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ORIGINAL ARTICLE

Do environmental variables predict the trophic structure of fish fauna in a subtropical river (Uruguay River Ecoregion)?

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ABSTRACT

Trophic interactions represent the routes through which energy flows upwards within ecosystems and the understanding of such structuring under varying environmental conditions is still challenging. Here we test the hypothesis that differences in environmental variables act as environmental filters on the composition and trophic structure of local the fish fauna of a subtropical mountain river. We predict that differences in the trophic structure of the fish fauna occur along the river continuum. Main environmental parameters have been measured and fishes were sampled quarterly between August 2013 and May 2014 at six sampling sites in the main channel of the Pelotas River, Upper Uruguay ecoregion. We collected 3848 individuals belonging to 38 species, 4 orders and 11 families. The most (82.1%) consisted of small- and medium-sized individuals. The species were classified into eight trophic guilds: aquatic insectivorous, carnivorous, detritivorous, detritivorous/aquatic insectivorous, herbivorous, iliophagous, omnivorous and piscivorous. In general, herbivorous and piscivorous guilds were the most representative in both number and biomass. Significant differences detected by Permanova were for richness, numerical abundance and biomass between all the sites sampled. Relationships between the environmental variables and the composition of trophic guilds were observed along the longitudinal gradient by RLQ and fourth-corner analyses. The abundance of guilds omnivorous, aquatic insectivorous and herbivorous increases with higher values of chlorophyll-*a* and vegetation cover, especially characterizing the upstream sites (S1, S2 and S3). On the other hand, the abundance of the iliophagous, detritivorous/insectivorous and piscivorous guilds increases with greater values of width, temperature, inorganic phosphorus and total solids, a fact observed in downstream sites (S4, S5 and S6). Thus, it was possible to identify a clear variation in the trophic structure of the fish fauna along the Pelotas River (upstream-downstream), in which the local variables were efficient in predicting environmental filters that influence the trophic organization. In this scenario, our study follows the longitudinal model and evidences a greater accumulation of energy in food webs in the upstream-downstream direction, which favors the greatest abundance of piscivorous, detritivorous and iliophagous verified in stretches of greater volume and dimensions of river. These results highlight the importance of the local variables and the interrelationships in the lateral connectivity processes along the river continuum.

Key words: Freshwater; lotic; trophic guilds; environmental filters; longitudinal gradient.

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INTRODUCTION

The understanding of ecosystem processes, especially environmental predictors in river systems, is a challenging ecological issue. Since the inception of the river continuum concept (RCC) (Vannote *et al.*, 1980) and the serial discontinuity concept (SDC) (Ward and Stanford, 1983), the environmental gradient assumptions in rivers were very strongly focused on longitudinal functions and processes. Thus, theoretical constructs, such as biotic and abiotic interactions on trophic structure and energy sources in ecosystems have been the attention of many studies in lotic environments (Carvalho and Tejerina-Garro, 2015; Leitão *et al.*, 2017; Röpke *et al.*, 2017). The

longitudinal distribution of aquatic organisms along a gradient of environmental conditions is a basic premise of the River Continuum Concept. Additional refinements and developments, with the inclusion of other variables, were discussed by Stanford and Ward (2001). In this regard, biological communities can adjust to environmental changes through species substitution as well as different forms of energy use.

Trophic interactions represent the routes through which energy flows upwards within the structure of ecosystems (Saint-Béat *et al.*, 2015). However, the understanding of this structuring under natural environmental conditions is still a challenge, which becomes even more promising, given the increasing

effects caused by anthropic impacts, such as deforestation and impoundments (Delariva *et al.*, 2013; Félix *et al.*, 2013; Furlan *et al.*, 2013; Schork *et al.*, 2013; Franchi *et al.*, 2014; Gandini *et al.*, 2014; Zeni and Casatti, 2014). In this sense, the use of trophic guilds is widely used in literature as a convenient method to summarize feeding habits data for a large group of species; i.e., non-taxonomic groups of species which exploit the same resource(s) (Gerking, 1994). This approach has been very useful in understanding the various trophic interactions exhibited by fish (Hargreaves *et al.*, 2017) as well as the functional trait selection (Mouillot *et al.*, 2013; Troia and Gido, 2015; Winemiller *et al.*, 2015; Fitzgerald *et al.*, 2017). Thus, trait-based approaches that focus on groups of co-occurring species with shared ecological traits, such as fish trophic guilds, may reveal a unique response of the fish community to environmental gradient (Macnaughton *et al.*, 2016) as well as anthropic disturbance.

Along the gradient of fluvial systems, a number of factors can drive and affect fish community structure, including geographic position and geomorphological history (Ibanez *et al.*, 2007; Esteves *et al.*, 2008; Félix *et al.*, 2013; Carvalho and Tejerina-Garro, 2015). In addition to these, alterations in the trophic guild composition pattern are attributed to environmental filters (Córdova-Tapia *et al.*, 2017), mainly those related to differences in water quality, energy input into the system (Vannote *et al.*, 1980) as well as the availability and supply of food (Bonato *et al.*, 2012; Wolff *et al.*, 2013). In this scenario, evolutionary characteristics of the fish fauna are selected, based on the environmental constraints, as well as the exploitation ability and adaptability in resource partitioning. These processes lead to the establishment of typical functional trophic groups in environmental gradients (Connel, 1980; Carvalho and Tejerina-Garro, 2015; Fitzgerald *et al.*, 2017).

In Neotropical region, the hydroelectric sector and construction of cascades of small hydropower plants have been promote drastic changes on plateau rivers and rivers of high-priority for conservation (Affonso *et al.*, 2015; Kliemann and Delariva, 2015; Latini and Pedlowski, 2016). Specifically, in Brazil's subtropical region, there are a limited number of studies on the trophic guilds of river fish. In addition, most of these studies have been focused in rivers that were already altered by dams (Mérona *et al.*, 2001; Loureiro-Crippa and Hahn, 2006; Luz-Agostinho *et al.*, 2006; Delariva *et al.*, 2013). In neotropical environments already studied, such as streams, their trophic status is largely dependent on allochthonous energy sources (Peres-Neto *et al.*, 1995; Wolf *et al.*, 2013; Nimet *et al.*, 2015). In floodplain systems, which are much more influenced by flood pulses, lateral connectivity promotes nutrient and energy exchange (Goulding *et al.*, 1988; Lowe-McConnell, 1999;

Esteves *et al.*, 2008; Leitão *et al.*, 2017; Röpke *et al.*, 2017). In plateau and embedded rivers although some of the above-mentioned premises are expected, local environmental heterogeneity, such as stretches with higher flow, rapids and differences in the marginal area/river width ratio can add important sources of differentiation along the longitudinal gradient. Moreover, the higher light incidence in the downstream reaches increases the autochthonous processes of energy upward flow (Melles *et al.*, 2012). Rivers with these characteristics are good models for testing perspectives in relation to trophic structuring as a key element of the spatial/temporal fluvial dynamics.

