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Do hydraulic units define macroinvertebrate assemblages in mountain streams of central Argentina?

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Abstract

Methods to assess the physical habitat provide important tools for many aspects of river management. Hydraulic units (defined as a homogeneous patch of flow type and substrate) were described in mountain streams of Central Argentina and the distribution of macrozoobenthos in these habitat units was analyzed. Four streams from the upper Carcarañá River Basin (Córdoba, Argentina) were sampled in two hydrological periods. Hydraulic units (as substrate and flow type), current velocity, depth, macrophytes and macroalgae were assessed. Three benthic samples were taken in each hydraulic unit. A total of 12 hydraulic units were registered, which varied seasonally in their proportional abundance. The highest values of taxonomic richness, total abundance, diversity and evenness were found in the low-water period. The most heterogeneous hydraulic units (characterized by substrate of diverse grain size) presented the highest richness, diversity and evenness, whereas the highest total abundance was observed in hydraulic units with homogeneous substrate, such as bedrock or gravel sand. Canonical correspondence analysis grouped samples and taxa mainly in relation to the hydraulic units, and temporal variation in macroinvertebrate assemblages was observed. We found that the interaction between hydrological and geomorphological conditions affected benthic assemblages and that their organization is important at a mesoscale. Therefore, hydraulic units may be considered important tools in assessing stream integrity in lotic systems of central Argentina.

Keywords: Macroinvertebrate assemblages; Benthos; Hydraulic units; Habitat; Stream; Diversity and abundance patterns

Introduction

Anthropogenic activities have strong effects on aquatic ecosystems leading to widespread modification of the physical habitat and consequently, of biotic communities and ecological functioning. The physical habitat of stream biota is a spatially and temporally dynamic entity, determined by the interaction of the structural features of the channel and the hydrological regime (Maddock, 1999). Methods to assess the physical habitat provide important tools for many aspects of river management, including river health monitoring, determination of river restoration strategies, and biodiversity assessment (Raven et al., 2002; Thomson, Taylor, Fryirs, & Brierley, 2001).

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Riverine systems can be studied considering a variety of spatial scales (Frissell, Liss, Warren, & Hurley, 1986). The scale in which knowledge is currently most lacking is at 'mesoscale'. This is a level of detail larger than the micro-habitat and smaller than river habitat features such as riffles and pools (Kemp, Harper, & Crosa, 2000). The mesoscale range from one to tens of meters and typical time scales of development are seasonal or yearly, from 1 month to a year (Baptist, 2001). The consideration of stream ecology at this scale may be important, because it is expected to provide useful tools in management (Harper & Everard, 1998) and river rehabilitation (Kemp, Harper, & Crosa, 1999).

Recent parallel developments in the fields of stream ecology and geomorphology have provided an opportunity to link 'biological' and 'physical' definitions of habitat. In ecology, definitions of the 'functional habitat' (Buffagni, Crosa, Harper, & Kemp, 2000; Harper, Smith, Kemp, & Crosa, 1998; Kemp et al., 1999) or the 'mesohabitat' concept (Armitage, Pardo, & Brown, 1995; Beisel, Usseglio-Polatera, Thomas, & Moreteau, 1998; Pardo & Armitage, 1997) describe habitat units, made up of substrate or vegetation types, which are identified as distinct by their macroinvertebrate assemblage (Kemp et al., 2000). On the other hand, physical habitat is also known as 'hydraulic biotope' (Wadeson & Rowntree, 1998) or 'hydraulic unit' (Thomson et al., 2001) by geomorphologists. According to these authors, these habitat units are patches of relatively homogeneous flow and substrate character and they are nested within geomorphic units such as riffles and runs. Hydraulic units are discharge (flow stage) dependent features, whereas geomorphic units are relatively more stable in the short term (Thomson et al., 2001). The usefulness of the procedures proposed by geomorphologists will depend on demonstrating that hydraulic units have ecological relevance so that patches of similar surface flow type, substrate and aquatic vegetation support similar biotic assemblages (Kemp et al., 2000; Thomson et al., 2001).

The Carcarañá River Basin is one of the most important fluvial systems of the central region of Argentina. Studies of water quality (Gualdoni & Corigliano, 1991), drift (Gualdoni, 1997; Oberto, Raffaini, & Corigliano, 2004) and functional community structure (Corigliano, 1989; Corigliano & Malpassi, 1998; Principe & Corigliano, 2006) have already been performed. However, research on macroinvertebrate assemblages associated with particular habitat units considering a mesoscale, is still lacking. Consequently, the characterization of local macroinvertebrate assemblages associated with different habitat units turns out to be essential, in order to use habitat assessment as a predictive tool for the evaluation of human actions on lotic ecosystems.

The main purpose of this study is to provide the answer to the following question: how valuable is the hydraulic unit concept to describe macroinvertebrate community structure in the study streams? Since it is known that substrate and flow influence macroinvertebrate distribution, and hydraulic units are defined by these two variables, we hypothesized that macroinvertebrate assemblages from different hydraulic units are distinct and therefore, these habitat units define the macroinvertebrate community. In this study, we identified and characterized dominant hydraulic units, and we examined the distribution of macroinvertebrate assemblages in these habitat units in order to test their ecological importance in mountain streams of central Argentina.

Materials and methods

Study area

The study was carried out in four streams of Chocancharava River and Ctalamochita River upper sub-basins, Córdoba, Argentina (Fig. 1). These rivers are the main tributaries of the Carcarañá River and belong to the La Plata River basin. This fluvial system is one of the most important in the central region of Argentina, since it supplies drinking water, irrigation and hydroelectric energy. Headwaters are in mountainous regions at about 2000 m a.s.l., where many small

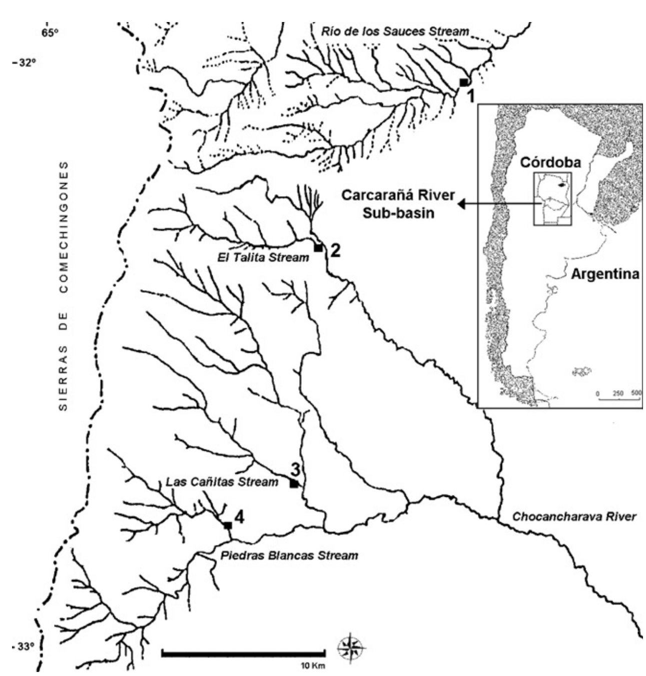

Fig. 1. Study sites in streams of Carcarañá River Sub-basin, Córdoba, Argentina: (1) Río de los Sauces, (2) El Talita, (3) Las Cañitas, (4) Piedras Blancas.

