Chironomid (Insecta: Diptera) assemblages along an Andean altitudinal gradient

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ABSTRACT: Chironomidae are an abundant, diverse and ecologically important group common in mountain streams worldwide, but their patterns of distribution have been poorly described for the Andes region in western-central Argentina. Here we examine chironomid assemblages along an altitudinal gradient in the Mendoza River basin to study how spatial and seasonal variations affect the abundance patterns of genera across a gradient of elevation, assess the effects of environmental variables on the chironomid community and to describe its diversity using rarefaction and Shannon's indices. Three replicate samples and physicochemical parameters were measured seasonally at 11 sites in 2000 and 2001. Twelve genera of chironomid larvae were identified, which belonged to 5 subfamilies. Chironomid composition changed from the headwaters to the outlet and was associated with changes in altitude, water temperature, substrate size and conductivity. We found a pronounced seasonal and spatial variation in the macroinvertebrate community and in physicochemical parameters. Environmental conditions such as elevated conductivity levels and increased river discharge occurring during the summer produced low chironomid density values at the sampling sites. The rarefaction index revealed that the sampling sites with highest richness were LU (middle section of the river) and PO (lower section). However, Shannon's diversity index indicated that LU had the lowest diversity as a consequence of the dominance of *Cricotopus* over the other genera found. We attribute the low diversity found in our aquatic system to the aridity of the sampling area, as has been demonstrated in studies of other similar lotic systems in this mountain region.

KEY WORDS: Macrobenthic invertebrates · Larvae · Mountain river · Benthos · Spatial gradients · Seasonal variations · Arid regions · Argentina

INTRODUCTION

Lotic ecosystems are highly heterogeneous in both time and space (Ward 1989), and the effects of variations in these dimensions on the dynamics and structure of aquatic communities and on the functioning of ecosystems has been extensively investigated in various freshwater environments (Burgherr & Ward 2001, Lencioni & Rossaro 2005, Finn & Poff 2005, Füreder et al. 2005). Over the longitudinal dimension, ecological conditions and assemblages of aquatic communities change (Füreder 1999), creating a gra-

dient of macroinvertebrate assemblages with respect to altitude (Milner et al. 2001). These gradients are especially pronounced in mountain stream systems.

Mountain streams are characterized by steep slopes, high turbulence, irregular beds and near-saturation levels of oxygen (Ward 1992, Füreder 1999). Their upper reaches are often undisturbed by humans, which leaves the resident ecological communities in many of these streams largely intact (Ward 1992). Consequently, mountain streams are potential reservoirs of biodiversity that may serve as indicators of large-scale perturbations such as climate change

(Kohler & Maselli 2009), atmospheric deposition of pollutants (Nodvin et al. 1995) and the spread of invasive species (Jaeger et al. 2008). Mountain streams can also exhibit distinctive environmental characteristics and flow regimes that relate to their runoff source (e.g. glacial melt, snowmelt or spring thaws; Füreder 1999, 2007, Lods-Crozet et al. 2001, Maiolini & Lencioni 2001, Milner et al. 2001). Hence high-altitude mountain streams are model systems for the study of longitudinal and seasonal patterns in benthic communities (Finn & Poff 2005).

In some mountain systems, zoobenthic communities are dominated mainly by members of Chironomidae and exhibit a great diversity in cold rivers with variations in altitude (Burgherr & Ward 2001, Lods-Crozet et al. 2001, Lencioni & Rossaro 2005). Members of the Chironomidae are distributed over a wide range of temperatures, pH, salinity, dissolved oxygen concentration, current velocity, depth, trophic state, altitude and latitude (Lindergaard & Brodersen 1995, Milner et al. 2001, Finn & Poff 2005). The chironomids have therefore been the object of extensive ecological and biogeographical studies (Brundin 1966, Ashe et al. 1987) because of their great plasticity (e.g. ecological amplitude) with respect to morphological, physiological and ethological adaptability (Coffman & Ferrington 1984).

The significant representation of the immature stages of Chironomidae within zoobenthos dynamics has prompted many research projects on their biology and taxonomy throughout the world (Wiederholm 1983, Lindergaard & Brodersen 1995, Paggi 2001, Rae 2004). The larval stage is the one most frequently recorded, usually reaching an abundance of 50 000 larvae m^{-2} (Coffman & Ferrington 1984). Nevertheless, the taxonomical identification of chironomid larvae is highly difficult because only a minimum percentage of the species has been described, and identification of the morphological characteristics is complicated (Pinder 1983).

Andean lotic systems in Argentina experience seasonal and longitudinal variations that are manifested in environmental variables (Miserendino & Pizzolon 2000, 2003, 2004, Mesa et al. 2009). In Patagonian mountain streams, seasonal fluctuations are evidenced by discharge and suspended sediment loads due to forestry and land use practices, while spatial variations show significant differences in substrate size and conductivity (Miserendino & Pizzolon 2003). Andean mountain streams are also affected by altitudinal variations (Miserendino 2009) that cause changes in the density and taxonomic richness of benthic communities along the longitudinal gradient

(Miserendino & Pizzolon 2000). There are several environmental parameters that are stressors of macroinvertebrate communities in Argentina's mountain systems, including: sudden increases in stream flow that result in peaks of abundance and richness of invertebrates during the dry season (Miserendino & Pizzolon 2000, Mesa et al. 2009, Scheibler et al. 2014); higher conductivity values, which strongly affect the presence of some macroinvertebrates (Miserendino & Pizzolon 2000) and result in changes in community assemblages along the longitudinal gradient (Scheibler & Ciocco 2011, 2013); acidic stress, which induces unfavorable effects on the community (Tripole & Corigliano 2005); and land use, a parameter that affects stream water quality and macroinvertebrate biodiversity (Miserendino et al. 2011). In Mendoza province in western-central Argentina, the diversity, ecological requirements and distribution of chironomid larvae have been previously described by Medina et al. (2008) and Scheibler et al. (2008). The present study focuses on the chironomid fauna of the Mendoza River system, and is significant in view of the scarcity of water in this region and the critical role that rivers play in providing water to the province's diverse human activities, including agriculture, energy production and manufacturing, and to the major cities.

The objectives of the study were to explore the spatial and seasonal distribution of chironomid assemblages (richness, faunistic composition and abundance) along the Mendoza River system in the Andes ridge using 2 sampling methods: (a) subsamples from 11 sites (Database 1) and (b) all data collected at 3 sites (Database 2). We also wanted to evaluate the effects of physical and chemical variables on chironomid communities (Database 1). Finally, we assessed the validity of working with subsamples by comparing results from rarefaction and Shannon's diversity indices (*H'*) using data from the 3 common sites of Databases 1 and 2.

MATERIALS AND METHODS

Study area

Mendoza province has an area of 150 839 km² and is located on the eastern border of the Andes (32° 00' to 37° 35' S, 66° 30' to 70° 35' W). The climate is continental, semi-arid to arid, with low annual rainfall (300 mm per year), intense sun radiation, daily freezing and thawing, and high summer temperatures (Corte & Espizua 1981). Spring and summer rains

originate from the Atlantic Ocean, and occur mainly along the eastern shoulder of the Andes on the potamon segment of the Mendoza River (Departamento General de Irrigación 1999). Winter snowfalls originate in the Pacific Ocean and snowmelt and glaciers provide most of the water for the streams of this region (Corte & Espizua 1981).

The basin of the Mendoza River, with an area of 18 484 km², is situated in the northwest of the province. Headwater tributaries are the Cuevas, Horcones, Tupungato and Vacas Rivers, all of which originate in the Andes. The main course of the Mendoza River, with a mean annual discharge of 50.6 m³ s⁻¹, extends for 300 km and flows into the Rosario (Guanachache) shallow lakes (Departamento General de Irrigación 1999). The Mendoza River, with its extensive headwater basin bordered by high mountains, is a typical high-altitude river containing an initial discharge area on the eastern shoulder followed by a low-velocity potamon segment near the shallow lakes (Villagra & Roig 1999).

