Longitudinal changes and indicator species of the fish fauna in the subtropical Sinos River, Brazil

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This study investigated the fish fauna in the subtropical Sinos River, considering species addition and replacement and the occurrence of indicator species along a longitudinal gradient. Patterns in fish assemblage ordination evaluated by correspondence analysis reflected the headwater and lowland river reaches. Uppermost sampling stations were characterized by species with restricted occurrence and medium abundance, whereas in the lowland most species were captured only once during the surveyed period and in low abundance. Species addition prevailed between the headwater sampling stations and both addition and replacement occurred between the lowland sampling stations. Nine species were characteristic for the headwater reach and 14 species for the lowland reach. © 2006 The Fisheries Society of the British Isles

INTRODUCTION

The longitudinal change in fish assemblage composition from headwater to lowland reaches is a common phenomenon and conceptual models explaining the underlying mechanisms are mainly based on temperate river research (Matthews, 1998). These models generally assume that habitat changes from headwater to lowland reaches influence fish distribution. Species richness usually increases in the downriver direction. The reason for this phenomenon is generally seen in the gradual increase in habitat diversity (Gorman & Karr, 1978; Reyes-Gavilán *et al.*, 1996). Additionally, physicochemical conditions in headwaters are more stressful and fewer fish species present adaptations to survive in such conditions (Matthews & Styron, 1981).

Two concepts have dominated the discussion about longitudinal changes of fish assemblage composition during the last 50 years: the European 'biozonation' concept and the North American 'species addition' concept. Both ideas have in common that fish assemblages reflect structural and physicochemical

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changes from the headwaters to the lowland reaches. The watercourse changes from a fast-running, turbulent, highly oxygenated and relatively cold stream with a low-temperature amplitude to a less turbulent and more turbid river of higher-temperature amplitude. The substratum tends to change from rocks, boulders and gravels to sand, silt and clay. The European biozonation concept suggests that temperate rivers can be divided longitudinally in four zones; each one is characterized by the occurrence of a principal indicator species: brown trout *Salmo trutta* L. in the upper headwater section, grayling *Thymallus thymallus* (L.) in the lower headwater section, barbel *Barbus barbus* (L.) in the upper lowland section and bream *Abramis brama* (L.) in the lower lowland section (Huet, 1959). Depending on the occurrence of dominant fish families, Jens (1980) suggests a concept that distinguishes between the salmonid region (headwater sections) and cyprinid region (lowland sections). The general idea of both authors is that species of one zone or region are replaced by other species in the next zone or region. The North American school advocates the concept of species addition. Changes in fish assemblages reflect a continuous downstream increase in habitat complexity, due to addition of species (Sheldon, 1968; Hocutt & Stauffer, 1975; Evans & Noble, 1979).

In the 1980s, Vannote *et al.* (1980) elaborated a conceptual framework for understanding the ecology of streams and rivers. The River Continuum Concept (RCC) conceptualizes the entire fluvial system as a continuously integrating series of physical gradients and associated biotic adjustments. Initially formulated to explain longitudinal changes in composition of macroinvertebrates in pristine temperate streams, the RCC was extended to encompass other groups like fishes (Toham & Teugels, 1998; Roper & Scarnecchia, 2001). Among the numerous tenets of the concept is the species replacement along the longitudinal gradient and the maximization of biotic diversity in middle reaches, as the result of highest environmental variability in these areas and spatial abundance shifts of functional feeding groups. The main concepts in fluvial ecology (*e.g.* zonation and RCC), however, are being questioned (Culp & Davies, 1982; Statzner & Higler, 1985; Miranda & Raborn, 2000). Some authors agree that the concepts of species replacement and addition might be complementary, because they would act on different spatial scales (Naimann *et al.*, 1988; Rahel & Hubert, 1991).

Studies in tropical streams describe species richness as positively related to habitat complexity (Peres-Neto *et al.*, 1995; Toham & Teugels, 1998), shelter availability (Abes & Agostinho, 2001) and volume (Garutti, 1988). Longitudinal changes of the river fish fauna in a subtropical Argentinean river seemed to follow the species addition concept, with the exception of the uppermost headwater section, which was dominated by introduced rainbow trout *Oncorhynchus mykiss* (Walbaum). Since thermal preference restricted rainbow trout to altitudes >800 m the species was substituted by native species in the lower river sections (Bistoni & Hued, 2002). These studies, however, made no attempt to identify characteristic groups in the investigated systems and further studies are necessary to confirm the patterns discussed above. Identifying fish species that characterize regions may help to understand distribution patterns along longitudinal gradients in rivers and constitute useful information in management (Matthews *et al.*, 1992) and in determining areas for conservation. This

information is extremely scarce for south Brazilian rivers, most of them already heavily impacted by agricultural and industrial activities. The subtropical Sinos River in Brazil's southernmost State Rio Grande do Sul is an example of an impacted, multiple use watercourse, which provides drinking water for 1·6 million inhabitants. In contrast to low water quality, the original river morphology is still preserved. Leal (1995) and Petry & Schulz (2001) provided a list of fish species from the flood-plain area and the longitudinal gradient of the Sinos River. The understanding of the underlying mechanisms influencing the fish fauna distribution as well as the occurrence of indicator species in this system still remains unknown. Therefore, the aims of the present study were (1) to investigate fish assemblages from the headwaters to downriver under the aspects of species addition and replacement and (2) to identify indicator fish species for each region.

