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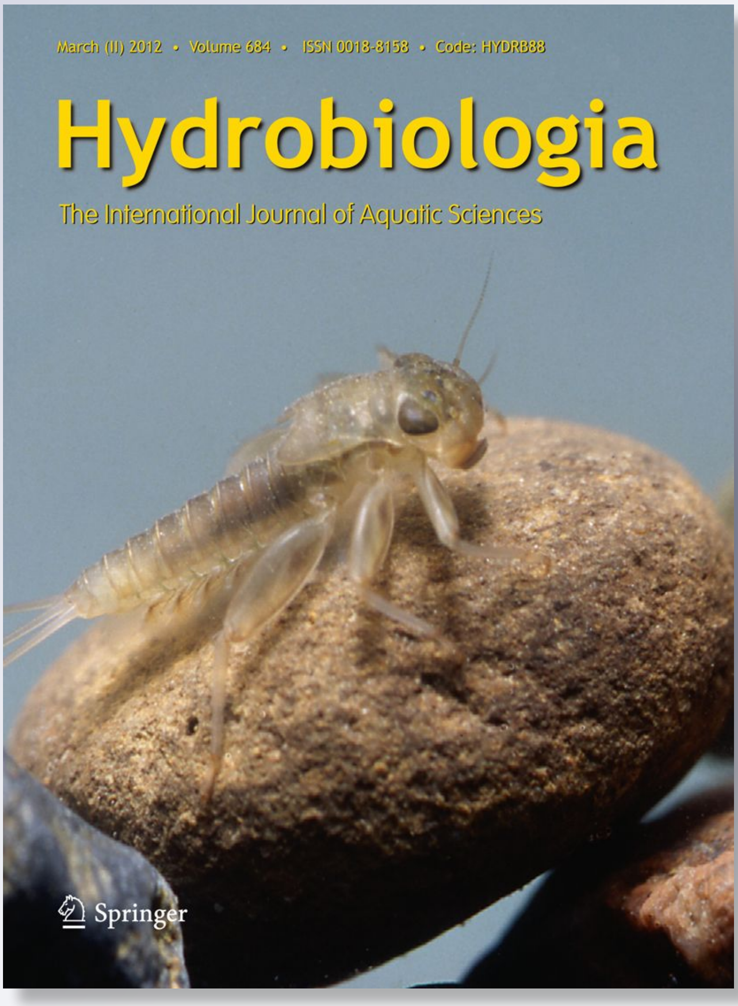

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PRIMARY RESEARCH PAPER

Chironomidae (Diptera) larvae assemblages differ along an altitudinal gradient and temporal periods in a subtropical montane stream in Northwest Argentina

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Abstract The objective of this study was to analyze the spatial and temporal dynamics of Chironomidae larvae assemblages in a subtropical mountain river basin of northwestern Argentina. We hypothesized that they would respond to (1) environmental changes along the altitudinal gradient in the *Yungas* forests; (2) environmental changes caused by spates (e.g., increased discharge or sediment transportation). We sampled five sites along an altitudinal gradient of ca. 1,500 m (from 680 to 2,170 m) during low-water and high-water period for 2 years. The Chironomidae larvae assemblages varied along the altitudinal gradient and between sampling periods based on an indicator species analyses and an ordination analyses (NMDS). The best indicator for high altitude sites was "Genus X" followed by *Onconeura* sp.2, "Genus 9", "Genus 10", and *Rheotanytarsus* sp.2; while *Rheotanytarsus lamellatus*, *Oliveiriella sanjavieri*, and *Thienemanniella* sp. were good indicators for low altitude sites. *O. sanjavieri* and *R. lamellatus* were the best indicators for high-water period. The most relevant environmental variables influencing their spatial and temporal distribution were altitude, water temperature, conductivity, and pH. This study is the first to analyze and describe in detail the spatial and temporal distribution of Chironomidae larvae assemblages in northwestern Argentina, and most of the taxa reported here are new records for the region.

Keywords Chironomids assemblages · Altitudinal gradient · Low-water period · High-water period · Neotropical

Introduction

The structure and composition of aquatic macroinvertebrates respond in a sensitive and predictable way to environmental changes from the headwaters to the mouth of the lotic systems (Vannote et al., 1980). Besides environmental factors, other variables such as historical features, natural and anthropogenic disturbances, and biological interactions influence the presence and abundance of macroinvertebrates in a particular portion of the river and their replacement along it.

Within the benthic macroinvertebrates, Chironomidae (Diptera) is the most widespread of all aquatic insect families (Pinder & Reiss, 1983; Merrit & Cummins, 1996; Ferrington, 2008); it is ubiquitous

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and diverse, and is the most abundant insect group in all types of freshwater (Armitage et al., 1995; Merrit & Cummins, 1996). Their immature stages (larvae and pupae) play an important role in all levels of the trophic webs in these systems; many are gathering collectors and filtering collectors, others are phytophagous and a few predators (Armitage et al., 1995; Merrit & Cummins, 1996). They constitute an important part of the diet of other invertebrates, fishes, amphibians, and birds. The larvae of some species show very broad ranges of tolerance which allow them to live in extreme conditions of salinity, current velocity, pH, and oxygen concentration (Coffman & Ferrington, 1996). The larval species composition of a particular site closely reflects the freshwater environment in which they live, thus they are good environmental indicators of medium or highly polluted environments (Brodersen & Anderson, 2002). The main factors that influence the distribution of the Chironomidae are temperature and the current regime, which indirectly condition food availability and substrate type (Lindegaard & Brodersen, 1995).

The spatial and temporal changes of the Chironomidae assemblages have been analyzed in different regions. For example, many studies carried out in the Holartic region have registered changes in the Chironomidae larvae assemblages along altitudinal gradients (Thienemann, 1954; Prat et al., 1983; Ward & Williams, 1986; Lindegaard & Brodersen, 1995). These studies reported that Orthocladiinae, Diamesinae, and Prodiamesinae are the predominant taxa in high mountain streams while Chironominae (particularly Chironomini) increase toward the mouth of these systems. Although little is known about the Chironomidae for the Neotropical region, a few studies have reported a similar pattern to the one described above (Tejerina & Molineri, 2007; Scheibler, 2007; Medina et al., 2008; Acosta, 2009).