The Pelotas River is classified as a mountain river (Uieda and Castro, 1999), with high slope and a range varying from 1600 to 160 m. By presenting such characteristics, this river has a high potential for hydropower generation, which has driven numerous projects for the implementation of power plants (Ministério do Meio Ambiente, Secretaria de Recursos Hídricos, 2006). In addition, the presence of endemic species and the lack of knowledge about the biology of the fish fauna in the region highlight the importance of this type of research. In this sense, the hypothesis tested here was that differences in local environmental variables act as environmental filters on the composition and trophic structure of local fish fauna. In this respect, it is predicted that differences in the trophic structure of the fish fauna occur along the river continuum. Thus, the goals of this study were: i) to identify the trophic guilds along the longitudinal gradient of the Pelotas River; ii) to test for possible differences in richness and abundance, in number and in biomass, of the trophic guilds among sampling sites and seasons; iii) to correlate the environmental variables with the composition of trophic guilds along the river continuum. It is expected a greater abundance of herbivorous and omnivorous guilds related to upstream stretches, while piscivorous, detritivorous and iliophagous guilds are more related to the downstream sites, associated with a gradual increase of autochthonous source of energy. In addition, it is also expected that trophic structuring is related to local environmental heterogeneity and lateral dynamics, which may provide different resources along the longitudinal gradient.

METHODS

Study area

The Upper Uruguay ecoregion encompasses the drainage basins of the Uruguay River upstream of Yucumã Falls. This region includes the Uruguay River and all of its tributaries, including the two forming rivers, the Canoas and the Pelotas. The Pelotas River arises in

the Serra Geral 64 km from the Atlantic Ocean and its basin is approximately 35,813 km². It flows inland until it meets the Canoas River, where it forms the main stem of the Uruguay. The Upper Uruguay flows over steep and rocky terrain marked by rapids and falls. High turbidity, low nutrients, and high flow contribute to low phytoplankton productivity along the Uruguay. Similarly, variable water levels, rapid flow, steep banks, and rocky substrates limit permanent aquatic vegetation along the main stem. The Upper Uruguay lacks a well-defined dry season since rainfall occurs throughout the year. Flooding tends to be brief, with waters flowing quickly through deep valleys with no marginal lakes or floodplains to absorb rising waters (Zaniboni-Filho and Schulz, 2003; Abell *et al.*, 2008).

In summer, rainfall distribution is uneven and evapotranspiration is high. The most pronounced debts occur in the fall and the weaker flows are found in March and April, with significant amplitudes between the maximum and the minimum, and an average flow of 258 m³/s. The vegetation of the region is composed of meadow areas that usually occur at altitudes above 800 meters and Mixed Ombrophilous Forest, which occupies almost half of the basin and has two formations: Mountain Forest (altitudes between 500 and 1000 meters) and High Mountain (above 1000 meters altitude) (Strassburger, 2005).

Sampling sections

Samples were taken quarterly (seasonally) between August 2013 and May 2014 at six sampling sites in the main channel of the Pelotas River (Fig. 1).

Environmental variables

At each sampling site, the main environmental variables were measured: water temperature, pH, conductivity, alkalinity, turbidity, transparency, color, total suspended matter, dissolved solids, dissolved oxygen, biochemical oxygen demand and chemical oxygen demand, chlorophyll-*a*, nutrients (total, inorganic and organic phosphorus; total, organic and ammonia nitrogen, nitrate, nitrite) and physical variables (width, flow and vegetation cover) (Supplementary Tab. 1).

Biotic data

Fish were collected under the license of the *Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis* (IBAMA) (Process IBAMA 1372, 1373, 1374 and 1376/2012). We used monofyllament gill nets (2.5; 3; 4; 5; 6; 7 and 8 cm between non-adjacent knots) and trammel nets (6; 7 and 8 cm between non-adjacent knots) with 20 m in length and with height ranging from 1.44 to 1.80 meters according to the mesh, set out at 16:00 h and inspected at 22:00 h and 8:00 h, remained exposed for 16 h.

After caught, fish were fixed in 10% formaldehyde and preserved in 70% alcohol.

Laboratory procedures and trophic categorization

Specimens were identified in the laboratory according to Serra *et al.* (2014) and in case of doubts, individuals were sent to experts for confirmation (specific case of *Hypostomus luteus* (Godoy, 1980), *Crenicichla celidochilus* Casciotta (1987) and *Astyanax cf. procerus* Lucena, Castro and Bertaco, 2013). Each specimen was measured (total and standard length in cm) and weighed (g), gutted and stomach were removed. According to size, species were classified as: small (<20 cm); medium (between 20 and 40 cm) or large (>40 cm) (*sensu* Baumgartner *et al.*, 2012). Voucher specimens were deposited in the fish collection of GERPEL (Grupo de Pesquisas em Recursos Pesqueiros e Limnologia), of the State University of Western Paraná and in the fish collection of Nupelia (Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura) of the State University of Maringá.

For specimens with full stomach (fullness equal to or greater than 30%) stomach contents were identified under optical and stereoscopic microscopes to the lowest taxonomic level possible. Food items were identified using the identification keys of Bicudo and Bicudo (1970) for algae and Mugnai *et al.* (2010) for invertebrates, and quantified according to the volumetric method; *i.e.*, the total volume of a food item taken by the fish population is given as a percentage of the total volume of all stomach contents (Hyslop, 1980), using graduated test tubes and a glass counting plate (Hellawell and Abel, 1971).

Data analysis

In this study, through the analysis of 853 stomachs, it was possible to make the trophic categorization of the 13 most abundant species (76.5% of the total numerical abundance). For most of these species, mainly *Astyanax* and *Bryconamericus*, besides being endemic to the region, there is no information in the literature about their biological aspects (Bonato *et al.*, 2018). For the other species (26), due to the low sample size, we used bibliographic information regarding each one (or, when unavailable, for the genus). Most of these species are considered trophic specialists (eight detritivorous species: *Hypostomus* and *Rineloricaria*; six piscivorous: *Crenicichla* and *Hoplias*). Thus, the determination of the trophic guilds for these species through the literature does not induce doubtful interpretations, since their morphological characteristics do not allow trophic guild change as a function of spatial variations in their diet. In addition, we were careful to select information about their diets in the study region (Uruguay basin).

For the determination of trophic guilds from the stomach contents matrix and bibliographic data, we adopted the criteria used by Mérona *et al.* (2001): more than 50% detritus/sediment in the stomachs: detritivorous; more than 50% aquatic insects in the stomachs: aquatic

insectivorous; similar proportions of detritus and aquatic insects: detritivorous/insectivorous; more than 50% various invertebrates in the stomachs: carnivorous; more than 50% fish in the stomachs: piscivorous; similar proportions of detritus and algae: iliophagous, more than