MATERIALS AND METHODS

STUDY AREA AND HABITAT DESCRIPTION

The Sinos River originates 700 m above sea level in the mountainous coastal region of northern Rio Grande do Sul, an almost pristine Atlantic forest environment. The occurrence of two waterfalls (>25 m) is restricted to the first 5 km. Downstream, the river flows 190 km west, discharging into the Guaíba Lake near the state capital Porto Alegre (Fig. 1). Sinos River headwaters suffer moderate impacts from small amounts of agricultural and domestic sewage and, in some restricted areas, from the clearing of
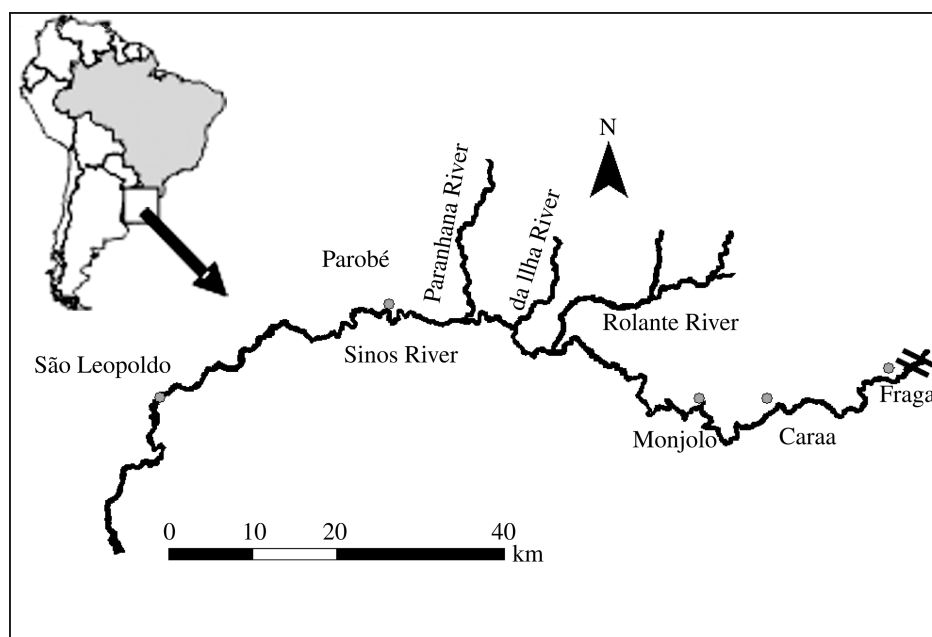

FIG. 1. Rio dos Sinos watershed with location of sampling stations (◉). ⟍, waterfalls above Fraga.

marginal tree vegetation. Two sampling stations, Fraga and Caraá, were located in this upstream section but downstream of the waterfalls. In this reach, the river is moderately entrenched, dominated by riffles with spaced pools and stable banks (B-type; Rosgen, 1994) and presents low water turbidity (Table I). The third sampling station, Monjolo, marks the transition between headwater and lowland reaches. Riffle–pool sequences are absent and turbidity increases. The most important tributaries, Rolante River, da Ilha River and Paranhana River, flow into the Sinos in the lowland section, below Monjolo. According to Rosgen (1994), this stretch can be classified as E-type, with high meander–width ratio, low width–depth ratio, low gradient and low deposition. Riparian vegetation is restricted to a narrow belt and domestic sewage is present at low levels. The fourth (Parobé) and fifth (São Leopoldo) sampling stations can also be considered E-type (Rosgen, 1994), but are heavily impacted by domestic and industrial sewage. Water quality is ranked as class four, which is the worst quality score in the official Brazilian ranking system (CONAMA, 1992). Although riparian vegetation is reduced, several wetlands are present in this stretch. In contrast to low water quality, habitat integrity is still high in most reaches. The river continuum is not interrupted by any dams, lateral connectivity to still existing wetlands is high in the middle and lower reaches and only the 3 km urban river stretch of São Leopoldo is channelized.

Elevation, declivity and stream order of sampling stations were determined by using maps from the Brazilian Ministry of Defence and from the Brazilian Institute of Geography and Statistics (scale 1:50,000). Physical characterization of the sampling stations followed Simonson *et al.* (1994), measuring 20 transects equally spaced by two mean river widths. Depth and current velocity were measured in five equidistant points at each transect, excluding the first 50 cm from both margins. Current velocity was measured in 60% depth of the water column by an electronic flow-meter (Marsh-McBirney, Flowmate 2000). Substratum composition (silt, sand, gravel and rock), occurrence of shelter (cover, which included undercut banks, aquatic macrophytes and large woody debris) and presence of riparian vegetation were estimated visually for each transect (Table I). Turbidity was measured upstream of the fishing site during 12 h by a programmable Hydrolab data sonde 4 in 15 min intervals.

