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## Research Paper

# Structure and Spatial-Temporal Dynamics of Chironomidae Fauna (Diptera) in Upland and Lowland Fluvial Habitats of the Chocancharava River Basin (Argentina)

*key words:* benthos, substrate, mountain streams, lowland river, Argentina

### Abstract

Structure of benthic Chironomidae assemblages and their spatial-temporal dynamic were analyzed in upland and lowland habitats from the Chocancharava River basin (Córdoba, Argentina). Sampling was performed in three tributary streams and in three lowland reaches of the river during high and low rainfall periods. Characteristic taxa of upland and lowland reaches and of the different habitats in these reaches were identified using the IndVal method. Chironomidae assemblages were different between upland and lowland reaches and among habitats in each reach, as assessed by Multiresponse Permutation Procedure and Canonical Correspondence Analyses. Substrate type and current velocity were the major explanatory variables structuring the assemblages in upland reaches whereas in lowland reaches current velocity and aquatic vegetation were the most important variables. The highest richness was found in the most complex habitat units in both upland and lowland stretches as assessed by Analyses of Variance. Chironomidae larvae responded to longitudinal changes of hydraulic variables and to local variations of fluvial habitats at different reaches.

### 1. Introduction

Distribution patterns of aquatic macroinvertebrates are influenced by hydraulic variables that define fluvial habitats (STATZNER *et al.*, 1988). Furthermore, small-scale differences in hydraulic conditions created by combinations of current velocity, water depth and substrate have an important role in the spatial distribution of macroinvertebrate assemblages (BROOKS *et al.*, 2005).

Habitat assessment provides important tools for many aspects of river management, including river health monitoring, determination of river restoration strategies, and biodiversity assessment (THOMSON *et al.*, 2001; RAVEN *et al.*, 2002). The understanding of species-environment relationships became essential for the development of this appraisal; therefore, every assessment will be more accurate if habitat preferences and indicator species are known (MCGEOCH and CHOWN, 1998; TICKNER *et al.*, 2000).

Despite their importance, knowledge of habitat preferences of aquatic invertebrates is rather scarce in Argentina (VELAZQUEZ and MISERENDINO, 2003; PRINCIPE *et al.*, in press) especially knowledge about preferences of chironomids. The Chironomidae family is of great significance in the structure and function of lotic systems due to its great abundance, diversity and occurrence (CRANSTON, 1995). Larvae, pupae and adults form an integral part

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of the food web, serving as food for larger invertebrates, fish, amphibians and birds (EPLER, 2001). Furthermore, larvae play an important role in organic matter processing and nutrient cycling (MERRITT *et al.*, 1984).

The chironomids of South America have very many species, but are little known (SPIES and REISS, 1996). In Argentina the identification of larvae has constituted a difficult task mainly due to the absence of local taxonomic keys. Although the development of a new regional key by PAGGI (2001) has facilitated the identification of Chironomidae larvae, few studies have been carried out on their ecology (but see PAGGI and RODRIGUES CAPITULO, 2002; MEDINA and PAGGI, 2004).

This study aims to analyze the structure and composition of Chironomidae assemblages in different habitat units from upland and lowland reaches in the Chocancharava River basin. We examined the spatial-temporal dynamic of the assemblages correlating taxa with measured habitat variables in order to investigate habitat preferences and factors influencing larvae distribution.

## 2. Methods

### 2.1. Study Area

The study was carried out in upland and lowland reaches from the Chocancharava River basin (Fig. 1, Table 1). Upland reaches belong to El Talita Stream, Las Cañitas Stream and Piedras Blancas Stream which are tributaries of the Chocancharava River. Lowland reaches correspond to different sections of the river located at about 35 km downstream from the confluence of the tributaries, where Río Cuarto city is situated. These reaches belong to a hydraulic transition zone between the rhithral and the potamal zones of the river. The Chocancharava River is one of the tributaries of Carcarañá River and belongs to La Plata River basin. This fluvial system is one of the most important in the central region of Argentina since it supplies drinking water and irrigation.

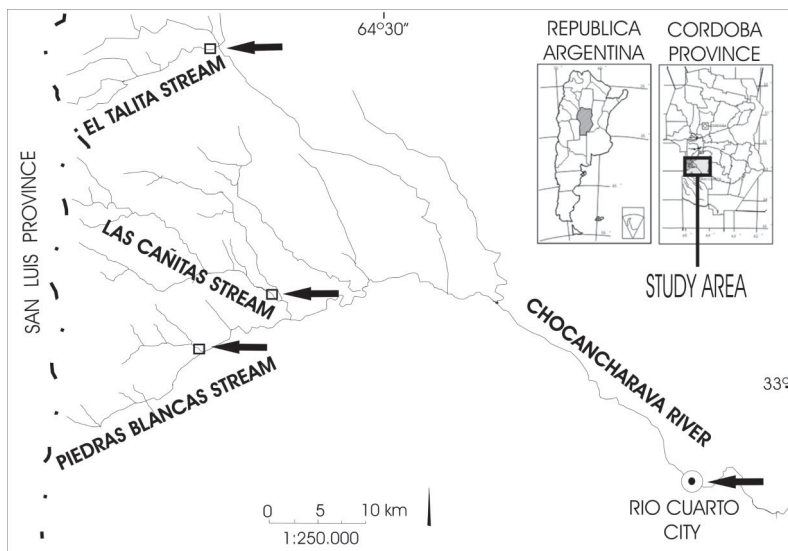


Figure 1. Study sites in upland and lowland reaches of Chocancharava River basin. Two reaches were considered in El Talita Stream, Las Cañitas Stream and Piedras Blancas Stream. Three reaches were considered in the lowland segment of the river at the point of Río Cuarto city.

Table 1. Location and characterization of sampling sites in tributary streams and in the lowland segment of the Chocancharava River. Standard deviation of mean channel width is shown in brackets.

	El Talita Stream	Las Cañitas Stream	Piedras Blancas Stream	Chocancharava River
<b>Altitude (m a.s.l.)</b>	875	672	732	454
<b>Stream order</b>	3	3	3	7
<b>Mean channel width (m)</b>	13 (5)	16 (2)	13 (3)	170 (46)
<b>Riparian vegetation cover (%)</b>	>95	75–84	>95	20–40
<b>Land use</b>	Agriculture-Recreation	Agriculture-Livestock grazing	Agriculture-Recreation	Urban
<b>River channel pattern</b>	Straight	Straight	Straight	Braided

The Chocancharava River basin 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 starts in October and ends in April (725 mm). The minimum rainfall (143 mm) occurs between April and September (CAPITANELLI, 1979). Maximum air temperature reaches 34 °C in summer (December–March) and decreases up to –5 °C in winter (June–September). The lithology of the upland reaches is characterised by the predominance of metamorphic (gneiss, schist, migmatite) and igneous rocks (granite), whereas eolic deposits (loess) are dominant in the lowland reaches. Basin vegetation changes in relation to the longitudinal gradient and its distribution is modified by human activities (CABIDO *et al.*, 2003).

