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ORIGINAL ARTICLE

Short spatial and temporal scale patterns of fish assemblages in a subtropical rainforest mountain stream

Juan José Rosso^{a,b,*}, Ezequiel Mabragaña^{a,b}, Esteban Avigliano^{b,c}, Nahuel Schenone^{b,c} & Juan Martín Díaz de Astarloa^{a,b}

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The fish fauna of a subtropical mountain stream in Argentina was surveyed for the first time. The abundance and occurrence of species were explored considering variation in hydrology, seasonality and the abiotic environment. We collected 221 individuals of 23 species from 10 families and four orders. Small sized species and small individuals dominated the fish fauna. The small characid *Astyanax saguazu* was the most conspicuous species. Hydrology, seasonal changes in water temperature and variation in water conductivity affected the abundance and distribution of fish. *Hypobrycon maromba* is recorded in Argentina for the first time.

Keywords: Argentina; Misiones; Ramos stream; fish; hydrology

Introduction

River ecosystems are complex environments. Early biological research in rivers attempted to define zones on the basis of site-specific characteristics and related these to longitudinal succession of fish, invertebrates and other freshwater biota (Hawkes 1975). The longitudinal nature of hydrological and geomorphological changes in watercourses has led to the development of one of the most influential concepts in river ecology: the river continuum concept (Vannote et al. 1980). Later contributions revealed several limitations of this concept and highlighted the more complex multi-dimensional nature of river ecosystems (Ward 1989; Junk et al. 1989; Thorp & Delong 1994). More recently, heuristic and comprehensive models considered river ecosystems as a complex array (not merely longitudinal) of interconnected river patches with unique ecological functioning (Thorp et al. 2006).

Intimately aligned with this spatial arrangement of river patches, fish assemblages at different reaches show drastic changes in species composition and structure. Earlier river ecologists already recognized that most, if not all, fish species differently thrive in different river reaches and described a longitudinal zonation of fish fauna for river ecosystems (Huet 1949; Illies & Botosaneanu 1963). For instance, fish assemblages at mountain headwater streams are largely regulated by

the harsh abiotic and hydrological fluctuating conditions that characterize these environments (Roux & Copp 1996). Mountain rivers are highly unstable because of the frequency and random nature of the disturbance hydrological events affecting these ecosystems (Beckinsale 1969). The intensity of disturbance associated with exceptional episodes in headwater streams is explained by the fact that energy is dissipated over a narrow corridor (Bravard & Gilvear 1996). Nevertheless, it is the coexistence and alternation of “normal” fluvial process and torrential process, which explain the features and biological responses in mountain lotic systems (Cummins et al. 1984; Minshall et al. 1985).

The Ramos stream, in Misiones province, Argentina, is a rainforest mountain tributary of the Acaraguá River, a tributary of the middle Uruguay River. Recent results from ichthyological surveys in tributaries of the Uruguay River in Misiones suggest the existence of a high, not widely anticipated diversity of fish species inhabiting these rainforest mountain streams (Araya et al. 2012). From the earliest contributions of the foreign ichthyologists in the nineteenth century to the most recent lists (Roa & García 1982; Azpelicueta et al. 1985; Braga & Azpelicueta 1986; Gómez & Chebez 1996) the species richness of the fish fauna in this region has been steadily increased. One of the latest revisions reported 243 species for Misiones province grouped in 38 families and 11 orders (López

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et al. 2005). More recently, at least 15 new species and records of the genera *Crenicichla* (Casciotta et al. 2006a, 2010; Lucena 2007; Casciotta & Almirón 2008; Piálek et al. 2010), *Australoheros* (Casciotta et al. 2006b; Řičán & Kullander 2008; Řičán et al. 2011), *Hoplias* (Oyakawa & Mattox 2009), *Rhamdella* (Bockmann & Miquelarena 2008), *Hisonotus* (Azpelicueta et al. 2007), *Pimelodus* (Almirón et al. 2009), *Cnesterodon* (Aguilera et al. 2009) and *Rineloricaria* (Rodríguez & Miquelarena 2005) were reported for this province. Nevertheless, many low order mountain streams, including the Ramos stream, are still unexplored. Moreover, comparatively, the tributaries of the Uruguay River in Misiones are less explored than their counterparts of the Paraná River (Menni 2004). At present, 61 fish species have been reported for the tributaries of the Uruguay River in Misiones (López et al. 2005; Araya et al. 2012). This is one of the ecoregions with the highest number of ichthyofaunistic endemisms in Argentina (López et al. 2002). Therefore, an accurate estimation of the actual diversity is crucial in order to planning conservation efforts.