The temporal variation of the Chironomidae assemblages is associated with spates and floods, which are common disturbances in streams and have been recognized as important features structuring invertebrate assemblages (Grimm & Fisher, 1989; Grimm, 1993). Some studies reported the influence of these disturbances on the abundance and richness of Chironomidae, some species disappear from the stream after the spates while others decrease in abundance but persist, showing that their behavior may vary greatly (Langton & Casas, 1999; Rossaro et al., 2006). However, most of these studies are based on pupal exuviae because information of the response of larval chironomids to temporal variation is very scarce.

In the subtropical mountain forest of northwestern Argentina (also known as *Yungas*), there are many studies that describe the assemblages of macroinvertebrates (Domínguez & Ballesteros Valdez, 1992; Domínguez & Fernández, 1998; Romero & Fernández, 2001; Fernández et al., 2001, 2002, 2009; Fernández & Molineri, 2006; Mesa & Fernández, 2007; Von Ellenrieder, 2007; Mesa, 2010a), but either they ignored the Chironomidae or only considered them at the family or subfamily level without further detail, except for Molineri (2008) and Tejerina & Molineri (2007) who identified part of the Chironomidae assemblages at the generic level. Thus, detailed information about their specific or ecological diversity for these latitudes is lacking. Studying their spatial and temporal dynamics in subtropical mountain streams will allow a better understanding of the functioning of these environments. Specifically, we aimed to: (1) describe the structure and composition of the Chironomidae larvae assemblages in a subtropical mountain river basin, (2) analyze their spatial distribution along an altitudinal gradient and their temporal variation during low-water period (spring) and high-water period (summer), and (3) relate the most relevant environmental variables (such as conductivity, water temperature, pH, current velocity, mean channel width, mean depth, and mean velocity) with the Chironomidae larvae assemblages in these streams. We hypothesized that the Chironomidae larvae assemblages (1) would respond to the environmental changes along the altitudinal gradient in the *Yungas* forests. We expected to find cold stenothermal taxa in high altitude sites and eurithermal taxa in low altitude sites; (2) would respond to the environmental changes caused by spates (e.g., increased discharge or sediment transportation). We expected to find different composition during low-water and high-water periods, such as less abundance and richness of Chironomidae during low-water period. This study provided detailed information about the Chironomidae larvae assemblages (at genus and species level when possible) at different altitudes and periods in a subtropical montane stream of Argentina; and is the first to take into account the larval stage of Chironomidae within this region.

Materials and methods

Study area

This study was undertaken in the Argentinean *Yungas* forests (Cabrera & Willink, 1973), a subtropical extension of tropical Andean montane forests; specifically in Lules river basin, a seventh-order catchment located in northwestern Argentina (Fig. 1). This basin has an altitudinal gradient that ranges from 400 to 4,500-m elevation (Mesa, 2006). Along this gradient, temperature, humidity, and precipitation vary, resulting in different vegetation belts: (1) at lower-elevation level (400–700 m) the piedmont forests have been replaced by sugar cane and citrus crops, (2) at mid-elevation (700–1,500 m) vegetation is characteristic of the lower montane zone (Selva Montana) where tree canopy is dominated by *Blepharocalyx salicifolius* (Kunth) O. Berg and *Cinnamomum porphyrium* (Griseb.) Kosterm, within this belt precipitation and biodiversity are the highest, and (3) at upper-elevation (above 1,500 m) forests tend to be monospecific and are dominated by *Podocarpus parlatorei* Pilg. and *Alnus acuminata* H.B.K. (Brown et al., 2001).

Mean annual rainfall is 1,141 mm, which is distributed in a monsoonal regime with dry winters-springs and rainy summers. The rainy season lasts from November to April, during which 80–90% of annual rainfall occurs (high-water period), whereas the dry period extends from April to October (low-water period) (data recorded by Obispo Colombres Meteorological Station of Tucuman province, period 1961–1990). Thus, during the rainy season these streams increase their discharge and transport more sediment than during the dry period when waters are less dynamics, allowing the proliferation of green algae.

Two main types of disturbances affect the richness and abundance of the aquatic macroinvertebrates community (including Chironomidae) in the Lules