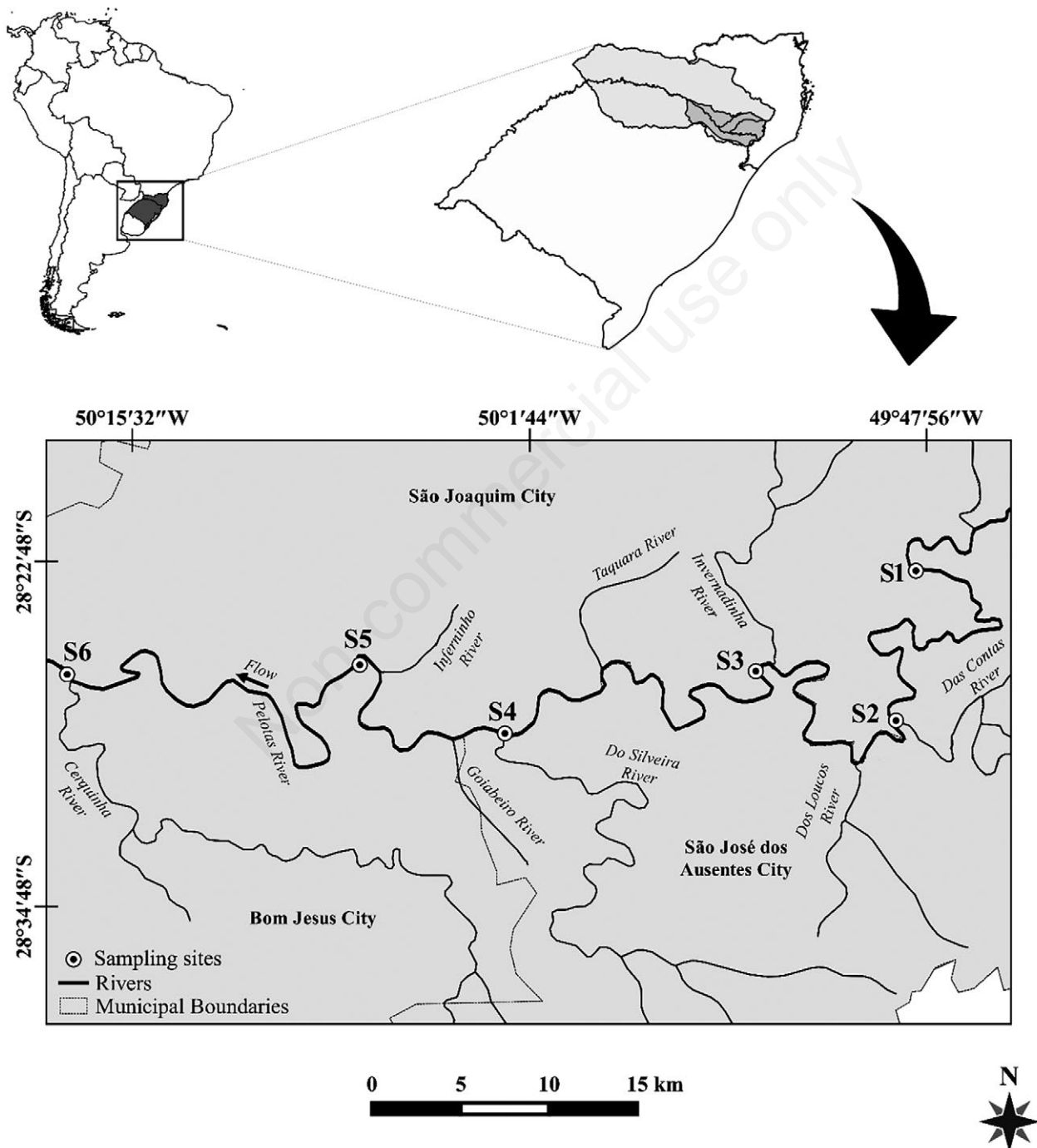


Fig. 1. Study area. Location of sampling sites in the Pelotas River (S1-S6), in Upper Uruguay ecoregion.

50% leaves/seeds in the stomachs: herbivorous; none of the above statements valid, and adding items from different origins (plant and animal): omnivorous. Finally, in our study, based on stomachs contents and on literature data, species were categorized into eight trophic guilds: aquatic insectivorous, carnivorous, detritivorous, detritivorous/aquatic insectivorous, herbivorous, iliophagous, omnivorous and piscivorous.

The trophic structure was evaluated considering species richness, abundance in number and biomass per trophic guild, and was indexed by catch per unit effort (CPUE, number of individuals in 1000 m² of net within 16 h) based on gill nets and trammel nets.

In order to test possible differences in the proportions of the trophic guilds (richness, numerical abundance and biomass), a two-way (sites and seasons) Permutation Multivariate Analysis of Variance (PERMANOVA) was run using the Bray-Curtis index obtained with 9999 permutations (Anderson, 2001).

In order to evaluate the relationship between the environmental variables and the trophic guilds, the RLQ analysis (Dolédec *et al.*, 1996) was applied to detect trait responses to environmental gradient along the Pelotas River. RLQ is a multivariate technique, derived from co-inertia, which allows relating of two or more matrices (Borcard *et al.*, 2011; Dunck *et al.* 2016; Santos *et al.* 2017). The RLQ results in scores for the samples, considering the relationship between trophic guilds and environmental variables along orthogonal axes. In the present study, the matrices used were: R ($n \times m$), in which n is the sampling sites and m , the local environmental variables; L ($n \times s$), where n is the sampling sites and s , the species; in which the samples correspond to the relative abundance (CPUE) of the species collected at each sampling site; Q ($s \times p$), in which s is the species and p , the trophic guilds (0: absence of the trait, 1: presence of the trait). We used permutation tests by the fourth-corner approach (Dray and Legendre, 2008) to test the relationship significance. Before carrying out RLQ analysis, due to the large number of environmental variables and possible correlations between them, we applied the Spearman correlation (ρ) between pairs of these variables to exclude one of the most correlated ($\rho > 0.50$).

In each matrix, an independent ordination was performed according to the nature of the data. The matrix L was transformed into square root to reduce the influence of the dominant species in the analysis of community structure (Sokal and Rohlf 1995) and subjected to a correspondence analysis (CA) (Legendre and Legendre, 2012), the R matrix was log-transformed and subjected to Hill-Smith analysis (Hill and Smith, 1976) and the matrix Q was analyzed by a Principal Component Analysis (PCA). The final result of RLQ is a linear combination of environmental variables (matrix R) and functional trait

(matrix Q) that maximizes covariance between these groups of variables, mediated by species abundance (matrix L).

All the analyses were performed in R environment version (R Core Team, 2015). For PERMANOVA, the 'vegan' package version 2.4-6 was used (Oksanen *et al.*, 2007) while for RLQ, the 'ade4' package version 1.7-10 (Dray and Dufour, 2007). Also, 'dudi.coa' was used to execute the CA with the matrix L, the 'dudi.hillsmith' to perform the Hill-Smith analysis with the matrix R and the PCA for the matrix Q.

RESULTS

Environmental variables

From the environmental variables, it was possible to observe that with the decrease in altitude in the upstream-downstream direction there was an increase in the channel width, reduction in flow and vegetation cover (Tab. 1). In relation to the water characteristics, the highest values of temperature and turbidity were found in the downstream sites (S4, S5 and S6). On the other hand, higher chlorophyll-*a* concentrations were observed at the upstream site (S1) (Tab. 1).

Trophic structure of the assemblage

We collected 3848 individuals belonging to 38 species, 4 orders and 11 families, of which the majority consisted of small- (46.2%) and medium-sized (35.9%) individuals. The most numerically abundant species were *Astyanax xiru* Lucena, Castro and Bertaco, 2013 (23.2%), *Bryconamericus patriciae* da Silva, 2004 (20.7%) and *Astyanax saguazu* Casciotta, Almirón and Azpelicueta, 2003 (10.5%). On the other hand, *Hoplias malabaricus* (Bloch, 1794), *Hypostomus luteus* (Godoy, 1980) and *Schizodon nasutus* Kner, 1858, were rare, totaling less than 0.1%. In biomass, *Hypostomus isbrueckeri* Reis, Weber and Malabarba, 1990 (18.5%), *Astyanax xiru* (13.5%) and *Rhamdia quelen* (Quoy and Gaimard, 1824) (10.1%) were the most representative, whereas *Australoheros taura* Ottoni and Cheffe, 2009, *Astyanax procerus* Lucena, Castro and Bertaco, 2013 and *Hyphessobrycon* sp., contributed with only 0.3% (Tab. 2).