With this background, two main questions arose when planning this research: 1, how diversified the Ramos stream is; and 2, whether its fish fauna shows

changes in abundance and distribution associated with spatial and temporal hydrological and environmental dynamics. Particularly, we aimed to test if this small headwater mountain stream behaves as a unique ecological patch (*sensu* Thorp et al. 2006) in relation to fish assemblage dynamics or if further partitioning of small patches may be identified. Accordingly, we documented the diversity of the fish fauna in this subtropical rainforest mountain stream of Misiones, Argentina, and evaluated patterns in fish species abundance and distribution associated to short spatial (different stream reaches) and temporal (two different hydrological and climatic seasons) variations.

Materials and methods

Study area

The study area is located (27°26' S and 54°55'–54°58' W) among the central highlands of Misiones province (municipality of Campo Ramón) surrounded by subtropical rainforests where thermal seasonality is evident but hydrological variation is not as predictable as temperature. The Ramos stream is a small mountain first-order tributary of the Acaraguá River (Figure 1). Three

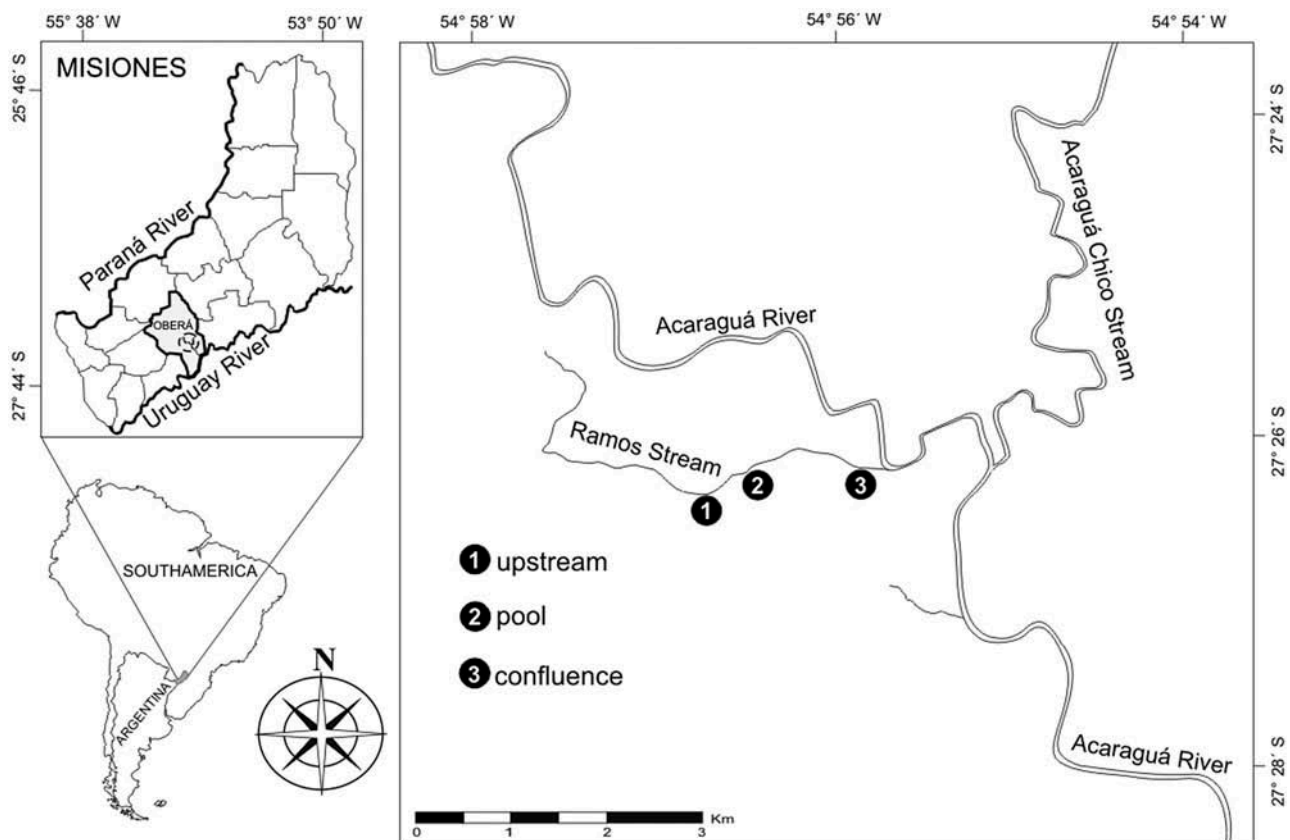


Figure 1. Map of the study area showing sampling locations in the Ramos stream, Misiones, Argentina.

different sampling sites were selected along the main course of the Ramos stream. An upstream site (1) was located in a shallow (less than 1 m deep) slowly flowing lotic reach where no signs of stagnation were observed. This site was the uppermost accessible reach of this ecosystem. The second site (2) was located 50 m downstream in a pool located shortly after a riffle-fall sequence. The third site (3) was located at the confluence of the Ramos stream with the Acaraguá River (Figure 1).

