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ORIGINAL ARTICLE

Temporal and altitudinal variations in benthic macroinvertebrate assemblages in an Andean river basin of Argentina

Erica E. SCHEIBLER,[1*] M. Cristina CLAPS,[2] Sergio A. ROIG-JUÑENT[1]

[1]Laboratorio de Entomología, IADIZA, CCT CONICET Mendoza. Avda. Ruiz Leal s/n. Parque Gral. San Martín, CC 507, 5500 Mendoza; [2]ILPLA, CCT CONICET La Plata, Boulevard 120 e/62 y 63, 1900 La Plata, Argentina
*Corresponding author: escheib@mendoza-conicet.gov.ar

ABSTRACT

Environmental variables and benthic macroinvertebrate assemblages were spatially and seasonally examined over two consecutive years (2000-2002) along a glacier and snowmelt river in the central-west of Argentina where lies the highest peak in America, Mount Aconcagua (6956 m elevation). The goal was to assess seasonal and altitudinal variability in benthic community structure and to define whether physical-chemical variables affect distribution of aquatic insects. The Mendoza River basin was characterised by high variability in flow and transparency, high conductivity, hard calcium sulphate water, neutral and alkaline pH, and dominant substrate composed of small blocks, cobbles, pebbles, and sand-silt. Richness of invertebrates was low, with the lowest taxonomic richness being recorded at the mouth. The dominant group with highest taxonomic richness was Diptera, although caddisflies, mayflies, beetles, and stoneflies were present. Seasonal and spatial variations in biotic and abiotic variables were detected. Maximal densities and taxonomic richness were recorded in autumn and winter. From Modified Morisita's Cluster analysis it was found that the system is divided into two groupings of sites related to each other by faunal composition. INDVAL revealed species turnover along the altitudinal gradient of some taxa: Andesiops, Massartellopsis, Edwarsina, Chelifera*, and Ceratopogonidae had preference for the headwaters (2835-2425 m elevation),* Smicridea murina *and* Baetodes *for the lower section (1413-1085 m elevation), and* Austrelmis *for the middle and lower sections. The middle section (1846-1727 m elevation) was a transition area where taxa from the headwaters and the lower section coexisted. Generalised Linear Models evidenced that altitude was the major factor determining macroinvertebrate assemblages along the large arid Mendoza River and that the physical-chemical variables that most influenced variation in community structure were: transparency, bicarbonate concentration, pH and substrate type. Our results suggest that benthic macroinvertebrate structure and environmental variables are affected in different ways by seasonal and altitudinal variations.*

Key words: Mendoza River, aquatic insects, community structure, hard environmental conditions, altitudinal gradient, Argentina.

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INTRODUCTION

Studies of longitudinal and seasonal variations in aquatic environments have been highly reported globally over several years (Maiolini and Lencioni, 2001; Milner *et al.*, 2001; Jacobsen, 2004; Füreder *et al.*, 2005; Miserendino, 2009). However, in the Central West Andes Mountains of Argentina, studies on macroinvertebrate communities following altitudinal and temporal gradients are limited. It is known that longitudinal studies contribute data on species distribution ranges and that turnover of macroinvertebrate assemblages (Milner *et al.*, 2001; Finn and Poff, 2005) in environmental gradients (Knispel and Castella, 2003) as well as description of these patterns are important contributions to ecological studies (Jacobsen, 2004). Furthermore, seasonal studies provide information about the variability of physical-chemical conditions experienced by mountain streams (Füreder, 1999; Knispel and Castella, 2003), which affects macroinvertebrate densities (Scheibler and Debandi, 2008). Mountain streams are significant systems for studying spatial biological processes (Finn and Poff, 2005) and are environments likely to be more affected by global climate change and human impact than rivers at lower altitudes (Burgherr and Ward, 2001; Finn and Poff, 2005). The physical, chemical and biotic variables elicit responses from macroinvertebrates that are reflected in the structure of aquatic communities (Cummins *et al.*, 2008). Both environmental (hydrologic, geomorphologic, and chemical) and biological features go through considerable changes, particularly in mountain streams, depending on the water source (Füreder, 1999; Füreder *et al.*, 2005). In biological terms, environmental variables determine that natural selection pressures have likely driven organisms to develop adaptive strategies for coping with each particular environment, depending on their ecological factors (dissolved oxygen, pH, conductivity, current speed, substrate typology, water hardness, nutrients, among others) (Wais de Badgen, 1992).

The Mendoza River basin is located in the Andean region (Morrone, 2006) in the northwest of Mendoza

Province in Central West Argentina. Five geomorphologic units are involved in the formation of this basin: Principal Cordillera, Frontal Cordillera, Pre-Cordillera, Uspallata depression and foothills. Each unit contributes different minerals to the Mendoza River, depending on the type of substrate composing it. The rivers that meet to form the Mendoza River contribute hard water with high saline content because they run in areas composed primarily of gypsum (evaporites). Variations in salinity also exhibit seasonal differences, the highest saline concentrations occurring in winter, with a notable decline toward summer because of increased river flows. From the headwaters (2425 m elevation) to the system's lower section (1235 m), the Mendoza River runs 100 km and receives the contribution of several streams that help decrease the salinity of its water, thus improving its physical-chemical quality and making it fit for human consumption (Armando, 1985). The importance of studying the Mendoza River basin lies in the multiple uses it is put to, as its waters are totally used for human consumption by the main urban and rural settlements in the province. Different establishments engaged in various activities: agriculture, horticulture, forestry, livestock, industry, tourism, water power and oil (Departamento General de Irrigación, 1997) are located across the Mendoza River basin area.

Here we characterise the physical, chemical and biological features of 11 sites sampled at different elevations in the Andean area. The study involves a description of the heterogeneity of benthic communities on both temporal and longitudinal scales. The first objective of our study was to assess seasonal and spatial variability in benthic community structure along a large river in the Central West Andes Mountains of Argentina. The study of relationships between invertebrate assemblages and environmental features is also an important community ecology theme and enhances knowledge about the functioning of rivers in arid zones, taking into account that the ecology of arid and semiarid streams remains relatively unexplored (Stevens *et al.*, 1997). For this reason, the second main objective of our research was to find out whether physical and chemical variables affect distribution of benthic communities and whether they characterise the ecological distribution range of each species.

METHODS

Study area

The Mendoza River basin comprises an area of 18,484 km^2 nestled in the Central Andes of Argentina in the north of Mendoza Province (32°00'-37°35'S; 66°30'-70°35'W). Born from the confluence of the Cuevas, Horcones, Tupungato and Vacas Rivers at the locality of Punta de Vacas (2394 m altitude), the river runs 300 km until draining into the Guanacache and Del Rosario Lakes. The waters of the Mendoza River are mostly fed by glaciers and snow melt from the Andes Mountains; an example of this are the Horcones and Vacas Rivers, which receive an input of melt water from glaciers located on Mount Aconcagua (6956 m elevation). The Mendoza River has an average annual discharge of 50.6 $m^3 s^{-1}$, which increases considerably between December and February (summer months) as a consequence of snow melting, reaching values between 90-120 $m^3 s^{-1}$. Rainfalls, with an annual average of 250 mm, occur in spring and summer, the contribution of rainwater to the Mendoza River being negligible. The regional climate can be defined as arid, of maximum continentality and typically temperate. The climate characterising the upper basin is typical of high mountain areas, with very cold winters where air masses coming from the Pacific Ocean produce the main meteoric contribution in the form of snow between the months of June and September. Environmental moisture is overall low and the thermal regime is characterised by strong fluctuations, which are not only seasonal but also daily (Departamento General de Irrigación, 1997, 2006).

The tributaries forming the Mendoza River have Andean vegetation composed of tall shrubs such as: *Adesmia pinifolia* Gillies ex Hook. and Arn., *Chuquiraga oppositifolia* D. Don, *Berberis empetrifolia* Lam. and *Adesmia aegiceras* Phil. The Uspallata valley (middle section) marks the start of the shrub-steppe. Among its most representative species we find *Larrea divaricata* Cav., *Lycium chanar* Phil. and *Scleropogon brevifolius* Phil., and toward the lower section *Larrea divaricata*, *L. cuneifolia* Cav. and *Bulnesia retama* Gillies ex Hook. and Arn. At its mouth, the Mendoza River crosses an area of crops containing shrubby slopes with *Larrea divaricata* and *L. cuneifolia* associated with *Bulnesia retama*; floodplain areas with cattails (*Thypha subulata* Crespo and RL Pérez-Mor.), reed beds (*Phragmites australis* Cav.), stands of pampas grass (*Cortaderia rudiuscula* Stapf.), and drains into a floodplain area with presence of *Prosopis alpataco* Phil., *Tamarix gallica* Linneo, *Baccharis salicifolia* Ruiz and Pavón and *Mikania mendocina* Phil. (Ambrosetti *et al.*, 1986; Carretero, 2000).

Site selection

From the headwaters towards the outlet of the studied system, we sampled 11 sites (Fig. 1). The watershed was subdivided into 3 sections following an altitudinal gradient. The first section was called *Headwaters* (2835-2425 m elevation) and the first four sampling sites were recorded: Cuevas River (CU: S 32° 49.443' W 69° 57.239'), Horcones River (HO: S 32° 49.326' W 69° 55.163'), Tupungato River (TU: S 32° 52.734' W 69° 46.054') and Vacas River (VA: S 32° 51.012' W 69° 45.382'). Upper Uspallata (UU: S 32° 37.210' W 69° 25.903') and Lower Uspallata (LU: S 32° 41.211' W 69°

21.504') sampling sites corresponded to the second subdivision: *the middle section* (1846-1727 m elevation). The third division, *lower section* (1413-1085 m elevation), was represented by the following sampling sites: Evarsa, (EV: S 32° 54.908' W 69° 14.251'), Potrerillos (PO: S 32° 57.335' W 69° 10.840'), Cacheuta (CA: S 33° 1.145' W 69° 6.818'), and Blanco Encalada (BE: S 33° 2.661' W 69° 0.159'). The last sampling site, the mouth, (LA: S 32° 45.459' W 68° 21.397'; 606 m elevation), had a fluctuating flow dynamics, with dry periods depending on Cipoletti dam, located in Blanco Encalada locality. Ten sites corresponded to running waters and LA to the lentic system.