## 2.2. Field and Laboratory Methods

Sampling was carried out in upland and lowland fluvial habitats during high (February–March 2003) and low rainfall periods (July–August 2003). In the upper basin, three streams were selected. In each stream two reaches of about 50 m each and separated by nearly 250 m were sampled. Three different habitats were sampled in each reach: 1) riffles, 2) coarse substrate runs and 3) fine substrate runs. Three replicate Surber samples (0.09 m<sup>2</sup>, 300 µm mesh size) were taken in each of these habitat units following a stratified random sampling design. A total of 108 benthic samples were collected in the upper basin (2 hydrological periods, 3 streams, 2 reaches, 3 habitat units and 3 replicates).

In the lowland segment of the river, three reaches of about 100 m each and separated by nearly 8 km were selected. In each reach, five different habitats, previously characterized (CORIGLIANO, 1989), were sampled: 1) unvegetated secondary channels, 2) secondary channels with highly mobile substrate, 3) backwaters in bars, 4) channels in bars and 5) vegetated secondary channels. An additional habitat unit (6) was sampled in one of the lowland reaches; it was a vegetated secondary channel in a calcrete riverbank. Three replicate samples were taken with a Hess sampler (0.07 m<sup>2</sup>, 300 µm mesh size) in each of these habitat units. A total of 96 benthic samples were collected in the lowland segment of the river (2 hydrological periods, 3 reaches, 5 habitat units, 3 replicates and an additional habitat in one reach) finding the total of 204 samples in this study.

Substrate composition was assessed in each habitat unit and sampling occasion. In upland reaches, this assessment was visually performed (GORDON *et al.*, 1994) and in lowland reaches, substrate samples were taken and sieve sets were used for grain size analysis in the laboratory. In each habitat the proportional abundance of aquatic vegetation was visually evaluated. Current velocity and sampling depth were measured with a Global Flow Probe FP101–FP201 for each replicate sample. Conductivity, pH, water temperature and turbidity were measured with portable sensors and water chemical analyses were performed using the portable laboratory Hach 2000 and colorimetric analyses (GREENBERG *et al.*, 1992) to characterize the studied reaches. The average values of the analyzed parameters in upland and lowland reaches are shown in Table 2.

Table 2. Physico-chemical characterization of water in tributary streams and in the lowland segment of the Chocancharava River during high and low rainfall period. Mean values are shown with standard deviations below. In the lowland segment of the river, values registered in the three studied reaches were considered. In each tributary stream, values registered in the two studied reaches were considered. Standard deviation is not shown when the variable was measure only in one reach. TDS: Total dissolved solids.

	High rainfall period				Low rainfall period			
	El Talita	Las Cañitas	Piedras Blancas	Chocancharava	El Talita	Las Cañitas	Piedras Blancas	Chocancharava
Temperature (°C)	21.00 1.13	18.40 0.00	15.50 0.28	22.90 0.62	11.90 0.49	11.00 2.12	13.00 0.00	11.10 2.23
Turbidity (utum)	0.20 0.10	2.50 0.80	0.80 0.60	53.20 5.82	1.60 0.64	1.00 0.14	1.00 0.80	22.10 8.80
pH	7.15 0.46	7.30 0.11	7.08 0.49	7.70 0.10	7.50 0.04	7.75 0.22	7.95 0.14	8.20 0.72
Conductivity (µS/cm)	63.20 4.81	99.20 15.06	101.90 12.10	267.00 4.58	81.30 14.78	145.10 0.07	138.20 0.49	336.30 3.21
TDS (mg/l)	30.00 2.12	48.00 0.36	48.00 6.36	125.30 2.52	38.00 7.07	69.00 0	66.00 1.41	159.30 4.51
Salinity (%)	0 0	0.05 0.07	0.05 0.01	0.10 0.10	0 0	0.1 0	0.1 0	0.2 0.2
NO <sub>3</sub> <sup>-</sup> (mg/l)	1.500	1.200	1.300	2.900	1.000	1.300	1.300	0.667 0.150
NO <sub>2</sub> <sup>-</sup> (mg/l)	0.025	0.021	0.021	0.017 0.030	0.020 0.010	0.010	0.020	0.020 0.001
SO <sub>4</sub> <sup>-2</sup> (mg/l)	1.80 0.85	1.00 0.41	1.00 0.10	16.00 1.73	1.00	1.00	1.0	30.00 1.00
PO <sub>4</sub> <sup>-3</sup> (mg/l)	0.17 0.11	1.00 0.38	0.31 0.15	0.85 0.89	0.27	0.27	0.18	0.487 0.270
Hardness (mg/l)	18.00 0.35	31.30 0.06	36.20 2.47	79.20 1.40	22.73	42.90 0.71	43.54 8.16	86.90 2.52
Alkalinity (mg/l)	26.00 0.35	45.00	47.20	109.10 6.67	27.19	55.60 2.12	47.60 6.01	108.20 1.67

Invertebrates were fixed with 4% formaldehyde solution. In the laboratory, chironomids were sorted, counted and preserved in 70% ethanol. The larvae were identified to genus level when possible, using the taxonomic keys by WIEDERHOLM (1983), EPLER (2001) and PAGGI (2001).

### 2.3. Data Analyses

Canonical Correspondence Analysis (CCA) with all data was performed. Two additional CCAs were carried out with upland and lowland data sets separately in order to explore Chironomidae larvae distribution in habitat units and to detect relations between taxa and habitat variables. CCAs were performed using the statistical package CANOCO version 4.02 (TER BRAAK and SMILAUER, 1998). Abundance data were  $\log_{10}(Y + 1)$  transformed and forward selection was run. Restricted Monte Carlo permutation tests were performed (199 permutations) for determining the significance of eigenvalues derived from the CCAs. Restricted permutations favoured the null model (completely random permutations) because benthic samples were collected in a special spatial structure (sampling scheme). Under this permutation scheme, in global CCA only samples collected in the same stretch (upland and lowland) and during the same hydrological period were permuted. In the CCAs carried out separately with upland and lowland data sets only samples collected in the same period and belonging to the same habitat were permuted. Some replicates of the upland habitats and the additional habitat unit (6, vegetated secondary channel in a calcareous riverbank) sampled only in one of the lowland reaches were respectively omitted in these CCAs since the performed restricted permutations required a balance design.

Differences between upland and lowland assemblages and among assemblages from different habitats were tested by Multiresponse Permutation Procedures (MRPP). The indicator value method (IndVal) proposed by DUFRENE and LEGENDRE (1997) was used in order to identify characteristic taxa of upland and lowland reaches and indicator taxa of the different fluvial habitats. The IndVal method identifies indicator species as those "characteristic" of a particular habitat. It combines measurements of the degree of specificity of a species to an ecological state, for example a habitat type, and its fidelity within that state. Species with a high specificity and high fidelity within a habitat will have a high indicator value. Good indicator species are thus those that are always present at sites in a given group and never occur in other groups (DUFRENE and LEGENDRE, 1997; MCCUNE and GRACE, 2002). Both MRPP and IndVal were performed using PC-Ord for Windows 4.25 (MCCUNE and MEFFORD, 1999).