Environmental and hydrological variables

All sites were sampled twice during 2011 (February and June) under different hydrological and meteorological conditions (warm and cold seasons, respectively). In order to characterize the environmental and hydrological conditions, pH, dissolved oxygen (mg l^{-1}), turbidity (NTU), water conductivity ($\mu\text{S cm}^{-1}$), water temperature, water depth, subsurface velocity and stream width were recorded at each sampling site. Environmental parameters were measured with a multi-parameter probe Horiba U-53G. Water depth and stream width were measured with a scaled rope. Subsurface (20 cm depth) velocity was measured by means of a device composed of a small sized float (to avoid wind interference) with a proportional load submersed (20 cm depth) underwater. This is an adaptation of the floating object method (Brower & Zar 1984).

Fish sampling

Fishing gears were selected to maximize capture of different species and sizes according to the physical constraints imposed at each sampling site. Accordingly, fish were caught using trammel and beach seine nets. The trammel nets are constructed with an outer mesh of 75 mm between knots and an inner mesh of 15 mm between knots. The beach seine net, intended to capture small fish, is 10 m long with a 12 mm mesh in the wings and a central bag (1.5 m) of 5 mm between knots. In all sites trammel-nets were deployed just before sunset and left overnight (12 h). When deployed, the trammel nets completely crossed the stream width. Additionally, we hauled the seine net during daylight. Both trammel and beach seine samplings were conducted twice at each site on both sampling dates. The confluence site was not surveyed with the seine net during winter sampling due to the constraints imposed by woody debris.

Collected fish were measured (standard length SL) to the nearest mm with a digital caliper and weighed to the nearest gram with a digital balance. Fish species were identified following Ringuelet et al. (1967) and available

updated literature of Neotropical fish fauna when necessary. Particularly, we revised literature of *Cyanocharax* (Malabarba & Weitzman 2003), *Hemiancistrus* (Cardoso & Malabarba 1999), *Astyanax* (Casciotta et al. 2003), *Bryconamericus* (Casciotta et al. 2002, 2004; Almirón et al. 2004), *Oligosarcus* (Menezes 1987), *Hypobrycon* (Malabarba & Malabarba 1994; Silva & Malabarba 1996; Almirón et al. 2001), *Hoplias* (Oyakawa & Mattox 2009), *Crenicichla* (Lucena 2007), *Hypostomus* (Reis et al. 1990), *Rineloricaria* (Rodríguez & Miquelarena 2005) *Steindachnerina* (Vari 1991) among many others. Voucher specimens were deposited at the fish collection of the Research Institute of Coastal and Marine Science (IIMyC, CONICET-Universidad Nacional de Mar del Plata, Argentina).

Data analysis

A Mann–Whitney test was applied to the environmental variables to evaluate differences between sampling seasons. This analysis aimed to characterize the seasonality of the system as a whole. For that reason we used the combined data of all sampling sites of each season as a single set and tested for differences between them.

Due to the lack of the seine sample at the confluence during winter, this site-date data was not included in further statistical analyses. At the remaining sites, species richness was calculated and the total specimens collected of each species computed as a measure of abundance. With these results, each site was further characterized by measuring the diversity (Shannon & Weaver 1949) of the fish community. Spearman Rank correlation coefficients among fish community attributes (total abundance, richness and diversity) and environmental variables were estimated in order to evaluate the influence of seasonality and hydrology. We also included in this analysis the abundance of those species ($n = 4$) that were present in all samples. Spatial and temporal patterns in fish community structure were evaluated by means of a similarity percentage analysis using matrices constructed with Bray–Curtis distance on standardized, $\log(x + 1)$ fish abundance data. In order to detect environmental variables “best explaining” patterns in fish community structure, the routine BIOENV of the statistical software PRIMER.5 (Plymouth Routines In Multivariate Ecological Research) was used. This procedure selects best variables by maximizing a rank correlation (Kendall coefficient) between the fish and environment similarity matrices.

The richness extrapolation estimator proposed by Chao (1987) $Chao1 = S + (a^2/2 \times b)$ was used in order to assess the collection efficiency, where S is the total number of species in the samples, a is the number of

species with only one individual and b is the number of species with just two individuals. The pattern in fish size distribution was explored using the formula of Sturges (1926) ($K = 1 + 3.32 \log n$), where K is the number of intervals, and n is the sample size. The range of the intervals derived from the ratio between the range of the total values and the number of intervals (K) suggested by the formulae.

Results

The environmental conditions

Hydrological and environmental conditions differed greatly between sampling dates. A warm high water period characterized the stream environment during February. Conversely, June was characterized by lower temperature and water velocity, maximum depth and shorter stream width (Table 1). Overall, the high water period was characterized by significantly higher water velocity (Z value = -1.7457 ; $p < 0.05$), conductivity (Z value = -1.7457 ; $p < 0.05$) and temperature (Z value = -1.7457 ; $p < 0.05$). Ramos stream had slightly alkaline and clear waters. Low values of dissolved oxygen were registered at the confluence with the Acaraguá River.