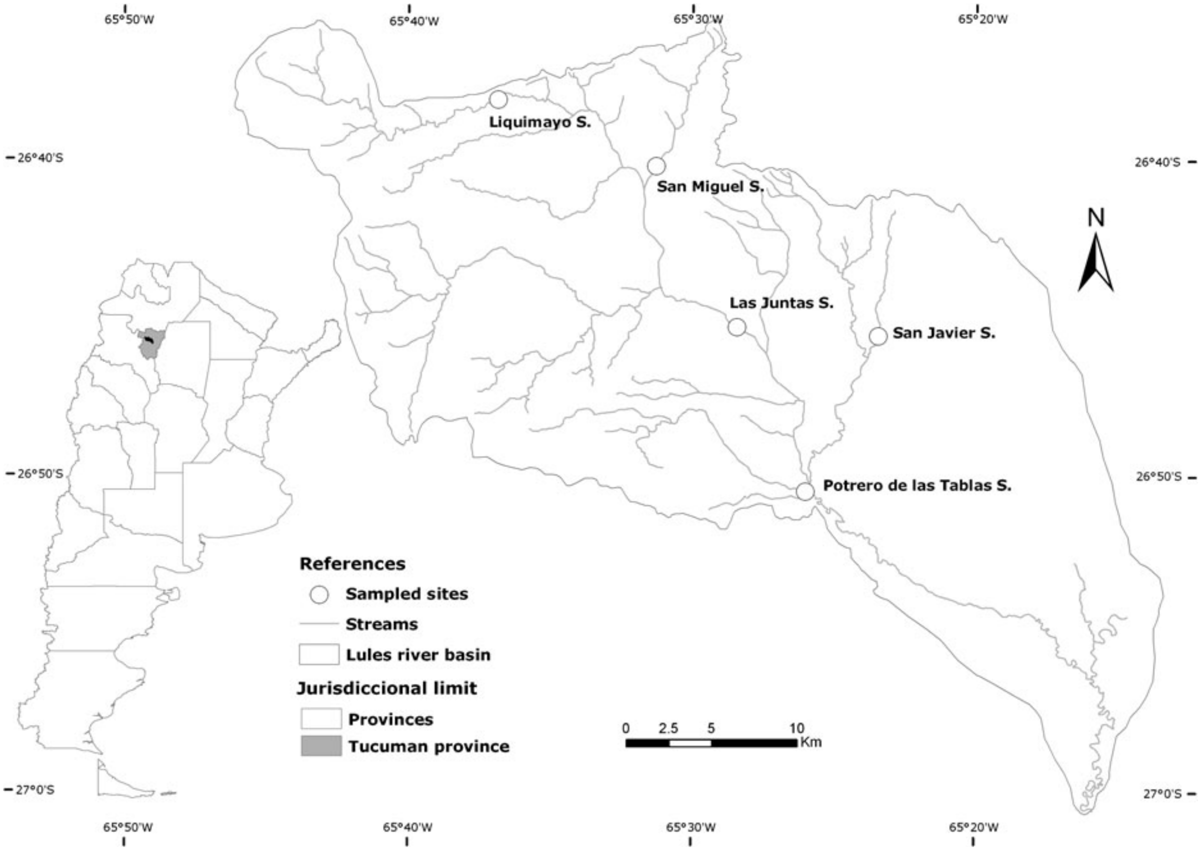

Fig. 1 Map of Lules river basin showing the sampling sites, Tucumán, Argentina

river basin. Spates which are a natural disturbance and occur during the rainy season, and human impact caused mainly by farming and cattle grazing. The latter disturbance modifies the riparian vegetation where exotic species are mixed with native species, being more pronounced in streams below 900-m elevation, whereas at higher elevations the riparian vegetation of the streams is better preserved (Mesa, 2010b).

Field and laboratory methods

We selected five sample sites (Liquimayo, San Miguel, Las Juntas, San Javier, and Potrero de las Tablas) along the Lules river basin which represented an altitudinal gradient of ca. 1,500 m (from 680 to 2,170 m) (Fig. 1; Table 1). In each site, we took two seasonal samples per year, during low-water period (September—early spring) and during high-water period (March–late summer) from Sept 2005 to March 2007 (four samples total for each site), except for Liquimayo stream where we took two samples in spring 2003 and summer 2004, and in Las Juntas where we took three instead of four samples due to climatic conditions ($n = 17$) (Table 1). Although Liquimayo samples were taken before the rest of the samples, no important climatic variation occurred during these years. Thus, we believe Liquimayo samples are comparable to the other ones.

In each site (and sampling period), we took three benthic samples (replicates) with a Surber sampler (0.09 m^2, 300 µm mesh size). All the material was fixed in 4% formaldehyde solution. In the laboratory, chironomids larvae were sorted, counted and identified to morphospecies using a stereoscopic microscopic with a 10× magnification. From each morphospecies, we chose those corresponding to the fourth stage larvae to make permanent microscope slides (@10,000 larvae in total). Larvae were mounted complete (including head capsules and body) following the conventional method proposed by Epler (2001). Larvae were identified using a compound microscope with 40× magnification to genus or species level when possible using the taxonomic keys (Wiederholm, 1983; Epler, 1995, 2001; Trivino-Strixino & Strixino, 1995; Merrit & Cummins, 1996; Paggi, 2001, 2009) and taxonomic descriptions to confirm appropriate identifications (Brundin, 1966;

Table 1 Environmental parameters measured in each sampling site and date

Site and altitude	Site code	Discharge (m^3/s)	Water temperature (°C)	Conductivity (µS/cm)	Mean width (m)	Mean depth (cm)	Mean velocity (m/s)	pH	Sample date
Liquimayo (LI)	LI_{L1}	0.78	14.4	57	8.8	13.1	0.72	7	Sep 03
2,170 m	LI_{H1}	0.367	11	57	9	10	0.55	7	Jan 04
San Miguel (SM)	SM_{L1}	0.01	20	166	1.4	0.07	0.13	8	Sept 05
1,300 m	SM_{H1}	0.49	19	33	3.6	0.45	0.6	6	Mar 06
	SM_{L2}	0.01	19	163	1.4	0.12	0.29	7	Sept 06
	SM_{H2}	0.07	17	145	1.4	0.17	0.33	6	Apr 07
Las Juntas (LJ)	LJ_{L1}	0.96	15	135	12.7	0.37	0.82	8	Sept 05
925 m	LJ_{L2}	0.89	15.5	129	13.4	0.43	1.06	6	Sept 06
	LJ_{H1}	4.27	21	108	4.27	0.64	1.32	6	Mar 07
San Javier (SJ)	SJ_{L1}	0.08	16	373	4.1	0.12	0.69	8	Sept 05
860 m	SJ_{H1}	0.10	19	276	3.8	0.1	0.31	7	Mar 06
	SJ_{L2}	0.06	20	270	4.2	0.13	0.63	6	Sept 06
	SJ_{H2}	0.24	20	229	2.6	0.27	0.44	7	Mar 07
Potrero de las Tablas (PT)	PT_{L1}	0.30	20	657	11.1	0.24	0.75	9	Sept 05
680 m	PT_{H1}	1.00	20	220	12	0.31	0.46	6	Mar 06
	PT_{L2}	0.15	19	569	5.8	0.25	0.58	8	Sept 06
	PT_{H2}	0.71	25	344	7	0.63	1.31	7	Mar 07

Codes: Sub-indexes L and H refer to low-water and high-water period, while 1 and 2 correspond to the first (2005) and second (2007) year of field sampling, respectively

Roback & Coffman, 1983; Tejerina & Paggi, 2009a, b). The rest of the material that was not used to make permanent microscope slides was preserved in 75% ethanol.

At each sampling occasion, we measured the following environmental variables: conductivity (with a portable sensor, Methrom E587), water temperature (with a standard thermometer), pH (with a pH paper), current and mean velocity (with a Global Flow Probe FP101–FP201), mean channel width (with meter tape), and mean depth (with a two meter ruler) (Table 1). Although nutrients and dissolved oxygen are important variables they were not measured due to lack of budget and equipment limitation.