Richness was measured considering the number of different taxa recorded and Shannon diversity index was calculated using natural logarithms. Three-way Analyses of Variance (ANOVAs) were used to elucidate the effect of hydrological period, habitat and tributary stream on richness, diversity and abundance of Chironomidae larvae from upland reaches. Abundance data were  $\log_{10} Y$  transformed in order to meet the assumptions of normality and homoscedasticity. The Student-Newman-Keuls' test (SNK) was used for a posteriori comparisons ( $P < 0.05$ ). Structural attributes of lowland assemblages was also compared between hydrological periods, among habitats and reaches by three-way ANOVAs. The additional habitat sampled only in one of the lowland reaches (vegetated secondary channel in a calcareous riverbank) was not considered in order to get a balance design for the performing of these analyses. In this case, abundance and richness data were  $\log_{10} Y$  transformed.

## 3. Results

Thirty one Chironomidae taxa belonging to four subfamilies were identified (Table 3). Orthocladiinae showed the highest generic richness (13 taxa). In upland reaches, this subfamily showed a proportional abundance of 89% in the high rainfall period, Chironominae 7%, and Tanypodinae 4%. In the low rainfall period the proportional abundances were: 64% for Orthocladinae, 18% for Chironominae, 18% for Tanypodinae. Podonominae was the less frequent and abundant (Table 3). In lowland reaches, the subfamily Chironominae was the most important with about 60% of proportional abundance in both rainfall periods. Orthocladiinae showed a proportional abundance of 35% in the high rainfall period and 38% in the low rainfall period. Tanypodinae were less important with a 6% of proportional abundance in the high rainfall period and only 0.5% in the low rainfall period. Podonominae were absent.

Table 3. List of aquatic Chironomidae collected from upland and lowland fluvial habitats in the Chocancharava River basin. Subfamilies are presented in phylogenetic order and genera in alphabetic order. Total abundance was calculated as the abundance from all samples ( $n = 204$ ) pooled together. See reference to habitats in Methods section.

Chironomidae Taxa	Frequency of occurrence (%)	Total abundance	Upland habitats	Lowland habitats
<b>Podonominae</b>	0.8	57	1, 3	
<b>Tanypodinae</b>				
<i>Ablabesmyia</i> sp.	3.3	758	1, 2, 3	5
<i>Apsectrotanytus</i> sp.	0.4	185	1	
<i>Djalmabatista</i> sp.	23.8	35819	1, 2, 3	1, 3, 4, 5, 6
<i>Labrundinia</i> sp.	2.9	417	1, 2, 3	
<i>Larsia</i> sp.	11.3	2460	1, 2, 3	2, 5
<i>Pentaneura</i> sp.	16.7	12751	1, 2, 3	
<i>Thienemannimyia</i> sp.	44.6	50448	1, 2, 3	1, 4, 5, 6
<b>Orthoclaadiinae</b>				
<i>Corynoneura</i> sp.	39.2	55098	1, 2, 3	1, 6
<i>Cricotopus</i> sp. 1	0.4	111	2	
<i>Cricotopus</i> sp. 2	0.8	173		3, 5
<i>Eukiefferiella</i> sp.	2.1	3946	1, 2	
<i>Lopescladius</i> sp.	29.2	24401	1, 2, 3	1
<i>Nanocladius</i> sp.	2.9	474	1, 2, 3	
<i>Onconeura</i> sp.	20.4	11016	1, 2, 3	1, 2, 4, 5
Orthoclaadiinae sp. 1	17.5	7695		1, 2, 3, 4, 5, 6
Orthoclaadiinae sp. 2	1.7	540		5
<i>Orthocladus</i> sp.	16.7	39693	2, 3	1, 2, 3, 4, 5, 6
<i>Parametrioctenus</i> sp.	20.4	14920	1, 2, 3	2, 3, 5, 6
<i>Paratrichocladius</i> sp.	43.3	291717	1, 2, 3	1, 2, 3, 4, 5, 6
<i>Thienemanniella</i> sp.	37.5	18423	1, 2, 3	1, 2, 3, 4, 5, 6
<b>Chironominae</b>				
<i>Chironomus</i> sp.	0.8	43		3, 5
<i>Cladotanytarsus</i> sp.	9.2	9509	1, 2, 3	
<i>Cryptochironomus</i> sp.	0.8	163	2, 3	
<i>Dicrotendipes</i> sp.	0.8	94		2, 5
<i>Parachironomus</i> sp.	1.7	141	1, 2	2, 3
<i>Paratanytarsus</i> sp.	1.7	1147	1, 2, 3	2
<i>Polypedilum</i> sp.	59.2	306414	1, 2, 3	1, 2, 3, 4, 5, 6
<i>Pseudochironomus</i> sp.	14.6	6416	1, 2, 3	1, 5
<i>Rheotanytarsus</i> sp.	13.3	11393	1, 2, 3	5
<i>Tanytarsus</i> sp.	20.4	33705	1, 2, 3	5

*Polypedilum* sp. was the most frequent and abundant Chironomidae (Table 3), followed by *Thienemannimyia* sp. and *Paratrichocladius* sp. *Thienemannimyia* sp. was indicator taxa of upland reaches (Table 4) but *Polypedilum* sp. and *Paratrichocladius* sp. were not indicators of any reach. However, *Polypedilum* sp. was indicator taxa of specific habitat units (Tables 5 and 6) when data sets were considered separately.

CCA performed with global data separated samples and taxa of upland reaches from those of lowland reaches (Fig. 2). The first four axes explained 22% of total variability of species data and 91% of species-environment relation (Eigenvalues: Axis 1: 0.348, Axis 2: 0.057, Axis 3: 0.042, Axis 4: 0.034; Total inertia: 2.193). Restricted Monte Carlo permutation test showed that all the axes were significant ( $F$ -ratio = 6.721,  $P = 0.005$ ) indicating a good relationship between Chironomidae taxa distribution and measured environmental

Table 4. Indicator values for Chironomidae taxa from upland and lowland reaches in the Chocancharava River basin. Monte Carlo test was used to assess the significance of each taxon as an indicator for a respective reach type. Only taxa with significant indicator values are listed.

UPLAND		
Taxa	Indicator Value	P-value
<i>Corynoneura</i> sp.	85.1	0.001
<i>Thienemannimyia</i> sp.	84.6	0.001
<i>Lopescladius</i> sp.	63.8	0.001
<i>Tanytarsus</i> sp.	42.5	0.001
<i>Paratrichocladius</i> sp.	38.5	0.027
<i>Djalmabatista</i> sp.	37.6	0.001
<i>Pentaneura</i> sp.	37.0	0.001
<i>Rheotanytarsus</i> sp.	28.7	0.001
<i>Onconeura</i> sp.	25.9	0.001
<i>Pseudochironomus</i> sp.	25.4	0.001
<i>Parametriocnemus</i> sp.	23.4	0.006
<i>Larsia</i> sp.	22.7	0.001
<i>Labrundinia</i> sp.	6.5	0.014
<i>Nanocladius</i> sp.	6.5	0.020
<i>Ablabesmyia</i> sp.	6.3	0.017
LOWLAND		
Taxa	Indicator Value	P-value
Orthocladiinae sp. 1	43.7	0.001
<i>Thienemanniella</i> sp.	39.7	0.003
<i>Orthocladius</i> sp.	39.4	0.001
Orthocladiinae sp. 2	4.2	0.033

variables. Variables related to substrate type were the major explanatory variables in the ordination analysis. The biplot of samples and environmental variables reflected a gradient mostly related to longitudinal changes in substrate variables. Samples from lowland reaches characterized by fine substrate (sand and silt-clay) were grouped on the right of the plot, whereas samples from upland reaches, characterized by coarse substrate (cobble), were grouped on the left. MRPP also showed that Chironomidae assemblages collected from upland and lowland reaches were different ( $A = 0.0390$ ,  $P < 0.0001$ ). In CCA, depth was also an important variable in separating the two main groups of samples and current velocity showed less explanatory power. Fifteen Chironomidae taxa showed significant indicator values for upland reaches (Table 4) and all these taxa were grouped in the CCA in relation to upland reaches (Fig. 2). The most representative taxa associated to these reaches were *Corynoneura* sp., *Thienemannimyia* sp. and *Lopescladius* sp., since they presented the highest indicator values. On the other hand, four taxa presented significant indicator values for lowland reaches, belonging all to the subfamily Orthocladiinae.