Fish fauna composition

During the study period we collected 221 individuals of 23 species from 10 families and four orders (Table 2). The *Chao1* index indicated a potential richness of 23.4 species. By far, this system was dominated by Characiformes. Almost 86% ($n = 190$) of the specimens collected belong to this order. Characiformes also dominated the sample in terms of biomass (78%). This order showed also the largest number of species (Figure 2a). The family Characidae accounted for 40% of the total species collected. Characidae also

dominated the abundance of the fish fauna (Figure 2b). The presence of large specimens of *Hoplias lacerdae* (Erythrinidae) in the confluence reversed this pattern in terms of biomass.

Small characids of the genus *Cyanocharax* and *Astyanax* dominated in abundance. Altogether, these species accounted for more than 66% of total fish collected (Table 2). More than 30% of fish collected in the Ramos stream were *Cyanocharax uruguayensis*. Both *Cyanocharax* species accounted for 42% of total fish abundance. Two species of *Astyanax* and *Steindachnerina aff. biornata* slightly surpassed the 5% of total fish abundance whereas the remainder 18 species were all below 5%.

Mean SL of collected species spanned one order of magnitude, from the smallest *Bryconamericus* sp. (23 mm SL) to the largest *H. lacerdae* (365 mm SL). In 83% of the species, specimens had a mean SL lower than 150 mm (Figure 3). More than 93% of fish collected were smaller than 146 mm SL (Figure 4).

Spatial and temporal patterns in species abundance and distributions

The small characid *Astyanax saguazu* was present in all sampled environments and in both periods (Table 2). Species of the genus *Cyanocharax* and *Hemiancistrus* cf. *fuliginosus* dominated in all reaches. Conversely, several species were confined to the confluence and did not progress further upstream. One specimen of *Hypobrycon maromba* was collected in the pool during cold low water conditions and represents the first documented record of this species in Argentina. Twenty species were collected during warm high water conditions whereas only 10 were found during the cold low water sampling. In particular, all species of Perciformes and Gymnotiformes were captured during warm high water conditions.

Table 1. Spatial and temporal variation of selected environmental and hydrological variables in the Ramos stream, Argentina.

	Warm high water period				Cold low water period			
	Upstream	Pool	Confluence	Mean	Upstream	Pool	Confluence	Mean
Temperature (°C)*	22.12	22.03	23.19	22.4	12.9	13	13.6	13.1
pH	nd	nd	nd	—	7.97	8.43	7.23	7.87
Turbidity (NTU)	3.3	2.7	4.7	3.5	nd	nd	nd	—
Conductivity ($\mu\text{S cm}^{-1}$)*	293	312	336	313.6	55.4	54.9	54.3	54.8
Dissolved oxygen (mg l^{-1})	9.41	9.96	6.76	8.71	nd	nd	nd	—
Water velocity (m s^{-1})*	0.13	0.09	0.07	0.09	0.03	0.02	0.01	0.02
Max. depth (m)	0.6	1.3	1.19	1.03	0.45	0.8	0.65	0.63
Stream width (m)	5.4	7.2	7.2	6.6	4.75	6.65	6.9	6.1

Notes: nd: not determined. Asterisks denote significance of the Mann–Whitney test on season means at $p < 0.05$.

Table 2. Spatial and temporal patterns in abundance of fish species in the Ramos stream, Argentina. The total fish collected, diversity and richness of the fish assemblages at each site are also reported.

	Upstream		Pool		Confluence		Ramos stream	
	Warm	Cold	Warm	Cold	Warm	Cold	Abundance	Total biomass(g)
Characiformes								
Acestrorhynchidae								
<i>Acestrorhynchus</i> sp.					3		3	182
Parodontidae								
<i>Apareiodon affinis</i>					10		10	322.1
Characidae								
<i>Astyanax abramis</i>			1		1		2	58
<i>Astyanax asuncionensis</i>			3		13		16	425
<i>Astyanax</i> cf. <i>fasciatus</i>					6		6	113
<i>Astyanax saguazu</i>	2	8	14	5	1	1	31	276.8
<i>Bryconamericus</i> sp.	1		1	2			4	2.2
<i>Bryconamericus ytu</i>				2			2	1.63
<i>Cyanocharax uruguayensis</i>	3	16	20	15	14		68	74.2
<i>Cyanocharax lepiclastus</i>	2	6	7	4	6		25	21.4
<i>Hypobrycon maromba</i>				1			1	1.2
<i>Oligosarcus oligolepis</i>	2	1				1	4	159.1
Curimatidae								
<i>Steindachmerina</i> aff. <i>biornata</i>		14		1			15	248.2
Erythrinidae								
<i>Hoplias lacerdae</i>					3		3	1758
Siluriformes								
Loricariidae								
<i>Hemiancistrus</i> cf. <i>fuliginosus</i>	1	3	2	1	1		8	455.7
<i>Hypostomus commersoni</i>			1		3		4	124
<i>Rineloricaria</i> sp.		1	1	1	1		4	22.4
Pseudopimelodidae								
<i>Microglanis cottoides</i>					1		1	9
Heptapteridae								
<i>Rhamdia quelen</i>	1		1				2	190
Perciformes								
Cichlidae								
<i>Crenicichla lepidota</i>					2		2	59
<i>Crenicichla missioneira</i>			1		2		3	59
<i>Gymnogeophagus</i> sp.			1		4		5	54
Gymnotiformes								
Sternopygidae								
<i>Eigenmannia virescens</i>					2		2	36
Total no. of fish	12	49	53	32	73	2	221	
Total biomass (g)								4651.9
Total no. of species	7	7	12	9	17		23	
Diversity	1.86	1.61	1.79	1.68	2.45		2.43	