Rivers and streams in the high Andean region show great variations in flow, with notable flow increases towards the summer (Videla & Suarez 1991). The main tributaries of the Mendoza River form in numerous high-altitude valleys and glacial cirques (around 3500–4000 m altitude), where most snowfall accumulates in winter and thaws in summer. Snowfall constitutes the largest contribution to the flow of Andean rivers (A. R. Villodas pers. comm.). Another contribution, although of lower proportions, comes from the partial melting of glaciers, which constitutes water reservoirs in years of poor snowfall (Videla & Suarez 1991). During the sampling period (2000 to 2002), snow precipitations were abundant and the major contributor of water to the basin.

Site selection

Eleven sampling sites were established along the Mendoza River system, and these spanned a range of altitudes, substrate compositions, hydrologic variables and human settlements. The river system was subdivided into 4 sections. The first 3 sections were lotic, the last was lentic. The headwater section contained the following sampling sites: the Cuevas River (CU), the Horcones River (HO), the Tupungato River (TU) and the Vacas River (VA). The sites of the second section, lying in the middle basin, were located on the upper Uspallata (UU) and lower Uspallata (LU) Rivers. The names of these segments refer to the position of the sampling sites with respect to the Uspallata River (velocity = 2 m³ s⁻¹). This river feeds water to the village of Uspallata (Scheibler & Debandi 2008). The lower basin was monitored at the following sampling sites: Evarsa (EV), Potrerillos (PO), Cacheuta (CA) and Blanco Encalada (BE). Finally, a single sampling site was established at the river's outlet (Lavalle, LA). This last site had a fluctuant discharge, with dry periods related to the unloading of the Cipoletti reservoir (Fig. 1, Table 1).
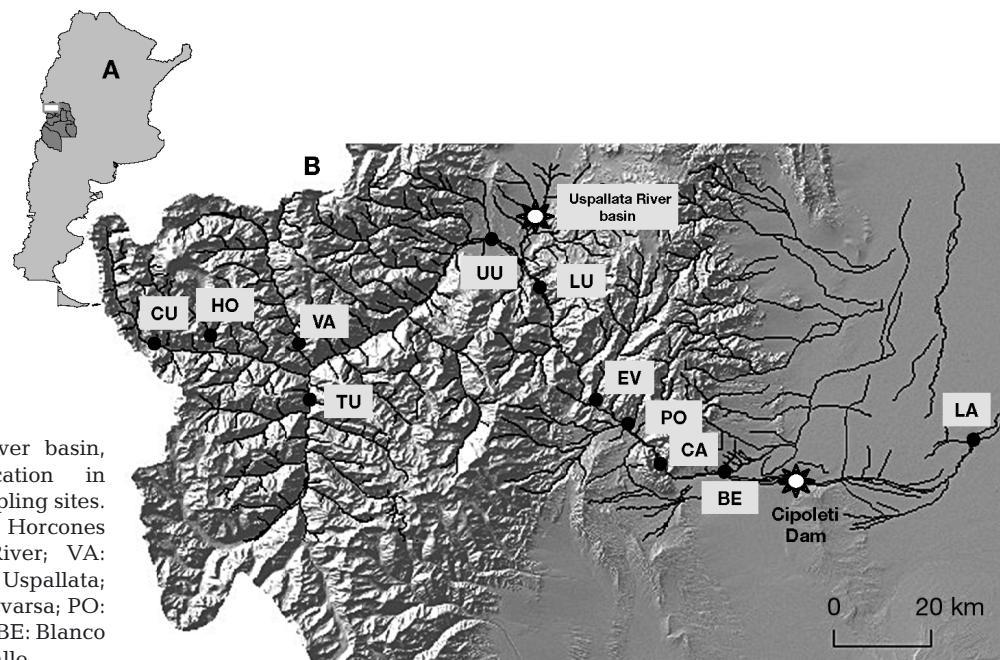

Fig. 1. The Mendoza River basin, showing (A) the location in Argentina and (B) the sampling sites. CU: Cuevas River; HO: Horcones River; TU: Tupungato River; VA: Vacas River; UU: upper Uspallata; LU: lower Uspallata; EV: Evarsa; PO: Potrerillos; CA: Cacheuta; BE: Blanco Encalada; LA: Lavalle

Table 1. Location and general characteristics of the sampling sites in the Andes, Argentina. 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. Discharge values are biannual means

	Stream order	Slope (%)	Altitude (m a.s.l.)	Latitude (S)	Longitude (W)	Location	Discharge ($m^3\ s^{-1}$)
CU	3	1.66	2835	32° 49	69° 57	Main mountain range	7.4
HO	2	24.00	2775	32° 49	69° 55	Main mountain range	–
TU	4	1.00	2447	32° 52	69° 46	Lower mountain range	24.0
VA	3	13.66	2425	32° 51	69° 45	Lower mountain range	3.4
UU	5	12.66	1846	32° 37	69° 25	Uspallata Valley	–
LU	5	1.16	1727	32° 41	69° 21	Uspallata Valley	–
EV	5	27.33	1413	32° 54	69° 14	Andes shoulder	46.8
PO	5	3.16	1355	32° 57	69° 10	Andes shoulder	–
CA	5	3.16	1235	33° 01	69° 06	Mountain foot	46.2
BE	5	1.33	1085	33° 02	69° 00	Mountain foot	–
LA	–	0.00	606	32° 45	68° 21	Plains	–

Environmental variables

The following physicochemical variables were measured for each sampling site: pH (Hanna pH Meter, HI 9025); conductivity (Hanna conductimeter HI 9033); transparency (Secchi disk); water and air temperature (mercury thermometer); water depth (graduated ruler); flow velocity (using the float method according to Gordon et al. (1994); slope (Dangavs 1995); stream order (Strahler 1957); and substratum composition, as the percent coverage of each fraction of large blocks (boulders), medium blocks, small blocks, cobbles, pebbles, gravel, sand and silt (Cummins 1992) (Table 1, see Tables A1 & A2 in the Appendix).

Water samples were collected from each sampling site and analyzed for the following chemical parameters according to APHA (1989): Ca^{+2}, Mg^{+2}, Na^+, K^+, CO_3^{-2}, HCO_3^-, Cl^-, SO_4^{-2}, total dissolved ions and total hardness. The discharge values for 5 sampling sites (CU, TU, VA, EV and CA) were obtained from the Departamento General de Irrigación of the Mendoza province (Tables 1 & A2).

Chironomid sampling and identification

Spatial and seasonal samples were obtained over 2 consecutive years (2000–2001 and 2001–2002). Triplicate samples were collected at random with a Surber sampler (300 µm pore size mesh net with an area of 0.09 m^2) near the riverbank at each site for the first 10 sampling sites. High discharge in the Mendoza River prevented the possibility of collecting samples from the middle of the channel, e.g. maxi-

mum EV discharge in summer 2001 was 119 $m^3\ s^{-1}$. A Petersen dredge (extraction area = 352 cm^2 per replicate) was used to sample the benthos at LA.

Chironomid larvae were identified by preparing permanent slides mounted in Euparal according to Paggi (2001) and voucher specimens were deposited in the Entomology Laboratory of IADIZA-CCT Mendoza, CONICET. Identifications were made to the genus level and based on criteria from Brundin (1966), Wiederholm (1983) and Paggi (2001). Identification to the genus level is the highest level of confidence existing at present in the study area (Scheibler et al. 2008, Medina et al. 2008). We have doubts about the identification of *Paralimnophyes* as the larvae are similar to *Limnophyes* larvae. Pupae or exuviae pupae are required to confirm genus identification. In addition, one of the genera found in the study area, belonging to the subfamily Orthocladiinae, was named Genus 9 by Roback (Roback & Coffman 1983).

Data analyses

Generalized linear models were applied to analyze significant differences between chemical and physical variables among sites and seasons using the data of both periods (2000–2001 and 2001–2002). Discrete data (conductivity) were analysed using a Poisson distribution with logarithm as a link function, and were 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, temperature, transparency, velocity, total dissolved ions and discharge) were analysed using a normal distribution and identity link, and were tested with *F*-tests. Detailed procedures for this type of analysis can be found in Crawley (1993) and McConway et al. (1999). For the different ion concentrations, only the data on total dissolved ions were used because this variable represents the sum of all individual ions. We also estimated the percent variation explained by the model for each response variable (conductivity, pH, transparency, etc.) as follows: % of explained variability = explained deviance (or variance for normal data)/total deviance (or variance) × 100. Statistical analyses were performed with GENSTAT 7.2.