Table 1. Location and environmental characterization of study sites in streams of Ctalamochita River and Chocancharava River sub-basins: (1) Río de los Sauces, (2) El Talita, (3) Las Cañitas, (4) Piedras Blancas

	Study sites			
	1	2	3	4
Latitude (S)	32°32′07″	32°39′45″	35°52′13″	32°54′17″
Longitude (W)	64°35′43″	64°44′47″	64°45′35″	64°50′40″
Altitude (m a.s.l.)	735	875	672	732
Stream order	4	3	3	3
Mean width (m)	8	8	15	16
Vegetative cover (%)	>95	>95	75–84	>95
Consumption of trees and shrubs by livestock (%)	0–5	0–5	5–25	0–5
% bank with deep, binding root masses[a]	65–85	>85	>85	>85
Management activities	Recreation	Recreation	Agriculture – livestock grazing	Recreation
River channel pattern	Straight	Straight	Straight	Straight
Dominant geomorphic units	Riffle – Run	Riffle – Run	Riffle – Run	Riffle – Run

[a]The percentage of bank with deep, binding root masses was assessed by visual estimation in both stream banks. All tree and shrub species were considered to provide such roots. In each bank, a transect was walked along the entire length of the study reach and root masses were assessed within a 2-m wide swath on each side of the transect.

streams join to form the main collectors at foothills. Then they flow through the pampean plain in a west–eastern direction into the Carcarañá River.

Streams in the upper sections have generally deep and narrow valleys, with riffles of coarse substrate and turbulent flow. In lower slope reaches, the stream bed is also composed of gravel and sand. This fluvial system is submitted to a highly dynamic hydrology, with short and intense floods in specific periods of the year (Cantero et al., 1998). The rainy season, from October to March has a maximum precipitation of 725 mm; the minimum precipitation (143 mm) occurs between April and September (Capitanelli, 1979). Maximum temperature reaches 34 °C in summer (December–March) and decreases up to -5 °C in winter (June–September). Vegetation of the study area, which is only partially shaded, changes in relation to the longitudinal gradient and its distribution is modified by human activities (Luti et al., 1979). Some species typical of downstream zones, such as *Acacia caven* (Mol.) Mol., *Geoffroea decorticans* (Gill.) Burk. and *Celtis tala* Planchon, also occur at this altitude along the stream banks and in the adjacent areas (Cabido et al., 2003). In some reaches there are also exotic species of ornamental trees and bushes.

Four sampling stations were selected in this study: Río de los Sauces, El Talita, Las Cañitas, and Piedras Blancas (Fig. 1). Location and environmental characteristics of sampling stations are shown in Table 1.

Sampling design

Sampling was carried out in four streams during high- (March 2003) and low-water period (July 2003). All streams were visited twice in each period because temporal replication is required to be sure that there are, in fact, seasonal differences in abundance (Underwood, 1994).

Three geomorphic units were selected in each site and sampling occasion and, in each of these geomorphic units, the dominant hydraulic unit was characterized by flow type and substrate character (Table 2). As flow and substrate are variables that varied seasonally and may differ among streams, not all hydraulic units were present in all streams and hydrological periods. Three replicate Surber samples were taken in each hydraulic unit following a stratified sampling design. A total of 144 benthic samples were collected (4 streams, 2 hydrological periods, 2 dates, 3 hydraulic units and 3 replicates).

Field and laboratory methods

Substrate composition and flow type were visually assessed (Gordon, McMahon, & Finlayson, 1994) in each hydraulic unit and assigned to a category (Table 2) proposed by Thomson et al. (2001). Maximum width and length of each hydraulic unit were measured and proportional abundance of macrophytes, macroalgae, twigs and leaves, and detritus were assessed.

Current velocity and depth were measured with a Global Flow Probe FP101–FP201 for each sample (three times in each hydraulic unit). Conductivity, pH, temperature and turbidity were measured with portable sensors on each sampling occasion. In order to characterize study sites, water chemical analyses were performed using the portable laboratory Hach 2000 and

Table 2. Classification of surface flow types (Wadeson & Rowntree, 1998) and substrate types (Thomson et al., 2001)

Category	Flow type	Category	Substrate type
F1	Standing water/swamp	S1	100% bedrock
F2	Scarcely perceptible flow	S2	80% bedrock
F3	Smooth surface flow	S3	30–60% bedrock, mixed with cobbles and pebbles
F4	Upwelling	S4	Predominantly boulders and cobbles
F5	Rippled	S5	60% cobbles
F6	Unbroken standing waves	S6	Mixture of cobbles and pebbles
F7	Broken standing waves	S7	Even mix of cobbles, pebbles and gravels
F8	Chute	S8	Pebbles, gravel and sand
F9	Free fall		

colorimetric analyses (Greenberg, Clesceri, & Eaton, 1992).

Benthic samples were taken using a Surber sampler ($0.09\,m^2$, $300\,\mu m$ mesh size). Invertebrates were preserved in 4% formaldehyde solution. At the laboratory, organisms were sorted, identified to the lowest possible taxonomic level, counted and kept in 70% ethanol. Abundance was calculated as number of individuals per m^2.

Data analyses

A detrended correspondence analysis (DCA) was performed in order to analyze hydraulic unit distribution in the study streams. This ordination technique, which is based on reciprocal averaging (Hill & Gauch, 1980), was performed considering proportional abundance of hydraulic units in each stream and date. Differences in the DCA scores among streams and between hydrological periods were tested with the Kruskal–Wallis test and the Mann–Whitney test, respectively.

In this paper, "taxonomic richness" is used instead of species richness (Malmquist, Antonsson, Gudbergsson, Skülason, & Snorrason, 2000) because not all the identifications were made at species level. Richness was measured considering the number of distinctive taxa recorded and Shannon diversity index and evenness were calculated using natural logarithms. Since not all hydraulic units were found in all sites and dates, Monte Carlo approximations of exact Kruskal–Wallis tests were used to compare macroinvertebrate abundance, richness, diversity, and evenness among the hydraulic units. This analysis allows one to ensure the most accurate test of statistical significance when the data set is unbalanced. In order to obtain comparable sample sizes, Abramsky et al. (1990) suggested using Monte Carlo simulations. The Monte Carlo approximation is a repeated sampling method. For any observed table, there are many tables, each with the same dimensions. The Monte Carlo method repeatedly samples a specified number of these possible tables in order to obtain an unbiased estimate of the true p value. Abundance, richness, diversity and evenness were also compared between the hydrological periods by the Kruskall–Wallis test. As in this case the data set was balanced, the usual asymptotic method was used.

