
HYDRAULIC PARAMETERS AND LONGITUDINAL DISTRIBUTION OF MACROINVERTEBRATES IN A SUBTROPICAL ANDEAN BASIN

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SUMMARY

The influence of hydraulic, substratum and physicochemical variables on the spatial distribution of macroinvertebrate assemblages was analyzed in eleven riffles in a subtropical Andean basin of Northwestern Argentina. Complex hydraulic variables (shear velocity, roughness shear velocity, inferred boundary Reynolds number, Reynolds number, Froude number, shear stress), substrate roughness, relative roughness, and physicochemical variables (water temperature, conductivity and pH) were used in order to identify those significantly related with

the distribution of macroinvertebrate assemblages. Water temperature, conductivity and pH were significantly higher in lower altitude sites, whereas substrate roughness, shear velocity and shear stress increased in upper sites. Total macroinvertebrate abundance was higher in lower reaches, whereas invertebrate diversity decreased from upper to lower sites. Longitudinal changes in hydraulic variables, substrate roughness and conductivity represent the major factors affecting the benthic invertebrates distribution of Lules River basin.

Introduction

The fluvial environment is characterized by many interacting physical factors that produce spatial and temporal heterogeneity and may exert a major influence on benthic invertebrates. Hydraulic and substratum conditions have been identified as two factors that affect the composition of assemblages, and the abundance and distribution of the constituent populations (Gronics and Davis, 1994; Quinn and Hickey, 1994; Biggs *et al.*, 2005; Brooks *et al.*, 2005). Other factors including light (Robinson and Minshall, 1986), resource availability (Richardson, 1993), temperature (Jacobsen *et al.*, 1997) and water chemistry (Ramírez *et al.*, 2006) have also been shown to play important roles. Grain size composition determines the heterogeneity and surface roughness of the substratum which, in turn, creates fine-scale patterns

of near-bed flow that influence organic matter retention and the distribution of benthic organisms (Culp *et al.*, 1983; Hart *et al.*, 1996). If habitat selection is based on hydraulic and substratum suitability, the spatial distribution of species should correspond to the spatial pattern of physical conditions.

The identification and explanation of spatial distribution of biotic organization have long been key objectives in the field of stream ecology (Hynes, 1970). The concept of "river continuum" (Vannote *et al.*, 1980) provides a widely cited framework for explaining longitudinal changes in structure and function of assemblages. The longitudinal dimension is therefore appropriate for examining coarse-scaled ecological patterns, including the distributional ranges of individual species and the turnover of entire assemblages. Mountain streams are well suited for examin-

ing longitudinal distribution because of the rapid change in major abiotic conditions (temperature, stream size and associated hydraulic conditions) with altitude. In South America, many studies have focused on altitudinal gradient of rivers, but were limited to qualitative data (Illies, 1964), to a single macroinvertebrate order (Dominguez and Ballesteros Valdez, 1992; Romero and Fernández, 2001) or to the family level of taxonomic resolution (Jacobsen *et al.*, 1997).

The purpose of the present study was to examine the longitudinal distribution of macroinvertebrate assemblages in a subtropical Andean basin of Northwestern Argentina. The study encompassed several complex hydraulic variables proposed for lotic studies (Statzner *et al.*, 1988; Davis and Barmuta, 1989) and physicochemical variables, in order to identify those significantly

related with the distribution of macroinvertebrate assemblages within riffles habitats. Because previous studies in mountain streams have shown that longitudinal position had a primary influence on assemblages structure, it is hypothesized that longitudinal changes in environmental variables would be an important explanatory variable of macroinvertebrate assemblages distribution in streams of Lules River basin. It therefore follows that sites of similar environmental conditions should have similar macroinvertebrate assemblages.

Another hypothesis is that longitudinal changes in hydraulic characteristics represent the major physical gradient along which the benthic assemblages are organized. This is in accordance with studies showing a significant influence of flow conditions on the distribution of macroinvertebrates (Jowett, 2003; Konrad *et al.*, 2008).