Data analyses

For a general description of the structure and composition of the Chironomidae larvae assemblages, we estimated the relative abundance of each subfamily for each stream and sampling period (low-water and high-water period).

To identify which larvae taxa were characteristic of each site and period, we performed two Indicator Species Analyses (Dufrene & Legendre, 1997). This method produces indicator values (IV) calculated as the product of the relative abundance and relative frequency of each species for every sites (or period). IV ranges from 0% (no indication) to 100% (perfect indication). Perfect indication occurs when a given taxa has the highest percentage abundance in a particular site (or period) and also is present in all samples of that site. We used a Monte Carlo test (1,000 permutations) to evaluate the statistical significance of the observed maximum IV for each larvae taxa. When we ran the Indicator Species Analyses for sampling period, we kept the different years separated to explore inter-annual variation.

To describe the spatial distribution and temporal variation of Chironomidae larvae assemblages, we performed a Non Metric Multi-dimensional Scaling (NMDS; Kruskal & Wish, 1978) based on a Bray–Curtis distance matrix (Legendre & Legendre, 1998) between sites in different periods ($n = 17$) calculated from larvae (e.g., genus or species) mean density (individuals/m^2). To improve the convergence of the NMDS, before running the ordination we log($x + 1$) transformed the species densities to reduce the variability within and among taxa. In computing similarity between two sites at a given period, the Bray–Curtis index compares the density of each taxon. Sites that share taxa with comparable densities are considered more similar; and as a result, are closer in the multivariate space (Jogman et al., 1995). The advantage of NMDS over other ordination methods is that no assumptions are made about how taxa are distributed along environmental gradients (Kenkel & Orloci, 1986). We performed an autopilot procedure (slow and thorough mode) to decide the best solution (McCune & Grace, 2002).We used a two-dimensional configuration because the final stress (an index of agreement between the distances in the graph configuration and the distances in the Bray–Curtis matrix) was 11.04 (most ecological community data sets have solutions with stress between 10 and 20) and was different from chance (Monte Carlo: 500 runs with randomized matrix, $P < 0.05$; McCune & Grace, 2002). To relate the environmental variables of each site with the Chironomidae larvae assemblage, we used Kendall's correlation coefficient (Sokal & Rohlf, 1995) between the scores in the axes of the NMDS and environmental parameters measured in each sampling occasion.

We performed multivariate analyses with PC-ORD 5 (McCune & Mefford, 1999) and univariate analyses with STATISTICA 6.0 (Statsoft, Inc., 2001).

Results

Structure and composition of Chironomidae larvae assemblages

We found 24,532 Chironomidae larvae across all sample sites. We identified 27 taxa belonging to four subfamilies and 23 genera (Table 2). Orthocladiinae and Chironominae showed the highest values of relative abundance and richness (48% and 13 genera, 46% and 9 taxa, respectively), while Tanypodinae and Diamesinae showed the lowest values. Tanypodinae had 5% of relative abundance with 4 taxa, and Diamesinae 1% with 1 taxon.

The relative abundance of the four Chironomidae subfamilies varied along the altitudinal gradient (Fig. 2). Orthocladiinae was more abundant in high altitude sites (Liquimayo 2,170 m) and decreased downstream. Chironominae showed the opposite pattern, being more abundant at lower altitudes (San

Table 2 Mean density (individuals/m^2) of Chironomidae larvae registered for each sampling site listed by subfamily and genus/species

Subfamily	Taxa	Code	LI (2,170 m)	SM (1,300 m)	LJ (925 m)	SJ (860 m)	PT (680 m)
Diamesinae	*P. cinerascens*	Parah	187	103	7	0	0
Tanypodinae	*Pentaneura* sp.	Penta	13	114	102	191	4
	Pentaneurini1	Pent1	7	0	0	0	800
	Larsia sp.	Larsi	0	17	1	41	9
	Apsectrotanypus sp.	Apsec	2	2	0	0	42
Orthocladiinae	"Genus 9"	Gene9	17	0	0	0	0
	"Genus 10"	Gen10	39	0	0	0	0
	Corynoneura sp.	Coryn	2	21	33	20	38
	Onconeura sp.1	Onco1	22	7	142	208	110
	Onconeura sp.2	Onco2	119	16	81	0	0
	Thienemanniella sp.	Thien	52	10	41	96	177
	O. sanjavieri	Olive	9	12	118	259	149
	Cricotopus	Crico	665	1,461	735	2,060	3,677
	"Genus X"	GeneX	146	7	6	0	0
	Nanocladius sp.	Nanoc	0	21	0	62	13
	Lopescladius sp.	Lopes	2	18	44	0	28
	Paracladius?	Parac	0	0	0	0	249
	Parametriocnemus sp.	Param	70	37	28	16	136
Chironominae	*Pseudochironomus* sp.	Pseud	30	215	425	11	0
	Tanytarsus sp.1	Tany1	33	313	13	15	2,928
	Tanytarsus sp.2	Tany2	0	1	0	1	0
	R. lamellatus	Rheo1	4	12	48	4,258	397
	Rheotanytarsus sp.2	Rheo2	176	2	285	0	1
	Polypedilum sp.	Polyp	13	6	148	866	681
	Harnischia complex	Harni	0	0	0	0	53
	Chironomus gr decorus	Chiro	0	0	0	0	662
	Dicrotendipes sp.	Dicro	0	0	0	7	11

Taxa abbreviations (code) used in the NMDS ordination diagram are provided. Names within quotes are not formally described taxa identified by other authors (see text). *?* denotes uncertain identifications

Javier 860 m). Diamesinae had a low abundance, peaking in Liquimayo and decreasing toward Las Juntas (925 m), being absent below this altitude, whereas Tanypodinae had low abundance along the whole gradient reaching a peak of 8% in Potrero de las Tablas (680 m) (Fig. 2).