The first axis of the CCA carried out with upland data set mainly separated riffle samples from run samples (Fig. 3). The first four axes explained 15.7% of total variability of species data and 90% of species-environment relation (Eigenvalues: Axis 1: 0.077, Axis 2: 0.060, Axis 3: 0.046, Axis 4: 0.023; Total inertia: 1.317). Restricted Monte Carlo permutation test showed that all the axes were significant ( $F$ -ratio = 3.557,  $P = 0.005$ ). The run samples and taxa were grouped on the right side of the plot and the second axis separated them in two

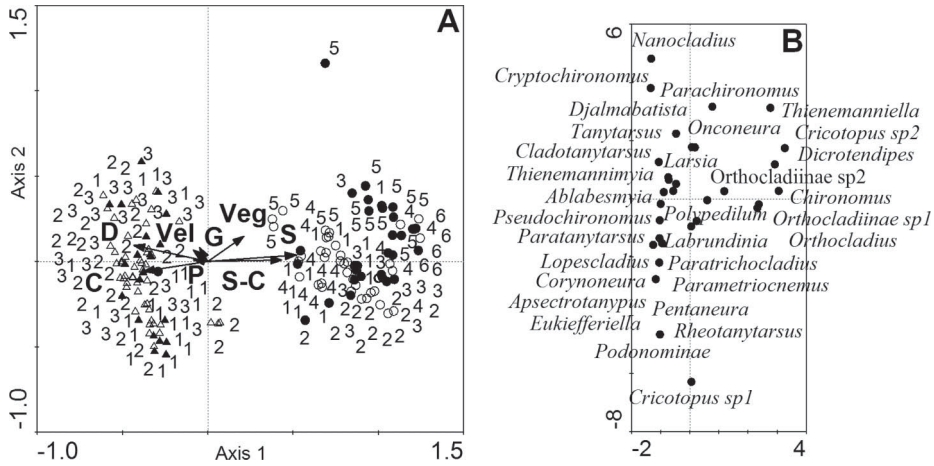


Figure 2. CCA Ordination of benthic samples and taxa from upland and lowland reaches. **A)** Ordination of samples in relation to Chironomidae larva abundances. Triangles correspond to upland reaches and circles correspond to lowland reaches. Close symbols correspond to the high rainfall period and open symbols correspond to the low rainfall period. Numbers represent habitats in the different reaches. See reference to habitats in Methods section. Environmental variables: Vel: current velocity, Veg: vegetation, D: depth, C: cobble, P: pebble, G: gravel, S: sand, S-C: silt and clay. **B)** Ordination of Chironomidae taxa.

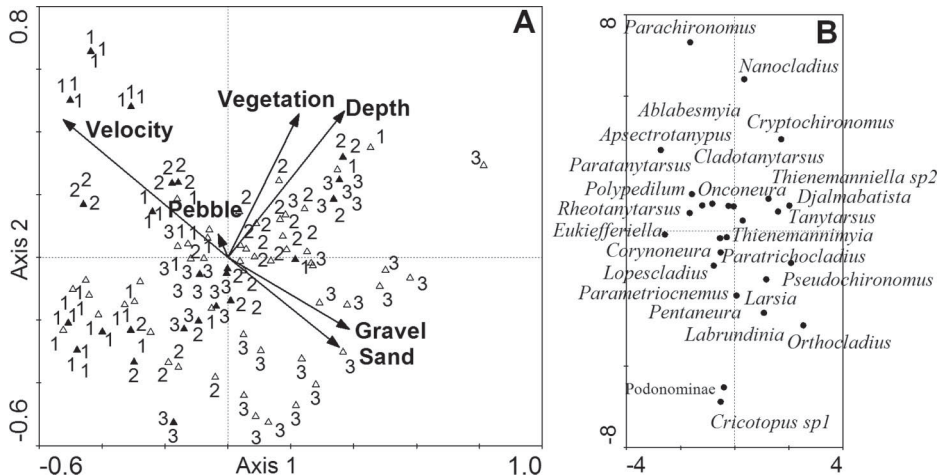


Figure 3. CCA Ordination of benthic samples and taxa from upland reaches. **A)** Ordination of samples. Close symbols correspond to the high rainfall period and open symbols correspond to the low rainfall period. Numbers represent upland fluvial habitats. See reference to habitats in Methods section. **B)** Ordination of Chironomidae taxa.



Table 5. Indicator values for Chironomidae taxa from the different upland fluvial habitats. Monte Carlo test was used to assess the significance of each taxon as an indicator for a respective reach type. Only taxa with significant indicator values are listed.

### 1) RIFFLE

Taxa	Indicator Value	P-value
<i>Polypedilum</i> sp.	67.2	0.001
<i>Rheotanytarsus</i> sp.	24.6	0.056
<i>Eukiefferiella</i> sp.	11.1	0.034

### 2) COARSE SUBSTRATE RUN

Taxa	Indicator Value	P-value
<i>Corynoneura</i> sp.	43.8	0.046

### 3) FINE SUBSTRATE RUN

Taxa	Indicator Value	P-value
<i>Thienemannimyia</i> sp.	49.3	0.012
<i>Larsia</i> sp.	25.3	0.010

different groups, in the upper right panel samples and taxa from coarse substrate runs were grouped and in the lower panel samples and taxa from fine substrate runs were. Differences in Chironomidae assemblages among the upland habitats were significant according to the MRPP analysis ( $A = 0.013$ ,  $P = 0.05$ ). These differences appeared when indicator values were analyzed (Table 5) since at least one significant indicator taxa was found for each habitat.