KEYWORDS / Aquatic Insects / Argentina / Subtropical Climate / Reynolds Number /

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PARÁMETROS HIDRÁULICOS Y DISTRIBUCIÓN LONGITUDINAL DE MACROINVERTEBRADOS EN UNA CUENCA ANDINA SUBTROPICAL

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RESUMEN

Se estudió la influencia de variables hidráulicas, de sustrato y variables físico-químicas sobre la distribución espacial de ensambles de macroinvertebrados en once rápidos de una cuenca subtropical andina del noroeste de Argentina. Variables hidráulicas complejas (velocidad de fricción, rugosidad de la velocidad fricción, número de Reynolds, número limitante de Reynolds, fuerza de fricción), rugosidad de sustrato, y variables físico-químicas (temperatura del agua, conductividad y pH) fueron utilizadas en virtud de identificar aquellas significativamente relacionadas con la distribución de la comunidad de macroinvertebrados. La temperatura del agua, la conductividad y el pH presentaron valores más altos en los sitios de menor

altitud, mientras que la rugosidad del sustrato, la velocidad y fuerza de fricción fueron mayores en los sitios de más altos. La abundancia total de macroinvertebrados fue mayor en los sitios de menor altitud, mientras que la diversidad de invertebrados disminuyó desde sitios superiores hacia los inferiores. Los cambios longitudinales en la hidráulica, rugosidad del sustrato y conductividad representan los factores de mayor incidencia en la distribución de los invertebrados bentónicos de la cuenca del Río Lules.

PARÂMETROS HIDRÁULICOS E DE MACROINVERTEBRADOS DISTRIBUIÇÃO LONGITUDINAL EM UMA BACIA ANDINA SUBTROPICAL

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RESUMO

A influência de variáveis hidráulicas, substrato e variáveis físico-químicas sobre a distribuição espacial das assembléias de macroinvertebrados foi investigada em onze rápido do um bacia hidrográfica subtropical Andina do noroeste da Argentina. Variáveis hidráulicas complexas (velocidade de fricção, rugosidade da velocidade de fricção, número de Reynolds, número de Reynolds limitando e força de fricção), rugosidade do substrato, rugosidade relativa e variáveis físico-químicas (temperatura, condutividade e pH) foram utilizados com o objetivo de identificar aqueles significativamente relacionadas com a distribuição

da comunidade de macroinvertebrados. A temperatura da água, condutividade e pH apresentaram os maiores valores em sites de baixa altitude, enquanto a rugosidade do substrato, a velocidade de fricção e força fricção foram maiores nos locais de maior altitude. A abundância total de macroinvertebrados foi maior em locais mais baixa altitude, enquanto a diversidade de invertebrados diminuiu de superior para os locais mais baixos. Alterações longitudinais na hidráulica, rugosidade do substrato e condutividade são importantes fatores ao longo do qual a comunidade bentônica Río Lules bacia é distribuído.

Material and Methods

Study area

The study was carried out at 11 sites in the Lules River basin (26°36'S, 65°45'W), a seventh order catchment located in Tucumán Province, Northwestern Argentina (Figure 1). The sites ranged from 650 to 1300masl (Table I). There were five lower sites (L1-L5) and six upper sites (U6-U11). The climate of Tucumán is dominated by the monsoon, a rainy season from November to March, during which 80% of annual rainfall occurs. The Yungas phytogeographical province, a mountain rainforest, covers almost all the watershed. This

highly diverse forest extends in Argentina between 22 and 28°S covering 3.9×10⁶ha (Brown, 2000).