The relative abundance of the four Chironomidae subfamilies also showed temporal variation (Fig. 3). Orthocladiinae was better represented during low-water period (57%) whereas Chironominae was more abundant in high-water period (68%). Tanypodinae and Diamesinae showed very low abundances (6% and lower) in both periods, with Diamesinae even being absent in high-water period (Fig. 3).

Spatial and temporal variation of Chironomidae larvae assemblages

Indicator species analysis showed significant association between some taxa and sampling sites (Table 3). "Genus X" (Orthocladiinae) was a very good indicator of Liquimayo site (2,170 m) followed by *Onconeura* sp.2 (Orthocladiinae), "Genus 9" (Orthocladiinae), "Genus 10" (Orthocladiinae), *Rheotanytarsus* sp.2 (Chironominae), and *Paraheptagyia cinerascens* (Diamesinae). *Rheotanytarsus* sp.2 was the only taxon of the Chironominae subfamily (Tanytarsini) with a significant indicator value for this high altitude site. *Pseudochironomus* sp. (Chironominae)

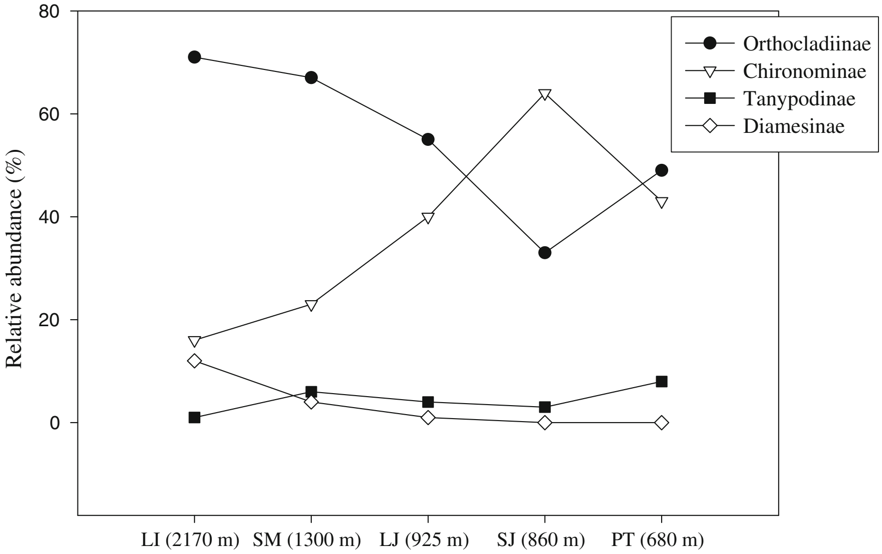

Fig. 2 Relative abundance of Chironomidae subfamilies along the altitudinal gradient

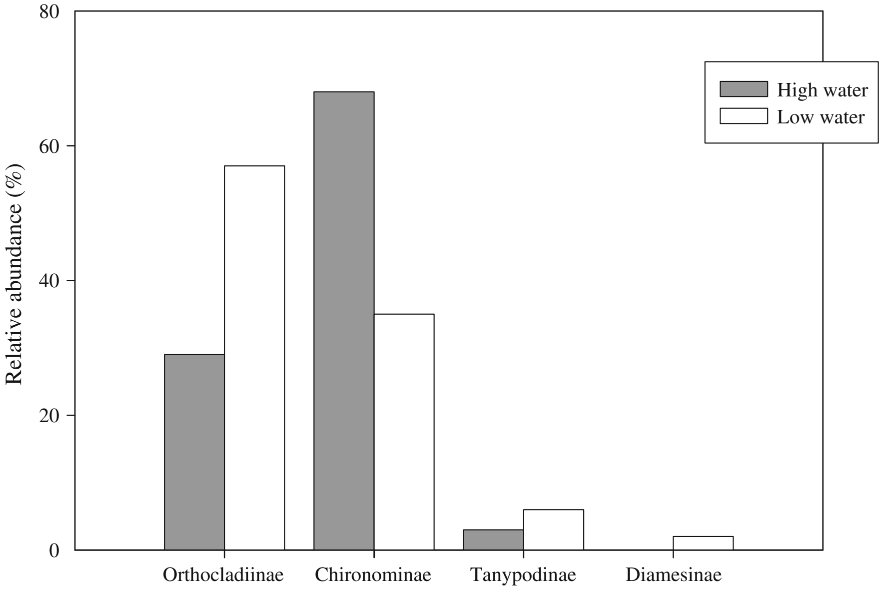

Fig. 3 Relative abundance of Chironomidae subfamilies in low-water and high-water period

was significantly associated with Las Juntas (925 m). *Rheotanytarsus lamellatus* was a good indicator for San Javier (860 m), followed by *Oliveiriella sanjavieri* (Orthocladiinae), *Nanocladius* sp. (Orthocladiinae), and *Pentaneura* sp. (Tanypodinae). Finally, *Thienemanniella* sp. (Orthocladiinae) was associated with the lower-elevation site Potrero de las Tablas (680 m) (Table 3).

Indicator species analysis also showed significant association between some taxa and sampling periods (Table 3). *Tanytarsus* sp.1 (Chironominae), *Pseudochironomus* sp., *Corynoneura* sp. (Orthocladiinae), *P. cinerascens*, *Cricotopus* (Orthocladiinae), *Onconeura* sp.2, *Rheotanytarsus* sp.2, *Parametriocnemus* sp. (Orthocladiinae), Pentaneurini 1 (Tanypodinae), "Genus 9" and "Genus 10" were associated with low-water period (only first year), while *R. lamellatus*, *O. sanjavieri*, *Onconeura* sp.1, and *Larsia* sp. (Tanypodinae) were associated with high-water period (only second year) (Table 3).