Most species of Siluriformes showed the same pattern of occurrence. Among Characiformes, the largest species (*Acestrorhynchus* sp., *Apareiodon affinis* and *Hoplias lacerdae*) and the largest *Astyanax* (*A. abramis*, *A. cf. fasciatus* and *A. asuncionensis*) were exclusively collected in summer. Only seven species occurred on both sampling dates.

Temporal and spatial patterns in the occurrence and abundance of species were reflected in the structure of fish assemblages. In particular, the percentage similarity analysis revealed a marked spatial variation in the structure of fish assemblages during

summer (Table 3). Temporal variation in fish assemblages (only for upstream and pool reaches) was less evident.

As suggested by the correlation analysis, richness and diversity of fish assemblages seemed to be affected by hydrology and the abiotic environment. Species richness was higher when stream width ($r = 0.94$; $p = 0.014$) and water depth ($r = 0.87$; $p = 0.053$) were higher. The diversity increased as the temperature ($r = 0.99$; $p < 0.001$) and conductivity ($r = 0.81$; $p < 0.10$) increased. The correlation analysis also showed that the abundance of

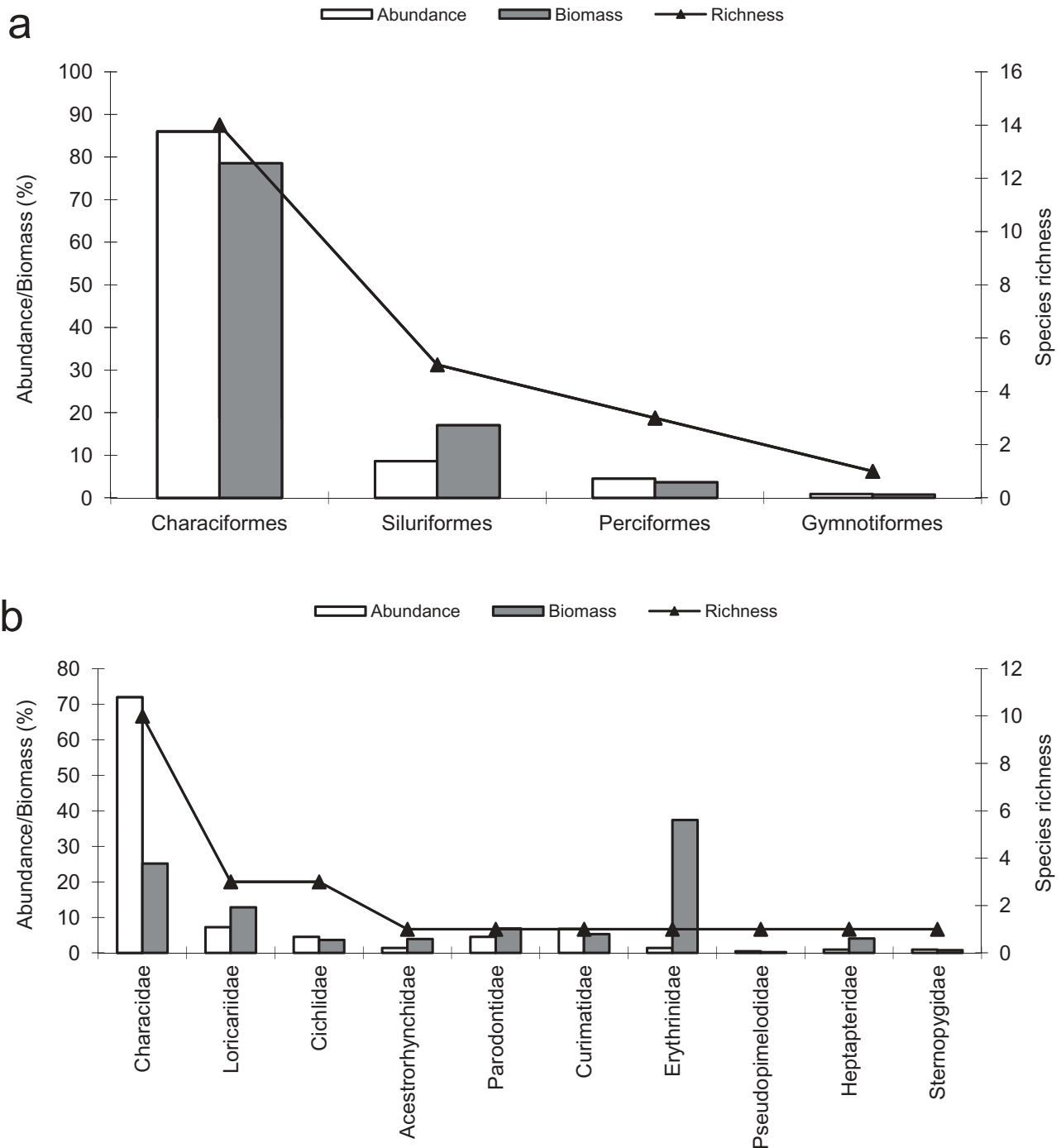


Figure 2. Comparison of the relative contribution of a, each order; and b, each family to the total abundance, biomass and species richness of fish collected in the Ramos stream, Misiones, Argentina.

Astyanax saguazu, *Cyanocharax uruguayensis*, *C. lepiclastus* and *Hemiancistrus* cf. *fuliginosus* was not related with the environmental variables.

The Kendall correlation coefficient ($r = 0.45$) of the BIOENV analysis showed that water temperature and velocity were the most influential environmental factors for the fish community structure.

Discussion

Species richness and composition of the fish fauna

The species richness of this small unexplored mountain stream paralleled other well-known lotic ecosystems of Misiones, such as the Cuña-Pirú creek ($n = 23$, Miquelarena et al. 2002) and the Uruguay River ($n = 22$, Miquelarena et al. 1997). The *Chao1* index