For a given hydraulic unit, the abundance of each taxon present was divided by the total abundance of that taxon recorded across all the units. This gave a measure (between 0 and 1) of the relative preference of each taxon for each habitat unit (Tickner, Armitage, Bickerton, & Hall, 2000). In order to analyze macroinvertebrate distribution in hydraulic units and associations of the assemblages with variables that influence habitat availability, canonical correspondence analysis (CCA) was performed (Ter Braak, 1986). Abundance data were $\log_{10}(Y+1)$ transformed and the Monte Carlo permutation test was applied to test the significance of taxa–environment relationships (199 permutations).

In order to test differences in macroinvertebrate assemblages between hydrological periods, DCA were carried out for each stream on macroinvertebrate abundance data. Differences in the DCA scores among the hydrological periods were tested with one-way analysis of variance (ANOVA). All multivariate analyses were performed, using the statistical package CANOCO version 4.02 (Ter Braak & Smilauer, 1998).

Results

Characterization and distribution of hydraulic units

Values of physicochemical variables were among the normal values for mountain streams of the central region of Argentina (Table 3). A total of 12 hydraulic units were registered in the study streams (Table 4). Categories S1 and S2 of substrate (Table 2) were not found in this study and four out of nine possible flow categories were registered. Hydraulic unit Nos. 1 and 11

Table 3. Physico-chemical characterization of water in study sites (1: Río de los Sauces, 2: El Talita, 3: Las Cañitas, 4: Piedras Blancas) during high and low water periods

	Study sites							
	High-water period				Low-water period			
	1	2	3	4	1	2	3	4
Temperature (°C)	18.55	17.75	18.68	17.95	9.82	8.58	11.77	12.72
	3.77	3.29	1.48	2.24	3.11	3.76	2.25	1.54
Turbidity (utm)	1.67	0.60	1.58	1.23	0.82	1.07	1.50	2.63
	1.08	1.04	0.92	0.51	0.23	0.25	0.66	1.70
pH	8.06	7.58	7.75	7.90	7.95	7.78	8.09	8.14
	0.31	0.38	0.23	0.36	0.10	0.10	0.17	0.10
Conductivity (μs)	172.63	59.33	103.73	108.13	202.93	72.97	137.97	132.87
	50.02	13.04	15.02	9.44	35.61	11.07	12.27	8.64
Total dissolved solids ($mg\,L^{-1}$)	81.67	28.00	49.33	51.33	95.67	34.00	65.33	62.67
	23.09	6.24	7.09	4.93	16.04	5.29	6.35	4.16
Salinity (%)	0.07	0.00	0.03	0.03	0.10	0.00	0.10	0.10
	0.06	0.00	0.06	0.06	0.00	0.00	0.00	0.00
NO_3^- ($mg\,L^{-1}$)	0.70	1.30	1.05	0.85	0.70	0.60	0.75	0.75
	0.57	0.28	0.21	0.64	0.71	0.57	0.78	0.78
NO_2^- ($mg\,L^{-1}$)	0.01	0.02	0.02	0.01	0.01	0.02	0.01	0.02
	0.01	0.00	0.01	0.01	0.00	0.01	0.00	0.01
SO_4^{-2} ($mg\,L^{-1}$)	2.67	7.33	1.67	8.00	2.00	0.50	0.50	0.50
	2.89	9.29	1.15	6.08	2.83	0.71	0.71	0.71
PO_4^{-3} ($mg\,L^{-1}$)	0.36	0.25	0.63	0.19	0.41	0.32	0.23	0.20
	0.06	0.11	0.32	0.11	0.04	0.06	0.06	0.03
Hardness ($mg\,L^{-1}$)	60.03	17.47	29.16	38.37	72.90	22.67	41.67	38.35
	18.21	1.38	3.78	1.89	6.51	0.09	3.04	5.86
Alkalinity ($mg\,L^{-1}$)	81.07	22.77	41.25	49.66	101.05	26.35	56.03	53.20
	25.48	5.17	5.30	3.48	1.63	1.20	2.38	4.85
Dissolved O_2 ($mg\,L^{-1}$)	13.50	11.90	10.70	10.00	13.10	13.50	11.80	10.00
						3.25	0.99	1.98

When variables were measured more than once, mean values are shown with standard deviations below.

were defined by smooth surface flow and rippled flow defined hydraulic unit Nos. 4, 6, 9, 10, and 12. These two flow types were found in runs. On the other hand, hydraulic unit Nos. 2, 5, and 7 were defined by the flow of unbroken standing waves, and hydraulic unit Nos. 3 and 8 were defined by the flow of broken waves. These two flow types with standing waves were registered in riffles.

Hydraulic unit No. 12, characterized by gravel-sand substrate and rippled flow, was the most frequent, being found in all streams and in both hydrological periods. There were differences in hydraulic unit composition among streams, especially in the low-water period (Fig. 2). In this period, hydraulic units were characterized predominantly by smooth surface flow. In the high-water period, unit No. 5 was dominant in all sites except in Río de los Sauces and El Talita and Las Cañitas showed a more similar hydraulic unit composition in this period.

The results of the DCA ordination showed that 42.8% of hydraulic unit proportional abundance was accounted by the first four ordination axes (eigenvalues: axis 1: 0.862, axis 2: 0.317, axis 3: 0.115, axis 4: 0.050; total inertia: 3.140). This analysis showed temporal more than spatial segregation of sites. The first axis separated sites belonging to different streams, although this segregation was not significant (K–W $= 2.80$, $p = 0.42$). El Talita and Las Cañitas were grouped almost together, indicating a high similitude between these two streams. Río de los Sauces seems to be the most different stream, since it was separated from the other sites. The second axis more clearly distinguished sites in relation to hydrological periods (M–W $= 50$, $p = 0.06$). However, temporal differences were not very clear since Río de los Sauces in the low-water period was grouped with sites from the high-water period.

Macroinvertebrate diversity and abundance patterns

From a total of 106 taxa, 76 were found in Río de los Sauces, 72 in El Talita, 69 in Las Cañitas and 70 in

Table 4. Characterization of hydraulic units in the study streams (1: Río de los Sauces, 2: El Talita, 3: Las Cañitas, 4: Piedras Blancas)

Hydraulic unit	Substrate type	Flow type	Mean current velocity ($m\,s^{-1}$)	Mean depth (m)	Geomorphic unit	Stream	Frequency (%)
1	80% Bedrock	Smooth surface flow	0.18	0.45	Run	1	2.0
2	80% Bedrock	Unbroken standing waves	0.73	0.09	Riffle	1	2.0
3	80% Bedrock	Broken standing waves	0.74	0.18	Riffle	1	4.0
4	Predominantly boulders and cobbles	Rippled	0.30	0.28	Run	2-3-4	20.8
5	Predominantly boulders and cobbles	Unbroken standing waves	0.52	0.20	Riffle	2-3-4	18.7
6	60% Cobbles	Rippled	0.27	0.22	Run	1-4	6.0
7	60% Cobbles	Unbroken standing waves	0.21	0.32	Riffle	3	2.0
8	60% Cobbles	Broken standing waves	0.53	0.21	Riffle	2-3	4.0
9	Mixture of cobbles and pebbles	Rippled	0.20	0.14	Run	1-3	4.0
10	Even mix of cobbles, pebbles and gravels	Rippled	0.23	0.17	Run	1-4	6.0
11	Pebbles, gravel and sand	Smooth surface flow	0.18	0.28	Run	1-3	4.0
12	Pebbles, gravel and sand	Rippled	0.28	0.26	Run	1-2-3-4	25.0

The frequency of each hydraulic unit was calculated over the total of 144 samples taken in this study.