In general, the most representative in number and biomass were the guilds herbivorous (23.9%) and piscivorous (24.6%), respectively (Fig. 2). The guild aquatic insectivorous was composed of five species, of small and medium size, in which *A. saguazu* was the one that contributed most in numerical abundance (51%). Two species represented the carnivorous guild, represented numerically mainly by *R. quelen* (80%). The detritivorous guild included eight species, mainly of medium size, and the most numerically abundant was *H. isbrueckeri*

(64.8%). The herbivorous guild was represented by three species, of which the most numerically abundant were *A. xiru* (89.7%) and *A. dissensus* (10.2%). Five small species composed the iliophagous guild, of which *S. biornata* and *S. brevipinna* were the most numerically abundant (66.1% and 22%, respectively). The omnivorous guild was composed of five species, mainly small-sized, and *A.*

paris was the most numerically representative species (83.8%). The piscivorous guild exhibited the highest richness, with 10 species, mainly of medium and large sizes, especially *O. brevioris* (37.9%) and *C. celidochilus* (18.7%) (Tab. 2).

Along the Pelotas River, regarding the species richness, there was no pattern related to the longitudinal

Tab. 1. Environmental characteristics and physicochemical water variables (mean and standard deviation) measured along the Pelotas River, between 2013 and 2014, in Upper Uruguay ecoregion.

Sites	S1	S2	S3	S4	S5	S6
Latitude	28°22'49"S	28°28'19"S	28°26'25"S	28°28'46"S	28°29'20"S	28°26'43.8"S
Longitude	49°48'31"O	49°48'60"O	49°53'25"O	50°02'36"O	49°51'57"O	50°17'48.4"O
Altitude (m)	1089	980	939	867	850	782
Width (m)	35	80	70	100	150	100
Flow	Rapid waters and backwaters	Rapid waters and deep wells	Rapid waters	Moderate flow	Moderate flow and backwaters	Backwater and rapid waters
River banks	Approximately 10 m forested	RB preserved with more than 50m, LB with approx. 10 m forested. Presence of Araucaria	Well preserved area, with ample protection of the banks	RB preserved with Araucarias and LB approx. 10 m forested	RB with mat of approx. 20 m. LB well preserved with presence of Araucaria	Presence of riparian vegetation of 50 m
Land uses in the surroundings	Extensive cattle raising, agriculture and apple cultivation	Apple cultivation and extensive cattle raising	Small areas of apple cultivation and pasture	Pasture	Pasture	Livestock and diverse family culture
Electric conductivity ($\mu\text{S cm}^{-1}$)	21.9±2.1	22.1±1	27.3±3.9	24.1±5.8	21.7±2.9	19.8±2.9
Water temperature ($^{\circ}\text{C}$)	18±7.1	18.1±6.4	18.9±8.2	19.6±7	19.3±6.5	20.1±7.2
pH	6.5±0.3	6.3±0.3	6.5±0.5	6.5±0.4	6.5±0.5	6.5±0.3
Alkalinity (mg L^{-1})	9.6±1.5	9.9±2.1	12.9±3.9	10.8±3.1	9.8±1.9	8±1
DO (mg L^{-1})	8.6±1.2	8.1±1.3	8.9±1.1	8.5±1.1	8.9±1.5	8.4±1.5
DO % SAT	89.1±10.1	84.2±9	94±9.8	90.9±3.8	96.1±4.4	90.7±5.1
Turbidity	7.4±2.3	7.9±7.4	7.4±0.3	9.8±5.6	7.8±2.9	8.9±3
Transparency (m)	1.5±0.9	1.5±0.7	1.7±0.6	1.4±0.7	1.2±0.2	2.5±0.3
Color (uH)	22.8±6.4	22.9±13.1	19.8±6.2	20±8.7	17.8±4.8	24.3±5.9
Organic nitrogen (mg L^{-1})	0.82±0.18	0.7±0.21	0.65±0.14	0.88±0.36	0.88±0.15	0.93±0.24
Ammonia nitrogen (mg L^{-1})	0.11±0.11	0.08±0.08	0.09±0.09	0.08±0.09	0.08±0.09	0.05±0.08
Total nitrogen (mg L^{-1})	0.7±0.45	0.68±0.47	0.67±0.42	0.77±0.59	0.74±0.51	0.68±0.44
Nitrite (mg L^{-1})	0.01±0.004	0.01±0.005	0.01±0.003	0.01±0.004	0.01±0.004	0.01±0.004
Nitrate (mg L^{-1})	0.59±0.35	0.59±0.42	0.57±0.39	0.68±0.55	0.66±0.46	0.62±0.43
Organic phosphorus (mg L^{-1})	0.011±0.003	0.011±0.006	0.015±0.006	0.016±0.006	0.012±0.003	0.011±0.004
Inorganic phosphorus (mg L^{-1})	0.007±0.004	0.006±0.001	0.008±0.002	0.011±0.006	0.007±0.002	0.008±0.003
Total phosphorus (mg L^{-1})	0.018±0.004	0.017±0.006	0.023±0.004	0.027±0.011	0.019±0.003	0.019±0.005
BOD (mg L^{-1})	4.9±2.4	2.8±0.9	4.8±1.9	4.3±1.8	4.5±0.9	3.9±2.2
COD (mg L^{-1})	8.6±5.6	9.8±7.5	10.5±7.2	13.1±7.5	18.1±13	15.5±18.2
Total solids (mg L^{-1})	47±39.9	75.7±60	96.2±100.1	100.5±107.1	94±77.6	55.5±83.2
Suspended solids (mg L^{-1})	4.8±6.2	19.7±36	37.3±47.3	20±30.6	20.3±27.8	21.2±32
Dissolved solids (mg L^{-1})	42.1±34.5	56±35.2	59±56.1	80.5±77.6	73.6±52	34.3±51.8
Chlorophyll- <i>a</i> ($\mu\text{g L}^{-1}$)	1.4±1.5	0.7±1.1	0.5±0.2	0.1±0.2	0.8±0.8	0.6±0.7

RB, right bank; LB, left bank; DO, dissolved oxygen; %SAT, percent saturation; BOD, biochemical oxygen demand; COD, chemical oxygen demand.

gradient. Higher richness of aquatic insectivorous was observed in S1 and S5, detritivorous, in S3 and S4, and in S6, iliophagous. In numerical abundance, the most representative guilds were herbivorous (S1 and S3), aquatic insectivorous (S2), detritivorous/aquatic

insectivorous (S4 and S5) and iliophagous (S6). In biomass, stood out herbivorous (S1), carnivorous (S2), detritivorous (S3) and piscivorous in the other sites downstream (Fig. 2).