Table 3 Indicator values (IV) for Chironomidae taxa along sampling sites and periods

Subfamily	Taxa	IV for sampling sites					IV for sampling periods			
		LI (2,170 m)	SM (1,300 m)	LJ (925 m)	SJ (860 m)	PT (680 m)	Low-water$_1$	Low-water$_2$	High-water$_1$	High-water$_2$
Diamesinae	*P. cinerascens*	**32***	9	1	0	0	**52****	1	0	0
Tanypodinae	*Pentaneura* sp.	3	26	16	**43***	0	31	10	6	24
	Pentaneurini1	1	0	0	0	18	**38****	0	0	0
	Larsia sp.	0	4	0	20	4	1	5	0	**32***
	Apsectrotanypus sp.	3	0	0	0	8	15	0	1	0
Orthocladiinae	"Genus 9"	**50****	0	0	0	0	**23***	0	0	0
	"Genus 10"	**50****	0	0	0	0	**23***	0	0	0
	Corynoneura sp.	1	10	9	10	22	**57****	11	0	10
	Onconeura sp.1	4	0	23	38	18	10	12	11	**43***
	Onconeura sp.2	**60****	4	16	0	0	**46***	3	1	0
	Thienemanniella sp.	14	1	5	19	**48***	21	8	6	36
	O. sanjavieri	1	1	17	**48***	21	9	19	5	**46***
	Cricotopus	8	14	8	25	41	**49***	32	2	16
	"Genus X"	**93****	0	0	0	0	23	1	4	0
	Nanocladius sp.	0	8	0	**34***	1	24	2	1	3
	Lopescladius sp.	1	4	15	0	19	18	0	4	11
	Paracladius?	0	0	0	0	9	8	0	0	0
	Parametriocnemus sp.	25	4	4	1	21	**41***	30	1	0
Chironominae	*Pseudochironomus* sp.	5	24	**43***	0	0	**63****	5	0	2
	Tanytarsus sp.1	1	7	0	0	46	**96****	2	0	0
	Tanytarsus sp.2	0	4	0	4	0	4	0	0	4
	R. lamellatus	0	0	0	**75***	5	1	5	0	**61***
	Rheotanytarsus sp.2	**45***	0	14	0	0	**46***	0	0	0
	Polypedilum sp.	1	0	5	54	31	24	4	2	41
	Harnischia complex	0	0	0	0	9	8	0	0	0
	Chironomus gr decorus	0	0	0	0	9	8	0	0	0
	Dicrotendipes sp.	0	0	0	7	5	4	0	8	0

Note * $P < 0.05$; ** $P < 0.001$

Numbers in bold indicate maximum IV for each taxa at each site and periods. Monte Carlo test was used to asses their significance. Subindex 1 and 2 correspond to the first (2005) and second (2007) year of field sampling, respectively

Spatial–temporal distribution of Chironomidae larvae assemblages in relation to environmental variables

Sampling sites segregated along two axes of the NMDS ordination based on their Chironomidae larvae composition. Axis 1 was associated with the altitudinal gradient, high altitude sites (e.g., Liquimayo, San Miguel) were positioned toward the positive side of axis 1 while lower sites (San Javier, Potrero de las Tablas) were placed toward the negative side of this axis (Fig. 4). Las Juntas grouped closer to higher sites during low-water period and closer to lower sites during high-water period. Axis 2 was associated with the temporal variation as high-water samples (H1, H2) were located toward the positive side (except for

