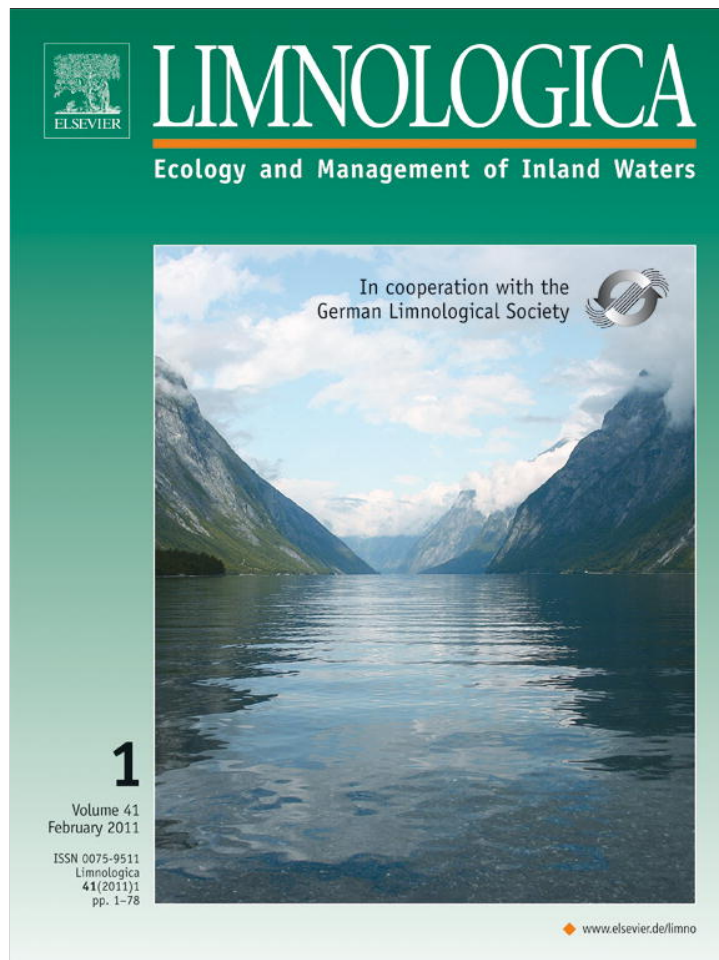


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Distribution of Macroinvertebrate assemblages along a saline wetland in harsh environmental conditions from Central-West Argentina

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ABSTRACT

The goal was to examine how macroinvertebrate taxonomic richness and density respond to spatial-temporal changes and to the influence of water physicochemical characteristics along the Bañado Carilauquen (BC). Benthic samplings were conducted seasonally and environmental parameters were recorded in five reaches of the BC. Cluster analysis was applied to compare taxonomic richness among sites. Community structure and spatial-temporal variation were explored using logarithmic regression. CCA was applied to explore the relationship between species and environmental variables. A total of 36 taxa were identified, predominantly insects. A growing gradient of conductivity and hardness was registered between headwaters (HD; relatively soft waters) and outlet (OL; very hard and saline waters). Total density of taxa showed significant differences among sampling sites and climate seasons. A decline in richness and density was observed from HD to OL. The spatial conductivity gradient is the major factor modulating macroinvertebrate distribution along this saline arid wetland. With the exception of the headwaters, hard, eutrophic, polysaprobic and contaminated waters such of those of the BC represent critical conditions for the development of macroinvertebrate assemblages.

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Introduction

The values traditionally attributed to non-arid wetlands also apply to most arid-zone wetlands, and hold economic, cultural, aesthetic, scientific, environmental, and conservation importance (Williams et al., 1990; Myers and Resh, 1999; Timms, 2005). The relevance of reliable surface water in arid environments has been long recognised, but more so in terms of human or animal uses than for its broader ecological significance (Box et al., 2008). Biological attributes of the natural saline aquatic ecosystems have high ecological and biogeographic value because they are usually exclusive to these kinds of habitats (Williams, 1985; Moreno et al., 2009). Saline lakes provide ideal conditions for ecological studies of aquatic ecosystems, because changes in the biological communities occur more often and more intensely than in freshwater lakes (Comín and Comín, 1992); their community structures and energy flux networks are simpler than in freshwater ecosystems (Hammer, 1986); and the variability of hydrological and physicochemical conditions in these water bodies provides excellent opportunities to examine environmental factors affecting communities such as those of macroinvertebrates (Villagrán-Mella et al., 2006; Timms, 2007).

Similarly to what occurs in other large countries of the Southern Hemisphere like Australia (Timms, 2005), around 60% of the total area of Argentina consists of arid lands (Cabrera and Willink, 1973). However, most of the scientific information about Argentina wetlands comes from the temperate-warm and humid areas of the North and Central East of the country, particularly the La Plata basin, which is the watershed with highest discharge in Argentina and the second largest in South America (Canevari et al., 1999). Aquatic macroinvertebrate assemblages in the arid/semiarid West of Argentina have been in general poorly studied (Modenutti et al., 1998). Available information comes almost exclusively from lotic systems in the Patagonian Andes (Miserendino and Pizzolón, 2000, 2004; Velásquez and Miserendino, 2003; Miserendino, 2007, 2009; Miserendino et al., 2008) and, to a lesser extent, from the Central West of Argentina (Scheibler, 2007; Scheibler and Debandi, 2008; Scheibler et al., 2008; Medina et al., 2008). There is no information on macroinvertebrate species from lentic water bodies from the vast Argentina Central West, or about the ways in which hydrological and physicochemical water conditions affect the distribution patterns of invertebrate macrofauna in this arid/semiarid environment.