According to physical characterization (Table I), the major gradient of habitat change downstream involved decreases in elevation and increases in river order, river depth, turbidity and heterogeneity of substratum type. Sampling stations were grouped in two river reaches based on their structural characteristics and on the classification method of natural rivers proposed by Rosgen (1994). Fraga and Caraá were headwater Monjolo, Parobé and São Leopoldo lowland reaches.

FISH SAMPLING

Four collections were conducted seasonally at each station, from March 1998 to December 1999. Seven gillnets (30–100 mm stretched mesh size) and three trammel nets (60–80 mm stretched inner mesh size) were set on the river margins between 1800 and 0700 hours. Additionally, each location was electrofished for 50 min with a 7·5 kW EFKO (Leutkirch Germany) generator at 700 V direct current, using a 5 m aluminum boat as the cathode, due to low conductivity values (30–100 μS cm^{-1}). Captured fishes were kept on ice until identification and measurement of total length (L_T) in the laboratory. Voucher specimens were deposited in the Ichthyological Collection of the Museu de Zoologia, Universidade do Vale do Rio dos Sinos.

DATA ANALYSIS

Patterns of fish assemblage structure (composition and abundance) were evaluated through correspondence analysis (CA) applied on the abundance per species data matrix. The first two axes of the CA (CA1 and CA2) were retained for interpretation because they explain most of the variability of the data matrix. Spatial variation related to headwater and lowland river reaches was tested by a *t*-test in CA1 and by Mann–Whitney

TABLE I. Location and physical characterization (mean ± s.e.) of the sampling stations along the Sinos River

		Fraga	Caraá	Monjolo	Parobé	São Leopoldo
Location		29°44′ S; 50°17′ W	29°46′ S; 50°26′ W	29°46′ S; 50°31′ W	29°40′ S; 50°54′ W	29°46′ S; 51°11′ W
Elevation (m)		160	40	18	10	7
Declivity (‰)		2·44	0·2	<0·01	<0·01	<0·01
River order		3°	4°	5°	6°	6°
Width (m)		13·12 ± 0·82	20·60 ± 1·31	14·80 ± 0·75	41·30 ± 1·50	40·23 ± 1·60
Depth (cm)		52·50 ± 4·38	90·59 ± 5·31	171·04 ± 4·04	268·44 ± 15·41	389·58 ± 16·70
Current velocity (ms^{-1})		0·21 ± 0·02	0·34 ± 0·03	0·26 ± 0·02	0·24 ± 0·02	0·14 ± 0·01
Substratum type (%)	Silt	—	—	20	90	100
	Sand	5	5	50	—	—
	Gravel	95	80	30	—	—
	Rock	—	15	—	10	—
Turbidity (NTU)		4·6 ± 0·1	4·7 ± 0·03	10·9 ± 0·12	22·2 ± 1·0	27·0 ± 1·5
Cover (%)		96·87 ± 1·79	37·50 ± 6·06	57·50 ± 5·97	11·88 ± 2·31	72·50 ± 5·85
Riparian vegetation (%)		82·5 ± 5·62	77·78 ± 5·77	38·13 ± 4·10	46·25 ± 3·15	77·50 ± 4·12

U-test in CA2 scores. The non-parametric test (Mann–Whitney) was employed because assumptions of normality (Shapiro–Wilk test) and homocedasticity (Levene test), even after transformation (square root and logarithmic) were not met.

Alterations in species composition along the longitudinal river gradient were evaluated by a β_2 diversity index (Harrison *et al.*, 1992), quantified between each adjacent sampling station. β_2 measures the amount by which regional diversity exceeds the maximum diversity attained locally. Formally, it is described as: $\beta_2 = (\gamma \alpha_{max}^{-1} - 1) (N - 1)^{-1}$, where γ = total number of species in both sampling stations, α_{max} = maximum number of species encountered at one sampling station and N = number of sampling stations. β_2 attains zero if adjacent sampling stations share all species and an increasing β_2 indicates an increasing degree of species turnover.

Indicator species for headwater and lowland reaches were determined based on occurrence and abundance of a given species considering each sample, as described by Dufrêne & Legendre (1997). Species with probability of type I error $<5\%$ ($P < 0.05$; resulted from the random Monte-Carlo reallocation procedure, based on 5000 permutations) were considered as potential indicators. The null hypothesis assumed that the value (I_I) for a given species i within a given river reach j could be found at random (McCune & Mefford, 1997). Multivariate and univariate statistical analyses were performed using the softwares PC-Ord 3·15 (McCune & Mefford, 1997) and Statistica (StatSoft, 2003), respectively. Significant level in all tests implies $P < 0.05$.

RESULTS

During the study, a total of 63 fish species was recorded. Seven of them (11%) were distributed among the five sampling stations at least at one sample. Fish species were neither evenly distributed along the river gradient nor strongly related to river order. Fraga (the uppermost sampling station) displayed the lowest species richness and abundance and São Leopoldo (the most downriver sampling station) the highest values for these assemblage attributes. Species richness in the other sampling stations varied between 33 and 34 (Table II).