Two different levels of sampling effort were used for the analysis of chironomid assemblages. Database 1 comprising around 30 chironomid larvae selected by random subsampling was adopted seasonally in triplicate at the 11 sampling sites. Database 2 comprised complete sampling of chironomid larvae: all larvae collected from VA, LU and PO (each belonging to one of the 3 sections of the lotic system) were sampled.

Database 1

Distribution of chironomid assemblages

To explore seasonal and spatial distribution and composition of chironomid assemblages, we calculated relative abundance (%) and taxonomic richness for each benthic subsampling, and for this purpose a data matrix was constructed with relative abundance (%) of each taxon per replicate, season and sampling site.

Prevalence of chironomids and environmental variables

To characterize the distribution of chironomid communities among sampling sites according to some environmental parameters (water temperature, altitude, substrate composition), and calculate the percentage of rithronic assemblages, we applied Lindergaard & Brodersen's (1995) methodology.

To investigate variations in the species data and the relationship between species composition and environmental variables over the total length of the river, we used a multivariate-ordination technique

from the CANOCO program (version 4.5). Environmental variables were standardized (Pielou 1984, ter Braak 1986). Because of the narrow ranges of explanatory variables, a redundancy analysis (RDA) was selected over a canonical correspondence analysis, following the recommendations of ter Braak & Smilauer (2002). Only environmental parameters with variance inflation factors <10 were retained in the analysis because a greater value would indicate multicollinearity among the variables (ter Braak & Verdonschot 1995). The significance of variation in the parameters and the overall significance of the ordination were tested with the Monte-Carlo permutation test (499 unrestricted permutations; p < 0.01).

A Pearson correlation analysis was used to assess differences in chironomid density and discharge between seasons.

Database 2: Community assemblage structure

Relative abundance (%), total and mean abundances (ind. m^{-2}), and taxonomic richness were calculated for each sampling site and each season. Generalized linear models (McCullagh & Nelder 1983) were employed to examine differences in larval density among seasons and sites, as well as site–season interaction. A Poisson distribution was assumed for the abundance data, and a logarithmic regression was applied. Genera with low abundances and frequencies (e.g. *Chironomus*, *Paraheptagyia*, and *Podonomopsis*) were excluded from the analysis. Annual differences in abundance were tested using an ANOVA, and tests were considered significant at or below the α-level of 0.05. GENSTAT Software, version 7.2 (2008), was used to conduct all statistical analyses.

Databases 1 and 2: Chironomid diversity

To determine whether chironomid community diversity was well represented in each sampling site, accumulation curves were applied. Because the accumulation curves showed that the sampling effort was not enough to represent the community diversity, we decided to apply the rarefaction method. EstimateS Software, version 9.1 was used to perform both analyses.

To compare the chironomid richness between the sampling sites among databases (1 and 2), rarefaction measurement and the conventional index of species diversity (Shannon's diversity index, *H'*) were

used to compare the taxonomic richness and taxonomic diversity of chironomid communities among sampling sites in the study area. Rarefaction was performed considering the minimal number of individuals sampled at a site per database. We calculated rarefied taxonomic richness and Shannon's diversity index for each database using the freely available EstimateS software (Colwell 2013). For applying both indices and maximizing their properties, we used the lowest taxonomic identification reached (genus), as applied by Fernández et al. (2001).

RESULTS

Environmental variables

In general, physical and chemical variables exhibited marked seasonal and spatial changes (Table 2). Mean water temperatures ranged from a minimum of 2°C at the headwaters to a maximum of 25.4°C at the outlet (Table A1). Air temperature fluctuated between 2–6°C (winter) and 30–36°C (summer). The pH values ranged from neutral to alkaline (Table A1), with the maximum pH registered in the winter 2000–2001 (mean = 8.7 ± 0.6). At the headwaters (CU, HO, and TU), conductivity values were higher than those recorded in the middle section of the basin, and the highest conductivity values were observed at the mouth of the basin (Table A2). Transparency decreased in spring and summer as a result of increased discharge. Mean biannual discharge was 26 m³ s⁻¹, with increases in summer (Fig. 2). Substrata at all sites (from CU to BE) consisted mainly of small boulders, cobbles, pebbles, sand and silt, whereas the river bottom at LA was composed entirely of sand and silt. Velocity was maximum at BE (2.13 m s⁻¹, summer 2002) and minimum at LA (0.17 m s⁻¹, autumn 2000).
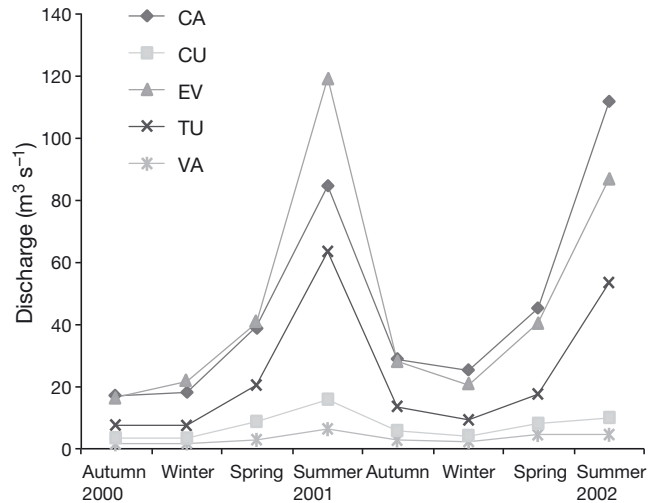

Fig. 2. Biannual mean seasonal values of discharge (m³ s⁻¹) at 5 sampling sites along the Mendoza River basin. See Fig. 1 for site abbreviations

During the sampling period, the water of the Mendoza River was extremely hard (EPA 1986, APHA 1989), with an average calcium-bicarbonate concentration of >300 mg l⁻¹.

Database 1

Distribution of chironomid assemblages

Eleven genera were identified, which belonged to 5 subfamilies (Table 3). The highest richness was recorded at the CU, LU and PO sampling sites, with an abrupt decrease in richness at LA (Table 3). Seasonally, maximum richness (11 genera) was detected in summer and minimum richness in spring (7 genera).

The Orthocladiinae were dominant across seasons and at all sampling sites except at LA, where this sub-

Table 2. Summary of generalized lineal model analysis used to examine differences in environmental variables among sampling sites and seasons

Physical-chemical variable	Site				Season			
	F	df	p	% Variability explained	F	df	p	% Variability explained
pH	20.73	10, 259	<0.001	8.24	295.31	7, 259	<0.001	82
Conductivity	46.99	10, 259	<0.001	49	35.87	7, 259	<0.001	26.07
Water temperature	64.35	10, 259	<0.001	33.84	145.19	7, 259	<0.001	53.39
Velocity	17.17	10, 259	<0.001	34.69	11.60	7, 259	<0.001	16.41
Transparency	2.79	10, 259	0.003	4.2	56.43	7, 259	<0.001	59.39
Discharge	43.75	4, 118	<0.001	37.5	26.29	7, 118	<0.001	39.5
Total dissolved ions	80.91	10, 259	<0.001	59	46.82	7, 259	<0.001	23.77

Table 3. Total relative abundance (%) of the chironomid assemblages, as well as total richness and Shannon's diversity index (H'). Superscripted numbers indicate Database 1 or Database 2