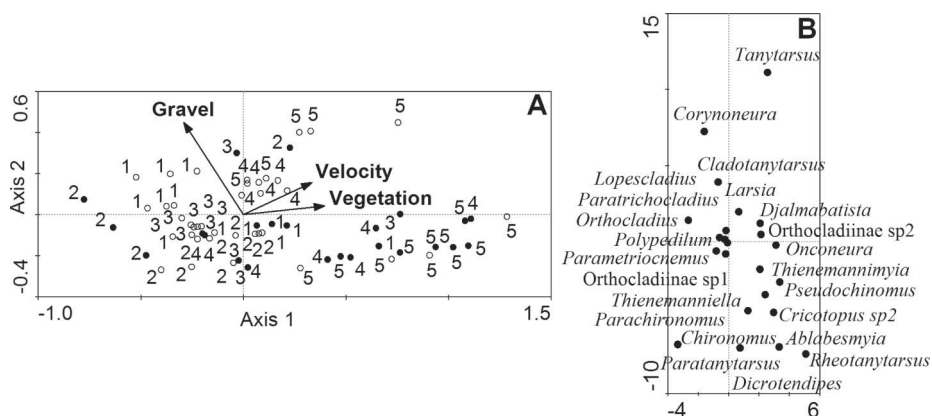


Figure 4. CCA Ordination of benthic samples and taxa from lowland reaches. **A)** Ordination of samples. Close symbols correspond to the high rainfall period and open symbols correspond to the low rainfall period. Numbers represent lowland fluvial habitats. See reference to habitats in Methods section. The habitat number 6 (vegetated secondary channel in a calcrete riverbank) which was sampled only in one of the lowland reaches were not considered in the CCA since restricted permutations required a balance design. **B)** Ordination of Chironomidae taxa.

The CCA performed with the lowland data set mainly separated samples from habitats which differ in current velocity and in the abundance of aquatic vegetation (Fig. 4). The first four axes explained 44.7% of total variability of species data and 100% of species-environment relation (Eigenvalues: Axis 1: 0.142, Axis 2: 0.029, Axis 3: 0.027, Axis 4: 0.999; Total inertia: 2.677). Restricted Monte Carlo permutation test showed that all the axes were significant ( $F$ -ratio = 1.919,  $P = 0.001$ ) indicating that the influence of vegetation, velocity and gravel on the structure of lowland Chironomidae assemblages was significant. Samples and taxa from habitats characterized by high current velocity and by the presence of aquatic vegetation were grouped on the right panel of the plot whereas samples and taxa from habitats with low current velocity were grouped on the left panel. Chironomidae assemblages were significantly different among lowland habitats as assessed by MRPP ( $A = 0.080$ ,  $P = 0.001$ ). When indicator values were analyzed, no taxon appeared as a significant indicator in four out of six habitats sampled in lowland reaches. Only vegetated habitats showed significant indicator taxa (Table 6). All the multivariate analyses did not show evidence of temporal segregation of the assemblages since samples from the same rainfall period were not clustered in the plots.

In the upland reaches, taxonomic richness showed dependence on the joint effects habitat-tributary stream and on the joint effect period-stream (Table 7). Diversity was influenced by habitat and by the joint effect period-stream; whereas total abundance depended on three joint effects: stream-period, stream-habitat and habitat-period.

In the lowland reaches, taxonomic richness was influenced by the individual effect of habitat and period (Table 7); diversity showed dependence on the joint effect habitat-period and on the joint effect habitat-reach; whereas total abundance depended on the joint effect reach-period-habitat.

In upland and lowland reaches the highest values of assemblage attributes were found in the low rainfall period (Fig. 5). In upland reaches, the highest richness and diversity were found in coarse substrate runs. On the other hand, in lowland reaches the highest richness

Table 6. Indicator values for Chironomidae taxa from the different lowland fluvial habitats. Monte Carlo test was used to assess the significance of each taxon as an indicator for a respective reach type. Only taxa with significant indicator values are listed. Only habitats 5 (secondary vegetated channel) and 6 (secondary vegetated channel in a calcrete riverbank) showed significant indicator taxa.

#### SECONDARY VEGETATED CHANNEL

Taxa	Indicator Value	$P$ -value
<i>Onconeura</i> sp.	57.1	0.002
<i>Djalmabatista</i> sp.	38.6	0.015
<i>Pseudochironomus</i> sp.	26.5	0.012
Orthocladiinae sp. 2	22.2	0.017
<i>Tanytarsus</i> sp.	16.7	0.042

#### SECONDARY VEGETATED CHANNEL IN A CALCRETE RIVERBANK

Taxa	Indicator Value	$P$ -value
<i>Thienemannimyia</i> sp.	56.4	0.001
<i>Polypedilum</i> sp.	47.6	0.013
<i>Parametriocnemus</i> sp.	43.4	0.002
<i>Orthocladius</i> sp.	34.8	0.039
Orthocladiinae sp. 1	28.3	0.050

Table 7. Summary of analysis of variance to examine the influence of habitat unit, hydrological period, stream (in upland reaches) or reach (in lowland reaches) and interaction terms on Chironomidae assemblage structure in upland and lowland reaches. Significant *P*-values are in bold.

UPLAND				LOWLAND			
Source of variation	<i>DF</i>	<i>F</i>	<i>P</i>	Source of variation	<i>DF</i>	<i>F</i>	<i>P</i>
Taxonomic richness				Taxonomic richness			
Habitat	2	3.27	0.0425	Habitat	4	6.88	<b>0.0002</b>
Hydrological period	1	80.00	<0.0001	Hydrological period	1	297.82	<b>&lt;0.0001</b>
Tributary stream	2	1.02	0.3649	Reach	2	0.07	0.9318
Habitat*period	2	2.50	0.0879	Habitat*period	4	1.48	0.2227
Habitat*stream	4	2.77	<b>0.0321</b>	Habitat*reach	8	1.07	0.4002
Period*stream	2	15.10	<b>&lt;0.0001</b>	Period*reach	2	0.45	0.6404
Habitat*period*stream	4	0.55	0.7002	Habitat*period*reach	8	1.14	0.3539
Shannon diversity				Shannon diversity			
Habitat	2	4.05	<b>0.0206</b>	Habitat	4	0.48	0.7476
Hydrological period	1	5.78	0.0183	Hydrological period	1	173.73	<0.0001
Tributary stream	2	20.47	<0.0001	Reach	2	0.02	0.9829
Habitat*period	2	0.17	0.8457	Habitat*period	4	7.52	<b>0.0001</b>
Habitat*stream	4	1.65	0.1684	Habitat*reach	8	2.43	<b>0.0239</b>
Period*stream	2	16.43	<b>&lt;0.0001</b>	Period*reach	2	0.70	0.5026
Habitat*period*stream	4	2.33	0.0619	Habitat*period*reach	8	1.81	0.0937
Total abundance				Total abundance			
Habitat	2	1.95	0.1484	Habitat	4	22.58	<0.0001
Hydrological period	1	140.05	<0.0001	Hydrological period	1	360.70	<0.0001
Tributary stream	2	8.77	0.0003	Reach	2	0.75	0.4772
Habitat*period	2	4.43	<b>0.0146</b>	Habitat*period	4	7.83	0.0001
Habitat*stream	4	3.25	<b>0.0154</b>	Habitat*reach	8	4.64	0.0003
Period*stream	2	8.70	<b>0.0004</b>	Period*reach	2	1.10	0.3414
Habitat*period*stream	4	0.59	0.6719	Habitat*period*reach	8	2.54	<b>0.0222</b>

was found in the vegetated secondary channel. The highest values of diversity were found in unvegetated secondary channels and the highest abundance was found in vegetated secondary channel and in backwaters in bars. Secondary vegetated channels in calcareous riverbanks, which were sampled only in one of the lowland reaches, presented high values of richness, diversity and abundance.