Ordination showed a longitudinal gradient in the Sinos River based on fish composition and abundance. CA1 (eigenvalue = 0·55) ordinated sampling stations in two main groups (headwater and lowland reaches) with significant differences between score values (t-test, d.f. = 18, $P < 0.01$) (Fig. 2). Although CA2 (eigenvalue = 0·25) accounted for some variability among samples, especially for Parobé and São Leopoldo, differences between river reaches scores were not significant (Mann–Whitney U-test, $k = 8, 12, P = 0.28$). Ordination was strongly influenced by fish distribution. Species positively correlated with CA1 were characterized by their occurrence in Fraga and Caraá, such as *Heptapterus mustelinus* (Valenciennes), *Rhamdella eriarcha* (Eigenmann & Eigenmann) and *Astyanax* sp. 2. Despite the restricted occurrence, these species were captured in all samples. Species like *Astyanax* sp. 1 and *Rineloricaria microlepidogaster* (Regan), although caught also in lowland sampling sites, were most abundant in upper stations. Species negatively correlated with CA1, such as *Platanichthys platana* (Regan), *Astyanax* sp. 3, *Gymnotus carapo* L. *Cheirodon interruptus* (Jenyns), *Lycengraulis grossidens* (Spix & Agassiz) and *Parapimelodus nigribarbis* (Boulenger), were captured only at São Leopoldo, in low abundance (<1% total abundance) and in only one sample.

TABLE II. Fish species, distribution and relative abundance (% of all individuals at a sampling station belonging to a particular species) along the Sinos River

Common name	Species name and authority	Code	L_T (cm)	Sampling station				
				Fraga	Caraá	Monjolo	Parobé	São Leopoldo
Biru	Steindachnerina biornata (Braga & Azpelicueta)	sbio	11·77 ± 0·27		1			
Violinha	Rineloricaria sp. 2	rin2	8·38 ± 0·98		1			
Bagre	Heptapterus mustelinus (Valenciennes)	hmus	7·30 ± 1·45	1	+			
Mandi	Rhamdella eriarcha (Eigenmann & Eigenmann)	reri	13·77 ± 0·48	5	3			
Lambari	Astyanax sp. 2	ast2	7·77 ± 0·90	1	1			
Canivete	Characidium pterostictum Gomes	cpte	6·94 ± 0·41	10	6	1		
Cará	Cichlasoma facetum (Jenyns)	cfac	9·13 ± 1·55	+	+	+		
Lambari	Bryconamericus iheringii (Boulenger)	bihe	8·28 ± 0·28	19	5	4	1	
Cascudo	Hemiancistrus punctulatus Cardoso & Malabarba	hpun	19·22 ± 0·22	11	19	3	3	
Joana	Crenicichla punctata Hensel	cpun	12·93 ± 0·82	3	4	3	1	
Tambicu	Oligosarcus jenynsii (Günther)	ojen	19·12 ± 0·70	2	+			2
Lambari	Astyanax sp. 1	ast1	12·54 ± 0·31	28	20	+		
Violinha	Rineloricaria microlepidogaster (Regan)	rmic	16·92 ± 0·41	9	7	+	+	+
Cascudo	Ancistrus brevipinnis (Regan)	abre	13·60 ± 0·29	5	6	1	1	+

TABLE II. Continued

Common name	Species name and authority	Code	L_T (cm)	Fraga	Caraá	Monjolo	Parobé	São Leopoldo
Jundiá	*Rhamdia quelen* (Quoy & Gaimard)	rque	25·36 ± 0·84	3	4	+	1	+
Cascudo	*Hisonotus* sp.	hisp	4·02 ± 0·58	+	+	3	+	3
Lambari	*Astyanax alburnus* (Hensel)	aalb	5·09 ± 0·41	1	1	7	22	9
Canivete	*Characidium* cf. *zebra*	czeb	4·62 ± 0·11	+	+	16	2	1
Branca	*Oligosarcus robustus* Menezes	orob	23·56 ± 0·27	+	1	3	3	10
Lambari	*Mimagoniates inequalis* (Eigenmann)	mine	5·33 ± 1·01		+		+	
Tuvira	*Eigenmannia virescens* (Valenciennes)	evir	17·45 ± 1·05		+			+
Mandi	*Microglanis cottoides* (Boulenger)	mcot	5·64 ± 0·44		1			1
Acará-topete	*Geophagus brasiliensis* (Quoy & Gaimard)	gbra	10·49 ± 0·51		1	2	2	3
Cará	*Gymnogeophagus gymnogenys* (Hensel)	ggym	7·25 ± 0·31		4	4	4	1
Biru	*Cyphocharax voga* (Hensel)	cvog	17·28 ± 0·16		4	3	6	20
Lambari	*Astyanax bimaculatus* (L.)	abim	8·28 ± 0·24		4	6	2	4
Grumatã	*Prochilodus lineatus* (Valenciennes)	plin	26·00 ± 1·02		+	1	2	+
Cará	*Gymnogeophagus labiatus* (Hensel)	glab	10·78 ± 0·68		4	1	1	