Benthic sampling

The 11 sites were sampled in September 2005-

2006 and March 2006-2007. Three Surber samples (area 0.09m², mesh size 300µm) were taken from riffle habitats. Benthic sampling of sites U10, U6, and U7 in March 2006 and on U9 in March 2007 could not be carried out because of high water levels. The samples were preserved in 4% formaldehyde prior to laboratory processing. Current velocity measurements were taken with a Global Water flow meter. Substrate size composition was assessed measuring 12 random rocks. Conductivity was measured with a pocket conductivity meter (Methrom E587). All environmental data were taken at each site in each sample date. Macroinvertebrate specimens were sorted and identified to

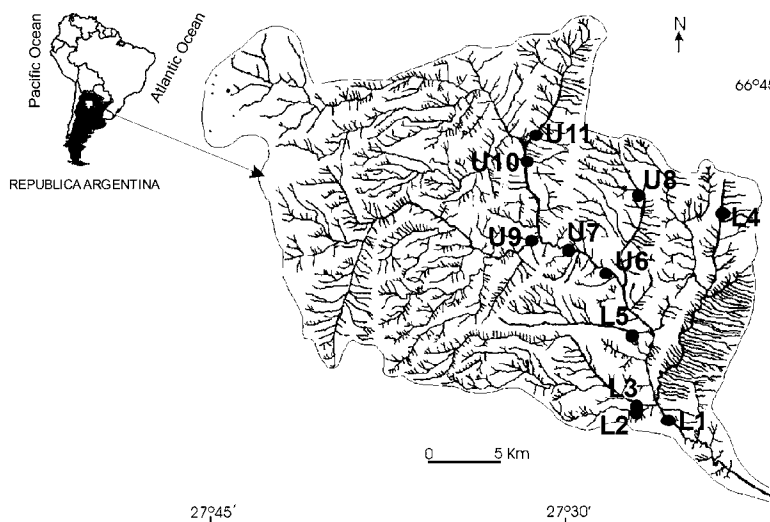


Figure 1. The eleven sampled sites on Lules River basin, Tucumán, Argentina. L1-L5: lower sites; U6-U11: upper sites.

the lowest taxonomic level. Samples were completely counted and identified.

Environmental variables and assemblage metrics

Substrate roughness (K_v) was measured using a modification of Winget's (1985) method, as

$$K_v = (5C_1 + 3C_2 + C_3)/9$$

where C: coarseness value (which refers to the following substrate size classes: >256mm= 4; 64-256mm= 3; 16-64mm= 2; and <16mm= 1), C_1 : the dominant substrate type; C_2 : 2nd most dominant substrate type, and C_3 : 3rd most dominant substrate type. If two substrate classes shared dominance, the larger particle size was considered dominant.

The calculated hydraulic parameters included

Shear velocity $U^* = \sqrt{gDs}$

Roughness shear velocity

$$U_r^* = U / (5.75 \log_{10}(12D/K_v))$$

Reynolds number $Re = (UD)/\nu$

Inferred boundary Reynolds number $Re^* = U_r^* K_v / \nu$

Froude number $Fr = U / (gD)^{1/2}$

Relative roughness $Rr = D/k_v$

Shear stress = $gsD\rho$

where g: acceleration caused by gravity; D: depth; U: mean current velocity; K_v : substrate roughness; s: slope; ρ : water density; ν : kinematic viscosity ($0.897 \times 10^{-6} m^2 \cdot s^{-1}$ at 25°C).

Invertebrate diversity and substrate heterogeneity was calculated using the Shannon-Wiener index (Magurran, 1989):

$$H' = -\sum p_i \log_{10} p_i$$

where p_i : proportion of individuals/stones belonging to the i_{th} taxon/size of stone.

Richness was calculated as the total number of species collected in each sampled site.

Last, each site was ranked in increasing order (lower to

upper sites) according to its altitude, to create a variable called longitudinal position (Doysi and Rabeni, 2001).

Data analysis

To assess differences in environmental variables and assemblage parameters between upper and lower sites, one-way ANOVAs were conducted. Hydraulic, physicochemical (except pH), substrate variables and total abundance were $\log_{10}(x+1)$ -transformed before this analysis in order to meet assumptions of homogeneity of variance and normality (Zar, 1996).