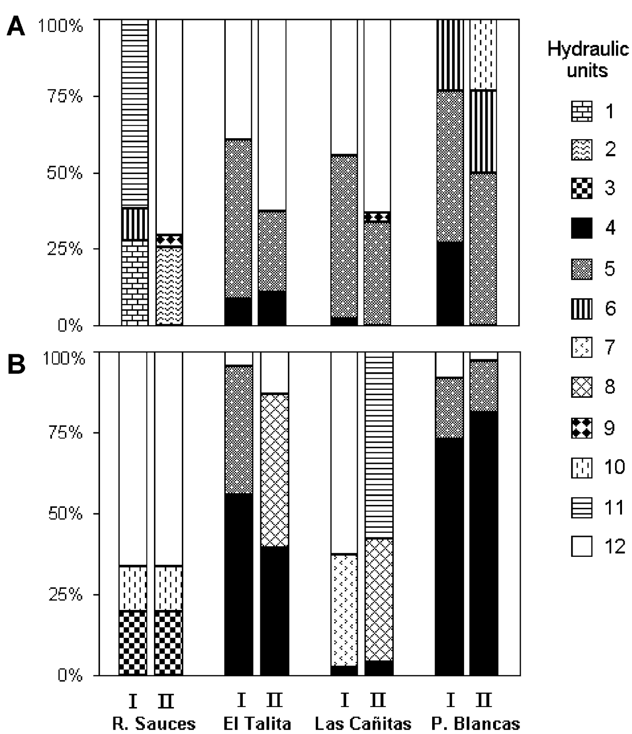

Fig. 2. Distribution and proportional abundance of 12 hydraulic units in the study streams. (A) High-water period. (B) Low-water period. Numbers I and II indicate different dates of each period in each stream.

Piedras Blancas. Total macroinvertebrate abundance, taxonomic richness, Shannon diversity and evenness were different among the hydraulic units in both hydrological periods, as assessed by exact Kruskal–Wallis tests (Table 5). The highest values of these community attributes were found in the low-water period, except for evenness which did not show differences between the hydrological periods (abundance: K–W = 27.90, $p<0.0001$; richness: K–W = 15.84, $p = 0.0001$; diversity: K–W = 3.35, $p = 0.0673$; evenness: K-W = 0.0003, $p = 0.9857$).

The highest total abundance was found in the hydraulic unit No. 10, characterized by a substrate of cobbles, pebbles and gravel and rippled flow (Fig. 3). The highest richness was found in unit No. 5 and the highest values of diversity were found in unit Nos. 5 and 7. Evenness and Shannon diversity showed a similar pattern of temporal variation among the different hydraulic units.

The general pattern of variation showed higher richness, diversity and evenness in the most heterogeneous hydraulic units (Fig. 3), which were characterized by substrate of diverse grain sizes (unit Nos. 4– 9). However, total abundance showed an inverse pattern, since the highest values were observed in hydraulic units with more homogeneous substrate (Fig. 3), such as bedrock or gravel sand (unit Nos. 1– 3, 10–12).

Table 5. Differences in macroinvertebrate community attributes among the hydraulic units in the different hydrological periods, measured by Monte Carlo approximations of exact Kruskal–Wallis tests

	Abundance		Richness		Diversity		Evenness	
	K–W	*p*	K–W	*p*	K–W	*p*	K–W	*p*
Hydraulic units								
High-water	27.91	<**0.001**[a]	23.73	**0.001**[a]	38.59	<**0.001**[a]	33.99	<**0.001**[a]
Low-water	16.19	**0.016**[a]	37.34	<**0.001**[a]	42.86	<**0.001**[a]	39.00	<**0.001**[a]

Monte Carlo significant *p* values are in bold.
[a]Monte Carlo significance based on 10,000 samples and seed 2,000,000.

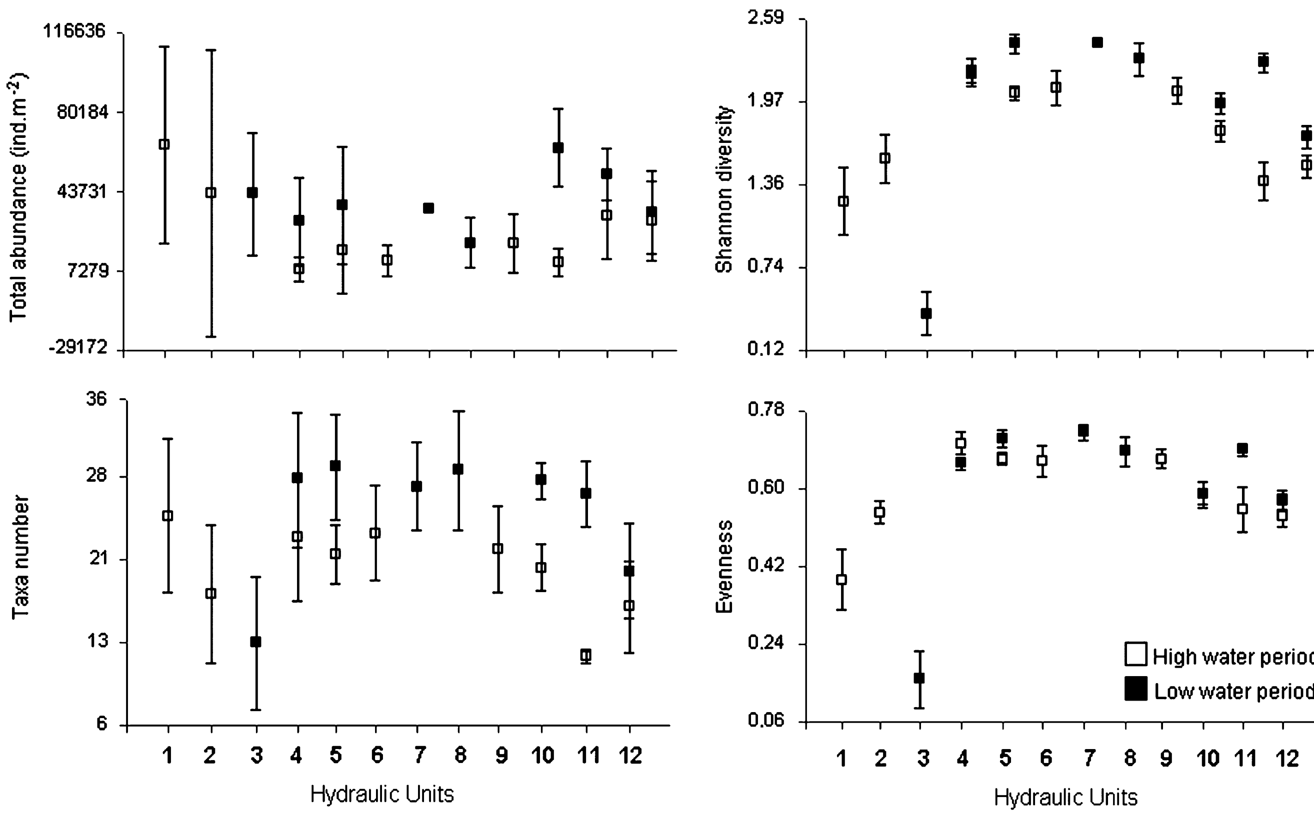

Fig. 3. Total macroinvertebrate abundance, taxonomic richness, diversity and evenness in hydraulic units of the study streams during the high- and the low-water periods. Mean values are shown with standard error.