The composition of the trophic guilds along the

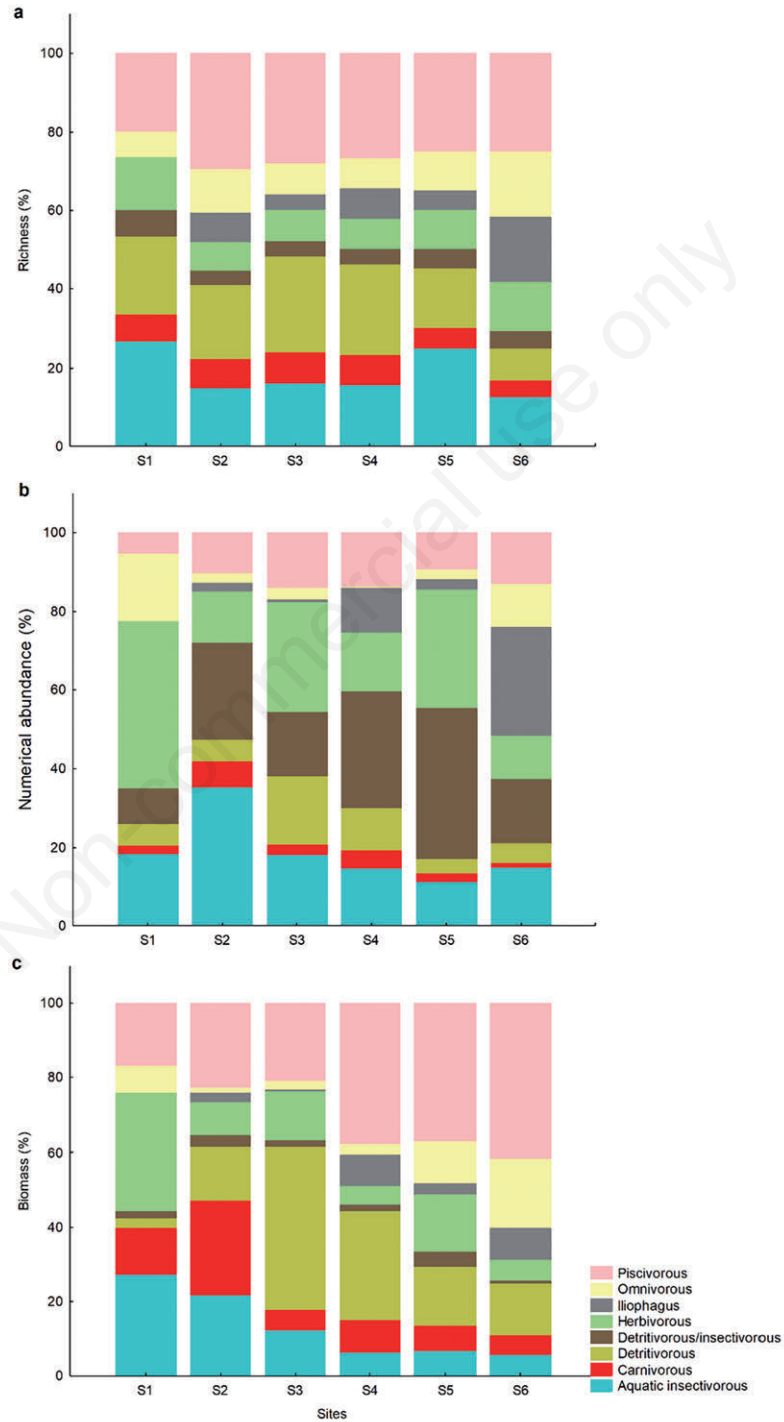


Fig. 2. Relative frequency of the: species richness (a), numerical abundance (b) and biomass (c) according to trophic guild along the longitudinal gradient Pelotas River, between 2013 and 2014, in Upper Uruguay Ecoregion.

longitudinal gradient of the Pelotas River presented richness, numerical abundance and biomass significantly different between the sites sampled (PseudoF=18.04; P=0.001; PseudoF=9.04; P=0.001, PseudoF=64.8; P=0.001, respectively) and between periods (PseudoF=41.0; P=0.001, PseudoF=10.54; P=0.001; PseudoF=3.36; P=0.005, respectively), with no significant interaction between the factors (PseudoF=-0.97; P=1, PseudoF=-7.71; P=1, PseudoF=0.82; P=0.55, respectively).

The first two axes of RLQ with eigenvalues of 0.15 and 0.06 for axes 1 and 2, respectively, accounted for 56.2% and 22.1% of the co-inertia and related the environmental characteristics of the sampling sites with the trophic guilds of the species (Fig. 3, Supplementary Tab. 2). The first RLQ axis was positively correlated with vegetation cover and chlorophyll-*a*, and negatively correlated with width, inorganic phosphorus and total solids. The second RLQ axis was positively correlated

with chlorophyll-*a* and inorganic phosphorus, and negatively with temperature, BOD and conductivity (Fig. 3a). The upstream sites (S1, S2 and S3) were segregated positively on RLQ axis 1 and correlations between trophic guilds in this axis indicated that the abundance of the guilds omnivorous, aquatic insectivorous and herbivorous increases with higher values of chlorophyll-*a* and vegetation cover (Fig. 3 b,c). On the other hand, the abundance of the guilds iliophagous, detritivorous/ insectivorous and piscivorous increases with higher values of width in the downstream sites (S4, S5 and S6) (Fig. 3 b,c). In turn, axis 2 segregated negatively detritivorous, correlated with higher values of BOD and temperature (Fig. 3b). Thus, it was possible to verify strong relationships between the local environmental variables and the composition of the trophic guilds in the sites distributed along the Pelotas River (Fig. 4, Supplementary Tab. 3). By the fourth-corner

Tab. 2. Fish species recorded in the study area. Systematic positions were based on Nelson (2006) for all orders, and the families of the order Siluriformes; Reis *et al.* (2003) for others families, except Characidae that follow Miranda (2009). Vouchers specimens: individuals deposited in Ichthyology Collection of GERPEL (CIG) and Fish Collection of Nupélia (NUP).

Taxonomic position/ species	Numerical proportion	Biomass ratio	SL (cm)	Trophic guild	Size	Voucher
CHARACIFORMES						
Parodontidae						
<i>Apareiodon affinis</i> (Steindachner, 1879)	0.13	0.06	9.2-11.5	Iliophagous* ¹	Small	CIG 2270
Curimatidae						
<i>Steindachnerina biornata</i> (Braga and Azpelicueta, 1987)	2.89	2.7	4.4-14	Iliophagous* ²	Small	CIG 2334
<i>Steindachnerina brevipinna</i> (Eigenmann and Eigenmann, 1889)	0.96	0.32	2-8.6	Iliophagous* ²	Small	CIG 2295
Anostomidae						
<i>Leporinus amae</i> Godoy (1980)	2.4	2.67	7.4-15.7	Aquatic insectivorous	Small	CIG 2285
<i>Schizodon nasutus</i> Kner (1858)	0.03	0.32	27	Herbivorous* ¹	Large	CIG 2373
Characidae						
<i>Astyanax aff. fasciatus</i> (Cuvier, 1819)	0.68	0.35	6.9-11.8	Omnivorous	Small	CIG 2276
<i>Astyanax dissensus</i> Lucena and Thofehrn (2013)	2.63	0.33	2.3-10.2	Herbivorous	Small	CIG 2265/2296
<i>Astyanax paris</i> Azpelicueta, Almirón and Casciotta (2002)	5.42	1.7	2.7-10.1	Omnivorous	Small	CIG 2276/2292
<i>Astyanax cf. procerus</i> Lucena, Castro and Bertaco (2013)	0.05	0.01	6- 6.1	Omnivorous* ³	Small	NUP 18138
<i>Astyanax saguazu</i> Casciotta, Almirón and Azpelicueta (2003)	10.5	2.56	2.8-12.1	Aquatic insectivorous	Small	CIG 2271/2629
<i>Astyanax xiru</i> Lucena, Castro and Bertaco (2013)	23.25	13.49	2.4-12.9	Herbivorous	Small	CIG 2267/2338
<i>Bryconamericus patriciae</i> da Silva (2004)	20.72	2.27	2-8.4	Detritivorous/ aquatic insectivorous	Small	CIG 2257/2362
<i>Oligosarcus brevioris</i> Menezes (1987)	3.91	9.32	2.2-25.6	Piscivorous	Medium	CIG 2341
<i>Oligosarcus jenynsii</i> (Günther, 1864)	0.83	2.29	8-24.7	Piscivorous	Medium	CIG 2331
Acestrorhynchidae						
<i>Acestrorhynchus pantaneiro</i> Menezes (1992)	0.03	0.04	16.4	Piscivorous* ⁴	Medium	CIG 2310
Erythrinidae						
<i>Hoplias australis</i> Oyakawa and Mattox (2009)	0.05	0.59	26.1-29.1	Piscivorous* ⁵	Large	CIG 2368
<i>Hoplias lacerdae</i> Miranda Ribeiro (1908)	0.68	9.66	9.6-54	Piscivorous	Large	CIG 2332
<i>Hoplias malabaricus</i> (Bloch, 1794)	0.03	0.31	27.1-27.1	Piscivorous* ⁵	Large	CIG 2365