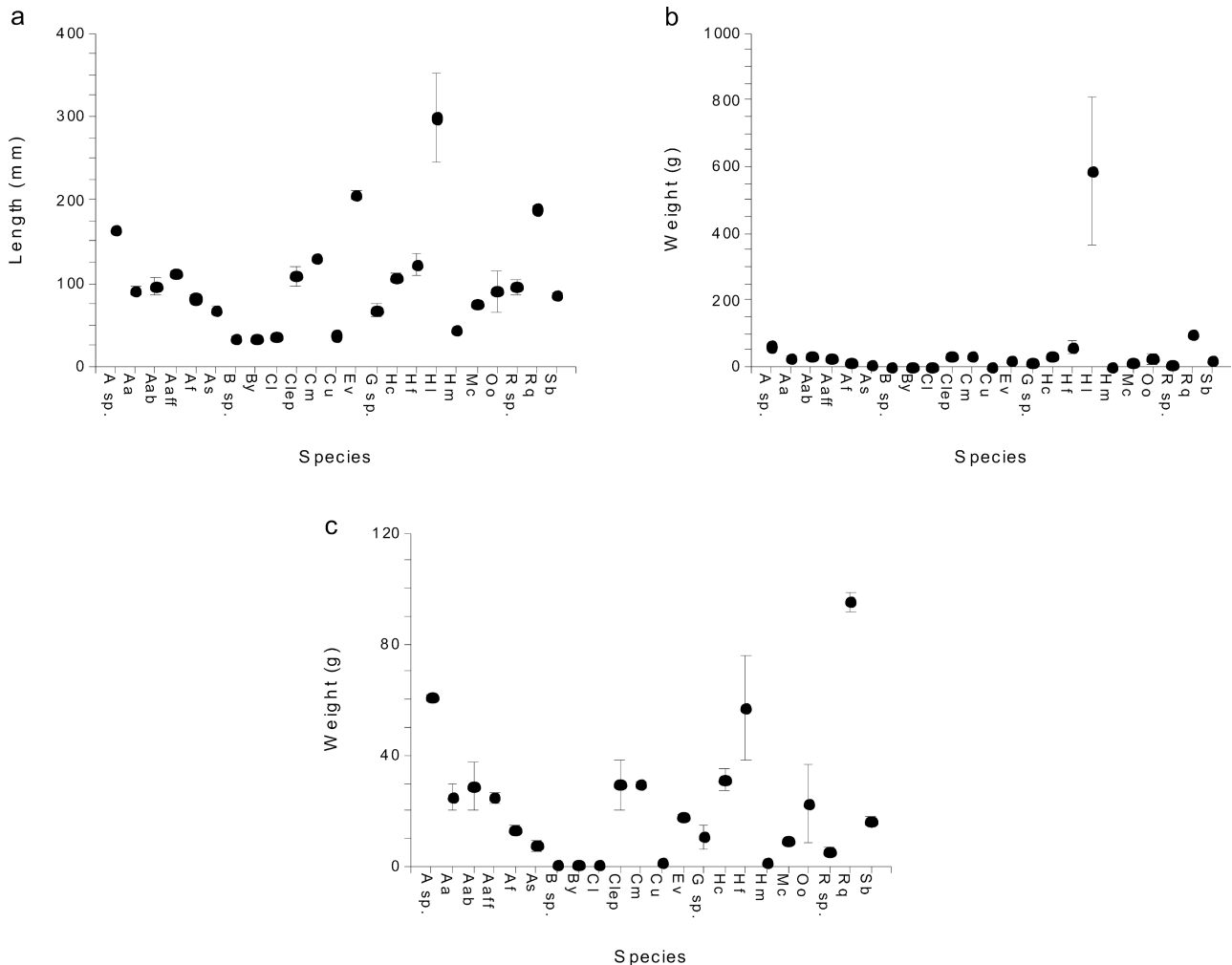


Figure 3. Means of a, standard length; b, weight of all fish species; and c, weight of all fish species except *H. lacerdae* inhabiting the Ramos stream. Error bars show one standard deviation. Abbreviations: A sp.: *Acestrorhynchus* sp.; Aa: *Astyanax asuncionensis*; Aab: *Astyanax abramis*; Aaff: *Apareiodon affinis*; Af: *Astyanax* cf. *fasciatus*; As: *Astyanax saguazu*; B sp.: *Bryconamericus* sp.; By: *Bryconamericus ytu*; Cl: *Crenicichla lepidota*; Clep: *Cyanocharax lepiclastus*; Cm: *Crenicichla missioneira*; Cu: *Cyanocharax uruguayensis*; Ev: *Eigenmannia virescens*; G sp.: *Gymnogeophagus* sp.; Hc: *Hypostomus commersoni*; Hf: *Hemiancistrus* cf. *fuliginosus*; Hl: *Hoplias lacerdae*; Hm: *Hypobrycon maromba*; Mc: *Microglanis cottoides*; Oo: *Oligosarcus oligolepis*; R sp.: *Rineloricaria* sp.; Rq: *Rhamdia quelen*; Sb: *Steindachnerina* aff. *biornata*.

indicated rather high collection efficiency, suggesting that the species richness of fishes in the Ramos stream may eventually reach slightly more than 23 species. Indeed, occasional later (June 2012) collections (Avigliano, personal communication) using the same sampling protocol, yielded two more species to this small stream, *Pimelodella* sp. and *Heptapterus mustelinus*. In addition to *Heptapterus mustelinus*, *Apareiodon affinis*, *Hypobrycon maromba*, *Oligosarcus oligolepis*, *Microglanis cottoides* and *Eigenmannia virescens* are new records for the tributaries of the Uruguay River in Misiones.

Not surprisingly, Characiformes and Siluriformes fishes dominated the fish fauna of the Ramos stream.

The dominance of these orders in fish assemblages of the Neotropics is well known (Lowe-McConnell 1987; Rodríguez & Lewis 1990; Langeani et al. 2007). Similarly, the large number of species of Characidae followed by several families with few or only one species is also a commonly observed pattern (Castro et al. 2004; Langeani et al. 2007). In particular, it has been shown that in South America, headwater reaches of lotic ecosystems are dominated by small characids (Buckup 1999). Moreover, the dominance of small characids seems to be characteristic of fish assemblages in Neotropical streams, regardless of their mountain or lowland nature. For instance, Casatti et al. (2006) mentioned that 26% of more than 7000