TABLE II. Continued

Common name	Species name and authority	Code	L_T (cm)	Sampling station				
				Fraga	Caraá	Monjolo	Parobé	São Leopoldo
Muçum	*Synbranchus marmoratus* Bloch	smar	23·70 ± 2·61		+	+		+
Barrigudinho	*Phalloceros caudimaculatus* (Hensel)	pcau	3·83 ± 0·44		+	+		+
Cascudo	*Hypostomus commersoni* Valenciennes	hcom	30·69 ± 1·92		1	+	1	+
Lambari	*Astyanax fasciatus* (Cuvier)	afas	11·70 ± 0·18		1	22	15	16
Lambari	*Hyphessobrycon luetkenii* (Boulenger)	hlue	4·40 ± 0·60		+	14	19	6
Limpa-fundo	*Corydoras paleatus* (Jenyns)	cpal	6·26 ± 0·73			1	1	2
Traíra	*Hoplias malabaricus* (Bloch)	hmal	19·61 ± 1·11			1	1	1
Lambari-bandeira	*Pseudocorynopoma doriae* Perugia	pdor	5·78 ± 0·20			2	4	8
Viola	*Loricariichthys anus* (Valenciennes)	lanu	29·03 ± 0·75			+	2	+
Porrudo	*Trachelyopterus lucenai* Bertoletti, da Silva & Pereira	tluc	13·95 ± 0·61			+		1
Violinha	*Rineloricaria* sp. 1	rin1	3·20 ± 0·00			+		
Violinha	*Rineloricaria cadeae* (Hensel)	rcad	14·13 ± 0·77			1		
Corcunda	*Charax stenopterus* (Cope)	cste	8·5 ± 0·00			+		

TABLE II. Continued

Common name	Species name and authority	Code	L_T (cm)	Sampling station				
				Fraga	Caraá	Monjolo	Parobé	São Leopoldo
Piapara	*Leporinus obtusidens* (Valenciennes)	lobt	36·30 ± 0·00			+		
Violinha	*Rineloricaria strigilata* (Hensel)	rstr	15·13 ± 0·44				2	+
Joana	*Crenicichla lepidota* Heckel	clep	12·78 ± 0·99				+	1
Cará	*Gymnogeophagus rhabdotus* (Hensel)	grha	8·00 ± 0·00				+	+
Tamboatá	*Hoplosternum littorale* (Hancock)	hlit	18·92 ± 0·63				+	2
Cascudo	*Hypostomus aspilogaster* (Cope)	hasp	26·34 ± 1·62				+	+
Guitarreiro	*Bunocephalus doriae* Boulenger	bdor	8·00 ± 0·24				+	+
Lambari	*Hyphessobrycon meridionalis* Ringuelet, Miquelarena & Menni	hmer	4·5 ± 0·00				+	
Lambari	*Diapoma speculiferum* Cope	dspe	5·15 ± 0·23				4	
Pintado	*Pimelodus maculatus* Lacepède	pmac	21·59 ± 1·20			+	1	
Tuvira	*Gymnotus carapo* L.	gcar	21·03 ± 3·71					+
Cará	*Cichlasoma portalegrense* (Hensel)	cpor	10·50 ± 0·00					+

TABLE II. Continued

| Common name	Species name and authority	Code	L_T (cm)	Sampling station				
				Fraga	Caraá	Monjolo	Parobé	São Leopoldo
Limpa-fundo	*Corydoras undulatus* Regan	cund	5·8 ± 0·00					+
Limpa-vidro	*Otocinclus flexilis* Cope	ofle	4·05 ± 0·45					+
Voga	*Schizodon jacuiensis* Bergman	sjac	19·50 ± 2·25					1
Mandi	*Parapimelodus nigribarbis* (Boulenger)	pnig	10·03 ± 0·24					+
Lambari	*Serrapinnus calliurus* (Boulenger)	scal	2·97 ± 0·07					+
Lambari	*Cheirodon ibicuhiensis* Eigenmann	cibi	5·7 ± 0·38					2
Lambari	*Cheirodon interruptus* (Jenyns)	cint	4·8 ± 0·35					2
Lambari	*Astyanax* sp. 3	ast3	9·57 ± 0·20					2
Sardinha prata	*Lycengraulis grossidens* (Spix & Agassiz)	lgro	14·45 ± 1·65					+
Lambari-branco	*Platanichthys platana* (Regan)	ppla	7·6 ± 0·20					+
Species richness				17	33	34	33	44
Fish abundance				781	1150	1058	1254	1584
β_2 diversity					0	0·26	0·26	0·18