Taxa	CU[1]	HO[1]	TU[1]	VA[1]	VA[2]	UU[1]	LU[1]	LU[2]	EV[1]	PO[1]	PO[2]	CA[1]	BE[1]	LA[1]
Orthocladiinae	**77.8**	**65.3**	**72.9**	**87.6**	**70.1**	**91.9**	**90.5**	**98.9**	**94.1**	**86.2**	**92.1**	**66.2**	**81**	
Cricotopus	61.1	58.7	66.1	70.3	54.8	86.5	86.9	98	86.6	68.2	89	63.4	79.8	
Onconeura	0.5					3.6	1.2	0.4	0.8	9	0.6		1.2	
Genus 9 Roback	13	4.4	6.8	11.7	5.6	1.8	1.2	0.2	2.5	9	0.3	2.8		
Paralimnophyes	3.2	2.2		5.5	9.7		1.2	0.2	4.2		1.1			
Parametriocnemus								0.1			1.1			
Podonominae	**21.1**	**23.9**	**25.4**	**9**	**6.5**	**7.2**	**2.4**	**0.7**	**2.5**	**1.2**	**0.3**		**2.4**	
Podonomus	18.9	23.9	23.7	9	6.5	7.2	2.4	0.6	2.5	1.2	0.3		2.4	
Parochlus	1.1													
Podonomopsis	1.1		1.7					0.1						
Diamesinae	**1.1**	**10.9**	**0.9**	**3.4**	**23**	**0.9**	**1.2**	**0.1**						
Paraheptagyi	1.1	10.9	0.9	3.4	23	0.9	1.2	0.1						
Chironominae			**0.9**					**0.1**		**3.6**	**4.3**	**33.8**	**14.3**	**100**
Polypedilum			0.9					0.1		1.2	4.1	12.7	14.3	62.1
Chironomus										2.4	0.2	21.1		37.9
Tanypodinae						**6**		**0.4**	**3.4**	**9**	**3.3**		**2.4**	
Pentaneura						6		0.4	3.4	9	3.3		2.4	
Total richness	8	5	5	5	5	5	7	10	6	7	9	4	5	2
Mean H'	1.17	1.12	0.95	1.09	1.23	0.55	0.59	0.14	0.6	0.9	0.51	0.98	0.68	0.69

family was absent (Table 3). The Podonominae and the Diamesinae were predominant in the headwaters, whereas the Chironominae were present only in the lower section of the basin and the outlet (LA). The Tanypodinae were recorded exclusively in the middle section, with the highest percentage occurring at PO. Seasonal changes in the relative abundance of the subfamilies of Chironomidae were observed: Orthocladiinae showed peak abundance in spring (at 90%), Podonominae in autumn (at 13%), Chironominae in summer (at 12%) and Tanypodinae in winter (at 4%).

Cricotopus was the most prevalent genus and was abundant during all sampling periods (Table 4) and at all sites (Table 3), showing the highest densities at UU, LU and EV. The maximum and minimum relative abundances of this genus were recorded in summer, at EV (100%) and CA (33%), respectively.

We observed a variation in the genera along the course of the river (Table 3). *Podonomopsis* (CU and TU) and *Parochlus* (CU) were found only at the headwaters. Maximal abundance of *Podonomus* was recorded at the high-altitude sites (HO: 2775 m; TU: 2447 m a.s.l.), with a clear decrease in this parameter downstream. Genus 9 (Roback) predominated at the headwaters, with the highest values at CU and VA. At the other sampling sites, the abundance of this genus was very low.

The genera *Polypedilum* and *Chironomus* were present throughout the lower section of the basin, including the outlet. The genus *Onconeura* was recorded along the entire course of the river, with its maximum abundance at PO. Specimens of *Pentaneura* were absent at the headwaters, whereas those of *Paralimnophyes* were more abundant in the lower section of the basin (EV) and at the headwaters (VA). The genera *Paraheptagyia*, *Podonomopsis* and *Parochlus* exhibited the lowest abundance along the course of the river.

A turnover of genera and a variation in their abundance over time were detected, although the taxa *Cricotopus*, *Onconeura*, Genus 9, *Paralimnophyes*, *Podonomus*, *Polypedilum* and *Pentaneura* were found during all seasons (Table 4).

Table 4. Mean relative abundance of the genera of Database 1 by season

Taxa	Autumn	Winter	Spring	Summer
Cricotopus	74.21	64.86	80.62	64.08
Onconeura	4.53	0.45	0	1.29
Genus 9 Roback	5.23	2.25	3.87	9.71
Paralimnophyes	1.74	3.15	0.39	2.58
Podonomus	11.50	10.81	8.52	7.77
Parochlus	0.35	0	0	0.32
Podonomopsis	0	0.45	0	0.97
Paraheptagyia	0	2.25	0.77	2.91
Pentaneura	0.70	6.76	0.39	0.65
Polypedilum	0.70	9	0.39	5.82
Chironomus	1.04	0	5.04	3.88

Table 5. Number of chironomid taxa and percent distribution of the subfamilies over a wide range of altitudes, water temperatures and substrate type. All taxa belonged 100% to rithronic groups. Subfamilies and season abbreviations: 1: Orthocladiinae; 2: Podonominae; 3: Diamesinae; 4: Tanypodinae; 5: Chironominae; F: fall; W: winter; Sp: spring; S: summer

Location	Altitude (m a.s.l.)	Water temperature (°C)	Subfamily (%)					Total number of taxa	Substrate type
			1	2	3	4	5		
Headwaters	2800–2400	F–W <4.0 Sp–S >8.0	75	20	5	0	0.2	6–8	Small block, cobble, pebble, sand–silt
Middle course	1800–1727	F–W 4.5–7.0 Sp–S 11.0–13.6	93	4	1	2	0.5	5–7	Small block, cobble, pebble, sand–silt
Lower course	1413–1085	F–W 5.4–8.6 Sp–S 11.0–16.4	81	1.5	0	4	13	4–7	Small block, cobble, pebble, sand–silt
Outlet	606	F–W 9.9 Sp–S 21.3	0	0	0	0	100	1	Sand–silt

Prevalence of chironomids and environmental variables

Application of the methodology of Lindergaard & Brodersen (1995) indicated that the subfamilies of Chironomidae showed a similar richness of genera except at the outlet, in spite of the significant differences in temperature and altitude along the river, a characteristic that might be related to the relatively constant substrate composition (Table 5).

According to the RDA analysis, chironomid assemblages located along the first axis were mainly related to conductivity, temperature and a gravel substrate. The environmental variables that were more significantly correlated with the canonical axes after performing the Monte-Carlo permutation test

were conductivity ($F = 17.00$, $p = 0.002$), gravel substrate ($F = 6.39$, $p = 0.002$), temperature ($F = 3.53$, $p = 0.008$) and water hardness ($F = 3.62$, $p = 0.03$). The inflation factors of all variables included in the analysis were less than 20 deviation units. On the basis of the variance in the species data, the percent total variance explained by the first 2 axes of the RDA was 66%. The first axis in the RDA biplot was strongly and positively correlated with conductivity. The genus *Polypedilum* was associated with the highest values of conductivity, as was the genus *Chironomus*, but the latter only to a minor degree. The second axis
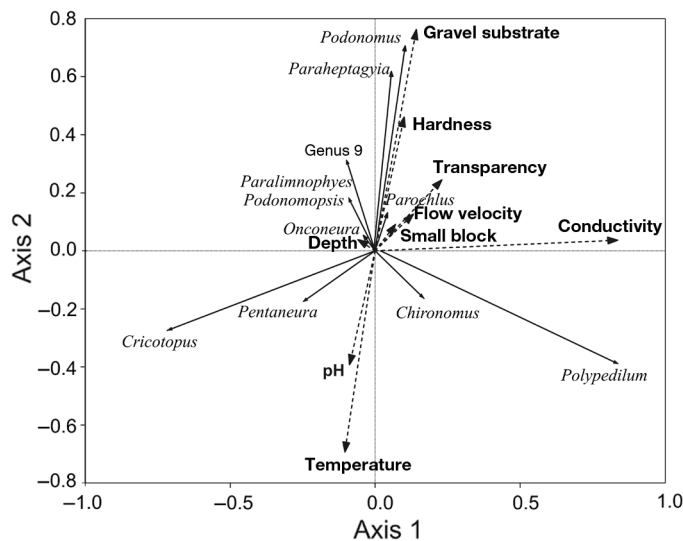
Fig. 3. Ordination diagram displaying the first axes of redundancy analysis (RDA) of the relation of the Chironomidae genera distribution (arrows with thick lines) with selected environmental characteristics (arrows with dashed lines) in the Mendoza River basin
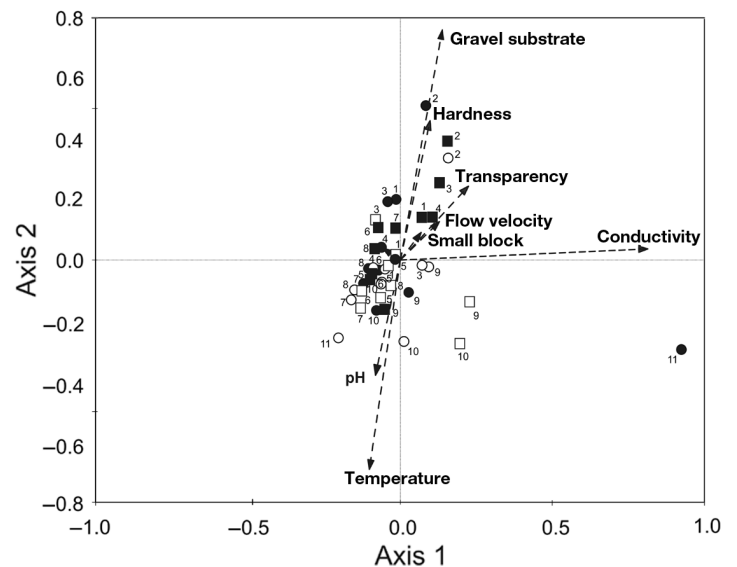
Fig. 4. Ordination diagram displaying the first axes of redundancy analysis (RDA) and showing the relationship between the seasonal samples with selected environmental characteristics (arrows with dashed lines) in the Mendoza River basin. White squares: summer; black squares: autumn; black circles: winter; white circles: spring. Numbers correspond to 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