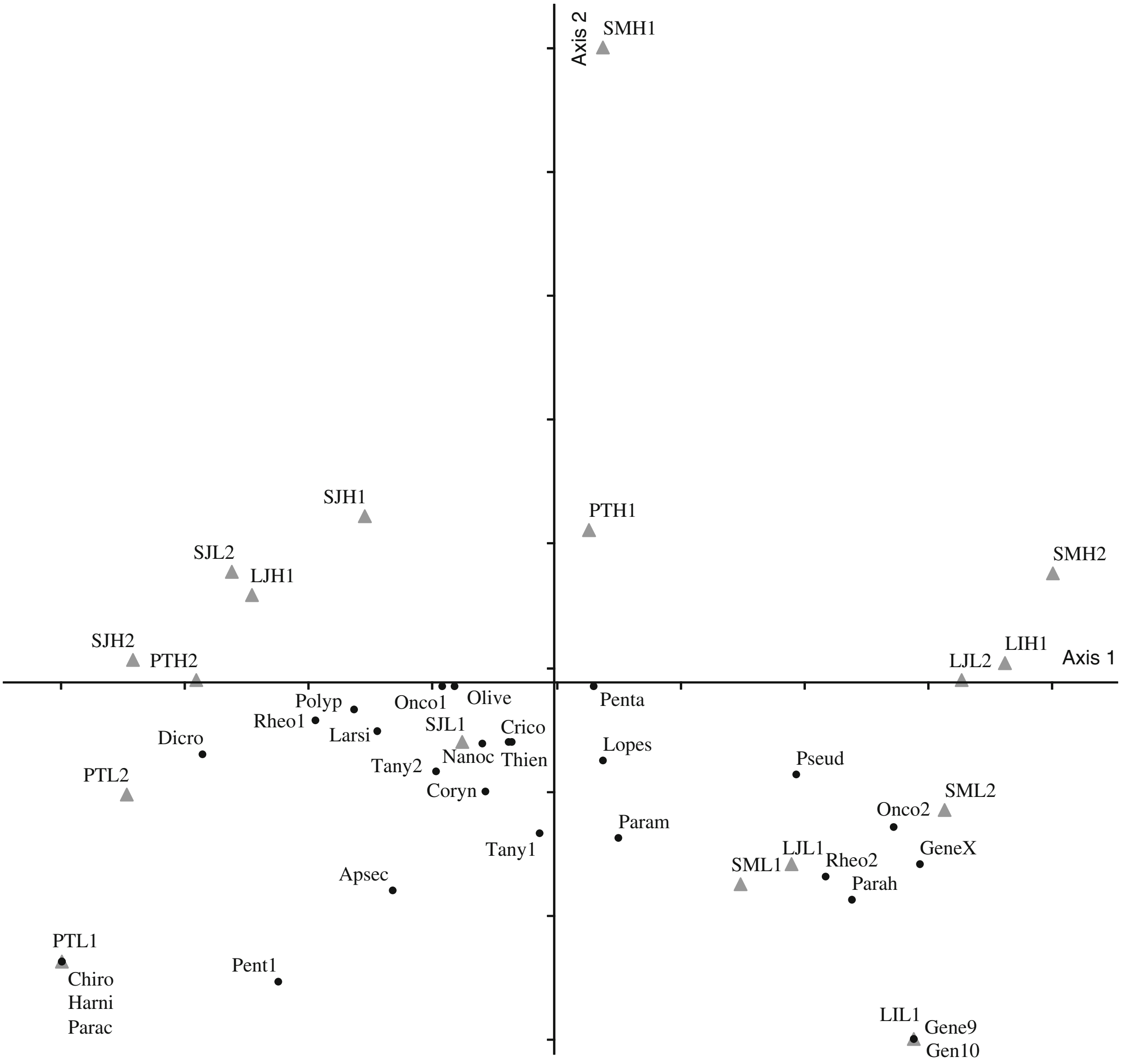

Fig. 4 Non-metric multidimensional scaling (NMDS) ordination diagram of sampling sites at a given period based on Chironomidae larvae composition. *Triangles* indicate sampling sites, see Table 1 for sites codes. *Circles* indicate optimal abundance of taxa, see Table 2 for taxa abbreviations

SMH1) while low-water samples (L1, L2) tended to be located toward the negative side of this axis (Fig. 4).

Kendall's correlation analyses identified that altitude was positively associated with axis 1 (high altitude sites, Liquimayo and San Miguel) while water temperature and conductivity were negatively associated with this axis (lower sites, San Javier and Potrero de las Tablas) (Table 4). Only pH was negatively associated with axis 2 (low-water samples, L1 and L2).

Discussion

Structure and composition of Chironomidae larvae assemblages

The Chironomidae larvae richness found in the Lules river basin was relatively high (27 taxa) and comparable to other Andean rivers (Brundin, 1966; Roback & Coffman, 1983; Scheibler, 2007; Tejerina & Molineri, 2007; Medina et al., 2008; Acosta, 2009).

Table 4 Kendall correlation coefficients between environmental parameters measured in each sampling site at a given period and their scores in the non-metric multidimensional scaling (NMDS) ordination

Environmental variables	Axis 1	Axis 2
Discharge (m^3/s)	0.015	0.191
Water temperature (°C)	**−0.517****	0.141
Conductivity (μS/cm)	**−0.554****	−0.111
Mean width (m)	−0.067	−0.156
Mean depth (cm)	0.125	0.022
Mean velocity (m/s)	−0.147	−0.088
Altitude (msnm)	**0.642*****	−0.096
pH	−0.274	**−0.600*****

Note *** $P < 0.001$; ** $P < 0.01$

For example, Roback & Coffman (1983) recorded 19 genera of Chironomidae for Venezuela, and 31 genera for Peru and Bolivia. Recently, Acosta (2009) reported 32 genera for Peru. At subfamily level, Orthocladiinae was consistently the most diverse, as found in many other studies of Andean rivers (Roback & Coffman, 1983; Scheibler, 2007; Tejerina & Molineri, 2007; Acosta, 2009).

The Chironomidae composition of our high altitude sites was similar to that of the Central-Andean and Andean-Patagonianstreams of Argentina. For example, Scheibler (2007) reported 13 taxa of Chironomidae in the Mendoza stream; eight of these [*Paraheptagyia*, *Pentaneura*, *Onconeura*, "Genus 9", *Cricotopus*, *Parametriocnemus*, *Polypedilum* (Chironominae), *Chironomus* (Chironominae)] were found in high altitude sites of our study (Liquimayo and San Miguel). In addition, Scheibler (2007) found *Podonomus* (Podonominae), *Parochlus* (Podonominae), and *Podonomopsis* (Podonominae); although we did not register *Podonomus* in this study, this genus was found in Liquimayo previously (Tejerina & Molineri, 2007). On the other hand, the Chironomidae composition found at low altitude sites of this study was similar to the composition of tropical–subtropical rivers, specifically to that reported for lowland streams of San Luis and Entre Rios (Argentina), where Chironominae was the most diverse subfamily (Medina & Paggi, 2004; Pave & Marchese, 2005). The common genera between those studies and this one were the Chironominae genera *Pseudochironomus*, *Tanytarsus*, *Rheotanytarsus*, *Polypedilum*, *Chironomus*, *Dicrotendipes*; the Orthocladiinae genera *Corynoneura*, *Cricotopus*, *Thienemanniella*, *Nanocladius*, *Lopescladius*; and the Tanypodinae genera *Apsectrotanypus* and *Larsia*.

Orthocladiinae and Chironominae were the most abundant subfamilies, but their relative contributions were different along the altitudinal gradient and between sampling periods. Orthocladiinae was abundant in high altitude sites and their abundance decreased gradually with altitude. The opposite happened with Chironominae which increased at low altitude sites. This distribution pattern coincides with the distribution pattern found in mountain rivers of other regions of Argentina (Miserendino, 2001; Medina et al., 2008; Principe et al., 2008; Scheibler et al., 2008); and also with the distribution pattern found in lotic systems in the northern hemisphere (Thienemann, 1954; Lindegaard & Brodersen, 1995). However, in Potrero de las Tablas (680 m, low altitude site) Orthocladiinae increased in abundance and was similar to Chironominae. This site showed some human impact (e.g., houses, trash and cattle, personal observation) that could result in nutrient enrichment of the water and algae proliferation. This site was characterized by the presence of filamentous algae favoring Orthocladiinae, mainly the phytophagous *Cricotopus*. According to Cranston and Reiss (1983), *Cricotopus* is tolerant to changing conditions, inhabit all types of freshwater, and is frequently associated with algae and aquatic macrophytes. Coinciding with our results, Mesa (2010a, b) reported that changes in land use in this site caused an increase in abundance of tolerant taxa of macroinvertebrates. On the other hand, Chironominae was more abundant during high-water period, whereas for the low-water period Orthocladiinae was the most abundant subfamily. Scheibler (2007) reported a similar behavior of the seasonal variation for Chironomidae in the Mendoza stream where Orthocladiinae reached their maximum abundance during the winter (low-water period) and Chironominae during the summer (high-water period).