Canonical correspondence analysis (CCA) was performed using CANOCO 3.0 (Ter Braak and Smilauer, 1998). The CCA was carried out to examine the relationship between the invertebrate and physicochemical data. An average of the three replicates was used in the analysis. Only those taxa representing >0.1% of the total invertebrates collected in the sites were used. All the invertebrate taxa and environmental data (except

TABLE I
ALTITUDE, DISTANCE FROM SOURCE AND LONGITUDINAL POSITION OF THE ELEVEN SAMPLED SITES OF LULES RIVER BASIN

Sites	Altitude (masl)	Distance from source (km)	Longitudinal position
L1	650	26.3	11
L2	680	27.5	10
L3	680	28.3	9
L4	860	33.8	8
L5	915	31.3	7
U6	925	35	6
U7	1070	38.8	5
U8	1080	40	4
U9	1105	42.5	3
U10	1265	42.5	2
U11	1360	43.8	1

pH) were $\log_{10}(x+1)$ -transformed to reduce the influence of numerically dominant taxa and standardize the scales of the environmental data. Forward stepwise regression was used to select the environmental variables in order to identify those that explained a significant ($p < 0.05$ using 999 Monte Carlo permutations) amount of variation in the benthic invertebrate assemblages.

Results

The general characteristics of upper and lower sites of Lules River basin are shown in Table I.

TABLE II
MEANS AND STANDARD ERRORS OF ENVIRONMENTAL VARIABLES AND ASSEMBLAGES PARAMETERS, AND RESULTS OF ANOVA (F) BETWEEN UPPER AND LOWER SITES

Variables	Upper sites	Lower sites	F
Water temperature (°C)	17.5 ±2.4	20.3 ±2.9	11.44**
Conductivity ($\mu S \cdot cm^{-1}$)	119.9 ±50	369.7 ±249	18.51***
pH	6.7 ±0.9	7.3 ±1	4.37*
Substrate heterogeneity	0.81±0.1	0.85 ±0.2	2.58
K_v	3.4 ±0.3	2.9 ±0.2	32.84***
U^*	3.8 ±0.9	3.1 ±1	5.78*
U_r^*	1.1 ±2.4	0.2 ±1	1.86
Re	90802 ±80	116381 ±99	0.69
Re^*	3842519.1 ±98	654063 ±70	3.09
Fr	0.3 ±0.1	0.3 ±0.2	0.25
Rr	0.14	0.19	0.5
Shear stress	15.5 ±7.2	10.6 ±6.7	5.81*
Invertebrate diversity	1.01 ±0.14	0.88 ±0.19	16.5***
Species richness	41.6 ±9.6	42.6 ±9.3	0.16
Total abundance	2966 ±1956	12037 ±8603	5.73*

Probabilities: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$; K_v : substrate roughness, U^* : shear velocity, U_r^* : roughness shear velocity, Re: Reynolds number, Re^* : roughness Reynolds number, Fr: Froude number, Rr: relative roughness.

Table II shows the values obtained for the environmental variables and assemblage parameters. All the calculated Reynolds numbers (Re) were >2000 and all the Froude numbers (Fr) were <1, indicating that the flow was sub-critical and turbulent (*sensu* Davis and Barmuta, 1989). Near-bed flows were classified as 'chaotic' (relative roughness $Rr \leq 3$; Davis and Grown, 1991). Water temperature, conductivity and pH exhibited a gradual decrease from lower to upper sites, being significantly higher in lower sites (ANOVA, $p < 0.05$). Substrate roughness (K_v) was strongly significantly related with upper sites (ANOVA, $F_2 = 32.84$, $p < 0.001$). Other variables that increase in upper sites were shear velocity (U^*) and shear stress (ANOVA, $p < 0.05$). Total abundance was significantly higher in lower reaches (ANOVA, $F_2 = 5.73$, $p < 0.05$), whereas invertebrate diversity decrease from upper to lower sites (ANOVA, $F_2 = 5.74$, $p < 0.05$).

Ordination analyses

The first two CCA axes (Figure 2) accounted for 34% of the cumulative variance of species data (Table III), with the first axis representing 32% of the species-environment relationship. The accumulated variation explained by the first two axes of the taxon-environment relationship in the CCA was 52%. Monte Carlo global permutation tests also demonstrated a significant macroinvertebrate-environment relationship ($p < 0.01$) along the first axis ($F = 7.45$, $p = 0.001$) and sub-

sequent canonical axes ($F=1.31, p=0.04$).