+, present but abundance <1%.
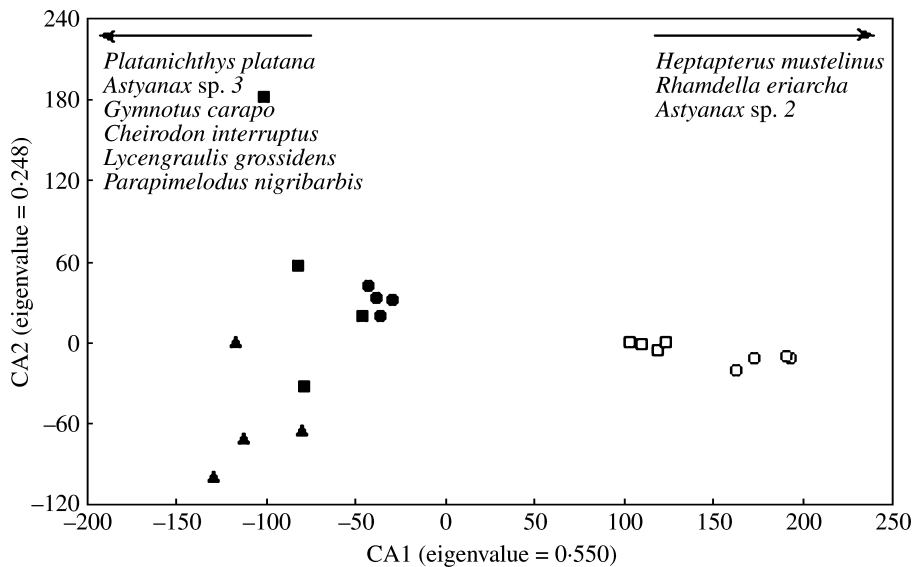
FIG. 2. Analysis of correspondence of samples from Sinos River, according to characteristics of fish assemblages: headwater [Fraga (○) and Caraá (□)] and lowland [Monjolo (●), Parobé (■) and São Leopoldo (▲)]. Arrows indicate fish species more correlated with CA1.

β_2 diversity indicated addition and replacement processes along the Sinos River. This index scored zero between headwater sampling stations, indicating an addition process in this stretch. Lowland reaches were characterized either by addition and replacement processes (Table II). Major heterogeneity was found between Caraá and Monjolo and between Monjolo and Parobé, showing identical values for β_2 (0·26). The number of added (10) and lost (nine) species was the same among these sampling stations. Between most downriver stations (Parobé and São Leopoldo) more species were added (19) than lost (eight), lowering the value of β_2 (0·18). Based on results of ordination and β_2 diversity, the stretch between Caraá and Monjolo marked the transition of fish assemblages composed by resident species with limited distribution to more complex assemblages.

According to I_I values (Table III), nine and 14 fish species were considered to be potential indicators of headwater and lowland reaches, respectively. Indicator species of headwaters are sedentary, characterized mainly by small size [Characiformes: *Astyanax* sp. 1, *Astyanax* sp. 2, *Bryconamericus iheringii* (Boulenger) and *Characidium pterostictum* Gomes], medium size and depressed [Siluriformes: *Ancistrus brevipinnis* (Regan), *Hemiancistrus punctulatus* Cardoso & Malabarba and *H. mustelinus*] or elongated body [Characiformes: *Steindachnerina biornata* (Braga & Azpelicueta) and Perciformes: *Crenicichla punctata* Hensel]. Indicator species of lowland included small [Characiformes: *Astyanax alburnus* (Hensel) and *Pseudocorynopoma doriae* Perugia, Siluriformes: *Corydoras paleatus* (Jenyns) and *Hisonotus* sp.], medium [Characiformes: *Astyanax bimaculatus* (L.) and *Astyanax fasciatus* (Cuvier), Perciformes: *Crenicichla*

lepidota Heckel and *Geophagus brasiliensis* (Quoy & Gaimard)] and large-sized species [such as piscivorous Characiformes: *Hoplias malabaricus* (Bloch) and *Oligosarcus robustus* Menezes, Siluriformes: *Loricariichthys anus* (Valenciennes) and *Pimelodus maculatus* Lacepède], some of them undergoing migrations, such as *Prochilodus lineatus* (Valenciennes) and *P. maculatus* (Tables II and III).

DISCUSSION

Distribution of fish fauna is rarely caused by one factor (Horwitz, 1978; Angermeier *et al.*, 2002). Despite the relevance of biotic interactions (Gilliam *et al.*,

TABLE III. Fish species (see Table II) indicator index (I_I) for the Sinos River reaches (↑ headwater and ↓ lowland)