Sampling

Benthic samplings were carried out seasonally over two successive years, between autumn 2000 and summer 2002, at all 11 sampling sites. At the first ten sampling sites, samples were collected with Surber net (300 µm pore size mesh net; area 0.09 m^2), whereas at LA we used a homemade Petersen dredge (extraction area: 352 cm^2). Three replications were made for each sampling site. All collected specimens were preserved in 95% alcohol for their later laboratory processing and taxonomic identification. Macroinvertebrates were identified to the lowest possible taxonomic level using the following keys: Johannsen (1970), Lopretto and Tell (1995) and Fernández and Domínguez (2001). Samples were deposited in the Entomology Laboratory of CCT Mendoza CONICET.

Conductivity (Hanna conductimeter HI 9033), pH (Hanna pH meter HI 9025), transparency (Secchi disk), water and air temperature (mercury thermometer; once per sampling site and season), depth (calibrated stick), current speed (the float method; measurements were applied a correction coefficient (0.85) according to Gordon *et al*., 1994), stream order (Strahler, 1957) and substrate compositions (Cummins, 1992) were measured at each sampling site. Water samples were collected from each sampling site and analysed for the following chemical parameters according to Jackson (1976): Ca^{+2}, Mg^{+2}, Na^{+}, K^{+}, CO_3^{-2}, HCO_3^{-1},

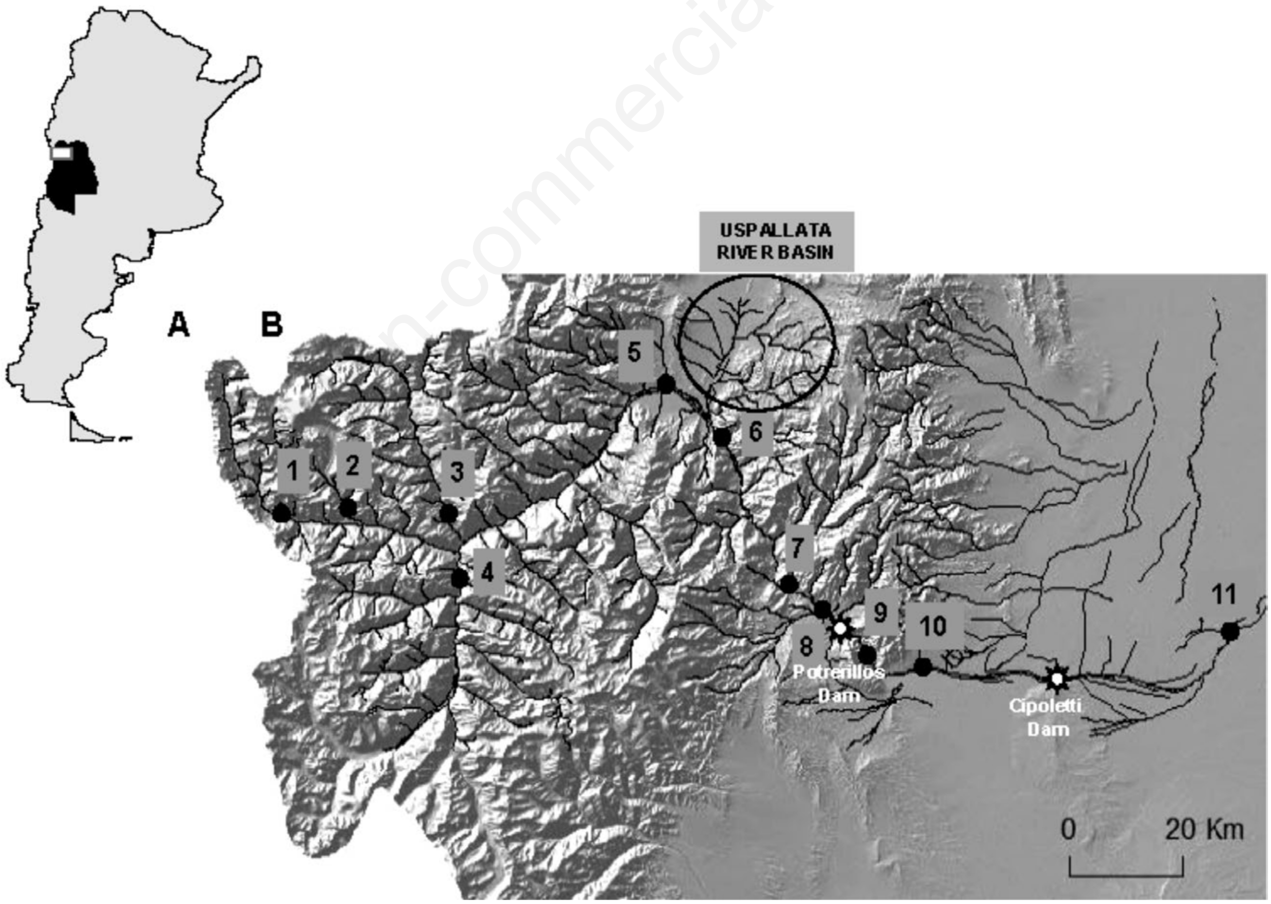

Fig. 1. Study area maps. A) Location of Mendoza Province. B) Sampling sites: 1, Cuevas River; 2, Horcones River; 3, Tupungato River; 4, Vacas River; 5, Upper Uspallata; 6, Lower Uspallata; 7, Evarsa; 8, Potrerillos; 9, Cacheuta; 10, Blanco Encalada; 11, Lavalle.

Cl^-, SO_4^{-2}, total dissolved ion, and total hardness. The discharge values of five sampling sites (CU, TU, VA, EV, and CA) were obtained from the Departamento General de Irrigación of Mendoza Province, Argentina.

Data analysis

Density (N) and taxonomic richness (S) were calculated for each benthic sample, and for this purpose a data matrix was constructed with densities (ind. m^{-2}) of each taxon per replicate, season and sampling site for the two years of sampling. Because the Chironomidae family (Diptera) was not identified to species level and its densities on our sampling sites were the highest compared to the rest of the community, we decided to exclude this family from the statistical analysis. However, as Chironomidae is a representative family of the macroinvertebrate community in our system, it was considered in some figures (Figs. 2 and 3) and in the descriptive parts of the text.

To check for normality, we applied the Shapiro-Wilks test (INFOSTAT, 2008). Since the data did not follow a normal distribution, nonparametric tests were used. When environmental variables were included as response variable in the Generalised Linear Models, they were log transformed. To explore variations in biotic (densities of abundant taxa, total density, richness) and abiotic (physical-chemical) variables, a temporal analysis was performed using seasons (S; autumn 2000, autumn 2001; winter 2000, winter 2001, spring 2000, spring 2001, summer 2001 and summer 2002) as factors, and a spatial analysis using sampling sites (SS) as factors. Moreover, for the biotic variables, we tested the interactions between both factors (SS; S). For this analysis we used Generalised Linear Models (GLM; GENSTAT software, version 4.2, 2005). Discrete data (density, richness) was analysed using Poisson distribution with logarithm as link function, and tested with χ^2. Because residual errors in the model showed overdispersion (*i.e.*, residual deviance was higher than the degree of freedom of the residual), the model was rescaled to correct for biases in the statistical test of hypotheses (Crawley 1993), using F tests instead of χ^2 as a measure of fit. Continuous data (pH, discharge, transparency, conductivity, current speed, *etc.*), were analysed using Normal distribution and identity link and tested with F. Detailed procedures for this type of analysis can be found in Crawley (1993) and McConway *et al.* (1999). Prior to the GLM analysis, in an exploratory fashion, a Spearman correlation analysis was performed among environmental variables to assess whether there was a high level of correlation between them. Only those Spearman's