Macroinvertebrate assemblages and habitat variables

CCA grouped samples and taxa mainly in relation to the hydraulic unit (Figs. 4 and 5). The summarized results of CCA are reported in Table 6. Monte Carlo test showed that all the axes were significant, indicating a good relationship between macroinvertebrate taxa distribution and measured environmental variables.

Flow and substrate type were important variables in the ordination analysis. The biplot of samples and environmental variables reflect a gradient mostly related to hydraulic conditions. The presence of macrophytes, macroalgae, and organic matter, such as detritus and twigs and leaves, were mainly associated with the second axis. Emergent vegetation showed less explanatory power. The first axis separates samples in relation to flow and substrate type (Fig. 4). On the right side of the plot, samples from coarse substrate and turbulent flow were grouped, whereas on the left-side samples were from fine substrate and smoother flow. The second axis separates samples in relation to the dominant aquatic vegetation. However, some hydraulic units with the same substrate type were not clearly separated in the plot, such as unit Nos. 4 and 5; and Nos. 11 and 12. An apparent temporal segregation was observed along axis 2, especially on the left side of the plot.

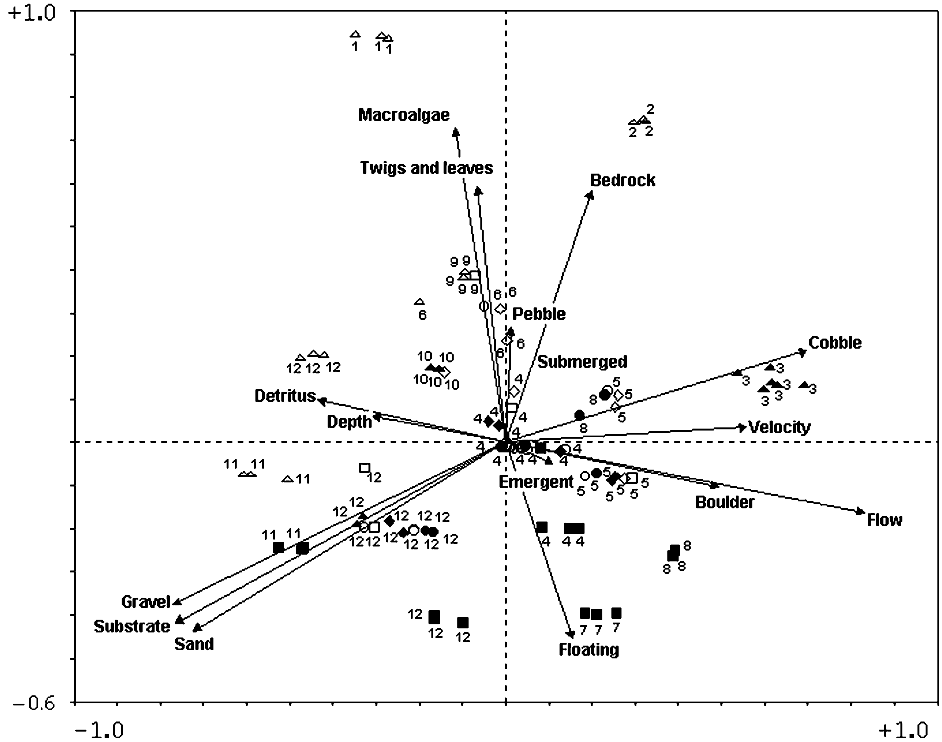

Fig. 4. CCA ordination of benthic samples from 12 different hydraulic units in relation to macroinvertebrate abundances registered in the study streams. Symbol codes are as follow: triangles: Río de los Sauces, circles: El Talita, squares: Las Cañitas, diamond: Piedras Blancas. Open symbols: high-water period, filled symbols: low-water period.

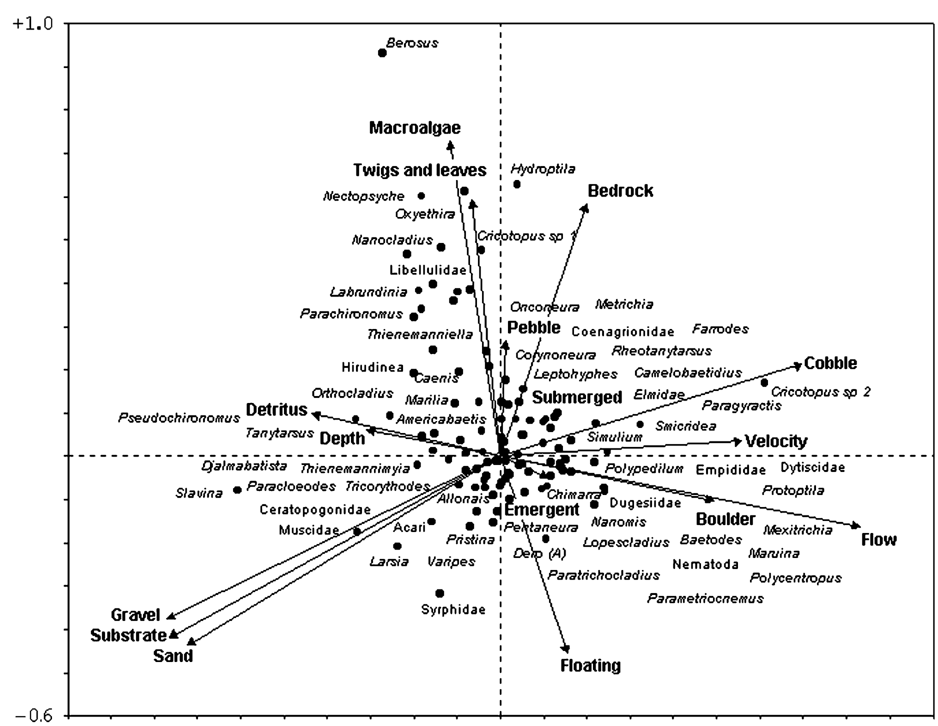

Fig. 5. CCA ordination of macroinvertebrate taxa. Only taxa with a frequency higher than 20% were included in the plot, but all were considered in the analysis.