#### 4. Discussion

Distribution pattern of Chironomidae subfamilies changes in relation to the longitudinal dimension of the river. Chironomidae fauna of upland streams is generally dominated by the subfamily Orthocladiinae, which is adapted to cool, well-oxygenated conditions (PINDER, 1995). On the other hand, Chironominae has been reported as the dominant chironomid subfamily in potamal communities (LINDEGAARD, 1995). Species of this subfamily are adapted to live in soft sediments and are better able to tolerate the higher temperatures and sometimes lower oxygen concentrations that occur in large lowland rivers (PINDER, 1995). In our study, Orthocladiinae was the most abundant subfamily in upland reaches and Chironominae

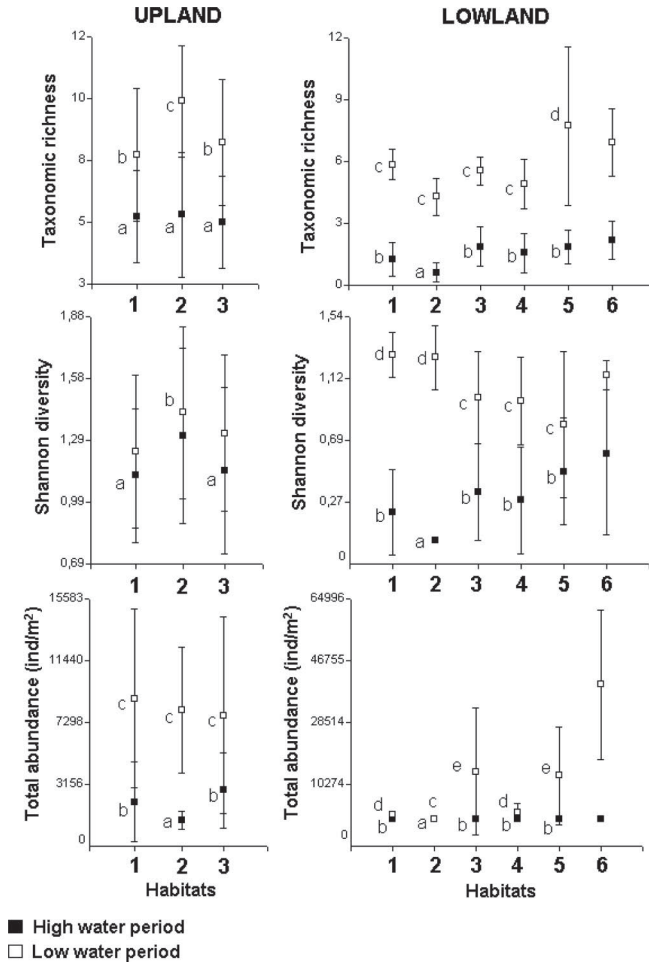


Figure 5. Taxonomic richness, diversity and total abundance of Chironomidae larvae in upland and lowland fluvial habitats during high and low rainfall period. Mean values are shown with standard deviation. See reference to habitats in Methods section. Different letters indicate significant differences tested by ANOVA (SNK test). Habitat number 6 (vegetated secondary channel in a calcrete riverbank) was not considered in ANOVAs but is presented in the figure in order to show mean values of assemblage attributes in this habitat unit.

dominated in the lowland segment of the river. However, in lowland reaches the number of Orthocladiinae taxa was similar to Chironominae. In fact, indicator taxa of lowland reaches were exclusively Orthocladiinae. River margins in the lowland section of the Chocancharava River are characterized by the presence of aquatic vegetation which determines a heterogeneous environment and provides refugia for invertebrates (COGERINO *et al.*, 1995; PRINCIPE and CORIGLIANO, 2006). It has been pointed out that aquatic vegetation facilitates the colonization of middle and lower reaches of rivers by Orthocladiinae and by other taxa characteristic of the rhithron (TOKESHI and PINDER, 1985). Additionally, our results showed that the presence of aquatic vegetation was one of the main variables conditioning the distribution of chironomids in lowland reaches.

Chironomidae assemblages were different between upland and lowlands reaches and among habitats in each reach. Distribution of the aquatic organisms changes in relation to hydrological and geomorphological conditions at different spatial scales: drainage, reach and habitat (HILDREW, 1996). Our results showed that the longitudinal variation in the assemblages was mainly conditioned by changes in substrate, as assessed by CCA. Current velocity was not an important variable explaining differences between lowland and upland assemblages since both sections of the river presented similar values of current velocity. When the upland data set was analyzed separately, samples and taxa ordinated not only in relation to substrate but also in relation to current velocity, since riffle samples (high current velocity) were separated first from run samples (low current velocity). Then, samples from runs characterized by different substrate were separated. On the other hand, current velocity and the presence of aquatic vegetation were the major explanatory variables conditioning the distribution of chironomids in lowland reaches. Substrate particle size, organic matter deposit, water depth and current velocity appeared to be the major factors affecting distribution of chironomids (LENCIONI and ROSSARO, 2005). These parameters may act together on the habitat preferences of Chironomidae larvae (SANSEVERINO and NESSIMIAN 1998). A positive relationship between the presence of macrophytes and the abundance and diversity of Chironomidae has also been demonstrated (MOORE, 1980). According to our results, the relative importance of habitat variables conditioning chironomid distribution changes in the longitudinal dimension of the river at a reach scale.

In upland reaches, the highest values of richness were found in coarse substrate runs which were characterized by low current velocity and substrate of cobble, pebble and gravel. In lowland reaches, richness was higher in marginal vegetated habitats. Coarse substrate runs and vegetated secondary channels are both heterogeneous and complex habitat units. Physically complex substrate types (wood, leaves, gravel or cobbles, macrophytes, mosses) usually support a more diverse zoobenthic community than structurally simple substrates (sand or bedrock) (LENCIONI and ROSSARO, 2005). The role of spatial heterogeneity in affecting the structure of communities has been highlighted by several authors (BEISEL *et al.*, 2000; VOELZ and MCARTHUR, 2000). Heterogeneous habitats potentially offer a great number of niches for invertebrates; they offer refugia and adequate conditions for feeding, since the probability of predation decreases. LENCIONI and ROSSARO (2005) suggested habitat heterogeneity as a better predictor of chironomid assemblages than large-scale patterns in landscape diversity. Heterogeneity created by different combinations of habitat variables may determine species richness and patch composition. Random patch dynamics may possess key attributes which drive chironomid community resistance and resilience to disturbances (SCHMID, 1993). The distribution of chironomids observed in the investigated reaches of the Chocancharava River indicates that larvae respond to longitudinal changes of hydraulics variables and to local variations of fluvial habitats at different reaches.

Orthocladiinae sp.1, *Thienemanniella* sp., *Orthocladus* sp. and Orthocladiinae sp. 2 were typical of lowland reaches, whereas fifteen taxa showed significant indicator values for upland reaches. *Corynoneura* sp., *Thienemannimyia* sp. and *Lopescladius* sp. were the most characteristic taxa of upland reaches since they presented the highest indicator values. The few indicator taxa registered in lowland reaches could be attributable to species of some genera may show rather different ecological preferences (MARZIALI *et al.*, 2006; ROSSARO *et al.*, 2006). Probably, more detail in the identification would provide quite different results adding more indicator taxa to the different reaches. For this reason, taxonomic studies should be encouraged in order to allow more accuracy in regional studies. On the other hand, the lowland stretch belongs to a hydraulic transition zone in which there is a gradual succession from rhithral to potamal conditions. In these zones species assemblages overlap therefore, few taxa may appear as indicators of lowland reaches.