was positively correlated with water hardness and substrate size (i.e. gravel) and negatively correlated with water temperature and pH. The genera *Podonomus*, *Paraheptagyia*, *Podonomopsis*, *Parochlus*, *Paralimnophyes* and Genus 9 were associated with the presence of the gravel substrate, low water temperature, transparency and neutral pH, conditions that characterized the headwaters, whereas the genera *Cricotopus*, *Pentaneura* and *Onconeura* formed the assemblage that was present in the middle section, with this reach having a higher water temperature and pH. *Polypedilum* and *Chironomus* were associated with high conductivity values obtained in the lower-basin section (Figs. 3 & 4).

Pearson's correlation coefficient showed a negative correlation between discharge and chironomid density in summer ($r = -0.82$, $p = 0.09$). In the other seasons (winter, autumn and spring), we found no significant correlations ($p > 0.60$).

Database 2: Community assemblage structure

The total density of chironomids, considering the 3 sampling sites (VA, LU and PO) along the longitudinal gradient, was 20 588 ind. m^{-2}. The Orthocladiinae exhibited the greatest taxonomic richness along with the highest density at 18 819 ind. m^{-2} (91% of total abundance), followed by Diamesinae at a density of 1222 ind. m^{-2} (6% of total abundance) and Podonominae at a density of 322 ind. m^{-2} (2% of total abundance). The contribution of Chironominae (*Polype-dilum* and *Chironomus*) was low in terms of density (119 ind. m^{-2}, 0.6% of total abundance), and that of Tanypodinae was also low (106 ind. m^{-2}, 0.5% of total abundance) (Table 6).

No significant differences in chironomid density were detected ($p = 0.43$) between the 2 sampling periods. Density peaks were recorded in the autumn (7162 ind. m^{-2}) and winter (9032 individuals m^{-2}) of both annual cycles; with a notable decrease in density towards the summer, mostly in Orthocladiinae (Table 6). The maximum mean density of Orthocladiinae occurred at LU, while Diamesinae and Podonominae predominated at VA.

Tanypodinae and Chironominae achieved their maxima at PO (Table 6), a sampling site in the lower sector of the river, where Diamesinae were absent.

Among the total identified genera, 86% of the larvae corresponded to *Cricotopus*, while the remaining 14% included members of the other 10 genera as well. Apart from *Cricotopus*, VA was characterized by the co-dominance of *Paraheptagyia*, *Paralimnophyes*, *Podonomus* and Genus 9. At LU, *Cricotopus* exhibited maximum density (13 575 ind. m^{-2}), while the other taxa were recorded at minimum densities compared to the respective values obtained at VA and PO. The genera *Pentaneura* and *Onconeura* were associated with one another, with both being registered at LU and PO. The highest densities of *Chironomus* and *Polypedilum* were recorded at PO (Table 6).

The analysis of Database 2 revealed that the densities of the genera displayed significant differences among sampling sites and seasons (Table 7). The

Table 6. Seasonal mean densities (ind. m^{-2}) of Chironomidae genera at each sampling site. Data are from Database 2

Taxa	Vacas				Lower Uspallata				Potrerillos			
	Autumn	Winter	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter	Spring	Summer
Orthocladiinae	897	783.5	94	71	2189	2438.5	1749.5	41.5	438.5	644.5	50	21.5
Cricotopus	855.5	472.5	83.5	46.5	2175	2422	1749.5	34.5	405.5	635	50	14.5
Paralimnophyes	22	261	0	4	0	11	0	0	27.5	0	0	0
Genus 9 Roback	19.5	50	10.5	20.5	5.5	0	0	1.5	0	0	0	2
Onconeura	0	0	0	0	8.5	0	0	5.5	5.5	2	0	2
Parametriocnemus	0	0	0	0	0	5.5	0	0	0	7.5	0	3
Podonominae	27.5	44.5	31.5	11.5	11	16.5	5.5	3	5.5	0	0	0
Podonomus	27.5	44.5	31.5	11.5	11	16.5	0	3	5.5	0	0	0
Podonomopsis	0	0	0	0	0	0	5.5	0	0	0	0	0
Diamesinae	0	516.5	71.5	18.5	0	0	5.5	0	0	0	0	0
Paraheptaghyia	0	516.5	71.5	18.5	0	0	5.5	0	0	0	0	0
Chironominae	0	0	0	0	0	0	5.5	0	11	27.5	0	16
Polypedilum	0	0	0	0	0	0	5.5	0	5.5	27.5	0	16
Chironomus	0	0	0	0	0	0	0	0	5.5	0	0	0
Tanypodinae	0	0	0	0	3	16.5	0	4.5	5.5	23.5	2	2
Pentaneura	0	0	0	0	3	16.5	0	4.5	5.5	23.5	2	2

Table 7. Percent variation in the abundance of each Chironomidae genus that explains each significant variable: sampling site (SS), season (S) and their interaction (SS × S). ns: not significant. Data are from Database 2

Taxa	Site	Season	SS × S
Cricotopus	28.6	54.0	11.8
Genus 9 (Roback)	45.3	24.8	ns
Onconeura	21.6	31.1	ns
Paralimnophyes	26.3	54.3	18.0
Parametriocnemus	19.7	50.9	ns
Paraheptagyia	36.1	61.4	ns
Pentaneura	24.9	54.4	ns
Podonomus	38.7	ns	ns
Polypedilum	34.8	43.0	ns

interaction between site and season showed significant differences only for the genera *Cricotopus* and *Paralimnophyes*. Overall, with the other genera present, the variation in density was more greatly determined by seasonality than by the location along the river (Tables 6 & 7).

Databases 1 and 2: Chironomid diversity

A total of 12 genera of Chironomidae were found in the study area, and 11 of them were shared by both databases. A comparison of the results obtained in Database 2 with those in Database 1 indicated an increase in taxon richness within the Orthocladiinae in the former, with the genus *Parametriocnemus* being present along with certain other genera at the selected sampling sites (VA, LU and PO), all of which genera were absent in Database 1.

The accumulation curves of Database 1 showed that chironomid diversity was richer at CU, LU and PO than at the other sampling sites (Fig. 5A). The accumulation curve of the chironomid community was steeper for CU compared with the rest of the sampling sites, suggesting a more even distribution of abundance among chironomid genera at this site (Fig. 5A). The expected richness in Database 2 for PO was 9 genera, followed by LU with 6 genera (Fig. 5B). VA, with 5 genera, reached a plateau with only 313 individuals sampled (Fig. 5B). When comparing richness obtained with subsamples and all data included (Database 1 vs. Database 2), we found that PO and LU had a higher richness than VA (Fig. 5C).