To be continued on next page

approach, significant positive correlations were observed between width and the detritivorous/insectivorous, iliophagous and piscivorous guilds (P-value adj.=0.02; 0.02 and 0.03, respectively); between DBO and temperature with detritivorous guild (P -value adj.=0.01 and 0.04, respectively). Negative correlations were significant only between turbidity and the carnivorous guild (P-value adj.=0.01).

DISCUSSION

The Pelotas River showed a high richness represented by eight trophic guilds, as well as a diversified trophic structure that varied spatially along the river continuum. Differences in the composition of the guilds between the sampling sites were mainly related to the upstream

presence of small-sized *Astyanax* species. On the other hand, in the downstream stretches it was observed that the most abundant species were small- to large-sized belonging to the guilds iliophagous (*Steindachnerina*), detritivorous (*Hypostomus*) and piscivorous (*Oligosarcus* and *Crenicichla*), respectively. We also verified that the use of allochthonous resources decreased along the longitudinal gradient (upstream-downstream), being the opposite for autochthonous resources. This pattern is expected by Vanote *et al.* (1980), meantime, we observed also that local environmental variables played an additional role in trophic structuring along the Pelotas River gradient.

Environmental conditions coupled with biotic interactions have a strong effect on the structuring and functional organization of fish assemblages (Hoeinghaus

Table 2. Continued from previous page.

Taxonomic position/ species	Numerical proportion	Biomass ratio	SL (cm)	Trophic guild	Size	Voucher
SILURIFORMES						
Loricariidae						
<i>Hemiancistrus fuliginosus</i> Cardoso and Malabarba (1999)	4.9	7.17	5.9-22.6	Aquatic insectivorous* ⁶	Small	CIG 2329
<i>Hypostomus commersoni</i> Valenciennes (1836)	0.13	0.61	16.3-21.3	Detritivorous* ⁷	Large	CIG 2366
<i>Hypostomus isbrueckeri</i> Reis, Weber and Malabarba (1990)	5.24	18.65	6.5-24.9	Detritivorous* ⁷	Medium	CIG 2354
<i>Hypostomus luteus</i> (Godoy, 1980)	0.03	0.11	17	Detritivorous* ⁷	Large	NUP 16848
<i>Pareiorhaphis hystrix</i> (Pereira and Reis, 2002)	0.08	0.04	8-9.9	Detritivorous* ⁸	Small	CIG 2333
<i>Rineloricaria anitae</i> Ghazzi (2008)	0.39	0.15	10.2-14.4	Detritivorous* ⁹	Medium	CIG 2297
<i>Rineloricaria capitonina</i> Ghazzi (2008)	1.07	0.44	10.1-15.3	Detritivorous* ⁹	Medium	CIG 2299
<i>Rineloricaria reisi</i> Ghazzi (2008)	0.83	0.33	8.7-15.3	Detritivorous* ⁹	Medium	CIG 2324
<i>Rineloricaria tropeira</i> Ghazzi (2008)	0.31	0.18	11.6-15.1	Detritivorous* ⁹	Medium	CIG 2298
Heptapteridae						
<i>Rhamdella longiuscula</i> Lucena and da Silva (1991)	2.66	2.21	9.2-20.8	Aquatic insectivorous	Medium	CIG 2349
<i>Rhamdia quelen</i> (Quoy and Gaimard, 1824)	2.87	10.13	11.1-34.2	Carnivorous	Large	CIG 2369
Pimelodidae						
<i>Iheringichthys labrosus</i> (Lütken, 1874)	0.13	0.38	14.3-20.5	Aquatic insectivorous* ¹	Medium	CIG 2326
<i>Pimelodus maculatus</i> Lacepède (1803)	0.29	3.41	22.9-32	Omnivorous* ¹⁰	Medium	CIG 2360
ATHERINIFORMES						
Atherinopsidae						
<i>Odontesthes</i> sp.	0.73	1.54	2.4-26.9	Carnivorous* ¹¹	Medium	CIG 2360
PERCIFORMES						
Cichlidae						
<i>Australoheros taura</i> Ottoni and Cheffe (2009)	0.03	0.04	7.2-9.2	Iliophagous* ¹²	Small	CIG 2246
<i>Crenicichla celidochilus</i> Casciotta (1987)	1.93	2.08	5.8-21.1	Piscivorous* ¹²	Medium	NUP 18131
<i>Crenicichla igara</i> Lucena and Kullander (1992)	2.5	2.74	5.1-19.4	Piscivorous* ¹²	Small	CIG 2279
<i>Crenicichla missioneira</i> Lucena and Kullander (1992)	0.21	0.31	13.1-15.6	Piscivorous* ¹²	Small	CIG 2307
<i>Crenicichla tendybaguassu</i> Lucena and Kullander (1992)	0.13	0.19	8.1-17	Piscivorous* ¹²	Small	CIG 2254
<i>Geophagus brasiliensis</i> (Quoy and Gaimard, 1824)	0.36	0.31	2.3-12.1	Iliophagous* ¹³	Small	CIG 2248

SL, standard lengths (minimum – maximum); size, small (<20 cm), medium (between 20 and 40 cm), large (>40 cm) (sensu Baumgartner *et al.*, 2012);*the trophic group was inferred by consulting bibliographical references (superscript numbers): 1. Teixeira and Bennemann (2007); 2. Giora and Fialho (2003); 3. Bonato *et al.* (2017); 4. Meurer and Zaniboni-Filho (2012); 5. Corrêa and Piedras (2009); 6. Langoni (2015); 7. Copatti and Copatti (2011); 8. Dias and Fialho (2011); 9. Ghazzi, 2008; 10. Lobon-Cervia and Bennemann (2000); 11. Rodrigues and Bemvenuti (2001); 12. Burress *et al.* (2012); 13. Meschiatti (1995).