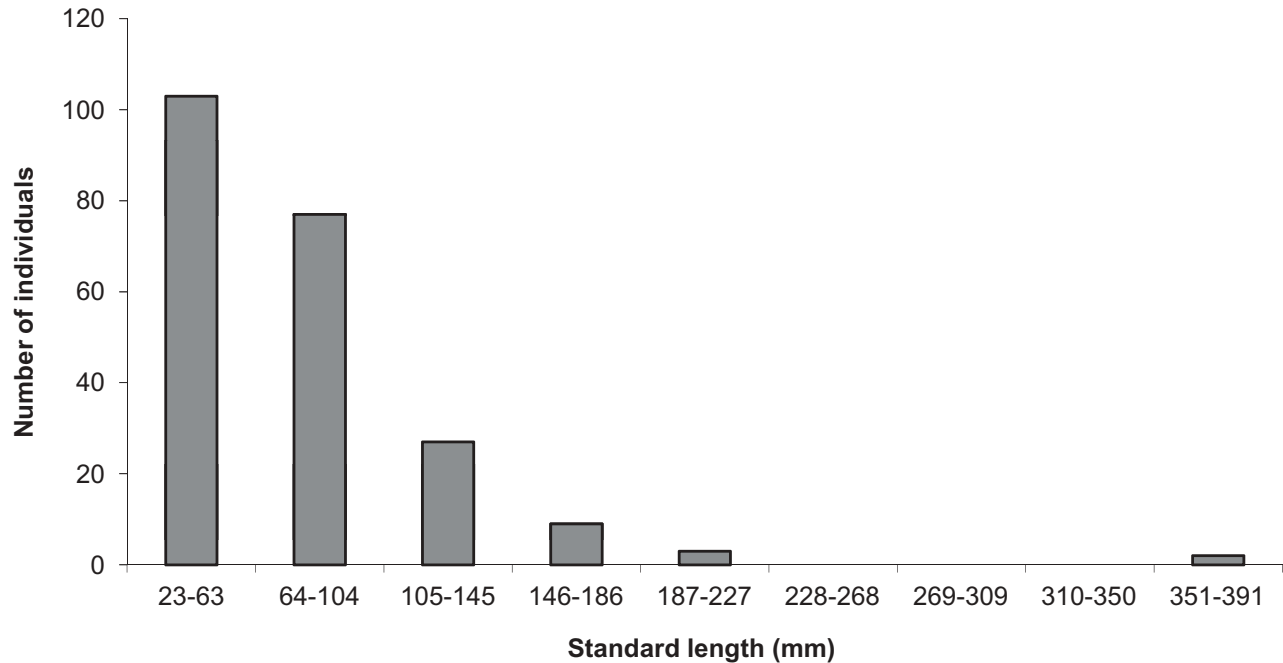


Figure 4. Frequency distribution of fish specimens ($n = 221$) grouped by body size (standard length in mm) in the Ramos stream.

Table 3. Matrix of Bray–Curtis similarity comparisons. Rows and columns labeled with the reach condition plus W for warm and C for cold periods.

	Upstream W	Pool W	Confluence W	Upstream C
Pool W	63.81			
Confluence W	29.78	53.04		
Upstream C	67.06	62.52	31.15	
Pool C	64.39	63.97	29.57	72.56

individuals collected in 35 grassland streams belong to *Astyanax altiparanae*. A similar dominance of *A. altiparanae* (17%) was identified in three headwater streams of the upper Paraná (Castro et al. 2004).

Species abundance and distribution

Our results showed that spatial variation in fish assemblage structure was stronger than temporal variation. This spatial variation would seem to be largely explained by the confluence site, since similarity between upstream and pool sites was rather high, both spatially and temporally. The same pattern was observed by Langeani et al. (2005) in the confluence of a small stream with the Tietê River. Confluence environments in river networks are typically populated by a large number of species, due to the presence of species exclusive to small tributaries plus the

occasional visitors from the main channel (Welcomme 1985). Indeed, it is widely recognized that fish species richness in lotic ecosystems increases from mouth to sea (Roux & Copp 1996). Spatial patterns in fish species abundance and occurrence may have strong implications in prey–predator dynamics. In this survey, the presence of large piscivores such as *Hoplias lacerdae* was only recorded at the confluence site. This leaves the uppermost reaches as a predator-free zone where most small species may take advantage of this situation. Indeed, a wealth of evidence suggests that piscivores can influence habitat use by small fishes in stream ecosystems (Matthews 1998).

The temporal analysis showed that very few species were collected in both sampling seasons. Sudden fast flooding events, as are commonly observed in the study area (Schenone, personal observation) may partially explain this pattern. Indeed, fish populations in headwater streams often present a lower level of adaptation to the largely fluctuating environmental dynamics, as the unpredictability of the short, sharp spates impedes development (Roux & Copp 1996). Besides hydrology, water temperature seemed to be a crucial factor determining temporal dynamics of fish assemblages. Indeed, the BIOENV analysis highlighted the importance of water temperature and flow velocity explaining spatial and temporal patterns in the structure of fish assemblages. Velocity is particularly important in running waters because it

influences metabolism and a large variety of behavioral characteristics (Petts & Amoros 1996). Moreover, correlation analysis further detected that water depth, stream width and water conductivity may be important for species richness and assemblage diversity. All these environmental factors have been shown to deeply regulate fish species abundance and occurrence in stream ecosystems (Matthews 1998). Particularly, hydraulic conditions at a local scale (0.1–100 m²), especially flow velocity, are seen as having a dominant influence on the patterns of fish species distribution and habitat selectivity (Stalnaker et al. 1989). Therefore, it could be suggested that hydrology, seasonal changes in water temperature and variation in water conductivity could be interactively influencing the abundance and distribution of fish in this subtropical rainforest mountain stream.

Our results revealed that a small headwater mountain stream, which could be seen as a unique ecological patch within the context of a river network, displayed evident spatial scale partitioning of fish assemblages intimately aligned with the variation of environmental variables. Understanding the effects of short-scale patterns in abiotic conditions and associated changes in biota is necessary for a more complete understanding of ecosystem ecology and therefore effective management (Barletta et al. 2010). In this respect our results represent an important contribution for planning management and conservation efforts in headwater mountain streams.

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