Spatial and temporal variation of Chironomidae larvae assemblages

The Chironomidae larvae assemblages differed among sites based on their indicator values. "Genus X" proved to be a very good indicator of Liquimayo (93%), being absent elsewhere. Accordingly, this morphospecies was identified in high altitude Andean streams of Peru (Prat et al., 2010). Also, *Onconeura* sp.2, "Genus 9", "Genus 10", *P. cinerascens* and *Rheotanytarsus* sp.2 were good indicators of this site. Roback and Coffman (1983) described "Genus 9" and "Genus 10" in high altitude streams of Bolivia and Scheibler (2007) found "Genus 9" and *P. cinerascens* in high altitude and low-temperature streams of Mendoza. At lower altitudes (below 860 m elevation), *R. lamellatus*, *O. sanjavieri*, *Nanocladius* sp., *Pentaneura* sp., and *Thienemanniella* sp. were good indicators. Principe et al. (2008) studied the fauna of Chironomidae in streams of Cordoba between 454 and 875 m of elevation and in agreement with our results, found *Thienemanniella* as a good indicator of 800-m elevation sites. These authors reported *Rheotanytarsus*, *Onconeura*, and *Nanocladius* as indicators of 875-m elevation site; these genera also characterized our site of 860 m (San Javier) in the Lules basin. At intermediate altitudes sites (Las Juntas, 925 m), only *Pseudochironomus* was revealed as a good indicator. Similarly, Maldonado & Goitia (2003), who studied the benthic macroinvertebrate community in Yungas streams of Bolivia, found no species that correlated with intermediate altitude streams.

The Chironomidae assemblages also differed between sampling periods based on their indicator values and between years within the same period. For example, the first low-water period and the second high-water period showed associations with different taxa while the other 2 years (second low-water period and first high-water period) had no associations, showing the relevance of the inter-annual variation. During the second high-water period (summer 2007) there was a prolonged period of rainfall which caused major flooding in nearby areas. During this period *R. lamellatus* showed the highest value (61%) suggesting it is a good indicator for the summer. During this period the discharge and current velocity were higher favoring the presence and abundance of rheobiontics species as *R. lamellatus*. Its larvae live within tubes that they build and adhere to different substrates, from where they capture suspended particles of debris with a mesh of silk used to gather food and for the construction of the tubes (Pinder & Reiss, 1983). Also, *O. sanjavieri* and *Onconeura* sp.1 showed relatively high indicator values (46 and 43%, respectively), being the only two species of Orthocladiinae that showed an increased abundance during this period. These genera have a wide distribution range and tolerate moderate temperatures, neutral to alkaline pH and high conductivity values (Krestian et al., 2010), coinciding with the conditions where they were collected in this study. Finally, *Larsia* sp. was the only genus of Tanypodinae that presented a relatively good indicator value (32%) for high-water period. On the other hand, we found a larger number of taxa (*P. cinerascens*, Pentaneurini 1, *Corynoneura* sp., *Parametriocnemus* sp., *Cricotopus*, *Onconeura* sp.2, "Genus 10", "Genus 9", *Rheotanytarsus* sp.2, *Tanytarsus* sp.1, and *Pseudochironomus* sp.) to be indicative of low-water period in the first year (winter 2005). This may be due to the fact that during this year the drought was greater than the following low-water year.

Spatial–temporal distribution of Chironomidae larvae assemblages in relation to environmental variables

The Chironomidae larvae assemblages varied along the altitudinal gradient and between sampling periods, and were related to environmental variables, such as temperature, conductivity, and pH. Lower sites (Potrero de las Tablas and San Javier) segregated together with mainly taxa of the Chironominae and Tanypodinae subfamilies (*R. lamellatus*, *Polypedilum* sp., *Tanytarsus* sp.1, Pentaneurini 1, *Larsia* sp., and *Apsectrotanypus* sp.) and were related with high-water temperatures and conductivity values (negative side of axis 1). On the other hand, Diamesinae ****(*Pareheptagyia cinerascens*) and most of Orthocladiinae genera characterized higher altitude sites (Liquimayo and San Miguel), with *Rheotanytarsus* sp.2 and *Pseudochironomus* sp. being the only genera within the Chironominae abundant in these sites. These results are consistent, as all these taxa are typical of cold water (Cranston & Reiss, 1983). Las Juntas segregated with low and high altitude sites depending on their sampling period. It was associated with high altitude sites during low-water period because it had *P. cinerascens*, *Onconeura* sp.2, *Pseudochironomus* sp., and *Rheotanytarsus* sp.2, among others. On the other hand, it was associated with low altitude site during high-water period because it had *R. lamellatus*, and *Polypedilum* sp., among others. This revealed that their taxonomic composition reflects its intermediate spatial position (925-m elevation) along the gradient. Sites sampled in the low-water period (winter) segregated together and presented alkaline pH (between 7 and 9) (negative side of axis 2) reflecting that the streams within this region are typically alkaline especially during this period (García et al., 2007). Potrero de las Tablas had the most alkaline pH value (9) and, as mentioned above, the maximum conductivity values in the first low-water period (winter 2005). For this sample period and site, we registered some exclusive taxa such as *Chironomus* gr. *decorus*, *Harnischia* complex (Chironominae), and *Paracladius*? (Orthocladiinae). Also *Dicrotendipes* sp. (Chironominae), *Apsectrotanypus* sp., and Pentaneurini 1 reached their optimum abundance in Potrero de las Tablas. Pinder & Reiss (1983) reported that these taxa are typical of calm water with low current velocity and inhabit fine sediment, coinciding with the conditions where they were registered in our study.

Overall, this study constitutes the first to describe in detail (at genus and species level when possible) the spatial and temporal Chironomidae larvae assemblage dynamics in a subtropical mountain river of northwestern Argentina. Moreover is the first to take into account the larval stage of Chironomidae within this region. Most of the taxa reported here correspond to new records for this region revealing important taxonomic, ecological, and biological aspects for the Chironomidae allowing a better understanding of the functioning in these lotic environments. In this sense, this study will be useful as a baseline for future studies, in management, conservation and monitoring programs. Also, this study coincides with other studies carried out mainly in temperate regions about the importance of altitude and related variables, such as water temperature, as factors structuring Chironomidae assemblages (Armitage et al., 1995; Lindegaard & Brodersen, 1995).

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