Table 6. Summary of CCA results of macroinvertebrates and environmental variables in the study streams

	Axes				
	1	2	3	4	Total inertia
Eigenvalues	0.118	0.073	0.058	0.034	1.307
Species-environment correlations	0.883	0.818	0.822	0.731	
Cumulative percentage variance					
Of species data	9.0	14.6	19.0	21.7	
Of species–environment relation	28.3	46.0	60.0	68.2	
Significance of Monte Carlo test (199 permutations)					
Axis 1: $F = 12.750$, p value $= 0.005$					
All canonical axes: $F = 4.282$, p value $= 0.005$					

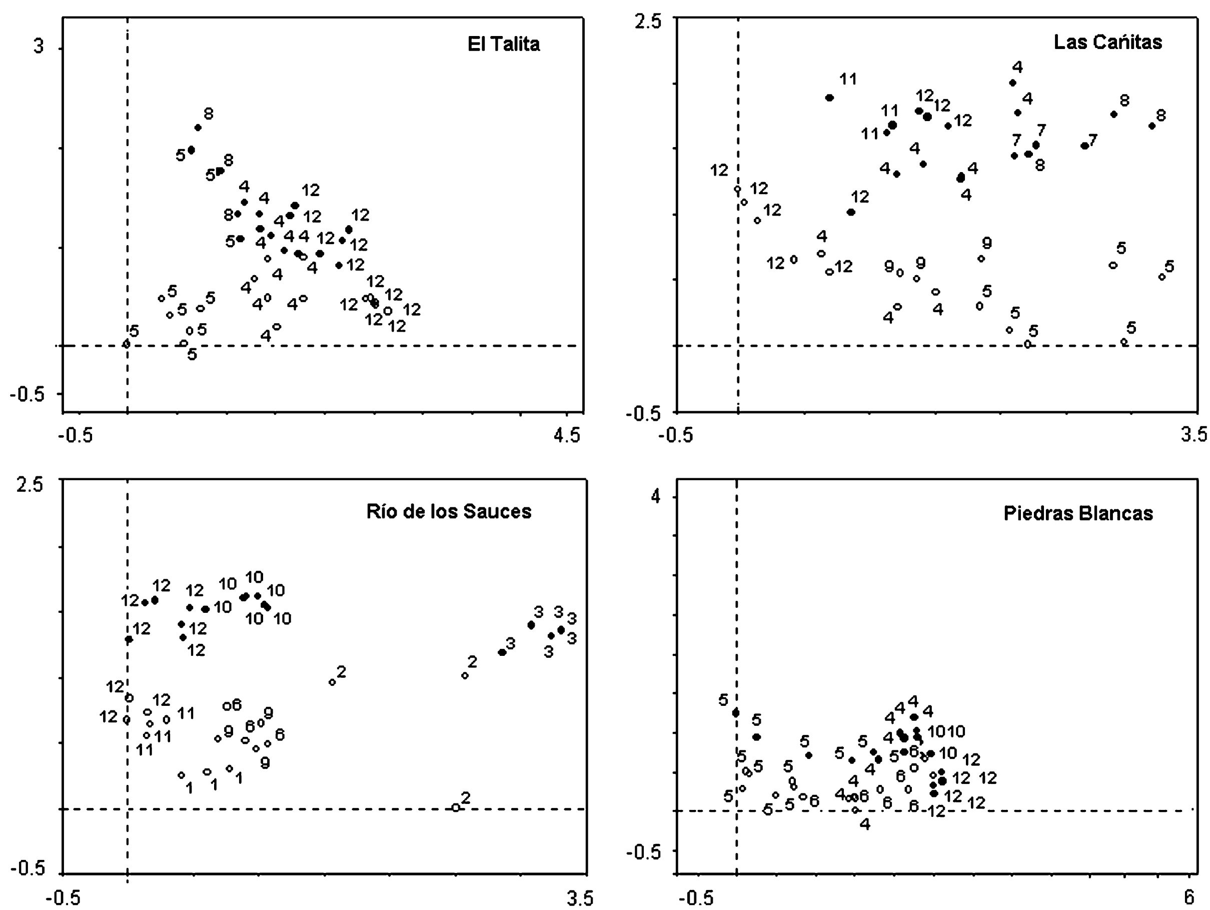

Fig. 6. DCA ordination of benthic samples from 12 different hydraulic units in each of the four streams of Carcarañá River sub-basin. Symbol codes are as follows: Open symbols: high- water period, filled symbols: low-water period.

The ordination shows that the main source of variation in the data set is the hydraulic unit composition. Superimposed over this is a temporal component, where samples from the low-water period are separated from those taken in the high-water period. Streams appear to have the least important effect on the ordination. As temporal segregation was not clear when all samples were included in the analysis, four different multivariate analyses were performed for each stream separately in order to test differences between hydrological periods. DCAs for each stream showed temporal differences in the macroinvertebrate assemblages (Fig. 6). In all streams, the first axis separated samples from different habitat units, whereas the second axis more clearly distinguished samples from different hydrological periods. The ordination scores of samples from the high-water period were significantly different from those of samples taken in the low-water period in all streams (Río de los Sauces: $F = 460.64$, $p < 0.0001$; El Talita: $F = 50.03$, $p < 0.0001$; Las Cañitas: $F = 163.82$, $p < 0.0001$; Piedras Blancas: $F = 4.66$, $p = 0.038$).

Ordination taxa with regard to the first two axes are presented in Fig. 5. Taxa occurring in habitats with coarse substrate, turbulent flow and high current velocity are positioned on the right side of the plot; those occurring in habitats with floating vegetation are in the lower quadrant. On the other hand, taxa from habitats of fine substrate and smooth surface flow occur on the left side; those taxa occurring in habitats with macroalgae and organic matter, such as detritus and twigs and leaves, are in the upper quadrant.

Typical taxa from hydraulic units characterized by substrate of bedrock were *Simulium* sp. and *Thienemanniella* sp. (Fig. 5, Table 7), but *Simulium* sp. were found associated mainly with more turbulent flow. *Baetodes* sp., *Camelobaetidius penai*, *Chimarra* sp., *Smicridea* sp. and *Parametriocnemus* sp. were taxa with high relative preference for habitats with substrate of boulders and cobbles and turbulent flow (Fig. 5, Table 7). Taxa associated mainly with hydraulic units characterized by gravel-sand substrate and smooth surface flow were the Ephemeroptera *Paracloeodes* sp., *Varipes* sp., *Tricorythodes popayanicus* and the Chironomidae *Tanytarsus* sp., *Pseudochironomus* sp. and *Thienemannimyia* sp. (Fig. 5, Table 7).

Investigation of taxon similarity among hydraulic units and among streams indicated that there were ubiquitous taxa that were found across all habitat units and streams. *Americabaetis* sp., *Leptohyphes eximius*, *T. popayanicus*, *Thienemanninyia* sp. and *Corynoneura* sp. were found in more than 80% of the samples, but they showed different habitat preference (Table 7). On the other hand, there were many rare taxa, since 44 out of 106 taxa were found in less than 5% of the samples. Assemblages were much more distinct within hydraulic units than within streams, with 42 taxa being found in all streams, compared with only 13 in all hydraulic units.