The arrangement of samples in relation to the 10 environmental variables showed a broad separation based on longitudinal distribution of macroinvertebrate assemblages. Upper sites were situated in the left side of the ordination, in the direction of increasing shear stress U^* , Re , Re^* , Rr , Kv and longitudinal position, whereas lower sites were situated in the right side of the ordination in the direction of increasing conductivity, pH and water temperature (Figure 2a). High hydraulic conditions were associated with the mayfly *Camelobaetidius penai*, the plecopteran species *Anacroneria* sp., the coleopteran species *Austrelmis* spp. (adult), *Neoelmis* spp. (adult), *Macrelmis* spp. (larvae) and Staphylinidae (adult), and the dipteran Tipulidae. Low hydraulic conditions and high level of physicochemical variables of lower sites were associated with the mayfly specie *Caenis ludicra*, the watermites *Atractides* spp., *Torrenticola Columbiana* and *Dodecabates dodecaporus*, the trichopteran specie *Metrichia* spp., and oligochaetes (Figure 2b).

Discussion

In support of the first hypothesis, the longitudinal distribution of Lules River basin was accompanied by a relatively predictable spatial arrangement of taxa. This finding reinforces previous studies suggesting that longitudinal environmental changes are among the most important factors with respect to the distribution of benthic invertebrates in high-gradient mountain streams (Ward, 1986; Burgherr and Ward, 2001; Finn and Poff, 2005; Helson *et al.*, 2006). Streams at high elevations present extremely harsh conditions, where the combination of physiologi-