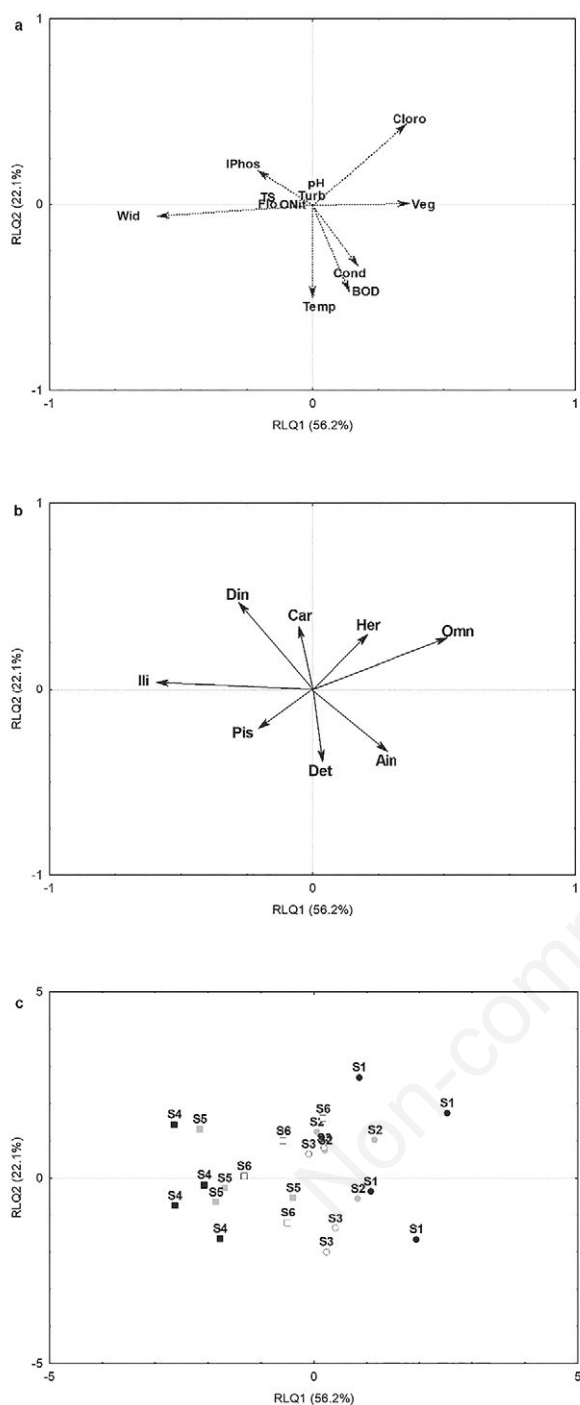


Fig. 3. Relationship between environmental variables and the first two axes of the RLQ analysis (a) of fish species along the longitudinal gradient Pelotas River, between 2013 and 2014, in Upper Uruguay ecoregion. Trait coefficients (b) and the sites scores (c) are also shown. Wid, width; Temp, temperature; Cond, conductivity; BOD, biochemical oxygen demand; Veg, vegetal cover; Cloro, chlorophyll-*a*; Turb, turbidity; TS, total solids; Flo, flow; ONit, organic nitrogen; IPhos, phosphorus inorganic; Omn, omnivorous; Her, herbivorous; Ain, aquatic insectivorous; Car, carnivorous; Det, detritivorous; Pis, piscivorous; Din, detritivorous/ insectivorous; Ili, iliophagous.

et al., 2011). Differences in the distribution of trophic guilds showed a relationship between the use of food resources and the environmental characteristics evaluated. Higher abundances of herbivorous and omnivorous were positively related to higher vegetation cover and chlorophyll-*a* in upstream sites, which evidences the strong relationship with the input of allochthonous material. The proportion of vegetation cover and the strong water flow in these upstream stretches are more limiting to primary production, but provide input of allochthonous resources, making them energetically favorable for some fish species, especially herbivorous. This fact is reinforced by the high abundance of *Astyanax xiru* at upstream sites. This species is also reported as herbivorous in studies conducted in adjacent basin (Bonato *et al.*, 2018). Moreover, omnivorous species, given their trophic plasticity (*A. aff. fasciatus*, *A. cf. procerus* and *P. maculatus*), are also favored by variations in the availability of resources. In addition, these species are considered more generalist and have morphologies that enable the exploitation of different compartments of the habitat. This strong relationship between morphology, foraging efficiency and habitat use has been well reported, especially for the genus *Astyanax* (Mise *et al.*, 2013; Neves *et al.*, 2015; Bonato *et al.*, 2018).

In the downstream sites, piscivorous, iliophagous and detritivorous, considered more specialist guilds, were significantly correlated with the increase in width, total solids, inorganic phosphorus and temperature, indicating that these environmental variables favor the success of these guilds downstream. In this context, piscivorous was the guild that exhibited the greatest species richness and was composed mainly by *Oligosarcus*, *Crenicichla* and *Hoplias*. These species of medium and large size present advantages in stretches characterized by greater width and depth, considering their swimming ability and visual acuity to capture prey. This finding is reinforced by Colloca *et al.* (2009), who observed a significant correlation between body size of predators and depth. Piscivorous species with a prey pursuit tactics, such as those of the genus *Oligosarcus* studied here, present a set of characteristics that increase the success of capture of mobile prey in the water column, such as compressed body together with terminal mouth and canine teeth (Nunes and Hartz, 2006). On the other hand, species that exhibit an ambush feeding tactics, such as *Hoplias* (Oliveira *et al.*, 2010), have an advantage in environments with high total solids load, as well as turbidity, due to the fact that species with low visual acuity are disadvantaged, making them potential prey that can be captured.

The increase in river width reduces the proportion of shaded water promoted by riparian vegetation, thus exposing the river bed to a higher solar incidence and, consequently, higher temperatures. These characteristics

influence the structural complexity of habitats, and in rivers, they alter the supply and availability of resources besides influence the co-occurrence of species (Suarez *et al.*, 2007; Carvalho and Tejerina-Garro, 2015). In this aspect, the increase in the availability of fine organic matter (like detritus; fragmented by the hydrological action and macroinvertebrates downstream) favor the detritivorous and iliophagous guilds (Nimet *et al.*, 2015). This is especially due to the trophic specializations exhibited by species belonging to these specialist guilds. For example, the presence of long intestine is characteristic of species of the family Loricariidae (Delariva and Agostinho, 2001) and Curimatidae (Bowen, 1983), which allows the absorption of detritus. In our study, these species were mainly represented by the genus *Hypostomus* and *Steindachnerina*, respectively. Besides the greater availability of organic detritus downstream, a greater solar incidence and the increase in temperature also promotes increased primary productivity, especially through the growth of periphytic algae attached to the rocky bottom (Pagotto *et al.*, 2011; Wolff *et al.*, 2013; Abilhoa *et al.*, 2016). The solar radiation acts directly on

the photosynthesis rate and determines the depth of the euphotic zone, whereas the temperature can act on phytoplankton productivity directly on the physiology of organisms and indirectly on the distribution of nutrients in the euphotic zone (Esteves, 2011). Thus, these environmental variables conferred an advantage to the detritivorous and iliophagous guilds, due to the increase in the availability of resource.

In large South American rivers with extensive floodplains, the high abundance of detritus/sediments favors the establishment of species with morphological characteristics specialized in efficient use of this type of resource, such as detritivorous (Delariva and Agostinho, 2001; Abujanra *et al.*, 2009). In our study, the presence of several representatives with detritivorous habit (*e.g.*, *Hypostomus* and *Rineloricaria*) at the downstream sites (S4, S5 and S6), demonstrates the dependence on solid materials coming from the displacement along the gradient. Suspended material tends to be deposited further downstream sites, where the width and depth are larger, as opposed to water velocity. This material provides energy sources to establish a food web based on detritus.