In upland reaches, *Polypedilum* sp., *Rheotanytarsus* sp. and *Eukiefferiella* sp. were indicator taxa of riffle habitats, characterized by coarse substrate and turbulent flow. *Polypedilum*

sp. is generally associated with fine sediments but some species can be also found in hard substrate (PINDER and REISS, 1983). *Corynoneura* sp. was the indicator taxon of coarse substrate runs. It has already been pointed out that this genus is mainly associated with coarse substrate. The larvae are often found in fissures in submerged stones because of their small body size (CRANSTON *et al.*, 1983). The indicator taxa of fine substrate runs were the Tany-podinae *Thienemannimyia* sp. and *Larsia* sp. FITTKAU and ROBACK (1983) have pointed out that sandy substrate is also preferred by these taxa in holartic streams.

In lowland reaches only habitats associated with riverbanks presented indicator taxa since in the other habitat units taxa which were common to all habitats occurred. Therefore, indicator taxa were not distinguished in these lowland habitats. Riverbank habitats allocated specific taxa, which seem to be able to colonize only this type of habitats in the lowland segment of the Chocancharava River. Most of these taxa are typical from upstream reaches since they are Orthocladiinae, Tany-podinae or Tanytarsini (LINDEGAARD, 1995). River margins in the lowland segment are characterized by the presence of aquatic vegetation which allows the colonization of typical taxa of the rhithron (TOKESHI and PINDER, 1985). In addition, the lowland studied reaches belong to a hydraulic transition zone in which there is a gradual succession from rhithron to potamal conditions. In these transition zones species assemblages overlap and some species live near the limits of their ecological tolerance (STATZNER and HIGLER, 1986).

Habitats associated to riverbanks in lowland reaches of the Chocancharava River are highly threatened since new urban planning projects pretend to modify banks in order to establish leisure places, eliminating natural aquatic vegetation and placing recreational infrastructure. As a consequence, aquatic communities living in these habitats may be endangered. Therefore, it would be important to apply conservation strategies in order to protect riverbanks since they present a high diversity of species (COGERINO *et al.*, 1995; PRINCIPE and CORIGLIANO, 2006).

Habitat preferences of aquatic macroinvertebrates from the central region of Argentina have not been widely investigated. This research adds information about the distribution of Chironomidae taxa in upland and lowland river sections. Upland reaches belong to tributary streams with scarce human impacts. These lotic systems, close to headwaters, may become an important resource of unpolluted waters for the future. On the other hand, lowland reaches are highly impacted by urban land use and present alteration of habitat quality mainly in areas associated to riparian zones (BOCCOLINI *et al.*, 2005). River condition may be assessed using aquatic invertebrates as indicators (ROSEMBERG and RESH, 1993), especially Chironomidae (LENCIONI and ROSSARO, 2005); but a better understanding of the ecological preferences of indicator taxa is needed (MCGEOCH and CHOWN, 1998; TICKNER *et al.*, 2000). This knowledge may allow the implementation of appropriate conservation and restoration strategies when necessary, in the lotic ecosystems of the central region of Argentina.

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## 6. References

- BEISEL, J.-N., P. USSEGLIO-POLATERA and J.-C. MORETEAU, 2000: The spatial heterogeneity of a river bottom: a key factor determining macroinvertebrate communities. – *Hydrobiologia* **422/423**: 163–171.

- BROOKS, A. J., T. HAEUSLER, I. REINFELDS and S. WILLIAMS, 2005: Hydraulic microhabitats and the distribution of macroinvertebrate assemblages in riffles. – *Freshw. Biol.* **50**: 331–344.
- BOCCOLINI, M. F., A. M. OBERTO and M. C. CORIGLIANO, 2005: Calidad ambiental en un río urbano de llanura. – *Biol. Acuática* **22**: 59–69.
- CABIDO, D., M. CABIDO, S. M. GARRE, J. A. GORGAS, R. MIATELLO, S. RAMBALDI, A. RAVELO and J. L. TASSILE, 2003: Regiones Naturales de la Provincia de Córdoba. Serie C. Publicaciones Técnicas. Agencia Córdoba. Dirección de Ambiente, Córdoba. 102 pp.
- CANTERO, G. A., M. P. CANTU, J. M. CISNEROS, J. J. CANTERO, M. BLARASIN, A. DEGIOANNI, J. GONZALEZ, V. BECERRA, H. GIL, J. DE PRADA, S. DEGIOANNI, C. CHOLAKY, M. VILLEGAS, A. CABRERA and C. ERIC, 1998: Las tierras y aguas del sur de Córdoba: propuestas para un manejo sustentable. UNRC, Río Cuarto. 119 pp.
- CAPITANELLI, R. G., 1979: Clima. – *In*: VÁZQUEZ, J. V., R. A. MIATELLO and M. E. ROQUÉ (eds.). Geografía Física de la Provincia de Córdoba. Ed. Boldt, Buenos Aires. pp. 45–138.
- COGERINO, L., B. CELLOT and M. BOURNAUD, 1995: Microhabitat diversity and associated macroinvertebrates in aquatic banks of a large European river. – *Hydrobiologia* **304**: 103–115.
- CORIGLIANO, M. C., 1989: Partición de recursos en el tramo anastomosado de un río de llanura. – *Rev. UNRC* **9**: 61–73.
- CRANSTON, P. S., D. R. OLIVER and O. A. SÆTHER, 1983: The larvae of Orthoclaadiinae (Diptera: Chironomidae) of the Holarctic region – Keys and diagnoses. – *In*: WIEDERHOLM, T. (ed.). Chironomidae of the Holarctic Region: keys and diagnoses. Part I. Larvae. Ent. Scand. Suppl. **19**: 1–457.
- CRANSTON, P. S., 1995: Introduction. – *In*: ARMITAGE, P., P. S. CRANSTON and L. C. V. PINDER (eds.). The Chironomidae. The biology and ecology of non-biting midges. Chapman and Hall, London. pp. 1–7.
- DUFRENE, M. and P. LEGENDRE, 1997: Species assemblages and indicator species: the need for a flexible asymmetrical approach. – *Ecol. Monogr.* **67**: 345–366.
- EPLER, J. H., 2001: Identification manual for the larval Chironomidae (Diptera) of North and South Carolina. North Carolina Department of Environmental and Natural Resources. Division of Water Quality, North Carolina. 526 pp.
- FITTKAU, E. J. and S. S. ROBACK, 1983: The larvae of Tanypodinae (Diptera: Chironomidae) of the Holarctic region – Keys and diagnoses. – *In*: WIEDERHOLM, T. (ed.). Chironomidae of the Holarctic Region: keys and diagnoses. Part I. Larvae. Ent. Scand. Suppl. **19**: 1–457.
- GORDON, N. D., T. A. MCMAHON and B. L. FINLAYSON, 1994: Stream hydrology, an introduction for ecologists. Wiley and Sons, New York. 526 pp.
- GREENBERG, A. E., L. S. CLESCERI and A. D. EATON (eds.), 1992: Standard methods for the examination of water and wastewater. American Public Health Association, Washington. 900 pp.
- HILDREW, A. G., 1996: Whole river ecology: spatial scale and heterogeneity in the ecology of running waters. – *Arch. Hydrobiol. Supp.* **113**: 25–43.
- LENCIONI, V. and B. ROSSARO, 2005: Microdistribution of chironomids (Diptera: Chironomidae) in Alpine streams: an autoecological perspective. – *Hydrobiologia* **533**: 61–76.
- LINDEGAARD, C., 1995: Classification of water-bodies and pollution. – *In*: ARMITAGE, P., P. S. CRANSTON and L. C. V. PINDER (eds.). The Chironomidae. The biology and ecology of non-biting midges. Chapman and Hall, London. pp. 385–404.
- MARZIALI, L., V. LENCIONI and B. ROSSARO, 2006: Chironomid species as indicators of freshwater habitat quality. – *Verh. Internat. Verein. Limnol.* **29**: 1553–1555.
- MCCUNE, B. and M. J. MEFFORD, 1999: Multivariate Analysis of Ecological Data. Version 4.25. MjM Software, Gleneden Beach, Oregon, U.S.A.
- MCCUNE, B. and J. B. GRACE, 2002: Analysis of Ecological Communities. MjM Software, Oregon, U.S.A.
- MCGEOCH, M. A. and S. L. CHOWN, 1998: Scaling up the value of bioindicators. – *Trends Ecol. Evol.* **13**: 46–47.
- MEDINA, A. I. and A. C. PAGGI, 2004: Composición y abundancia de Chironomidae (Diptera) en un río serrano de zona semiárida (San Luis, Argentina). – *Rev. Soc. Entomol. Argent.* **63**: 107–118.
- MERRIT, K. W., R. W. CUMMINS and T. M. BURTON, 1984: The role of Aquatic insects in the processing and cycling of nutrients. – *In*: RESH, V. H. and D. M. ROSENBERG (eds.). The ecology of aquatic insects. Praeger Publishers, New York. pp. 134–163.
- MOORE, J. W., 1980: Factors influencing the composition, structure and density of a population of benthic invertebrates. – *Arch. Hydrobiol.* **88**: 202–218.