For Database 1, Shannon's diversity index (*H'*) highlighted CU, HO and VA as the most diverse sites, and UU, LU and EV as the sites exhibiting lower

diversity, whereas for Database 2, the site with the lowest diversity was LU (Table 3).

Orthocladiinae and Chironominae were both more abundant in autumn and winter in Database 2 (high densities of *Cricotopus*, and low densities of *Paralimnophyes*, Genus 9, *Onconeura* and *Parametriocnemus*), whereas in Database 1 the maxima of the Orhocladiinae occurred in spring (high densities of *Cricotopus*, and low abundance of *Paralimnophyes*) and the highest densities of Chirono-
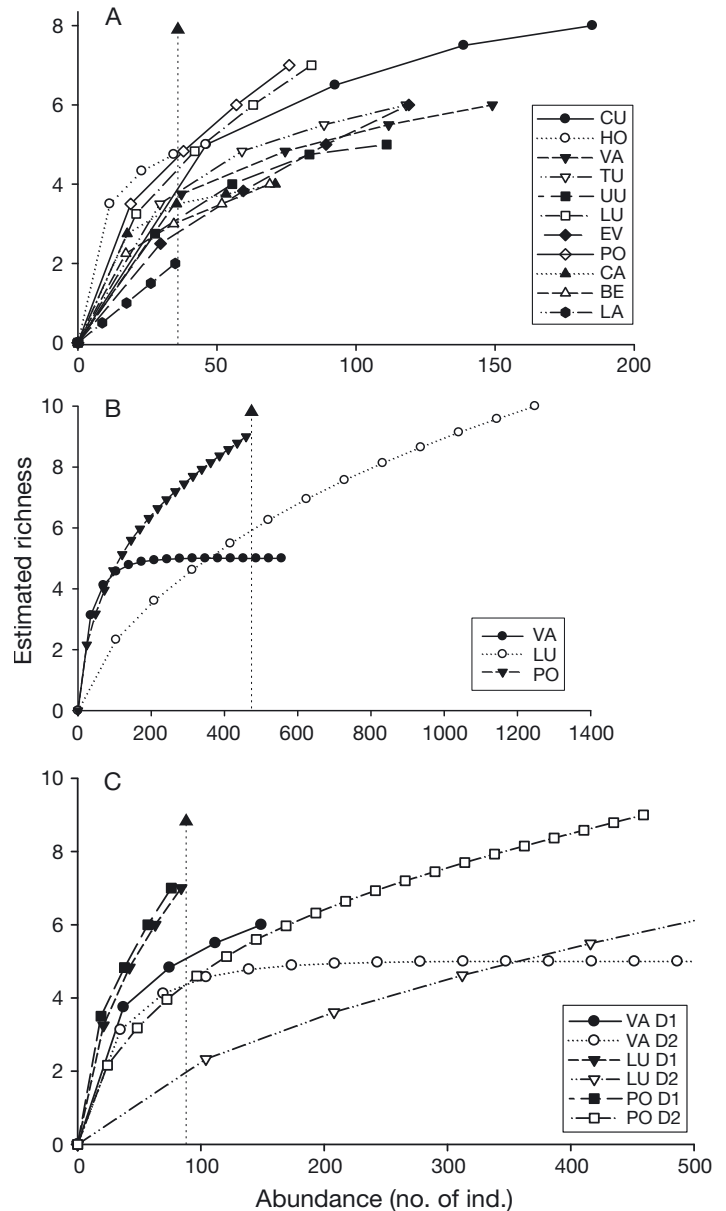

Fig. 5. Accumulation curves obtained by rarefaction after randomly mixing the samples 100 times for the sampling sites of the Mendoza River basin. (A) Database 1; (B) Database 2; (C) both Database 1 (D1) and Database 2 (D2). Vertical dashed arrow indicates sampling site with lowest abundance. See Fig. 1 for site abbreviations

minae were in summer (equal abundance of *Polypedilum* and *Chironomus*).

Paralimnophyes, recorded in Database 1 at VA and LU, were also found at PO. Furthermore, *Paremetriocnemus* was recorded at LU and PO and *Podonomopsis* and *Polypedilum* at LU in Database 2; these 3 genera were absent from those respective sites in Database 1.

Some of the results coincided between the 2 databases: for example, dominance of the members of Orthocladiinae in terms of taxonomic richness and abundance over space and time. Podonominae and Diamesinae predominated at the headwaters, whereas Chironominae were significant in the lower section of the basin. Tanypodinae, absent at the headwaters, were abundant in the middle and lower section, with the highest abundance at PO. *Cricotopus*, exhibiting maximum density at LU, was the most abundant and frequently occurring genus at all sampling sites.

DISCUSSION

Database 1

Distribution of chironomid assemblages

Most of the genera of Chironomidae recorded at our study sites are distributed worldwide (Ashe et al. 1987). Our results suggest that in the western-central region of Argentina, chironomids are dominant in high-elevation river communities. The chironomid community we studied belongs to the temperate Andean-Patagonia region, characterized by the presence of the subfamilies Orthocladiinae and Podonominae (Ashe et al. 1987), which together represented approximately 90% of the total chironomid fauna, found in the lotic section of Mendoza river basin, with less than 10% representation of Chironominae. In the tropical lowlands of South America (Ashe et al. 1987) the Chironominae subfamily is dominant (77.7%). Following Cranston's (1995) classification, the chironomid assemblages of the Mendoza River basin were found to be composed of cold stenothermic taxa (Podonominae, Diamesinae and Orthocladiinae) at the headwaters and warm eurythermic taxa (Chironominae) in the lower section and outlet (e.g. LA). In addition, Chironominae was the only subfamily present at the mouth. However, the abundance of Tanypodinae was always low. This spatial pattern over the altitudinal gradient coincided with that reported by Lindergaard & Brodersen (1995) for the Northern Hemisphere.

Prevalence of chironomids and environmental variables

The distribution pattern of the genera in the Mendoza River basin was strongly affected by environmental conditions. Altitude, conductivity, pH, water temperature, depth, transparency and substrate size were the most influential variables affecting the distribution of the Chironomidae in the Mendoza River. High-elevation rivers are characterized by low temperatures, discharge fluctuations, unstable substrates and elevated concentrations of suspended solids, resulting in harsh environmental conditions for the development of macroinvertebrate fauna (Ward 1992, Füreder 1999). Moreover, in streams and rivers of glacial origin, invertebrate communities must also tolerate the stress caused by marked channel instability during the melting season (Lods-Crozet et al. 2001). Nevertheless, chironomids have become adapted to these kinds of habitats (Lencioni & Rossaro 2005) and are one of the macroinvertebrate families most capable of surviving in such extreme environments (Lods-Crozet et al. 2001). In the Mendoza River basin, during the melting season (summer), stressful environmental conditions caused by increments in suspended solids (Scheibler 2007) and river discharge (present study) were associated with low chironomid density. Our results confirm a negative correlation between discharge and chironomid density in summer. Indeed, species richness in arid regions has been found to be notably low relative to areas with higher precipitation (Wright & Burgin 2010). Similar research on different aquatic environments in the Mendoza province has also reported low taxonomic richness (Scheibler 2007, Scheibler & Debandi 2008, Scheibler et al. 2008, Scheibler & Ciocco 2011).

The genus *Cricotopus* proved to be abundant and dominated the assemblages along the altitudinal gradient of the Mendoza River. Within the river basin, this genus has become adapted to a wide range of environmental conditions. The larvae of *Cricotopus* feed on algae (Fittkau 1969) and are commonly recorded in flowing waters (Wiederholm 1983). *Cricotopus* larvae in the Mendoza River had diatoms in their digestive tracts as well as fine-grained inorganic sediments. This observation agrees with that of Peralta & Claps (2001), who concluded that in the absence of riparian vegetation, primary production is mainly autochthonous.

Our results showed that *Podonomus*, *Parochlus*, *Podonomopsis*, *Paraheptaghyia*, Genus 9 and *Paralimnophyes* were located at the headwaters and were

associated with low temperatures and gravel sub-strate. In rivers of glacial origin, the larvae of Dia-mesinae and Podonominae have been recorded at high altitudes (Burgherr & Ward 2001, Milner et al. 2001, Lencioni & Rossaro 2005) and in rivers with similar physical characteristics (Ward 1992). At the headwaters of the Mendoza River, high water miner-alization and degree of hardness were also observed jointly with the presence of sedimentary rocks (e.g. gypsum; Armando 1985). The presence of Podo-nominae and Diamesinae in those harsh conditions demonstrated that these taxa may inhabit different types of habitats but are conditioned by temperature and dissolved oxygen concentrations (Cranston 1995).