Species	I_I Headwater	Lowland	P	Species	I_I Headwater	Lowland	P
aalb	4	96	0·01 ↓	hlue	0	100	0·07
abim	23	77	0·02 ↓	hmal	0	100	0·00 ↓
abre	89	11	0·01 ↑	hmer	0	100	1·00
afas	1	99	0·00 ↓	hmus	100	0	0·00 ↑
ast1	99	1	0·00 ↑	hpun	87	13	0·00 ↑
ast2	100	0	0·00 ↑	lanu	0	100	0·00 ↓
ast3	0	100	1·00	lgro	0	100	1·00
bdor	0	100	0·48	lobt	0	100	1·00
bihe	85	15	0·00 ↑	mcot	65	35	0·26
cfac	90	10	0·08	mine	43	57	1·00
cibi	0	100	1·00	ofle	0	100	0·49
cint	0	100	1·00	ojen	49	51	0·72
clep	0	100	0·03 ↓	orob	5	95	0·02 ↓
cpal	0	100	0·02 ↓	pcau	60	40	1·00
cpor	0	100	1·00	pdor	0	100	0·02 ↓
cpte	94	6	0·00 ↑	plin	17	83	0·02 ↓
cpun	72	28	0·01 ↑	pmac	0	100	0·04 ↓
cste	0	100	1·00	pnig	0	100	1·00
cund	0	100	1·00	ppla	0	100	1·00
cvog	13	87	0·03 ↓	rcad	0	100	0·23
czeb	4	96	0·06	reri	100	0	0·00
dspe	0	100	1·00	rin1	0	100	1·00
evir	60	40	1·00	rin2	100	0	0·40
gbra	23	77	0·01 ↓	rmic	97	3	0·00
gcar	0	100	1·00	rque	88	12	0·00
ggym	39	61	0·13	rstr	0	100	0·25
glab	81	19	0·59	sbio	100	0	0·01 ↑
grha	0	100	0·25	scal	0	100	1·00
hasp	0	100	0·19	sjac	0	100	0·49
hcom	65	35	0·88	smar	69	31	0·71
hisp	7	93	0·02 ↓	tluc	0	100	0·15
hlit	0	100	0·18				

1993), fish fauna distribution is determined largely by micro-habitat suitability (Ross *et al.*, 1990; Matthews, 1986) and physiographic characteristics (Gorman & Karr, 1978; Felley & Felley, 1987; Rahel & Hubert, 1991; Leclerc & Desgranges, 2005; Robinson & Rand, 2005). Longitudinal distribution patterns of fish fauna were first described for mountain rivers in temperate regions, where abrupt changes in fauna composition were observed in relatively short distances (Huet, 1959; Sheldon, 1968; Matthews, 1986; Rahel & Hubert, 1991). As shown in several studies in tropical and subtropical rivers (Ibarra & Stewart, 1989; Peres-Neto *et al.*, 1995; Toham & Teugels, 1998; Abes & Agostinho, 2001; Bistoni & Hued, 2002; Hoeinghaus *et al.*, 2004), the results of the present investigation have supported most of these temperate-generated patterns.

Addition and substitution are the prevalent processes in fish longitudinal distribution in lotic systems. An additive pattern is generally reported for fish assemblages in systems lacking major thermal or geomorphic transitions (Evans & Noble, 1979), as a result of increased habitat diversity and greater environmental stability (Horwitz, 1978). Zonation with species replacement is expected in mountainous regions, where average temperatures typically increase as altitude decreases (Huet, 1959; Rahel & Hubert, 1991). Although Neotropical diversity is well documented [>6000 fish species (Reis *et al.*, 2003)], little is known about actual factors responsible for patterns of fish fauna change. In the Sinos River, both substitution and addition processes marked the longitudinal distribution of the fish fauna.

Beta diversity indices are employed to measure how species composition changes along environmental gradients (Harrison *et al.*, 1992; Lorance *et al.*, 2002; Thomaz *et al.*, 2003). In the Sinos River headwater region, factors such as position along the longitudinal gradient and the similarity in environmental characteristics may have contributed to the relatively higher homogeneity (specifically, the absence of turnover) in composition and abundance of fish fauna among samples and sampling stations. Species addition prevailed between Fraga and Caraá and both processes (addition and replacement) occurred between the other sampling stations. Species turnover was high between Caraá and Monjolo and between Monjolo and Parobé. These high β_2-diversity values were probably caused by different effects. The river stretch between Caraá and Monjolo is characterized by the transition between the headwater and lowland region. Mean depth increases drastically from 90 to 171 cm and substratum changes from predominantly gravel to silt and sand. Fish assemblage in Caraá was dominated by mid-sized benthic pimelodid and loricariid species, as well as small-sized characids, both benthic and from the water column. Loricariids like *A. brevipinnis* or *H. punctulatus* display morphological characteristics adapted to high flow velocities: a compact hydrodynamic body shape with large pectoral fins, which prevent displacement. These species feed on periphyton and insect larvae (Power, 1990; Hahn *et al.*, 1997). The small benthic characid *C. pterostictum* also possesses relatively large pectoral fins, which are used in support when the species 'sits' on the bottom and 'waits' for drifting prey. Small water column characids of the genus *Astyanax* or *Bryconamericus* are strong swimmers, which dart into the current for feeding from low-current microhabitats. Only one species, *C. punctata*, is piscivorous. At the first lowland site Monjolo, these typical headwater species are substituted by members of the

lowland fish fauna, like *Cyphocharax voga* (Hensel), *P. lineatus* and *G. brasiliensis*, which are characterized by a laterally compressed body shape, which favours maneuverability in benthic feeding under low-current conditions. More piscivorous species (*C. lepidota*, *H. malabaricus* and *O. robustus*) are present. Except for the piscivorous *H. malabaricus* (ambusher), the predominant sit-and-wait feeding strategy in headwaters is substituted by an active search at lowland sites.