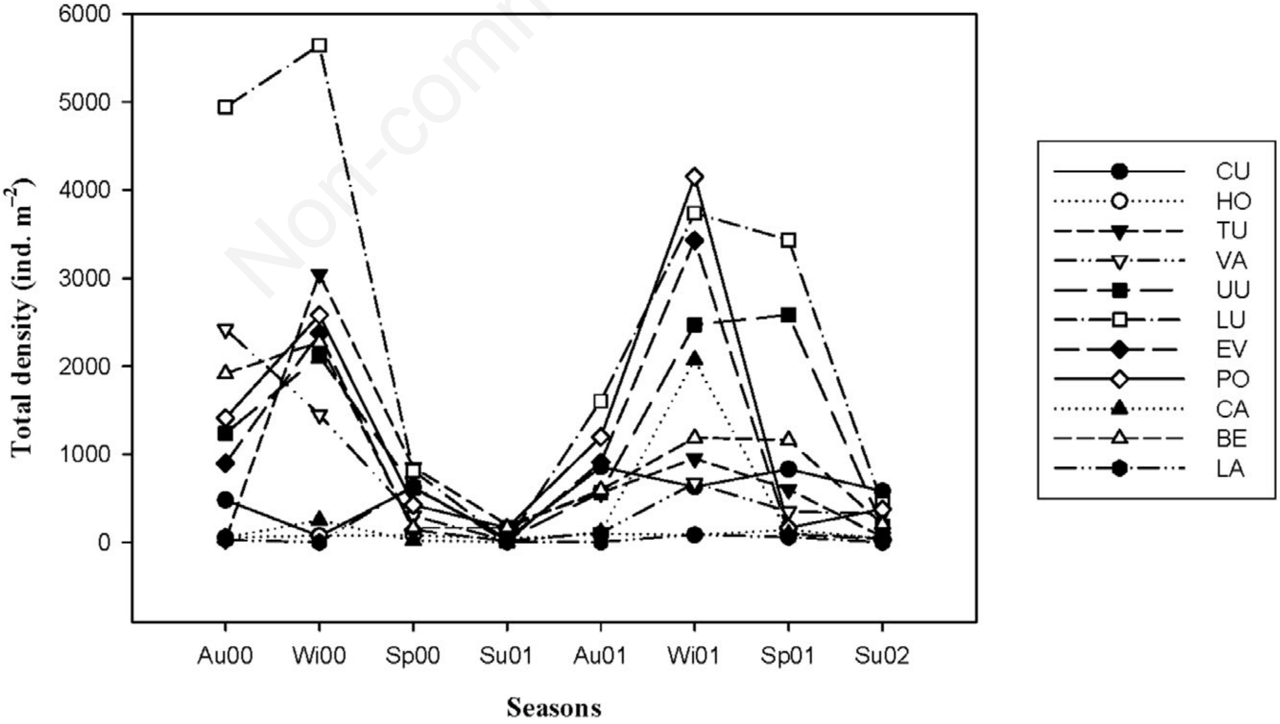

Fig. 2. Seasonal and spatial variation in total abundance averages for all 11 sampling sites. AU, autumn; WI, winter; SP, spring; SU, summer; CU, Cuevas River; HO, Horcones River; TU, Tupungato River; VA, Vacas River; UU, upper Uspallata; LU, lower Uspallata; EV, Evarsa; PO, Potrerillos; CA, Cacheuta; BE, Blanco Encalada; LA, Lavalle.

correlation coefficients (rho=δ) showing P≤0.05 were considered to be significant. Water and air temperature were excluded from the statistical analysis because these data were only taken once per season and sampling site and these data did not represent the thermal regime of the river. To detect the influence of abiotic variables on each biotic variable (total density, richness, and density of the most abundant taxon) we used a multiple regression, assuming Poisson distribution (GLM environment). The abiotic variables used were those non-correlated variables obtained with the Spearman analysis detailed above. For both GLM analyses we estimated the percent variation explained by the model for each response variable (total density, richness, environmental variables and taxon density) as follows: % of explained variability=explained deviance (or variance for normal data)/total deviance (or variance) *100. A Mann-Whitney U analysis was used to assess differences in each variable: biotic (density and richness) and abiotic (physical-chemical variables) between the two years. Piper Diagram (Baca and Threlkeld, 2000) was applied for the hydrochemical classification of water. Analyses were performed by year and season, and because the results obtained from both sampling cycles (2000-2001 and 2001-2002) were similar, the diagram was made based on the average of water chemical variables for the two consecutive sampling years.

In order to quantitatively compare taxonomic richness and densities among sampling sites, and to observe how macroinvertebrate communities were distributed along the Mendoza River Basin, a Modified Morisita's Similarity Cluster Analysis was applied, using unweighted pair group method (UPGMA; software MVSP version 3.11, Multi-Variate Statistical Package 2000). A total density matrix of each taxon per sampling site for the two years was used for this analysis. To determine composition of assemblages typical of the river sections, the indicator-value index (INDVAL) proposed by Dufrêne and Legendre (1997) was calculated for each taxon in every section. The species present in all three sections at IndVal indices higher than 10 were considered to be all-habitat.

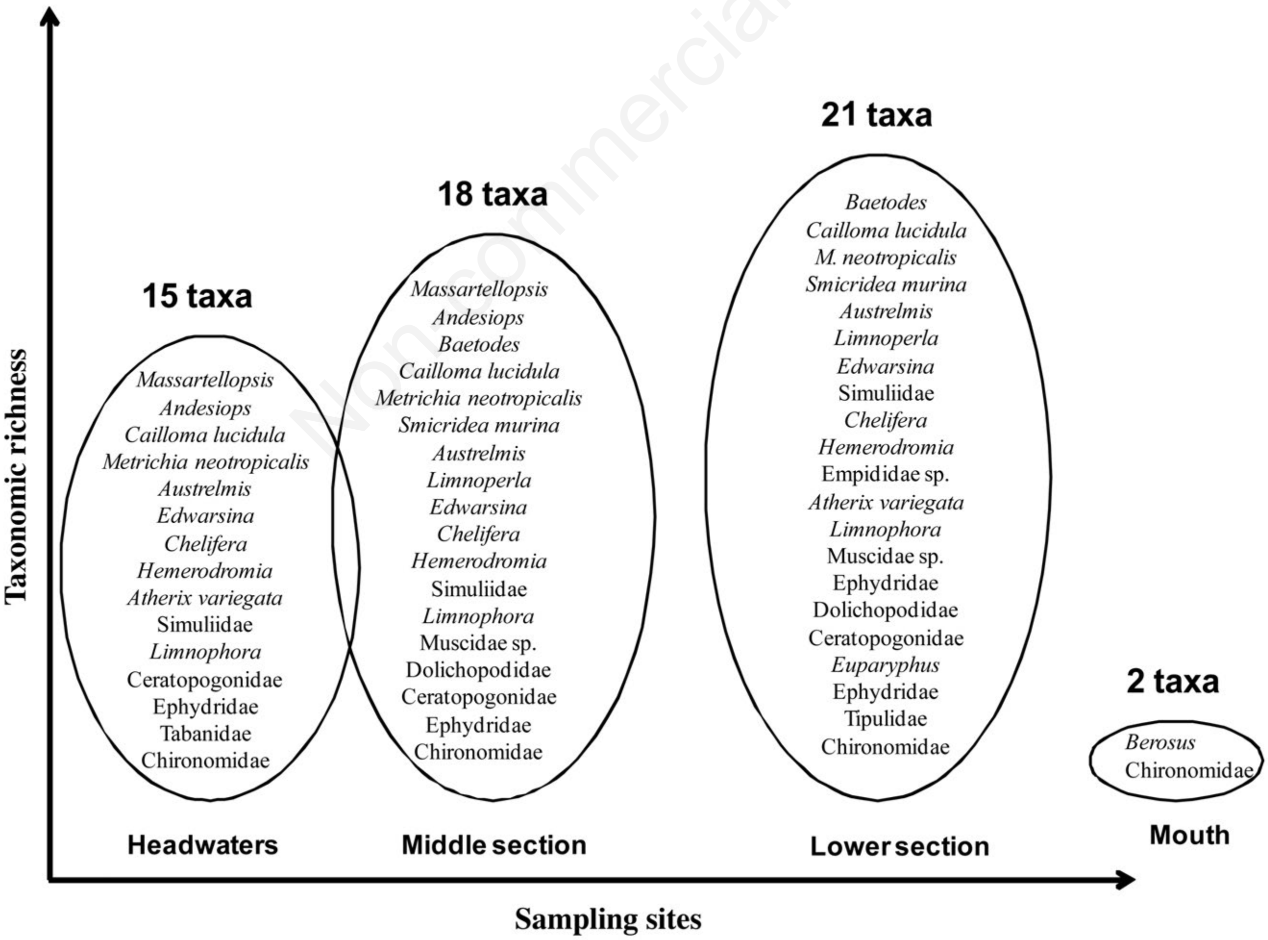

Fig. 3. Graphic representation of taxonomic richness along the Mendoza River.

RESULTS

Environmental conditions

The following variables were excluded from the GLM analysis: Ca^{+2} (δ=0.8121; P<0.0001), Mg^{+2} (δ=0.7201; P<0.0001), Na^{+} (δ=0.6026; P<0.0001), Cl^{-} (δ=0.6615; P<0.0001), SO_4^{-2} (δ=0.7329; P<0.0001), total ions (δ=0.8645; P<0.0001), total hardness (δ=0.8520; P<0.0001) because they were significantly correlated with conductivity; and depth due to its being correlated with transparency (δ=0.4021; P<0.0001).

The waters of the Mendoza River are characterised as being hard (Tab. 1; EPA, 1986; APHA, 1989), overall calcium sulphate waters at all sampling sites and in all seasons (Fig. 4). Water pH values ranged between neutral and alkaline (Tab. 1), exhibiting significant variations only among seasons ($F_{7-259=}16.10$; P<0.001; % of explained variability=82). Water temperature increased from the headwaters toward the outlet, mean water temperature was recorded at HO sampling site (1.9°C) while maximal values were found at LA sampling site (25.4°C). Recorded conductivity values were high (range 364-5290 $\mu S\ cm^{-1}$), the highest variation was recorded among sampling sites ($F_{10-259=}77.66$; P<0.001, % of explained variability=55), with LA exhibiting the highest conductivity values (5290 $\mu S\ cm^{-1}$); while the lowest variation was explained by seasons ($F_{7-259=}57.53$; P<0.001, % of explained variability=28.33). Current speed ranged between a minimum of 0.14 $m\ s^{-1}$ (LA) and a maximum of 1.81 $m\ s^{-1}$ (BE), showing significant differences among sampling sites ($F_{10-259=}17.17$; P<0.001, % of explained variability=34.69) and seasons ($F_{7-259=}11.60$; P<0.001, % of explained variability=16.41). Transparency presented significant differences among seasons ($F_{7-259=}56.43$; P<0.001, % of explained variability=59.39), with maximum values of 0.40 m in autumn and minimum values of 0.01 m in summer, and minimum differences among sampling sites ($F_{10-259=}2.79$; P=0.003, % of explained variability=4.2). The minimum discharge was recorded at CU (autumn 2000=1.45 $m^3\ s^{-1}$) and maximum flow at EV (summer 2001=119.11 $m^3\ s^{-1}$). Mean bi-annual discharge was 25.55 $m^3\ s^{-1}$, there being significant differences among sampling sites ($F_{4-118=}43.75$; P<0.001; % of explained variability=37.5) and seasons ($F_{7-118=}26.29$; P<0.001; % of explained variability=39.5). Bicarbonate and potassium concentration exhibited higher variations