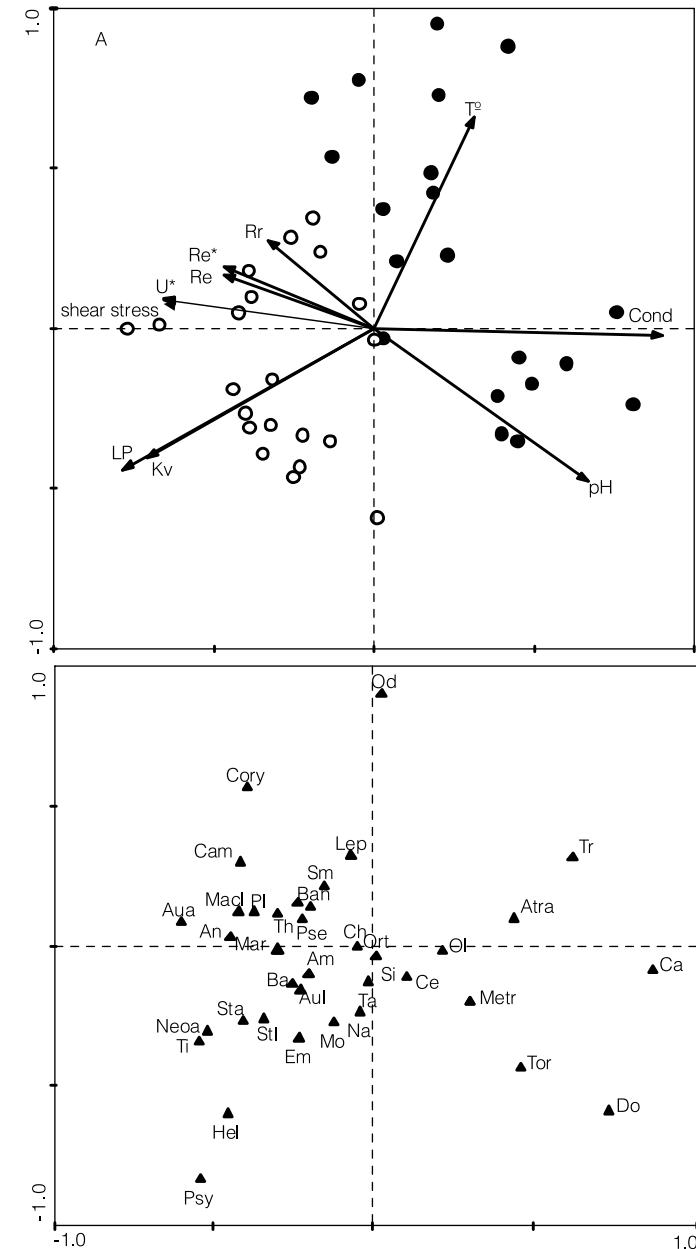


Figure 2. a: ordination diagram (canonical correspondence analysis) of upper sites (open circles) and lower sites (closed circles). Re : Reynolds number, Re^* : roughness Reynolds number, Rr : relative roughness, U^* : shear velocity, Kv : substrate roughness, LP : longitudinal position, $Cond$: conductivity, T° : water temperature. b: species ordination. Full names of taxa codes are given in Table III.

cally demanding conditions make survival, development, and reproduction difficult. Whereas abundance declined with increasing altitude, the diversity increased in upper sites. The general increase of abundance in lower sites may be caused by other supporting factors. A few opportunist species find a rich environment of increased solar radiation and consequently somewhat higher

water temperatures than at higher elevations.

A great variation in benthic assemblages data was explained by the hydraulic variables, which is consistent with previous studies showing that the distribution of benthic organisms is strongly influenced by hydraulic conditions (Wetmore *et al.*, 1990; Lancaster and Hildrew, 1993; Quinn and Hickey, 1994; Rempel *et*

al., 2000; Jowett, 2003). This observation was in accordance with the second hypothesis, that longitudinal changes in mean and near bed flow parameters are important factors in determining the assemblage distribution of benthic invertebrates in the Lules River basin. Hydraulic conditions become more important at higher in elevation or latitude in the Lules River basin. Variables such as shear velocity, shear stress and Reynolds number were significantly related to the distribution of macroinvertebrates at these sites.

Additionally, the association between hydraulic variables and total abundance of benthic invertebrates was negative: lower sites with lower values of hydraulic variables showed the highest macroinvertebrate abundance. Doysi and Rabeni (2001) and Brooks *et al.* (2005) reported a lack of relationship between invertebrate abundance and hydraulic parameters.

Hydraulic variables were positively related with invertebrate diversity, with the highest diversity in upper sites where flow conditions were maximum. This result was in agreement with several authors finding a positive relationship between diversity and flow conditions (Degani *et al.*, 1993; Brooks *et al.*, 2005). Many invertebrates have an inherent need for currents and also exhibit a higher tolerance limit with this variable (Hynes, 1970; Minshall, 1984).

The hydraulic habitat preferences of lotic invertebrates result from the balance of a variety of requirements of the organisms, including the energy costs and benefits for food and oxygen acquisition of maintaining their position in turbulent environments (Wiley and Kohler, 1980; Jowett *et al.*, 1991; Georgian and Thorp, 1992). High water turbulence of

TABLE III
LIST OF DOMINANT TAXA (RELATIVE
CONTRIBUTION>0.1%) IDENTIFIED IN LULES RIVER BASIN

Order	Family	Taxa	Abbrev.
Plecoptera	Perlidae	<i>Anacroneuria</i> sp.	An
Ephemeroptera	Baetidae	<i>Americabaetis alphus</i>	Am
		<i>Baetodes huaico</i>	Bah
		<i>Baetodes</i> spp.	Ba
		<i>Camelobaetidius penai</i>	Cam
		<i>Nanomis galera</i>	Na
	Caenidae	<i>Caenis ludicra</i>	Ca
		<i>Leptohiphes eximius</i>	Lep
		<i>Tricorythodes popayanicus</i>	Tr
	Leptophlebiidae	<i>Thraulodes</i> spp.	Th
	Coleoptera	Elmidae	<i>Austrelmis</i> spp. (larvae)
<i>Austrelmis</i> spp. (adult)			Aua
<i>Macrelmis</i> spp. (larvae)			Macl
<i>Neolmis</i> spp. (adult)			Neoa
Psephenidae		<i>Psephenus</i> sp.	Pse
Staphylinidae		larvae	Stl
		adult	Sta
Megaloptera	Corydalidae	<i>Corydalis</i> sp.	Cory
Prostigmata	Hygrobatidae	<i>Dodecabates dodecaporus</i>	Do
		<i>Atractides</i> sp.	Atra
	Torrenticolidae	<i>Torrenticola columbiana</i>	Tor
Trichoptera	Helicopsychidae	<i>Helicopsyche</i> sp.	Hel
	Hydroptilidae	<i>Metrichia</i> spp.	Metr
		<i>Mortoniella</i> spp.	Mo
	Hydropsychidae	<i>Smicridea</i> spp.	Sm
Diptera	Chironomidae	Orthoclaadiinae	Ort
		Tanypodinae	Ta
		Chironominae	Ch
		<i>Simulium</i> sp.	Si
	Simulidae	<i>Simulium</i> sp.	Ce
	Ceratopogonidae		Em
	Empididae		Psy
	Psychodidae	<i>Maruina</i> sp.	Mar
		Tipulidae	
	Odonata		
		Oligochaeta	Ol