Between Monjolo and Parobé all three major tributaries join the Sinos River main-stem. Areas of confluence were found to be of higher diversity, either in temperate (Matthews, 1986) or in tropical rivers (Fernandes *et al.*, 2004). The reason for higher diversity may be caused by the fact, that adventitious stream are of a lower order than the main-stem, thus locally mixing lower-order fauna with faunal components, which typically occur in higher orders. The result may be a nodal distribution of diversity (Fernandes *et al.*, 2004). Additionally, the lateral connectivity to adjacent flood-plains increases in the stretch between Monjolo and Parobé. The most frequent species at Parobé were *A. alburnus* and *Hyphessobrycon luetkenii* (Boulenger), small surface-dwelling characids, typically found in wetlands. These results correspond the expectations based on the RCC, which predicts higher diversity in the middle reaches. Studies in Cameroon showed a distribution pattern similar to that in the Sinos River (Toham & Teugels, 1998). Species richness and assemblage composition changed along the longitudinal gradient. As in the Sinos River, upstream sites displayed a pattern of species addition, while intermediate and downstream sites showed a pattern of species loss and substitution. In a subtropical Australian river system, however, changes in species richness were more related to species addition than to replacement (Hutchison, 1993). In the temperate River Seine basin in France, highest fish diversity was found in medium-sized rivers, corresponding to the RCC (Oberdorff *et al.*, 1993).

A major difference between a temperate and a subtropical river is the lower-temperature amplitude of the latter. Zalewski *et al.* (1990) found that rheophilic species in headwaters of Polish rivers tend to avoid stressful conditions by seasonal migrations. Not a single species of the Sinos headwater is known to migrate. As in the temperate Polish rivers, periphyton is the most important primary producer. Armoured catfishes feed directly on the basis of the trophic pyramid (periphyton) and characids like *C. pterostictum*, mainly on drifting ephemerid larvae, which is typical for the first consumer level. The residency in the Sinos River headwater fauna reflects probably the more homogenous conditions, which guarantee food availability during all seasons. Although higher mean temperature favours the primary production and, consequently, food availability during all seasons, residency has its price: it requires morphological adaptations to high flow conditions, which occur frequently due to torrential subtropical rain.

Ecotone effects in fish fauna composition have been observed between lotic and lentic environments (Willis & Magnuson, 2000) and between upper and lower stretches of several hydrographic basins (Toham & Teugels, 1998; Shibatta *et al.*, 2002; Hoeinghaus *et al.*, 2004). Several authors emphasized fish fauna dependence on biotope heterogeneity in tropical flood-plains (Agostinho *et al.*, 1993, 2004; Fernandes *et al.*, 2004). The number of fish species shared

among Sinos River sampling sites was relatively low (11%), a tendency observed also in other South American riverine systems of similar (Garutti, 1988; Abes & Agostinho, 2001; Pavanelli & Caramaschi, 2003; Hoeinghaus *et al.*, 2004) or higher elevational gradient (Peres-Neto, 1995; Videla & Bistoni, 1999).

Indicator species of the Sinos River probably reflect differences in environmental conditions. Factors such as body size, shape and feeding strategies differ between the indicator species of headwaters and lowland stretches. Morphological similarities such as small size and flattened body shape were characteristic of indicator species of the rithron environment (such as the armoured catfishes and the pimelodids). As demonstrated in other studies (Ross *et al.*, 1990; Toham & Teugels, 1998; Leclerc & Desgranges, 2005), substratum composition certainly exerts a strong influence on headwater species also in the Sinos River. Indicator species of lowland stretches in the Sinos River showed, in general, medium to large size. All headwater species are sedentary, characterized by a relatively short life span. Lowland indicator species such as *P. maculatus* and *P. lineatus*, however, require different habitats during their life cycle, migrating long distances to reach sites for feeding, spawning and early development (Zaniboni Filho & Schulz, 2003). The greater number of lowland indicator species compared to headwaters may be attributed to the greater heterogeneity in species composition among Monjolo, Parobé and São Leopoldo sampling sites. For fish assemblages of the upper Paraná River flood-plain, a greater number of indicator species was related to river channels, where fish species exhibit fewer ecological restrictions and great diversity of feeding habits and reproductive strategies (Da Luz *et al.*, 2004). As Characidae and Loricariidae families predominate among indicator species of headwaters (44 and 22%) and lowlands (43 and 14%), characterization of the longitudinal gradient based on dominance of fish families seemed not to be applicable to the Sinos River. Although not demonstrated, factors such as size and life history strategies seemed to be more important for ecological characterization of fish fauna longitudinal distribution and indicator species in the Sinos River than taxonomic aspects. The study of factors operating at different levels within the river system, especially fine scale evaluation (Leclerc & Desgranges, 2005), may contribute to understanding factors that determine fish species distribution in the Sinos River. Vilella (2002) confirmed a strong relation between micro-habitat factors and faunal distribution in a first-order stream located in the Maquiné River basin, which borders the Sinos River basin. Intensifying such studies in the order to contemplate the whole drainage basin with the inclusion of the tributaries, the lateral gradient (river channel and flood-plain) and species autoecology certainly will contribute for determining strategic areas for fish fauna conservation in the Sinos River.

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