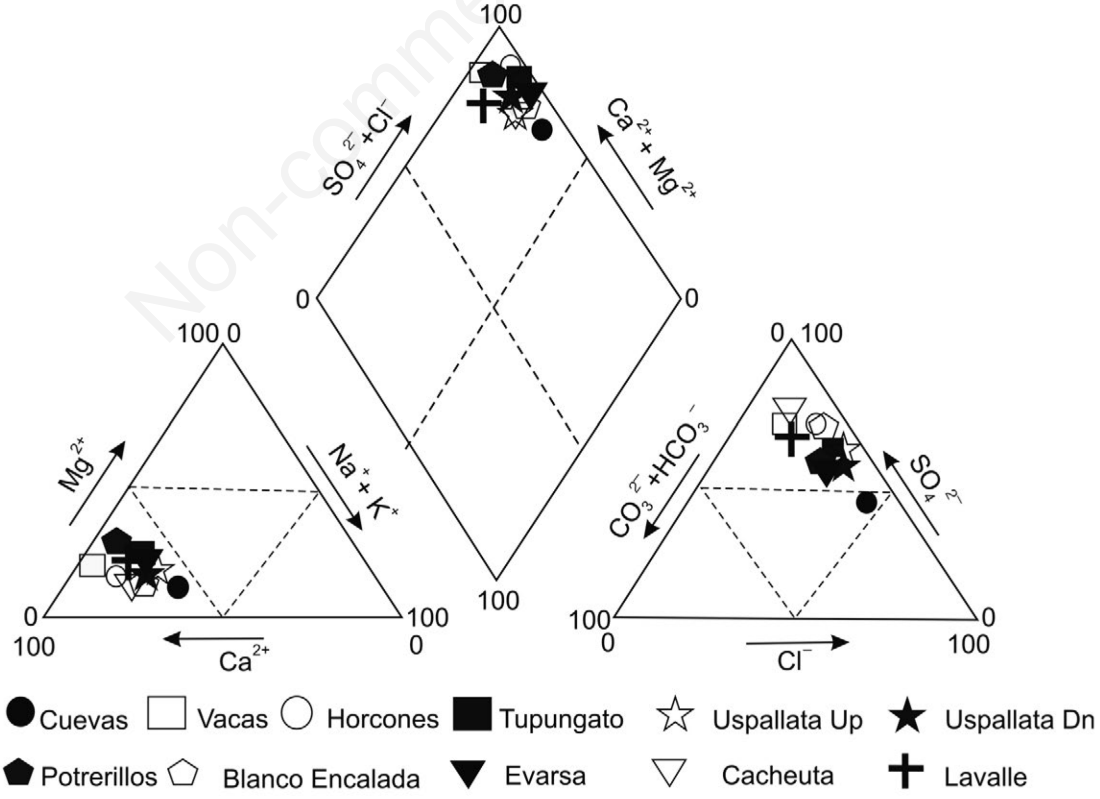

Fig. 4. Ternary diagram for surface water anions and cations. All seasonal data for the 11 sites for both sampling years (2000-2002). Proportions are based on data in $mg\ L^{-1}$.

Tab. 1. Mean values and ranges (in parentheses) of environmental variables for the 11 sampling sites in Mendoza River basin.

	CU	HO	TU	VA	UU	LU	EV	PO	CA	BE	LA
Current speed ($m\ s^{-1}$)	0.72 (0.91-0.55)	0.92 (1.47-0.44)	0.78 (1.06-0.56)	0.99 (1.49-0.69)	0.81 (1.14-0.55)	0.52 (0.91-0.31)	0.67 (1.55-0.45)	0,77 (1.46-0.32)	0.78 (1.41-0.39)	0.95 (1.81-0.48)	0.42 (1.2-0.14)
Depth (m)	0.21 (0.28-0.07)	0.15 (0.25-0.06)	0.28 (0.7-0.06)	0.22 (0.4-0.1)	0.23 (0.45-0.09)	0.32 (1.30-0.09)	0.24 (0.35-0.15)	0.22 (0.4-0.1)	0.18 (0.25-0.08)	0.13 (0.3-0.07)	0.31 (1.2-0.06)
Transparency (m)	0.12 (0.28-0.02)	0.10 (0.25-0.02)	0.17 (0.33-0.04)	0.13 (0.20-0.03)	0.12 (0.31-0.02)	0.16 (0.36-0.01)	0.13 (0.29-0.01)	0.14 (0.4-0.02)	0.13 (0.25-0.01)	0.1 (0.3-0.01)	0.1 (0.21-0.01)
Water temp. (ºC)	5.35 (10-2)	5.44 (11.1-1.9)	7.17 (12.3-2.4)	8.90 (14.1-4.8)	9.06 (14.7-2)	8.76 (14.5-4.5)	9.1 (15.3-4.6)	9.72 (14.4-5.6)	11.25 (16.1-6.2)	11.97 (16.4-6.6)	15.61 (25.4-7.9)
Air temp. (ºC)	12.00 (24-3)	14.00 (29-4)	15.00 (27-2)	15.00 (30-7.6)	16.67 (34-5.4)	13.51 (23-2.3)	15.74 (28.5-5)	15.7 (31.8-4)	17.6 (28.5-7)	20.11 (36-6.4)	21.12 (32.8-10.7)
pH	7.70 (8.8-6.61)	8.11 (8.8-7.18)	8.27 (9.2-7.5)	8.30 (9.3-7.04)	8.36 (9.5-7.09)	8.20 (9.2-6.85)	8.3 (9.3-7.32)	8.3 (9.3-6.94)	8.33 (9.6-7.39)	8.4 (9.5-7.4)	8.52 (10.2-7.64)
Conductivity ($\mu S\ cm^{-1}$)	1556 (2110-950)	1551 (1939-1124)	967 (1174-742)	549 (620-445)	954 (1237-672)	882 (1059-640)	851 (1054-621)	836.4 (1043-621)	833 (1057-364)	851 (1022-642)	1696 (5290-713)
Ca^{+2} ($mg\ L^{-1}$)	186.50 (240-148)	199.55 (270-86.4)	127.75 (154-88)	79.45 (88-50)	127 (150-100)	123 (156-90)	123 (142-106)	124.25 (146-100)	119 (136-100)	109.2 (130-80)	175.6 (260-114)
Mg^{+2} ($mg\ L^{-1}$)	27.51 (42.6-19.45)	33.21 (39.5-24.3)	21.70 (30.4-12.2)	14.40 (18.2-12.2)	20.67 (32.83-12.16)	19.07 (25.53-9.73)	19 (24.3-8.51)	17.8 (22.8-12.2)	20.8 (35.3-12.16)	23 (33-8.51)	33.5 (60.8-14.59)
Na^{+1} ($mg\ L^{-1}$)	64 (143-5.5)	49 (105.2-23)	21 (37-3.2)	16 (23-4.14)	28.12 (52.9-8.74)	23.72 (41.4-2.3)	29.1 (48.3-6.21)	33 (47-20)	25 (40.25-11.5)	26 (41.4-2.76)	47 (117.3-9.43)
K^{+1} ($mg.L^{-1}$)	4.01 (4.3-3.91)	3.66 (3.91-3.52)	3.62 (3.91-3.13)	3.52 (4.3-1.95)	3.37 (3.91-2.24)	3.42 (4.3-1.56)	3.96 (7.82-1.56)	3.47 (4.3-0.8)	3.66 (3.91-3.12)	3.86 (3.91-3.52)	3.86 (4.3-3.51)
HCO_3^{-2} ($mg\ L^{-1}$)	150 (220-91)	146 (183-85)	107 (171-61)	116 (171-49)	115.14 (183-48.8)	130.38 (176.9-61)	119.71 (171-73.2)	137.52 (195.2-73.2)	123.52 (159-73)	125 (171-49)	169.27 (293-110)
Cl^{-1} ($mg.L^{-1}$)	176 (319-50)	97 (142-60.35)	103 (195-39)	29 (46-14)	89.19 (145.55-42.6)	84.31 (106.5-39.05)	77.2 (106-35)	67.4 (102.9-35.5)	85.6 (106.5-53.25)	83 142-43	133 (213-43)
SO_4^{-2} ($mg\ L^{-1}$)	338 (576-78)	467 (641-268)	221 (338-119)	155 (197-86)	238.14 (329.3-185.7)	207.12 (290-163)	236 (340-100.3)	241 (380-113.3)	210 (309.12-120)	216 (312-93)	343.32 (653-212)
T. hardness ($mg\ L^{-1}$)	526 (775-47)	595 (825-36)	367 (490-37)	227 (280-27)	402.5 (490-34.5)	347 (490-34.5)	347 (450-33)	350 (430-30)	346 (485-32)	328 (425-34)	538 (900-34.5)
Total dissolved ions ($mg\ L^{-1}$)	945 (1446-667)	996 (1305-665)	605 (736-487)	414 (455-345)	625.05 (774.42-456)	587 (722-444)	607.52 (732.3-442)	625 (719-482)	588 (671-473)	586 (680-451)	905 1382-506

CU, Cuevas River; HO, Horcones River; TU, Tupungato River; VA, Vacas River; UU, Upper Uspallata; LU, Lower Uspallata; EV, Evarsa; PO, Potrerillos; CA, Cacheuta; BE, Blanco Encalada; LA, Lavalle.

between seasons (HCO_3^{-1}=$F_{7\text{-}259=}$35.66, P<0.001, % of explained variability=43; and K^+=$F_{7\text{-}259=}$19.11, P<0.001, % of explained variability=33) than among sampling sites (HCO_3^{-1}=$F_{10\text{-}259=}$7.97, P<0.001, % of explained variability=14; and K^+=$F_{10\text{-}259=}$3.18, P<0.001, % of explained variability=8). The dominant substrate was preferably composed of small blocks, cobbles, pebbles and sand-silt, except for LA where it was composed of sand and silt (Tab. 2). Stream order varied between 2 (HO) and 5 (UU, LU, EV, PO, CA and BE). The Cuevas and Vacas Rivers were of Strahler order 3 and the Tupungato River of Strahler order 4. Tab. 1 shows the mean bi-annual values for the environmental variables measured.