Discussion

Characterization and distribution of hydraulic units

A total of 12 hydraulic units, defined considering flow type and substrate, were observed in the study streams. Heterogeneity of geomorphic units such as runs and riffles can be assessed considering hydraulic variables and substrate character (Thomson et al., 2001; Wadeson & Rowntree, 1998). Some studies have characterized fluvial habitats considering not only substrate and flow but also aquatic vegetation (Armitage & Cannan, 1999; Buffagni et al., 2000; Tickner et al., 2000) and others have considered leaf and litter packs (Baptista, Buss, Dorville, & Nessimian, 2001; Velásquez & Miserendino, 2003). Kemp et al. (1999) found that each habitat was associated with distinct depth–velocity conditions. These studies have reported up to eight mesohabitats, probably because sampling was carried out only in one season or hydrological period. Although some authors have considered temporal variations (Baptista et al., 2001; Velásquez & Miserendino, 2003), they found not more than seven habitat types. Most of these studies did not take into account flow type as a descriptive variable of fluvial habitats. Since flow type introduces a lot of variability, at a reach level and between the hydrological periods, a higher diversity of fluvial habitats at a mesoscale was found in this study.

All works about habitats at a mesoscale agree in that these habitat units differ in their physical structure and in their hydraulic characteristics. These units should be defined in relation to hydraulic variables, substrate type and macrophytes (Buffagni et al., 2000). However, the relative importance of each of these variables changes in relation to local characteristics of each riverine system. In this study, hydraulic units were defined considering substrate and flow type. Depth, current velocity, presence of macrophytes, macroalgae and some types of organic matter were also considered. However, macrophytes, macroalgae and organic matter were not abundant in the study streams.

Important variations of hydraulic units were not observed among the study streams, except in Río de los Sauces where some exclusive habitats were registered. These differences may be probably due to particularities at a drainage scale since Río de los Sauces is the unique stream that belongs to the Ctalamochita River sub-basin, whereas the other streams belong to the Chocancharava River sub-basin.

The variability in the results found in studies about habitats at a mesoscale, ratifies the importance of considering local particularities, which have influence in the definition of fluvial habitats and, at the same time, make the elaboration of theoretical generalizations in relation to this concept difficult.

Diversity and abundance patterns

The highest values of richness, diversity, and evenness were found in the most heterogeneous hydraulic units, which were composed of substrates of diverse grain sizes. The lowest values were found in homogeneous hydraulic units composed almost exclusively of bedrock and in those characterized by fine substrate of gravel and sand. Flow type did not have any influence on diversity, since the highest values were found not only in habitats from riffles distinguished by turbulent flow but also in habitats from runs with smoother flow. Similar results were found by Beisel et al. (1998) and they

Table 7. Proportional abundances of the most frequent taxa in the hydraulic units of the study streams

Taxa	1	2	3	4	5	6	7	8	9	10	11	12	Total abundance
Nematoda	0.00	0.00	0.00	**0.31**	**0.29**	0.06	0.00	0.03	0.00	0.04	0.02	0.24	2755
Allonais sp.	0.00	0.00	0.00	**0.24**	0.09	0.00	0.11	0.08	0.01	0.13	0.12	**0.21**	149,063
Acari	0.00	0.00	0.00	0.23	0.06	0.00	0.04	0.05	0.00	0.01	**0.32**	**0.29**	88,975
Americabaetis sp.	0.14	0.05	0.00	**0.17**	0.04	0.03	0.01	0.01	0.05	0.09	0.08	**0.32**	989,321
Baetodes sp.	0.00	0.00	0.00	0.02	**0.65**	0.01	0.09	0.23	0.00	0.00	0.00	0.00	28,023
Camelobaetidius penai *Traver and Edmunds*	0.01	0.03	0.01	0.12	**0.64**	0.07	0.00	0.00	0.08	0.03	0.00	0.01	116,609
Paracloeodes sp.	0.00	0.00	0.00	0.08	0.01	0.00	0.00	0.00	0.02	0.01	0.15	**0.73**	194,557
Varipes sp.	0.00	0.00	0.00	0.14	0.13	0.00	0.02	0.00	0.03	0.00	0.00	**0.67**	70,369
Caenis sp.	**0.17**	0.01	0.00	0.09	0.04	0.04	0.00	0.01	0.04	0.09	0.13	**0.37**	101,000
Leptohyphes eximius Eaton	0.01	0.08	0.03	0.14	**0.28**	0.02	0.04	0.04	0.03	**0.21**	0.01	0.11	409,707
Tricorythodes popayanicus Dominguez	0.00	0.00	0.00	**0.18**	0.08	0.04	0.01	0.01	0.01	**0.18**	0.03	**0.47**	722,513
Farrodes sp.	0.01	0.00	0.00	0.14	**0.30**	0.08	0.01	0.00	0.18	**0.24**	0.00	0.05	12,638
Coenagrionidae	0.00	0.00	0.00	**0.32**	**0.28**	0.13	0.00	0.02	0.15	0.08	0.00	0.01	28,847
Chimarra sp.	0.00	0.00	0.03	0.04	**0.86**	0.00	0.04	0.02	0.00	0.01	0.00	0.00	40,157
Smicridea sp.	0.05	0.01	0.04	0.08	**0.76**	0.03	0.00	0.01	0.00	0.01	0.01	0.00	18,434
Mexitrichia sp.	0.00	0.00	0.00	**0.36**	**0.53**	0.03	0.03	0.02	0.03	0.00	0.00	0.00	3765
Marilia sp.	0.00	0.00	0.02	0.10	**0.18**	0.03	0.00	0.02	0.09	**0.42**	0.02	0.12	12,332
Elmidae	0.02	0.02	0.03	0.17	**0.35**	0.04	0.02	0.03	0.07	**0.19**	0.00	0.05	81,959
Simulium sp.	0.00	0.03	**0.59**	0.02	**0.24**	0.00	0.03	0.07	0.00	0.01	0.00	0.00	390,276
Ceratopogonidae	0.00	0.00	0.00	**0.31**	0.04	0.04	0.05	0.07	0.03	0.11	0.10	**0.23**	2877
Polypedilum sp.	0.01	0.12	0.03	0.12	**0.39**	0.01	0.03	0.04	0.02	0.05	0.04	**0.13**	83,445
Tanytarsus sp.	0.09	0.00	0.00	0.10	0.00	0.01	0.00	0.00	0.01	0.02	**0.20**	**0.58**	85,132
Rheotanytarsus sp.	0.03	0.16	0.01	0.15	**0.35**	0.01	0.00	0.01	0.01	**0.24**	0.00	0.01	11,140
Pseudochironomus sp.	0.08	0.00	0.00	**0.12**	0.01	0.02	0.00	0.01	0.00	0.10	0.11	**0.55**	10,780
Djalmabatista sp.	0.00	0.00	0.00	**0.49**	0.02	0.07	0.00	0.00	0.01	0.05	0.05	**0.30**	40,041
Pentaneura sp.	0.00	0.00	0.00	**0.32**	0.22	0.00	0.00	0.07	0.00	0.06	0.02	**0.29**	9773
Thienemannimyia sp.	0.04	0.00	0.00	0.11	0.05	0.03	0.00	0.00	0.03	0.14	**0.20**	**0.38**	118,216
Corynoneura sp.	0.04	0.02	0.00	**0.36**	**0.22**	0.09	0.00	0.01	0.03	0.12	0.01	0.09	66,746
Thienemanniella sp.	0.11	**0.78**	0.00	0.05	0.02	0.03	0.00	0.00	0.01	0.00	0.00	0.02	16,524
Onconeura sp.	**0.28**	0.02	0.03	0.04	0.14	0.01	0.02	0.03	0.05	0.06	0.11	**0.21**	10,967
Lopescladius sp.	0.00	0.00	0.00	**0.25**	0.10	0.00	0.07	**0.26**	0.06	0.06	0.01	0.18	24,583
Paratrichocladius sp.	0.00	0.00	0.03	**0.30**	0.18	0.00	0.11	0.12	0.00	0.00	0.04	**0.22**	125,655
Parametriocnemus sp.	0.00	0.00	0.01	0.22	**0.64**	0.00	0.00	0.02	0.00	0.05	0.00	0.06	6040
No. of samples	3.00	3.00	6.00	30.00	27.00	9.00	3.00	6.00	6.00	9.00	6.00	36.00	144
Total number of taxa	22.00	22.00	26.00	36.00	36.00	31.00	30.00	35.00	29.00	32.00	27.00	36.00	106
Total abundance (Ind. m^{-2})	184,315.00	128,257.00	256,448.00	629,780.00	626,873.00	104,365.00	107,217.00	116,839.00	116,440.00	416,079.00	249,123.00	1,167,924.00	4,103,658
Diversity	1.23	1.55	0.39	2.18	2.16	2.08	2.41	2.29	2.06	1.89	1.82	1.62	
Evenness	0.39	0.54	0.16	0.67	0.68	0.66	0.73	0.68	0.67	0.59	0.62	0.56	