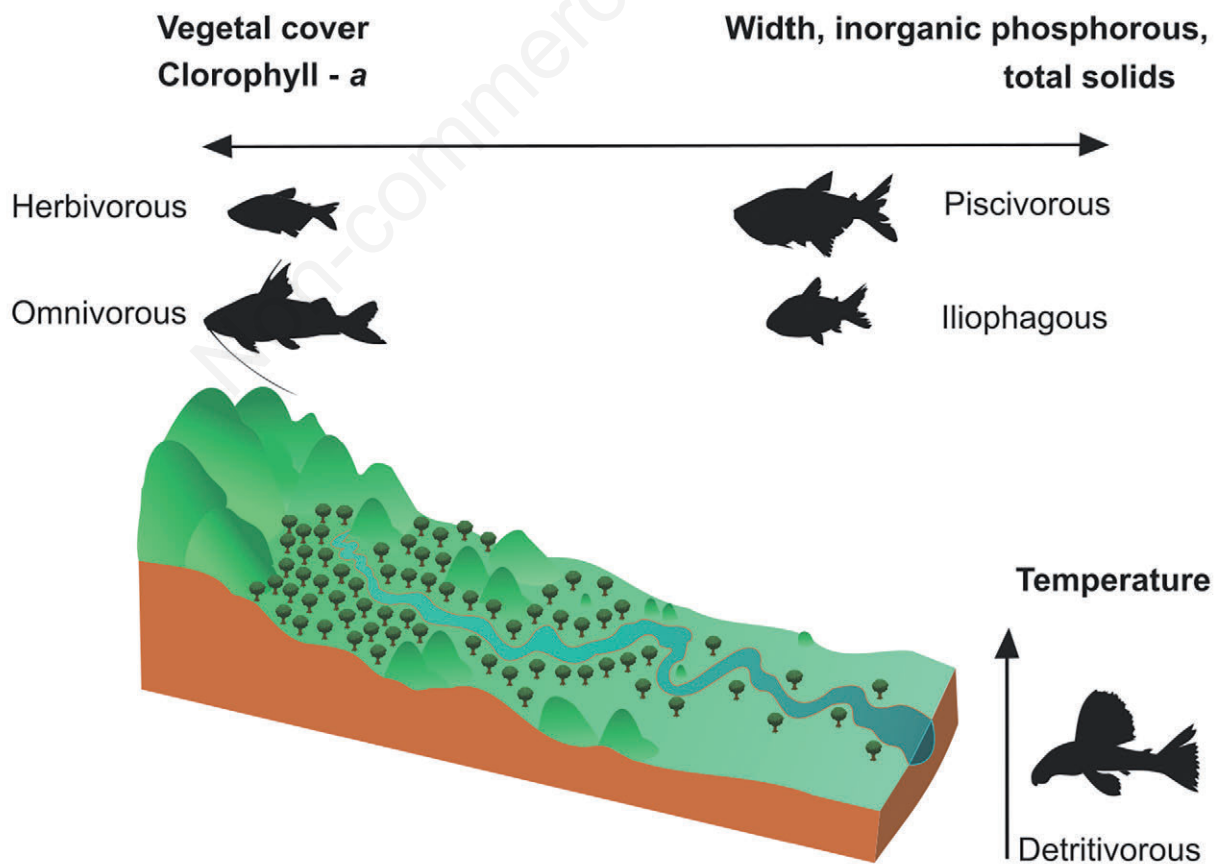


Fig. 4. Schematic representation summarizing the results of the RLQ analysis. Increasing width (from upstream to downstream sites).

Our results support the hypothesis of a proportional shift from generalist guilds, such as herbivorous and omnivorous to those more specialized, such as detritivorous and piscivorous, along the longitudinal gradient of the river. In this sense, we highlight the negative correlation between turbidity and carnivorous guild. In downstream stretches, in addition to the larger dimensions and increment of detritus, as discussed above, the lower flow velocity favors the sedimentation and, consequently, greater transparency. Added to this process are important increases in the richness of food sources, which together with higher primary productivity favor the selection of more specialized trophic groups, especially those linked to higher trophic levels. In this sites, carnivorous species, mainly the persecutors, are favored (Angermeier and Karr, 1983; Ibañez *et al.*, 2007; Wolff *et al.*, 2013). This switch of trophic functions can be related to the decrease in altitude, which affects longitudinal variations in environmental parameters (Angermeier and Karr, 1983; Pouilly *et al.*, 2006). In temperate regions, for example large European rivers, the richness of trophic guilds also increases downstream, and there are clear changes in guild structuring. However, the fish fauna is mostly composed of generalists and the trophic guild specializations are more constrained (Aarts and Nienhuis, 2003; Howeth *et al.*, 2016; Macnaughton *et al.*, 2016) than those verified in our study.

In the neotropical region, in rivers under strong influence of hydrological regimes, such as the Xingu River, the functional diversity is related to processes that promote functional similarity (for example, abiotic filtration), which strongly influence communities (Fitzgerald *et al.*, 2017). Furthermore, in rivers of the Tocantins-Araguaia River basin, Carvalho and Tejerina-Garro (2015) emphasize that the environmental conditions and spatial components drive the structural complexity of the habitat, consequently, the coexistence of species, since heterogeneous habitats can sustain more species with different traits. In this regard, specialist trophic guilds (detritivorous, iliophagous and piscivorous) are more associated with more stable water flow environments, whereas generalists are more abundant in places with greater hydrological variability (Poff and Allan, 1995). In this scenario, our study follows the longitudinal model and evidences a greater accumulation of energy in food webs in the upstream-downstream direction, which favors the greatest abundance of piscivorous, detritivorous and iliophagous verified in stretches of greater volume and dimensions of river.

Considering the Brazilian scenario whose public policies promote the implantation of small hydropower plants (Pelicice *et al.*, 2017), without considering the changes that occurred after the formation of the reservoirs in sequence, we highlight some considerations based on

our results. Cascade reservoirs mainly alter flow velocity, sedimentation, longitudinal connectivity processes and ecotone (Agostinho *et al.*, 2008; Santos *et al.* 2017). The substitution of lotic for lentic environment causes changes particularly in the water retention time, sediment characteristics, nutrients and limnological variables (Franchi *et al.*, 2014; Schork and Zaniboni-Filho, 2017), which were strongly correlated with selection of trophic guilds in our study. In this sense, questions about the influence of these impoundments on the trophic structure can be raised. It would be reasonable to expect possible implications: i) reduction of the detritivorous and iliophagous guilds due to the alteration of the lotic stretches with rocky bottoms; ii) the increase of generalist guilds and explorers of the water column, such as omnivorous fish; iii) homogenization of the trophic guilds along the longitudinal gradient. Thus, we emphasize the need for further researches that specifically assess the species loss and further impairment in regulated rivers by small hydropower plants in cascade. These studies will contribute towards guiding sustainability policies for the ecosystem services of plateau rivers.

CONCLUSIONS

Our study verified a marked longitudinal variation in the trophic organization of the fish assemblage along the Pelotas River, where differences in the composition of the guilds suggest specific trophic structuring related to local environmental characteristics. Variables such as vegetation cover, chlorophyll-*a*, width, inorganic phosphorus, total solids and temperature were related to the composition and abundance of trophic guilds along the upstream-downstream gradient, and can be considered as environmental filters. In this way, our results highlight the importance of the contribution from allochthonous sources of energy in upstream stretches, as well as the local variables and the interrelations in the processes of lateral connectivity, along the river continuum. These findings assume a relevant role for conservation and resource management practices, considering that future changes in the dynamics of the Pelotas River due to the construction of small hydropower plants (SHPP) may eliminate or alter the main trophic structuring forces verified here. As a consequence, they will irreversibly alter local environmental characteristics, directly affecting the fish community and the trophic structure.

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