Macroinvertebrate assemblage compositions

From the analysis of 264 Surber samples, after the two consecutive year effort, a total of 20,906 specimens of aquatic insects were found, grouped into 20 families corresponding to five orders (Plecoptera, Ephemeroptera, Trichoptera, Coleoptera, and Diptera). Fifteen families were common throughout both sampling years, the five non-common families for both sampling periods were, during the 2000-2001 annual cycle: Dolichopodidae and Tabanidae; during the 2001-2002 annual cycle: Tipulidae, Stratiomyidae, and Hydrophilidae.

From the bi-annual analysis it was found that the order Diptera (total bi-annual density: 184,076 ind. m^{-2}) was represented by 12 families. Chironomidae presented high densities at all sampling sites, exhibiting total relative abundances ranging from 77 to 97%, followed by Empididae (total relative abundance: 2.54%), Simuliidae (2%), Blephariceridae (1.1%), and Muscidae (0.5%), with the remaining Diptera families showing total relative abundances below 0.14%. Trichoptera were represented by three families (total bi-annual density: 30,500 ind. m^{-2}): Hydropsychidae (85%), Hydrobiosidae (12%) and Hydroptilidae (3%). Ephemeroptera (13,865 ind. m^{-2}) were composed of two families: Leptophlebiidae (5.4%) and Baetidae (94.6%). Coleoptera (6,176 ind. m^{-2}) presented two families: Elmidae (99.82%), and Hydrophilidae (0.18%). Plecoptera were represented only by the family Gripopterygidae, showing a total density of 121 ind. m^{-2}.

Community structure: density and richness

From the analysis of the macroinvertebrate community structure (without Chironomidae family), it was observed that total density, as well as taxonomic richness, showed significant differences among sampling sites (total density: $F_{10\text{-}259=}$50.87; P<0.001; % of explained variability=42.01; richness: $\chi^2_{10\text{-}259=}$26.03, P<0.001, % of explained variability=48.46), seasons (total density: $F_{7\text{-}259=}$33.65; P<0.001; % of explained variability=19.45; richness: $\chi^2_{7\text{-}259=}$6.35, P<0.001, % of explained variabil-

Tab. 2. Mean values and ranges (in parentheses) of inorganic substrate proportion for the 11 sampling sites in Mendoza River basin.

Inorganic substratum (%)	CU	HO	TU	VA	UU	LU	EV	PO	CA	BE	LA
Big block	0.13 (0-1)	5.45 (0-100)	11.39 (0-50)	7.17 (0-30)	-	-	0.6 (0-5)	-	1.88 (0-5)	-	-
Median block	0.63 (0-5)	3.64 (0-10)	12.17 (5-20)	3.04 (0-10)	5.68 (0-25)	-	6.2 (5-10)	-	5 (0-10)	-	-
Small block	10.63 (0-40)	15 (5-35)	23.91 (15-50)	5 (0-10)	12.5 (0-35)	12.5 (0-30)	13.20 (0-30)	15 (0-35)	18.75 (10-35)	5.40 (0-30)	-
Pebble	36.88 (0-80)	16.14 (5-30)	12.61 (10-20)	17.39 (10-30)	39.77 (20-50)	35 (30-40)	38.60 (25-50)	43.75 (35-60)	26.25 (10-40)	41.6 (20-50)	-
Cobble	23.13 (0-50)	29.09 (10-40)	16.17 (0-30)	32.39 (0-50)	21.82 (0-40)	30.63 (20-40)	15.2 (5-40)	27.5 (15-40)	27.5 (20-50)	42.4 (30-70)	-
Gravel	5 (0-15)	21.27 (0-45)	9.04 (0-20)	13.91 (0-30)	5.91 (0-25)	3.75 (0-10)	-	-	0.63 (0-5)	0.6 (0-5)	-
Sand-silt	16.25 (0-40)	12.95 (5-25)	14.7 (4-20)	22.83 (15-35)	15.68 (10-35)	18.13 (10-35)	21.40 (0-40)	13.75 (10-20)	20.63 (5-30)	8.8 (0-15)	100 (100-100)

CU, Cuevas River; HO, Horcones River; TU, Tupungato River; VA, Vacas River; UU, Upper Uspallata; LU, Lower Uspallata; EV, Evarsa; PO, Potrerillos; CA, Cacheuta; BE, Blanco Encalada; LA, Lavalle.

ity=8.27) and interaction between them (total density: $F_{70-259=}$4.21; P<0.001; % of explained variability=24.32; richness: $\chi^2_{70-259=}$1.59, P=0.001, % of explained variability=20.72). Sampling site was the factor that best explained variability in richness and total density deviance.

Fig. 2 shows the seasonal and spatial variation in averages of total macroinvertebrate density. Over the two annual sampling cycles, total density of the aquatic insect community followed the same pattern, it increased in autumn, reached its highest level in winter, and decreased toward spring until becoming almost nonexistent in summer. LU recorded maximum total density in both sampling periods. Taxon richness exhibited a similar pattern to that of total density, with autumn and winter being the seasons with highest taxonomic richness. Richness increased from the headwaters toward the lower basin, with the lower basin showing the highest taxonomic richness. The mouth presented the lowest taxonomic richness (Fig. 3).

Spatial and temporal density analysis of macroinvertebrates

For all five orders, the highest percentages of variation were observed among sampling sites (Tab. 3). The Leptophlebiidae, with the genus *Massartellopsis*, presented maximum abundance at TU and VA, showing maximum density at VA in winter 2000 (111 ind. m^{-2}) and spring 2001 (88 ind m^{-2}), and at TU in autumn 2001 (78 ind m^{-2}) and summer 2001 (77 ind. m^{-2}). The family Baetidae was represented by two genera: *Andesiops* and *Baetodes*. *Andesiops* was dominant in the headwaters at CU and TU, with spring 2000 (CU: 1,188 ind. m^{-2}, TU: 1,511 ind. m^{-2}) and winter 2001 (CU: 1,267 ind. m^{-2}) being the seasons exhibiting highest density. *Baetodes* presented maximum density at BE (autumn 2000: 889 ind. m^{-2}, spring 2001: 733 ind. m^{-2}) and LU (summer 2002: 633 ind. m^{-2}). The family Hydrobiosidae (*Cailloma lucidula* Ulmer) was predominant in the middle section of the river (UU: 366 ind. m^{-2} spring 2001, LU: 444 ind. m^{-2} winter 2000) and at the system's headwaters (TU: 243 ind. m^{-2} winter 2000 and 144 ind. m^{-2} spring 2000; VA: 166 ind. m^{-2} winter 2000). Hydropsychidae (*Smicridea murina* MacLachlan) showed maximum densities in the lower section: BE was the site where they were more predominant (autumn 2000: 3166 ind. m^{-2}; winter 2000: 4,311 ind. m^{-2}), followed respectively by PO and EV (winter 2001: 3844 and 1799 ind. m^{-2}). Elmidae (*Austrelmis*) were dominant in the middle and lower sections, specifically at UU (winter 2000: 366 ind. m^{-2}), LU (winter 2000: 477 ind. m^{-2}), PO (autumn and winter 2000: 409 and 300 ind. m^{-2} respectively) and BE (autumn and winter 2000: 466 and 766 ind. m^{-2} correspondingly). Chironomidae predominated at UU, LU, EV and PO, showing maximum total densities (> 40,000 ind. m^{-2}) in the winter of both sampling periods. Blephariceridae had maximum abundance at CU (spring 2000: 222 ind. m^{-2}), followed with lower density by TU (spring 2000: 166 ind. m^{-2}) and UU (autumn 2000: 122 ind. m^{-2}). Simuliidae showed maximum abundances at TU (summer 2001: 366 ind. m^{-2}), UU (spring 2000: 244 ind. m^{-2}, autumn 2001: 221 ind. m^{-2}) and EV (winter 2001: 287 ind. m^{-2}). Empididae exhibited maximum densities during the first sampling cycle, in autumn (655 ind. m^{-2}) and winter (945 ind. m^{-2}). Tab. 4 shows the mean densities of collected aquatic insects per sampling site considering both sampling periods together.

Tab. 3. Percentage of variation in density of each order explained by each significant variable: sampling site, season and relevant interaction.

Order	SS	S	SS*S
Diptera	39.00	11.14	24.28
Trichoptera	55.68	20.63	14.13
Ephemeroptera	43.03	9.34	32.64
Coleoptera	54.49	15.54	14.48
Plecoptera	28.77	22.55	21.94

SS, sampling site; S, season.

From the study of macroinvertebrate density, it can be concluded that autumn and winter 2000, followed by winter 2001 were the seasons showing the highest taxonomic density. Notwithstanding, some taxa such as *Edwarsina*, *Andesiops*, and *Baetodes* had peaks of abundance also in spring.

Heterogeneity of benthic communities along the altitudinal gradient

From Morisita's Similarity grouping analysis it was found that the system is divided into two groupings of sites related to each other by faunal composition (Fig. 5). The first grouping comprises the headwater sampling sites grouped into two clusters; the first cluster includes VA and TU and, the second CU and HO. These two groups had a good association between sampling sites, presenting a 90% similarity. The second cluster, with an association of 79%, encompasses six sampling sites corresponding to the middle and lower sections. The sites with the highest similarity index were VA and TU (95%). LA showed no similarity to any of the sampling sites.

All sections had exclusive faunal elements. *Massartellopsis* and *Andesiops* presented a high IndVal value (92 and 96, respectively) for the headwaters, which indicates their affinity with this section, whereas *Edwarsina*, *Chelifera*, and Ceratopogonidae, despite being present in all three river sections, had IndVal values that confirm their preference for the headwaters (74, 82 and 78, respectively). The middle section (UU, LU) was a transition area where taxa from the headwaters and the lower section coexisted, with *Limnoperla* and *Euparyphus* being representative of the section, as indicated by IndVal values (60 and

Tab. 4. Mean density of taxa collected at each sampling site in both sampling periods (2000-2002).

