for a specific type of substrate have been documented elsewhere (Ferreira and Casatti 2006). According to Leal et al. (2011), species that were selective with respect to substrate included mostly Siluriformes benthic species. Given that these species spend most of their time, and perform most of their foraging close to the substrate, it is not surprising that they are more specialized in this aspect than nektonic species. Species typically nektonic such as member of Characiformes swim continuously across various sections of the water column (Casatti and Castro 2006) and are less likely to be associated to substrate. Moreover, habitat structure may act in conjunction with anthropogenic influences (e.g., pasture, agricultural, urban and industrial activities) and historical factors (e.g., dynamic of local species colonization and extinction) to determine structure of fish community with eventual modulation of seasonal hydrologic variables.

Our study demonstrates that the habitat structure, more than physico-chemical variables, has a major role in structuring local fish assemblages on regulated rivers. On the other hand, despite seasonal changes in physico-chemical variables, only slight changes in structure of fish assemblages were found which could be associated to reduced flow changes. A sampling design that encompasses different river reaches and between-year variations should be implemented to corroborate this study's findings. Revealing and incorporating information on environmental influences on fish assemblages in riverine systems is a first step towards developing management strategies. Policies and restoration measures can benefit from these findings, since uses of lotic systems are increasing in tropical areas with losses of environmental quality.

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