In other semi-arid environments of Argentina, the tribe Pentaneurini (Tanypodinae) was reported to predominate in streams located at moderate alti-tudes (1560 to 1690 m a.s.l.) that are characterized by low temperatures and high flows (Medina & Paggi 2004). The larvae of *Pentaneura* can survive in rithronic environments with such high flows due to their small size and by living under stones (A. C. Paggi pers. comm.). The presence of the subfamily Chironominae in the lower sector of the Mendoza River basin is in agreement with results obtained for other major rivers (Ashe et al. 1987), indicating that certain *Chironomus* larvae prefer environments with high salinity (Wiederholm 1983, Scheibler & Ciocco 2011, 2013). In lotic environments, tempera-ture and current velocity influence food availability, while discharge determines substratum particle size (Lindergaard & Brodersen 1995), which strongly affects chironomid microdistribution (Lencioni & Rossaro 2005). Substrate size (Principe et al. 2008) and depth (Lods-Crozet et al. 2001) are also influen-tial in the distribution of chironomids. Whereas the size of the particles in the sediment notably controls the pattern of species richness within the chirono-mid community (Rae 2004), habitat heterogeneity is the main variable influencing the abundance of chironomid assemblages (Burgherr & Ward 2001, Füreder et al. 2005, Lencioni & Rossaro 2005). In the Mendoza River basin, chironomid richness was the highest at the headwaters (CU), in the middle sec-tion (LU) and in the lower section (PO), with a marked decrease at the mouth (LA) of the basin. Decreased richness has been previously reported in numerous studies of altitudinal gradients in both temperate and tropical regions (Illies 1964, Hynes 1971, Allan 1975, but see Finn & Poff 2005). In addi-tion, LA exhibited fluctuating flow dynamics, with dry periods depending on the Cipoletti dam, located in the Blanco Encalada locality, which, added to the poverty of substrate heterogeneity (only sand and silt) and the high impact of human activities in this area (large agricultural impact), caused this sam-pling site to have the lowest richness in the system under study.

Database 2: Community assemblage structure

Chironomid assemblage structure was found to be similar for Databases 1 and 2: the highest densities and taxonomic richness were detected for Ortho-cladiinae, followed in decreasing density and rich-ness by Diamesinae, Podonominae, Chironominae and Tanypodinae. The same subfamily compositions were registered from northwestern Argentinean mountain streams (Tejerina & Molineri 2007). The dominance of the Orthocladiinae subfamily was also detected in a Patagonian river basin (Miserendino & Pizzolon 2003) and in glacier-fed streams from Europe (Lods-Crozet et al. 2001).

The highest taxonomic richness was recorded at LU, the middle section of the Mendoza River. This is because this section of the river is a transition area where species of the upper and lower sections coexist (Scheibler et al. 2014). Diamesinae and Podonominae had the highest density at VA (headwater sampling site). As other chironomid studies point out, these cold stenothermic subfamilies in mountain systems are present at high elevations (Lencioni & Rossaro 2005, Tejerina & Molineri 2007, Scheibler et al. 2008).

The results of this method showed that the varia-tion in density was more greatly determined by sea-sonality than by the location along the river. The highest chironomid density in autumn and winter indicated in the results of Database 2 is consistent with the findings obtained in studies of other moun-tain streams, e g. in a subtropical Andean basin of Argentina (Mesa et al. 2009) and several streams in the Alps (Burgherr & Ward 2001, Lencioni & Rossaro 2005). In all of these lotic environments, the increase in discharge during the summer, coupled with a high suspended-solid concentration, produced unfavourable conditions for macroinvertebrate assemblages. The increase in density of Chironomidae during the autumn could be related to habitat diversification, such as was noted by Aburaya & Callil (2007) in a tropical river where increases in density during the low-water periods enable habitat restructuring, which enhances survival of resident organisms.

Cricotopus was the genus with the highest densi-ties at VA, LU and PO. The results showed that this genus has adapted to a broad range of environmental

conditions. Nonetheless, due to a lack of systematic studies in the area, and thus the inability to determine *Cricotopus* spp. to species or morphospecies level, our information on the distribution range of *Cricotopus* species was limited. Further sampling of pupae, pupal exuviae and adults will be necessary to achieve a more accurate taxonomic determination.

Databases 1 and 2: Chironomid community diversity

We concluded that the results obtained from Database 1 were sufficient to characterize the turnover of species assemblages along the longitudinal gradient of the Mendoza River basin. Our suggestion is based on the minimal variation observed between both database methods in both relative abundance of the dominant taxa and taxonomic richness. In contrast, to assess seasonal variations in chironomid fauna, we found that application of Database 2 was better as this method yielded more consistent results in the present study compared with the results obtained when considering the entire macroinvertebrate community. Density and taxon richness of the invertebrate community peaked during autumn and winter (Scheibler et al. 2014).

The rarefaction index revealed that the sampling sites with the highest richness were LU and PO, and this result was consistent between both databases. However, Shannon's diversity index showed LU to be the least diverse site, which is due to the dominance of the genus *Cricotopus* over the other genera found at this sampling site.

The accumulation curves show that only the Chironomidae at VA (Database 2) was capable of reaching the highest taxonomic richness in the chironomid community. Evidently, to be able to describe the diversity of the chironomid community of the Mendoza River basin, it is necessary to maximize sampling effort, regardless of the method used. However, this is the first study of seasonal and spatial patterns of chironomid assemblages in this Andean region, and systematic studies on Chironomidae have not yet been carried out. For a better understanding of chironomid variations in this arid region, future studies that maximize sampling effort (considering pupae, pupal exuviae and adults) and thus determine the species diversity are necessary.

In the system investigated here, a succession of chironomids was detected from the headwaters to the outlet as a function of variations in altitude, water temperature, substrate size and conductivity. The first 10 sampling sites (from CU to BE) had higher habitat heterogeneity compared to LA. In alpine streams, habitat heterogeneity was shown to be an important factor in predicting chironomid assemblages (Lencioni & Rossaro 2005). In recent years, the headwaters of mountain rivers have been the subject of greater attention on account of their lesser exposure to human activities compared with downstream sections (Maiolini & Lencioni 2001). In addition, the benthic communities recorded at high altitudes are more sensitive to environmental changes within their immediate environment (Füreder 2007). For these reasons, the macroinvertebrate communities of these ecosystems are especially good indicators of systematic climate change in the form of global warming (Burgmer et al. 2007, Kohler & Maselli 2009). Because of the high-altitude origin of the Mendoza River, the discharge regime and the physicochemical parameters exhibit pronounced seasonal and spatial changes. We recorded low values of chironomid diversity at all sampling sites, which may be the consequence of unfavourable environmental conditions. However, in glacial stream ecosystems with harsh conditions within different regions across Europe, the species richness of chironomid assemblages was found to be much higher (for example, 39 genera recorded; Lods-Crozet et al. 2001) than in the Andean river of the present study, with only 11 genera recorded. We attribute these low diversities to the aridity of the sampling area, as has been demonstrated in studies of other similar high-altitude lotic systems (Scheibler & Debandi 2008, Scheibler et al. 2008, 2014).