	CU	HO	TU	VA	UU	LU	EV	PO	BE	CA	LA
Plecoptera											
Limnoperla sp.	0	0	0	0	2.50	0.46	0	0.92	0.88	0.46	0
Ephemeroptera											
Baetodes sp.	0	0	0	0	0.50	49.00	16.80	11.04	91.08	5.50	0
Andesiops sp.	184.67	12.55	140.96	25	7.50	5.54	0.44	0	0	0	0
Massartellopsis sp.	2.29	2.5	12.00	13.43	2.00	0.46	0	0	0	0	0
Trichoptera											
Cailloma lucidula Ulmer	11.00	2.00	24.96	16.78	36.23	45.25	13.20	10.08	03.08	0	0
Smicridea murina MacLachlan	0	0	0	0	13.59	56.29	139.04	380.88	454.56	9.67	0
Metrichia neotropicalis Schmid	0.92	0.50	0.48	0	0.50	16.8	4.84	7.33	3.96	0	0
Coleoptera											
Austrelmis	0	0	0.48	0.48	46.32	61.79	16.32	60.88	66.48	4.58	0
Berosus sp.	0	0	0	0	0	0	0	0	0	0	0.46
Diptera											
Atherix sp. Walker	0	0	0.48	0	0	0	0	0	0.88	0	0
Edwarsina sp.	25.33	7.00	15.83	15.87	10.05	5.04	1.76	1.83	2.20	1.83	0
Ceratopogonidae	0.46	0.50	0.48	7.26	0.50	0	0	0.46	0.44	1.38	0
Chironomidae	272.08	48.68	565.78	529.13	1126.95	2283.83	861.44	808.29	365.52	301.67	102.96
Dolichopodidae	0	0	0	0	0	9.92	0	6.46	0.44	0	0
Chelifera sp.	0.46	1	16.30	95.13	7.00	10.63	1.32	1.38	2.64	0.92	0
Hemerodromia sp.	0.46	0.50	8.17	17.78	7.05	15.21	5.28	1.83	3.08	4.58	0
Empididae sp.	0	0	0	0	0	0	0	0	0.88	0	0
Ephydridae	0.46	0	0	0	0.50	0	0	0.92	1.32	0	0
Limnophora sp.	5.96	0.50	2.39	6.70	9.09	4.58	1.32	3.67	1.76	0.46	0
Muscidae sp.	0	0	0	0	0	0.92	1.32	0.92	0	0	0
Simuliidae	9.63	1.50	32.26	8.13	35.64	21.63	19.88	12.83	11.88	2.75	0
Euparyphus sp.	0	0	0	0	0	0.46	0	0	0	0	0
Tabanidae	0	0.50	0	0	0	0	0	0	0	0	0
Tipulidae	0	0	0	0	0	0	0.88	0	0	0	0

CU, Cuevas River; HO, Horcones River; TU, Tupungato River; VA, Vacas River; UU, Upper Uspallata; LU, Lower Uspallata; EV, Evarsa; PO, Potrerillos; CA, Cacheuta; BE, Blanco Encalada; LA, Lavalle.

50, respectively). *Smicridea murina* (IndVal 75) and *Baetodes* (IndVal 57) were characteristic of the lower section. *Cailloma lucidula*, Simuliidae, and *Hemerodromia* can be considered all-habitat. The genus *Austrelmis* presented very similar IndVal values for the middle (43) and lower (45) sections, so it is not possible to specify preference between both sections.

Generalised linear model analyses revealed that altitude explained between 45 and 13% of the variability in density of the following taxa along the altitudinal gradient: *Massartellopsis* (F_{10-259}=3.32; P<0.001; % of explained variability=45), Blephariceridae (F_{10-259}=14.8; p<0.001; % of explained variability=34.3), *Andesiops* (F_{10-259}=23.96; P<0.001; % of explained variability=23), *Cailloma lucidula* ($F_{10-259=}$14.8; P<0.001; % of explained variability=28.64), *Chelifera* ($F_{10-259=}$33.67; P<0.001; % of explained variability=38.55), Simuliidae (F_{10-259}=7.17; P<0.001; % of explained variability=19), *Baetodes* (F_{10-259}=14.83; P<0.001; % of explained variability=18.75), *Austrelmis* (F_{10-259}=21.31; P<0.001; % of explained variability=19) and *Smicridea murina* (F_{10-259}=20.72; P<0.001; % of explained variability=15.37). *Massartellopsis*, Blephariceridae, *Andesiops*, *Cailloma lucidula*, *Chelifera*, and Simuliidae presented higher densities at high elevations, whereas *Baetodes*, *Austrelmis*, and *Smicridea murina* showed higher densities at lower elevation sites.

Finally, it is important to mention that the filling phase of the *Potrerillos reservoir*, located in the Andean Corridor between Potrerillos and Cacheuta localities (Mendoza, Argentina), started in the second year of sampling (period 2001-2002). Although the building of the dam did not affect the faunal composition of the insect fauna collected, notable changes were observed in the densities of *Baetodes*, *Smicridea murina*, and *Austrelmis* between the two sampling years upstream and downstream of the dam (Sampling sites: EV, PO, CA and BE). Results of GLM analyses evidenced significant differences (P<0.001) among sampling sites and seasons for the genera *Baetodes* (% of explained variability per sampling site=40.85; % of explained variability per season=27.17), *Smicridea murina* (% of explained variability per sampling site=46.29; % of explained variability by seasons=26.65) and *Austrelmis* (% of explained variability per sampling site=45.25; % of explained variability per season=3.35), with major spatial differences being observed. Although *Baetodes* had similar total densities over the two sampling periods, its maximum density was recorded at BE in the spring of 2001 while it was absent in the spring of 2000, and the same happened in the winter of 2001 at Evarsa and in the spring of 2001 at Potrerillos. *Smicridea murina* displayed a similar pattern to that of *Baetodes*, and although they had similar total abundances in the two sam-

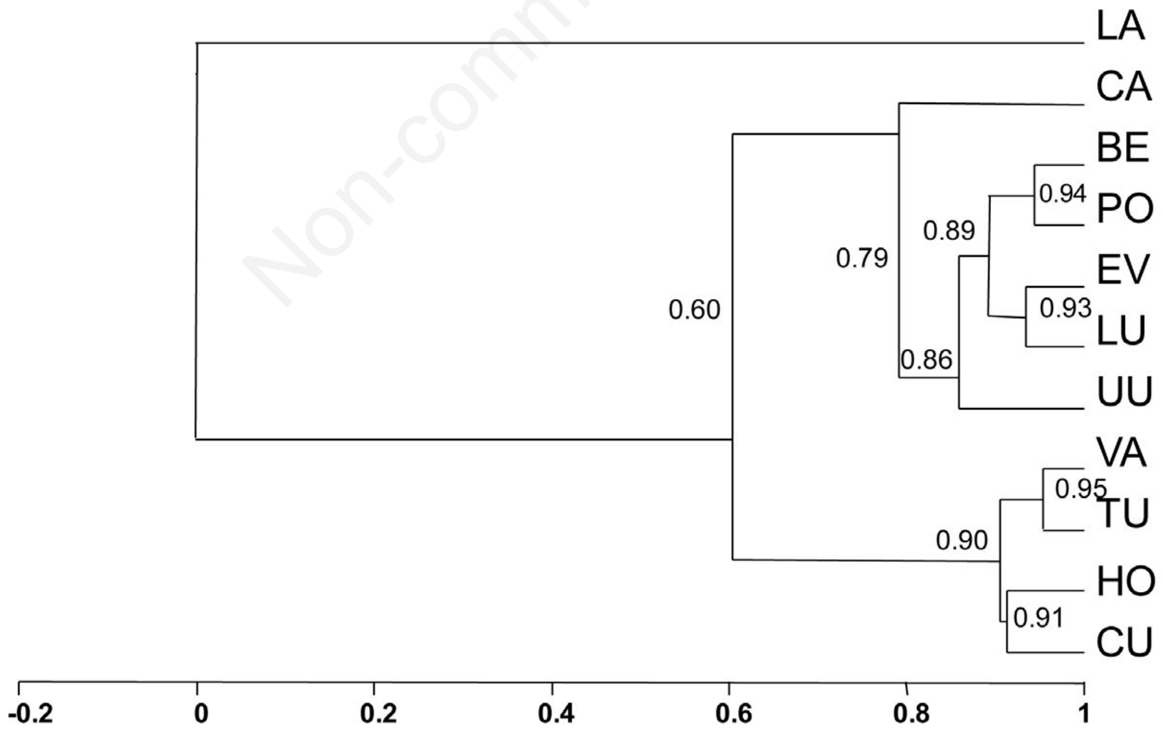

Fig. 5. Modified Morisita's Cluster showing similarity between benthic communities along the Mendoza River basin. CU, Cuevas River; HO, Horcones River; TU, Tupungato River; VA, Vacas River; UU, upper Uspallata; LU, lower Uspallata; EV, Evarsa; PO, Potrerillos; CA, Cacheuta; BE, Blanco Encalada; LA, Lavalle.

pling years, high densities were recorded in the winter of 2001 at EV and PO, tripling and almost quadrupling the values obtained for the same season in the previous period (2000-2001). *Austrelmis* showed higher total abundances during the first sampling period, its densities declining towards the second sampling cycle.

Macroinvertebrate relationships with physical-chemical variables

From the GLM analysis performed between taxa and environmental variables, it was found that the variables that had a greater influence on the variation in density of most taxa were: transparency, bicarbonate concentration, pH and substrate. Each type of substrate explained, to varying degrees, the changes occurred in the density of taxa; gravel was the substrate that best explained the variation in density of *Smicridea murina* (% of explained variability=30). Environmental variables explained between 78-51% of the deviance in *Austrelmis*, *Smicridea murina*, *Andesiops*, *Chelifera*, and *Baetodes*, whereas for Simuliidae, *Edwarsina*, *Cailloma lucidula*, *Massartellopsis*, *Metrichia neotropicalis*, and *Limnophora* it was physical-chemical variables that explained between 15-34% of the deviance of each taxon (Tabs. 5 and 6).