These measures of habitat preference were calculated by dividing the abundance of each taxon in a hydraulic unit by the total abundance of that taxon recorded across all the units. The highest values of proportional abundance for each taxon are in bold. Flow type and substrate that correspond to each hydraulic unit are shown in Table 4.

suggested that the substrate may be a primary determinant of community structure.

In several studies, the lowest values of richness and diversity were found in habitats with fine substrate (Armitage & Cannan, 1999; Baptista et al., 2001; Brunke, Hoffmann & Pusch, 2001; Tickner et al., 2000; Velásquez & Miserendino, 2003); these results agree with those we have found in this study. On the other hand, habitats with abundant aquatic vegetation allocate the highest diversity (Armitage & Cannan, 1999; Buffagni et al., 2000; Principe & Corigliano, 2006; Tickner et al., 2000) since these habitat units are highly complex. In this study, the highest diversity and richness were also found in the most complex habitat units, which were defined by substrate of diverse grain size. Beisel, Usseglio-Polatera, and Moreteau (2000) found that faunal richness was also higher in a heterogeneous environment composed of numerous substrates. Such a mosaic potentially offers a great number of niches for invertebrates. These habitat units are preferred by many species because they offer refugia and adequate conditions for feeding, since the probability of predation decreases. On the other hand, in habitats of finer substrate, the instability of the substrate and the low organic matter availability lead to a low diversity and richness (Hawkins, 1984). A very homogeneous mosaic offers a low variety of niches and shelters fewer taxa (Beisel et al., 2000). Habitat heterogeneity is an important factor influencing macroinvertebrate distribution (Vinson & Hawkins, 1998), richness and diversity patterns in lotic ecosystems (Pringle et al., 1988; Voelz & McArthur, 2000). This heterogeneity, generated by different combinations of habitat variables, may determine species richness and patch composition. The presence of a range of refugia, each likely to be used by different sets of species, must be largely responsible for the increment in the resilience and resistance of the system in the face of a disturbance (Townsend, Scarsbrook, & Dolèdec, 1997).

The highest values of abundance, richness, diversity and evenness were observed in the low-water period. Some authors reported the same temporal variation in diversity and abundance patterns (Baptista et al., 2001), while others did not observe temporal variations (Brunke et al., 2001). Habitats are more stable during the dry season due to a lower frequency and intensity of scouring floods. Thus, time for macroinvertebrate colonization is longer thereby allowing the increment of the species number and abundance.

Macroinvertebrate assemblages and habitat variables

Most of the hydraulic units we found in this study allocated different macroinvertebrate assemblages. The CCA showed that the main source of variation was the faunal composition in the hydraulic units. This may indicate that the study streams have quite similar hydraulic units and that macroinvertebrate assemblages differ more in relation to habitat variables at a mesoscale than in relation to particular characteristics of each stream at a larger scale. Tickner et al. (2000) found similar results. Although they observed many ubiquitous taxa in all mesohabitats and reaches, the assemblages were more different among mesohabitats.

Temporal variations in the assemblages were less important, although some differences were observed, as was assessed by DCA in each stream. Similar results have already been reported (Armitage & Cannan, 1999) but in studies of Patagonian streams, an important temporal variation of macroinvertebrate assemblages in each habitat was observed (Velásquez & Miserendino, 2003).

In this study, we found that some of the hydraulic units characterized by the same substrate but different flow allocated quite similar macroinvertebrate assemblages, since they were not clearly separated in the CCA. This result may indicate that probably flow type may not be the appropriate variable to define habitat units in all cases. However, this result was not found in all hydraulic units characterized by the same substrate; therefore, assemblages from most of the hydraulic units were distinct.

Each habitat unit of a lotic system is associated with a particular macroinvertebrate assemblage, whose composition is determined mainly by substrate character and flow type (Baptista et al., 2001; Brunke et al., 2001; Tickner et al., 2000). According to Ladle and Ladle (1992) the preference for one substrate or another is determined at first by the oviposition behavior of the organisms. But this distribution may be modified during the life of aquatic organisms by multiple factors, which make them move by passive drift or active migration. The relative importance of variables that determine organism distribution in different habitats can change in relation to the stage of the organism's life history.

Our results suggest that the interaction between hydrological and geomorphological conditions affects benthic assemblages and that their organization is importat at a mesoscale. Mesohabitats provide a means of categorising streams at a scale which has ecological relevance, but which can also be used to improve stream assessment for management purposes (Armitage et al., 1995; Harper & Everard, 1998). If habitat units possess predictable and distinct biological communities, study and management of streams would be facilitated (Armitage & Cannan, 1999; Tickner et al., 2000). Furthermore, greater confidence and efficiencies in sampling programs would result, and the emphasis presently placed on habitat restoration and conservation would have more a biological basis (Rabeni, Doisy, &

Galat, 2002). In this sense, hydraulic units may be considered to be important tools in assessing stream integrity in lotic systems of central Argentina.

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