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Table A1. Mean (±SD) values of hydrological features and physical parameters of the 11 sampling sites on the Mendoza River in the 2 sampling periods. P1: 2000–2001; P2: 2001–2002. For site abbreviations, see Table 1

Site	Sampling period	Flow velocity (m s⁻¹)	Depth (m)	Transparency (m)	Water temperature (°C)	Air temperature (°C)	pH	Main substrate
CU	P1	0.78 (0.1)	0.22 (0.1)	0.12 (0.1)	4.4 (2.5)	13.5 (7.7)	7.9 (1.0)	Small block, pebble, sand–silt,
	P2	0.91 (0.2)	0.21 (0.1)	0.13 (0.1)	6.3 (3.3)	10.1 (7.1)	7.5 (0.6)	cobble, pebble
HO	P1	0.93 (0.1)	0.13 (0.1)	0.07 (0.1)	4.4 (3.1)	15.7 (9.9)	8.4 (0.6)	Small block, cobble, pebble,
	P2	1.24 (0.5)	0.17 (0.1)	0.13 (0.1)	6.5 (3.9)	12.9 (7.9)	7.9 (0.5)	sand–silt, pebble, gravel
TU	P1	0.88 (0.2)	0.32 (0.3)	0.17 (0.2)	6.8 (3.9)	16.0 (7.6)	8.6 (0.8)	Big, median and small blocks, cobble
	P2	0.97 (0.2)	0.24 (0.1)	0.19 (0.1)	7.5 (4.3)	13.3 (9.0)	8.0 (0.3)	Small block, pebble
VA	P1	1.16 (0.4)	0.26 (0.1)	0.15 (0.1)	8.1 (3.5)	15.5 (9.9)	8.5 (1.0)	Big block, cobble, pebble, sand–silt
	P2	1.19 (0.3)	0.16 (0.0)	0.11 (0.1)	9.7 (3.7)	13.7 (6.8)	8.1 (0.2)	Pebble, sand–silt
UU	P1	0.84 (0.2)	0.24 (0.2)	0.10 (0.1)	8.2 (4.5)	15.1 (10.5)	8.7 (1.1)	Small block, cobble, pebble, sand–silt
	P2	1.07 (0.3)	0.23 (0.1)	0.15 (0.1)	10.0 (4.3)	18.2 (14.5)	8.1 (0.2)	Cobble, pebble
LU	P1	0.73 (0.4)	0.17 (0.1)	0.17 (0.2)	7.6 (2.1)	15.7 (8.1)	8.6 (0.9)	Small block, cobble, pebble,
	P2	0.71 (0.1)	0.23 (0.1)	0.14 (0.1)	9.9 (5.2)	11.3 (9.5)	7.8 (0.7)	sand–silt, cobble, pebble
EV	P1	1.11 (0.6)	0.20 (0.0)	0.10 (0.1)	8.5 (3.6)	15.9 (9.8)	8.6 (0.9)	Small block, cobble, pebble
	P2	0.77 (0.2)	0.28 (0.1)	0.16 (0.2)	9.7 (5.1)	15.6 (9.4)	7.9 (0.4)	Cobble, sand–silt
PO	P1	0.84 (0.6)	0.20 (0.1)	0.14 (0.2)	9.6 (3.9)	17.2 (11.2)	8.5 (1.1)	Cobble, pebble
	P2	0.98 (0.2)	0.25 (0.1)	0.15 (0.1)	9.9 (4.9)	14.2 (9.8)	8.0 (0.4)	Cobble, pebble
CA	P1	0.53 (0.1)	0.15 (0.1)	0.06 (0.0)	10.1 (4.0)	16.3 (10.0)	8.6 (0.9)	Cobble, pebble
	P2	1.32 (0.3)	0.22 (0.1)	0.2 (0.1)	12.4 (4.4)	18.9 (7.4)	8.0 (0.3)	Small block, pebble, cobble, sand–silt
BE	P1	0.75 (0.1)	0.13 (0.1)	0.07 (0.0)	11.1 (5.0)	18.9 (10.9)	8.8 (1.0)	Cobble, pebble
	P2	1.50 (0.5)	0.15 (0.1)	0.12 (0.1)	12.8 (3.8)	21.3 (10.6)	8.1 (0.3)	Cobble, pebble
LA	P1	0.23 (0.1)	0.14 (0.1)	0.08 (0.1)	15.3 (6.9)	22.6 (6.9)	9.1 (0.7)	Sand–silt
	P2	0.74 (0.5)	0.24 (0.3)	0.07 (0.04)	15.9 (7.2)	19.7 (9.6)	8.0 (0.3)	Sand–silt

Table A2. Mean (±SD) values of chemical variables of the 11 sampling sites on the Mendoza River during each sampling period

Site	Sampling period	Conductivity (µS cm⁻¹)	Ca²⁺ (mg l⁻¹)	Mg²⁺ (mg l⁻¹)	Na⁺ (mg l⁻¹)	K⁺ (mg l⁻¹)	HCO₃²⁻ (mg l⁻¹)	Cl⁻ (mg l⁻¹)	SO₄²⁻ (mg l⁻¹)	Total dissolved ions (mg l⁻¹)	Total hardness (mg l⁻¹)
CU	P1	1584 (518)	185 (45)	32 (8)	70 (74)	4 (0.2)	145 (54)	160 (133)	390 (131)	985 (386)	487 (318)
	P2	1527 (285)	188 (32)	23 (4)	58 (38)	4 (0.0)	156 (27)	192 (107)	286 (158)	906 (236)	565 (97)
HO	P1	1642 (356)	208 (84)	35 (4)	69 (29)	4 (0.2)	143 (42)	105 (37)	533 (128)	1097 (216)	585 (372)
	P2	1460 (244)	191 (65)	31 (5)	29 (7)	4 (0.2)	149 (32)	89 (15)	402 (129)	894 (238)	605 (180)
TU	P1	970 (187)	131 (22)	23 (6)	20 (19)	4 (0.2)	98 (30)	87 (57)	258 (55)	621 (111)	339 (207)
	P2	965 (151)	125 (25)	20 (9)	22 (2)	4 (0.4)	116 (45)	120 (51)	184 (71)	589 (95)	394 (65)
VA	P1	541 (71)	76 (18)	14 (1)	13 (9)	3 (1)	101 (40)	24 (9)	156 (49)	387 (34)	185 (112)
	P2	557 (79)	83 (4)	15 (3)	19 (5)	4 (0.2)	131 (31)	33 (10)	154 (22)	440 (22)	269 (13)
UU	P1	966 (275)	126 (20)	20 (6)	30 (25)	3 (0.7)	105 (25)	88 (52)	247 (72)	620 (148)	398 (72)
	P2	941 (245)	128 (21)	21 (11)	26 (12)	4 (0.2)	125 (69)	91 (23)	229 (28)	631 (164)	408 (91)
LU	P1	890 (204)	126 (23)	22 (5)	22 (14)	3 (1.0)	128 (38)	81 (33)	227 (53)	601 (110)	326 (203)
	P2	874 (149)	120 (21)	17 (5)	26 (11)	4 (0.4)	133 (54)	88 (15)	187 (24)	573 (112)	368 (58)
EV	P1	882 (191)	124 (15)	18 (6)	26 (22)	3 (1.0)	101 (25)	67 (36)	257 (73)	594 (125)	308 (190)
	P2	820 (137)	123 (13)	19 (8)	32 (18)	5 (2.0)	139 (39)	88 (15)	215 (87)	621 (119)	385 (59)
PO	P1	872 (201)	120 (18)	18 (4)	32 (10)	3 (2.0)	111 (26)	52 (18)	268 (93)	604 (105)	305 (186)
	P2	801 (147)	129 (20)	18 (3)	35 (14)	4 (0.2)	163 (31)	83 (16)	214 (84)	645 (10)	396 (57)
CA	P1	802 (309)	117 (15)	22 (9)	26 (9)	4 (0.3)	113 (35)	83 (24)	223 (59)	588 (68)	311 (195)
	P2	865 (116)	121 (12)	19 (7)	24 (12)	4 (0.2)	134 (22)	88 (23)	197 (64)	587 (90)	381 (44)
BE	P1	852 (167)	106 (11)	25 (8)	25 (17)	4 (0.2)	128 (55)	65 (15)	223 (68)	577 (73)	292 (173)
	P2	850 (135)	112 (22)	21 (8)	26 (14)	4 (0.0)	122 (43)	101 (29)	209 (78)	595 (100)	364 (61)
LA	P1	1333 (612)	181 (60)	35 (19)	34 (26)	4 (0.3)	150 (44)	113 (49)	379 (191)	895 (361)	518 (358)
	P2	2059 (1957)	171 (44)	32 (11)	59 (42)	4 (0.2)	189 (88)	153 (45)	308 (112)	915 (324)	558 (150)