Discharge significantly affected distribution of *Andesiops* ($F_{1\text{-}118}$=84.04; P<0.001; % of explained variability=14.23), *Cailloma lucidula* ($F_{1\text{-}118}$=31.75; P<0.001; % of explained variability=13), Blephariceridae ($F_{1\text{-}118}$=17.54; P<0.001; % of explained variability=8.7), and *Massartellopsis* ($F_{1\text{-}118}$=62.43; P=0.013; % of explained variability=2.7). Also flow-caused variations in total abundance and richness were recorded, accounting respectively for 13.4% and 16.1% of the total deviance. Taxonomic richness was affected by most of the physical-chemical variables (except big block, medium block and conductivity). Environmental variables accounted for 45% of total richness deviance (Tabs. 5 and 6).

Inter-annual differences

Only environmental variables experienced significant inter-annual differences. The physical-chemical variables that showed significant differences were: pH (Value of U:

Tab. 5. Proportion of variation in density by taxon, variation in richness accounted for by each physical chemical parameter (P≤0.05).

Biotic variables	C	T	pH	V	HCO_3^-	K^+
Massartellopsis	6.24	-	-	-	-	2.89
Andesiops	4.49	13.40	13	-	-	-
Baetodes	2.79	-	1.37	2.18	8.12	-
Cailloma lucidula	-	9.24	1.83	1.25	7	4.71
Smicridea murina	1.01	6.60	4.48	-	4.60	-
Metrichia neotropicalis	-	10.30	2.21	3.75	-	-
Austrelmis	-	5.93	3.20	0.70	7.70	-
Blephariceridae	2.40	-	7.60	-	-	-
Chelifera	13.20	7.34	-	0.74	13.26	12.02
Simuliidae	2.60	2.14	-	-	2.18	1.70
Limnophora	-	5.13	-	-	-	-
Richness	-	5.16	1.90	1.41	3.42	1.43

C, conductivity; T, transparency; V, velocity; HCO_3^{-2}, bicarbonate; K^+, potassium.

Tab. 6. Proportion of variation in biotic variables (taxon density, richness and diversity) explained by each type of substrate (P≤0.05).

Biotic variables	BB	MB	SB	P	C	G	SS
Massartellopsis	6.87	2.67	-	-	-	3.36	4.20
Andesiops	4.21	5.41	-	2.50	-	-	9.89
Baetodes	6.48	8	10	4.42	1.59	8.25	-
Cailloma lucidula	1.39	-	1.22	3.28	-	-	2
Smicridea murina	7	6.12	-	6.48	0.9	30	0.82
Metrichia neotropicalis	0	4.71	3.70	3.38	-	4.06	-
Austrelmis	12.08	1.68	-	8.21	2.08	8.58	7.31
Blephariceridae	-	-	1.58	-	1.98	-	-
Chelifera	7.23	-	2.38	1.52	1.07	-	1.44
Simuliidae	-	-	-	6.92	-	-	-
Limnophora	3.34	-	-	4.96	1.93	-	8.34
Richness	-	-	1.20	20.82	3	2.20	2.59

BB, Big block; MB, median block; SB, small block; P, pebble; C, cobble; G, gravel; SS, sand-silt.

4141.5; P<0.001), current speed (Value of U: 4996.5; P <0.001), transparency (Value of U: 7090.5; P=0.025), depth (Value of U: 6987; P=0.016), magnesium concentration (Value of U: 7279.5; P=0.054), bicarbonate concentration (Value of U: 6213; P<0.001), chloride concentration (Value of U: 6353.5; P<0.001), big block (Value of U: 6006; P<0.001), boulder (Value of U: 6352; P<0.001) and gravel (Value of U: 5795; P<0.001).

DISCUSSION

In the present study, the orders showing higher richness and abundance were Diptera, Trichoptera, Ephemeroptera and Coleoptera, with dipterans composing 78% of the benthic community. In Patagonian rivers located at high altitudes and latitudes, dipterans are the group of aquatic insects with the highest specific richness and greatest predominance (Miserendino and Pizzolón, 2000), and in a glacier-fed alpine stream 65% of the invertebrate community is represented by Chironomids (Knispel and Castella, 2003), which is consistent with findings for the Mendoza River. However, in several mountain streams there is a higher contribution of the taxonomic richness of the orders Plecoptera, Ephemeroptera, and Trichoptera to the benthic community (Maiolini and Lencioni, 2001; Figueroa *et al.*, 2003; Miserendino and Pizzolon, 2003), and overall higher invertebrate richness (Finn and Poff, 2005; Bogan and Lytle, 2007; Brown *et al.*, 2007). Nevertheless, in the Uspallata stream, a tributary of the Mendoza River, it was found that Diptera and Ephemeroptera compose 60% of the benthic community, with low diversity of the orders Plecoptera, Trichoptera, and Coleoptera (Scheibler and Debandi, 2008).

Altitude was the major factor determining macroinvertebrate assemblages along the large arid Mendoza River and explained the maximum taxon deviance, such as occurs in Patagonian rivers (Miserendino and Pizzolón, 2000, 2003; Miserendino, 2009) and Alpine streams (Finn and Poff, 2005) where faunal composition was determined mainly by altitude. There was turnover in taxon spatial distribution and in faunal composition of aquatic insects at the different sections of the river basin (upper, middle and lower sections) as predicted by the theory of longitudinal zonation (Ward, 1989), albeit a 60 percent similarity in faunal composition occurred among sampling sites corresponding to the lotic system according to results obtained from the grouping analysis. Studies conducted in the Rocky Mountain streams of Colorado (USA) found species turnover along the longitudinal gradient and a negative relationship between altitude and taxonomic richness (Finn and Poff, 2005), such as was observed in this system.

About the turnover of taxa along the longitudinal gradient of the watershed studied, we can conclude that: *Andesiops* was associated with *Massartellopsis*, a genus exclusive to the headwaters that presented low densities; both genera are very sensitive to changes in environmental conditions (Fernández and Domínguez, 2001; Figueroa *et al.*, 2003). From LU up to BE, *Andesiops* and *Massartellopsis* were replaced by *Baetodes*, a genus that has a wide temperature range (Ramírez *et al.*, 2004). Temperature and altitude are two major factors determining distribution of mayflies (Domínguez and Ballesteros Valdez, 1992). CU, HO, TU sites (headwaters) of the Mendoza River were at the highest altitudes (2835-2425 m). and recorded the lowest temperature values (1.9-2.4 °C). Our results confirm a great influence of altitude on the density of mayflies, so it could be predicted that this variable might play a major role in the turnover of the Ephemeroptera genera in our study. *Edwarsina* (Blephariceridae) was found to have higher density in the headwaters of the Mendoza River, coinciding with the presence of this family in upper reaches of Andean-Patagonian streams (Miserendino and Pizzolón, 2000). The habitat found in the headwaters meets the environmental requirements for survival of Blephariceridae larvae: clean oxygenated running waters (Winterbourn, 1981), beneath facets of smooth surface rocks or boulders, free of embedded sedimentary material; their distribution is limited to hills of mountain regions. Empididae had their maximum abundance at VA whereas Simuliidae exhibited maximum densities at TU and on sites located in the middle section. Both families were found in upper reaches of mountain systems, not very far from the glacial source of these systems (Maiolini and Lencioni, 2001). Nevertheless, the Simuliidae were present at 10 sampling sites along the Mendoza River. Simuliidae larvae choose sites with nonstop and swift water flow, stony substrates free of algae and mud that allow them to anchor, and clear and well oxygenated waters with good turbulence (Coscarón Arias, 2001), all of which conditions occur along the Mendoza River (except LA sites). *Smicridea murina* was the most abundant Trichoptera species found in the Mendoza River basin. It was recorded at UU (middle section) and its relative abundance began to grow until reaching its peak in the lower section of the river (PO, CA and BE). The genus *Smicridea* was the most abundant taxon in Patagonian plateau and mountains (Miserendino and Pizzolón, 2000). The family Hydropsychidae characterises the higher-order reaches of Andean rivers in Patagonia (Miserendino, 2009). In streams of semiarid environments, *Smicridea* have great abundance and it has been observed that distribution of hydropsychids is generalised and can be related to an increase in fine particulate organic matter (Vallania *et al.*, 1998). Hydropsychids are an important family of Trichoptera that inhabit running waters in most part of the world. They are extremely important to the ecology of running water systems because of their ubiquitous appearance, abundance and large biomass. The genus *Austrelmis* was present in the middle and lower sections, as well as *Smicridea murina*.

Elmids are the only coleopterans present in torrential streams because they extract dissolved oxygen from water with their gills, the plastron; therefore they inhabit environments with oxygenated water and rocky substrate, with their life cycle being totally aquatic (Archangelsky, *personal communication*). The family Chironomidae exhibited high densities at all sampling sites. Immature stages (larvae and pupae) are an important link in the ecology of benthic communities in most natural and artificial water bodies, in either surface or deep, running or stagnant waters, over broad areas or in small reservoirs (Coffman and Ferrington, 1996). Plecopterans showed low frequency of appearance, density and genus richness in the present study. Factors primarily affecting the spatial distribution of Plecoptera larvae are: altitude, river order and human influence (Bispo *et al.*, 2002). The very low density and sporadic frequency of plecopterans found in the Mendoza River could be due to the contribution by the drift of its tributaries located between Uspallata and Potrerillos localities, for their presence, abundance and richness is very conspicuous in the lower-order streams surrounding the area (Scheibler, 2007). Plecopterans added to the mainstream come from the contribution of its associated riparian environments, environments that constitute the lateral dimension of the river system (Ward and Standford, 1991).