- PAGGI, A. C., 2001: Diptera: Chironomidae. – *In*: FERNANDEZ, H. R. and E. DOMINGUEZ (eds.), Guía para la determinación de los artrópodos bentónicos sudamericanos. Universidad Nacional de Tucumán. Facultad de Ciencias Naturales e Instituto Miguel Lillo. 282 pp.
- Paggi, A. C. and A. RODRIGUES CAPÍTULO, 2002: Chironomids composition from drift and bottom samples in a regulated north-patagonian river (Rio Limay, Argentina). – *Ver. Int. Verein. Limnol.* **28**: 1229–1235.
- PINDER, L. C. V. and F. REISS, 1983: The larva of Chironominae (Diptera: Chironomidae) of the Holarctic region – Keys and diagnoses. – *In*: WIEDERHOLM, T. (ed.), Chironomidae of the Holarctic Region: keys and diagnoses. Part 1. Larvae. *Ent. Scand. Suppl.* **19**: 1–457.
- PINDER, L. C. V., 1995: The habitats of Chironomidae larvae. – *In*: ARMITAGE, P., P. S. CRANSTON and L. C. V. PINDER (eds.), The Chironomidae. The biology and ecology of non-biting midges. Chapman and Hall, London. pp. 107–133.
- PRINCIPE, R. E. and M. C. CORIGLIANO, 2006: Benthic, drifting and marginal macroinvertebrate assemblages in a lowland river: temporal and spatial variations and size structure. – *Hydrobiologia* **553**: 303–317.
- PRINCIPE, R. E., G. B. RAFFAINI, C. M. GUALDONI, A. M. OBERTO and M. C. CORIGLIANO, 2007: Do hydraulic units define macroinvertebrate assemblages in mountain streams of central Argentina? – *Limnologica* in press.
- RAVEN, P. J., N. T. H. HOLMES, P. CHARRIER, F. H. DAWSON, M. NAURA and P. J. BOON, 2002: Towards a harmonized approach for hydromorphological assessment of rivers in Europe: a qualitative comparison of three survey methods. – *Aquatic Conserv. Mar. Freshw. Ecosyst.* **12**: 405–424.
- ROSEMBERG, D. M. and V. H. RESH. (eds.), 1993: Freshwater biomonitoring and benthic macroinvertebrates. Chapman & Hall, New York. 488 pp.
- ROSSARO, B., V. LENCIONI, A. BOGGERO and L. MARZIALI, 2006: Chironomids from Southern Alpine running waters: ecology, biogeography. – *Hydrobiologia* **562**: 231–246.
- SANSEVERINO, A. and J. L. NESSIMIAN, 1998: Habitat preferences of Chironomidae larvae in an upland stream of Atlantic Forest, Rio de Janeiro State, Brazil. – *Verh. Internat. Verein. Limnol.* **26**: 2141–2144.
- SCHMID, P. E., 1993: Random patch dynamics of larval Chironomidae (Diptera) in the bed sediments of a gravel stream. – *Freshw. Biol.* **30**: 239–255.
- SPIES, M. and F. REISS, 1996: Catalog and bibliography of neotropical and Mexican Chironomidae. (Insecta, Diptera). – *Spixiana Suppl.* **22**: 61–119.
- STATZNER, B. and B. HIGLER, 1986: Stream hydraulics as a major determinant of benthic invertebrate zonation patterns. – *Freshw. Biol.* **16**: 127–139.
- STATZNER, B., J. A. GORE and V. H. RESH, 1988: Hydraulic stream ecology: observed patterns and potential applications. – *J.N. Am. Benthol. Soc.* **7**: 307–360.
- TER BRAAK, C. J. F. and P. SMILAUER, 1998: CANOCO Reference manual and User's guide to Canoco for Windows: software for Canonical Community Ordination (version 4). – Microcomputer power, Ithaca, New York. 352 pp.
- TICKNER, D., P. D. ARMITAGE, M. A. BICKERTON and K. A. HALL, 2000: Assessing stream quality using information on mesohabitat distribution and character. – *Aquatic Conserv. Mar. Freshw. Ecosyst.* **10**: 170–196.
- THOMSON, J. R., M. P. TAYLOR, K. A. FRYIRS and G. J. BRIERLEY, 2001: A geomorphological framework for river characterization and habitat assessment. – *Aquatic Conserv. Mar. Freshw. Ecosyst.* **11**: 373–389.
- TOKESHI, M. and L. C. V. PINDER, 1985: Microhabitats of stream invertebrates on two submersed macrophytes with contrasting leaf morphology. – *Hol. Ecol.* **8**: 313–319.
- VELÁSQUEZ, S. M. and M. L. MISERENDINO, 2003: Habitat type and macroinvertebrate assemblages in low order Patagonian streams. – *Arch. Hydrobiol.* **158**: 461–483.
- VOELZ, N. J. and J. V. McARTHUR, 2000: An exploration of factors influencing lotic species richness. – *Biodivers. Conserv.* **9**: 1543–1570.
- WIEDERHOLM, T., 1983: Chironomidae of the Holarctic Region: keys and diagnoses. Part 1. Larvae. – *Ent. Scand. Suppl.* **19**: 1–457.

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