Abbreviations of taxa used in CCA are also shown.

the upper sites restricts faunal assemblage to those species capable of dealing with harsh conditions. The dominance of *Camelobaetidius penai* in upper sites is made possible by using holdfast structures to maintain their position (Wallace and Merrit, 1980). Lloyd and Sites (2000) found a positive association between some Elmidae species with simple and complex hydraulic characteristics. In addition, the plecopteran species *Anacroneuria* sp. prefers high altitude habitats with highly turbulent conditions (Tomanova Tedesco, 2006).

The report of Statzner *et al.* (1988) that substrate is less important than complex hydraulic characteristics in determining the organization of benthic assemblages was not supported by this study. Substrate roughness was significantly related with the distribution of benthic invertebrate fauna of Lules River basin. A significant effect of substrate roughness has also been found in other studies, where species richness and abundance both declined with increasing roughness (Quinn *et al.*, 1996; Brooks *et al.*, 2005). This observation was

in agreement with the results of the present study, in that upper sites with higher values of substrate roughness had the lowest macroinvertebrate abundance. This fact could be related with the turbulence created by the substrate elements that would make difficult for invertebrates to hold position. In addition, several invertebrate taxa such as *Neolmis* spp. (adult) and Tipulidae shredders were found to be positively associated with substrate roughness. This is consistent with Culp *et al.* (1983) and Rempel *et al.* (1999), where the distribution of many shredder taxa was influenced by substrate roughness. Large substrate material with a rough surface topography could facilitate the retention of organic matter and create microhabitats of reduced hydraulic stress for foraging (Holomuzki and Messier, 1993).

A greater supply of fine detritus, expected in areas of low turbulence, would explain the association with lower sites of Oligochaeta, ephemeropterans *Caenis ludicra*, *Tricorythodes popayanicus*, and *Leptohiphes eximius* collector gatherer taxa. The preference of *C. ludicra* and *T. popayanicus* for these streams could be explained by their adaptability to fine substrata, slow currents, low dissolved oxygen and elevated water temperatures (Nolte *et al.*, 1997; Kasangaki *et al.*, 2006). The higher periphyton biomass expected in lowland streams of greater light availability could favour scrape feeders such as *Hydroptila* spp. and *Metrichia* spp. (Merrit and Cummins, 1984), and this study found that these two species showed preferences for lower altitude streams in the studied basin. In addition, water conductivity had a great influence over several watermites species; how-

ever, Goldschmidt (2004) found that water chemistry had minor influence on the differentiation of watermites in Costa Rica, but conductivity seems to have some influence; the increase of this variable from upper to lower sites could be related with the lithology of the basin, and this factor had a strong influence on macroinvertebrate distribution.

In conclusion, the results suggest that mean and near bed hydraulic conditions, conductivity as well as substrate roughness, represent major factors along which benthic invertebrates are distributed in the Lules River basin. On the other hand, significant biological differences in macroinvertebrate assemblages among hydraulic habitats in the study riffles were found. The spatial distribution of taxa would reflect their morphological and trophic suitability to particular environmental conditions within each benthic habitat.

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