In the Mendoza River basin there were significant spatial-temporal and inter-annual variations in environmental variables. Seasonality generated greater differences in pH, potassium and bicarbonate concentration, and transparency; whereas spatial differences were more marked for conductivity, discharge and velocity. Temporal and spatial variations are distinctive of running waters (Burgherr and Ward, 2001; Maiolini and Lencioni, 2001; Bradley *et al.*, 2002). Temporal variability depends on regional factors like climate (Richards *et al.*, 1997) which involves variables such as water temperature, discharge and flow pattern (Hawkins *et al.*, 1997). Water flow markedly increased toward the summer period as a result of the melting of snow and glaciers, significantly affecting macroinvertebrate richness and total abundance. Significant seasonal differences in water flow due to melting of the snow of mountain glaciers certainly cause differences in physical-chemical parameters between seasons (Peralta and Claps, 2001; Füreder, 2005; Bogan and Lytle, 2007); as well, streams in different types of environments: neotropical, tropical, arid and mountain environments, undergo highly seasonal changes in biotic (benthic assemblage composition and richness) and abiotic conditions due to flow variations (Burgherr and Ward, 2001; Miserendino and Pizzolón, 2003; Füreder, 2005; Bogan and Lythle, 2007; Scheibler and Debandi, 2008). Despite this, variations in taxon richness were largely affected by spatial heterogeneity and, in a lower proportion, by temporal variations, such as our results confirmed (sampling site was the factor that most explained variability in richness and total density deviance). However, maximum macroinvertebrate densities and taxonomic richness were recorded in the seasons of autumn and winter, indicating that these periods could provide better conditions for survival of invertebrates than spring and summer when snow and glacier melting occurs. During winter and autumn there were favourable environmental conditions for development of macroinvertebrate communities such as: greater transparency, lower water temperature, lower water flow and current speed, and consequently higher substrate stability, the same as found for other mountain river systems of glacial origin (Brittain and Milner, 2001; Burgherr and Ward, 2001). Towards the summer, when water flow increased as a result of spring ice melting, transparency diminished because of increased suspended solids (maximum 1,400 mg L^{-1}) (Scheibler, 2007) and a notable reduction was recorded in invertebrate density and richness.

Considering the results obtained from the GLM analyses applied, the physical-chemical variables significantly affecting aquatic insect distribution were: type of substrate, transparency, bicarbonate concentration, total hardness, current velocity and pH. Conductivity affected only some taxa (mayflies, *Smicridea murina*, some Diptera), while not altering richness. Conductivity did not affect the presence of ephemeropterans along the Mendoza River, in contrast to what was reported for Patagonian Andean streams where conductivities of 500 $\mu\text{S cm}^{-1}$ represented a saline barrier for ephemeropterans and plecopterans, which were absent under these conditions (Miserendino and Pizzolón, 2000). In lotic systems of temperate regions it has been found that variation in species richness of aquatic insects along an altitudinal gradient could be related to the temperature range shown by the different river reaches (Miserendino and Pizzolón, 2000). In the Mendoza River, the broadest temperature range was found in the middle and lower sections, and these conditions were associated to the highest taxonomic richness recorded. However, in our region, water temperature measurements should be done periodically to understand whether this variable really affects richness variations and distribution of the species. In addition, in the lotic system studied, variation in macroinvertebrate richness was affected primarily by substrate. The environmental heterogeneity generated by the combination of gravel, cobble, pebble, and boulder, along with the roughness and texture of the substrate surface, contributes to increasing macroinvertebrate diversity and abundance, contrasting with substrates composed of sand that reduce detritus retention and oxygen availability (Allan and Castillo, 2007), causing decreased invertebrate richness, as occurred at the mouth of the aquatic system studied. Moreover, diverse substrate composition benefits many taxa for it increases permeability of the hyporheos region, which allows water to flow and contributes to the transport of gases and nutrients that are important to survival of aquatic organisms (Allan and Castillo, 2007).

Richness increased from the headwaters towards the lower section. The highest taxonomic richness and total density was found at LU, located in the middle section of the basin, a middle-order site at mid altitude, in keeping with findings for mountain streams in the centre and south of Argentina (Corigliano *et al.*, 1996; Miserendino, 2009). Identifying areas with high species richness is very important from a biodiversity perspective because they act as species reservoirs for rehabilitation of systems degraded by human impacts (Bradley *et al.*, 2002) and these high richness areas constitute perfect systems to detect global climate change trends toward the future .The lowest taxonomic richness was recorded at LA; this site, which lies downstream of Cipoletti dam, showed a fluctuating flow dynamics with dry periods depending on the dam's activity and a dominant substrate composed of sand, where the highest conductivity values (5290 µS cm^{-1}) were recorded, and is an area with intensive agricultural activities. It is known that dams have detrimental effects on rivers and their aquatic biota because they alter water quality, habitat and assemblage composition (Allan and Castillo, 2007) which, added to land use, cause LA to be the poorest site in terms of faunal composition and subjected to great changes in environmental variables.

The increase in faunal richness towards the middle and lower sections of the river could be explained by the contribution of better quality waters (lower salinity) by the tributaries that flow between both sections and also by the increase in habitat heterogeneity (increased organic matter and sediments) afforded by said tributaries, as attributed by Knispel and Castella (2003) in glacier-fed streams. The Mendoza River was characterised as being a system with riffles and whirlpools in the headwaters, middle and lower sections, whereas depositional areas were located at LA. Some authors suggest that mountain river riffles/whirlpools have more species diversity and richness than depositional areas (Hynes, 1970; Buffagni and Comin, 2000). Low taxonomic richness was detected in the studied system for the orders Ephemeroptera, Trichoptera and Coleoptera. The low richness recorded in the Mendoza River concurs with that recorded in the phytoplankton (Peralta and Claps, 2001). Reduced richness does not indicate lower water quality but is related to the lower number of niches afforded by the environment. This decrease affects precisely two of the groups with greater requirements for habitat quality, mayflies and caddisflies (Gualdoni and Corigliano, 1991). In addition, the dominance of certain taxonomic groups (*e.g.*, Diptera), such as occurs at the mouth of the Mendoza River, alerts us about impoverishing processes (Magurran, 1988).

The absence of riparian vegetation could be an explanatory factor of the low richness found in the system, because of its contribution to erosion control and its provision of shelter for invertebrates (Rosenberg and Resh, 1993). Another variable that could account for the low richness found in this mountain system is the absence of aquatic macrophytes. The tufts of aquatic angiosperms increase habitat heterogeneity; they provide refuge to avoid currents and protection against predation, supply building material for portable cases and act as support sites for attachment of epiphytic algae (Ward, 1992). By observation of the material obtained from the total samples studied, it can be mentioned that the building materials for the portable cases of most aquatic insects that carry their cases came from the riverbed, containing mostly gravel and sand, and that epilithic algae were attached to rocks, forming the periphyton. Peralta and Claps (2001) found that diatoms were the dominant group on most sampling sites and seasons in the Mendoza River, and that 69% of the diatoms belonged to the benthic habitat. Therefore, it could be concluded that diatoms are a major feed source for benthic invertebrates from the Mendoza River, considering the absence of riparian vegetation. One more factor that could also be related to the low richness observed is the low autochthonous production in glacier-fed streams, particularly in summer, due to highly unfavourable conditions (unstable substrate, high values of suspended solids, high discharge variations) (Füreder, 1999).

This is the first and only survey of macroinvertebrates in the Mendoza River basin, before the second reservoir, Potrerillos Dam, was built. Our results confirmed changes in density for *Smicridea murina*, *Austrelmis* and *Baetodes* due to the building of the dam, so further studies will have to be conducted upstream and downstream of the dam to analyse the effect produced by this continuum discontinuity and the intensity of human impact.

Finally, spatial and temporal studies in high mountain systems are relevant to recognise biotic fluctuations and, in consequence, to detect global climate change (Oertli *et al.,* 2008). Additionally, knowledge of the environmental requirements and distribution ranges of the species in this kind of harsh environment is useful to identify biological variations when climate changes occur, and to distinguish bioindicator species of the health status of freshwater ecosystems. Several studies have demonstrated biological (composition, distribution, phenology) variations with climate change (Hassall *et al.*, 2007; Chessman 2009). Because of this, features of individual species (like thermal tolerances, rheophily, habitat selection, among others) require to be determined to recognise those species most at risk of extinction.

CONCLUSIONS

In the Andean river studied, seasonal and altitudinal variations were detected both in environmental variables and macroinvertebrate communities such as has been reported around the world by several freshwater studies (Maiolini and Lencioni, 2001; Milner *et al.*, 2001; Jacobsen, 2004; Füreder *et al.*, 2005; Miserendino, 2009). We can conclude that this arid system was characterised by harsh environmental conditions (high discharge, highest values of conductivity, absence of riparian vegetation, hardness) for the development of aquatic insect life. Despite this, sensitive taxa like *Andesiops*, *Massartellopsis*, *Cailloma lucidula*, and *Edwarsina*, among others, (Scheibler, 2007) were found in these hard conditions. In addition, altitude was the most important factor determining macroinvertebrate assemblages along this mountain river and, to a lesser extent, type of substrate, transparency, bicarbonate concentration, total hardness, current speed, conductivity and pH. It is known that altitude is a variable that involves other spatially correlated environmental variables (Finn and Poff, 2005). We can determine two groups which are similar in macroinvertebrate assemblage composition; one group located at high elevations (headwaters) and the other group occurring at middle and lower altitudes in the river basin. We also found a transition area in the middle section of the Mendoza River basin where species of the upper and lower sections coexist. During periods of favourable conditions (autumn and winter), invertebrate density and taxon richness peaked, however, sampling site was the factor that best explained variability in richness and total density deviance. Our results confirm that benthic macroinvertebrate structure and environmental variables respond in different ways to seasonal and longitudinal variations.

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