Macroinvertebrates are among the most diverse and abundant constituents of the biota of freshwater wetlands, and have been reported as key components of these ecosystems (Sharitz and Batzer, 1999). In saline water bodies, the occurrence of

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macroinvertebrates depends, among other factors, on water permanence (Moreno et al., 2009) and hardness (Thorp and Covich, 2001). In lentic ecosystems, high levels of conductivity result in significant drops in abundance and taxonomic richness of macroinvertebrate fauna (Piscart et al., 2005; Quintana et al., 2006; Timms, 2007; Waterkeyn et al., 2008; Carver et al., 2009). In arid/semiarid environments, where rainfall is seasonal, variable and significantly less than the evaporation rate, hydrological and chemical water conditions depend, among other factors, on the seasonally variable interactions between surface waters and groundwater (Jolly et al., 2008). Additionally, the chemistry of lake water depends on several factors such as geo-lithology of the watershed substrate, salinisation due to anthropogenic processes, climate and atmospheric changes and biological disturbances (Timms, 2005). High salinity and significant variations in water level along with high solar radiation and poorly permeable soils make up stressful environments. However, macroinvertebrate communities respond to spatial-temporal changes in saline waters from arid/semiarid regions, with insects, particularly dipterans and coleopterans, being the best adapted group for these critical conditions (Vidal Abarca et al., 2004).

The Bañado Carilauquen is one of the major components of the endorheic wetland system denominated “Laguna Llanquanelo”, a saline lake located in the South of Mendoza Province, Central West of Argentina. The word “Bañado” is a geographic term and means a wetland under arid conditions. This saline wetland is one of the dryland sites with highest biodiversity (avifauna in particular) in Argentina and worldwide (Sosa, 2005; Coconier, 2005). The area harbours dozens of thousands of specimens of nearly 100 bird species, several of which are migratory and use the area as a resting and feeding site in their inter-hemisphere travels (Blendinguer and Alvarez, 2002; Coconier, 2005). For this reason, Laguna Llanquanelo was designated as provincial fauna reserve in 1980 and included as a RAMSAR site in the list of wetlands of international importance in 1995. Simultaneously, its subsoil contains extensive oil reserves that have been exploited since the 1930s. In addition to oil production and mining, overgrazing, poaching, and pollution, among others, have been mentioned as threats to the area's sustainability (Sosa, 1995; Iglesias and Pérez, 1999).

In spite of the importance of mentioned conflict, information about the biological and the physicochemical attributes of the Llanquanelo watershed is scarce. Peralta and Fuentes (2005) have characterized the Bañado (from the requirements of the species found in plankton and microbenthos communities) as eutrophic and saprobic, with records of hydrocarbon in the middle reaches, and a growing deterioration of water quality and plant cover from the headwaters toward the outlet. Ciocco and Scheibler (2008) studied the malacofauna at the Bañado and confirmed the growing salinity gradient from the less saline waters at the headwaters to the extremely saline and hard waters of the outlet-lake. Together with the salinity gradient, the Bañado has spatial heterogeneity due to water permanence. Despite the stable lentic conditions of the headwaters, the water volume of the Bañado Carilauquen shows significant seasonal variations from the middle reaches to the outlet due to high evaporation rates (Peralta and Fuentes, 2001), whereby the shallowest points of the middle reaches are exposed to desiccation.

The goal of the present study is to examine how spatial-temporal changes and physicochemical water characteristics affect the taxonomic richness and density of benthic macroinvertebrates in this arid wetland. In particular, we hope to test whether in harsh environmental conditions and at the whole-Bañado scale the highest salinity levels correspond with the lowest levels of macroinvertebrate richness and abundance, despite the spatial heterogeneity caused by seasonal variations in water permanence.

Materials and methods

Study area

The Bañado Carilauquen (BC) is located West of Laguna Llanquanelo (LL), a saline lake averaging 0.30 m in depth (maximum: 2 m), that comprises about 65 000 ha and lies at an altitude of about 1300 m. a.s.l. between 35°30'–36°S and 69°–69°15'W in the Central West of Argentina (Fig. 1). The Malargüe River is the major tributary of the LL. Also the Chacay, Álamo, Mocho, and Durazno streams contribute to the watershed system, as well as various semi-permanent watercourses, notable among which is the Carilauquen “stream” which runs for about 10 km from West (headwaters) to East (outlet into lake), draining the BC into the LL. Maximum depth of the BC is approximately 2 m (headwaters and isolated pools) and mean depth is around 0.20 m. Both the headwaters and the outlet-lake always have water; in contrast to shallow middle reaches, which undergo periods of desiccation. Salt deposits occur between the lake and the system's marshes. Flooded grounds are silt-clay soils, and the dominant vegetation is composed of hygrophilous macrophytes such as *Scirpus californicus*, *Cortadeira selloana* and *Chara vulgaris* (Sosa et al., 1989; Peralta and Fuentes, 2005; Méndez, 2005).

From the biogeographic perspective, the Llanquanelo watershed system is located in the Andean region, specifically in the Patagonian Sub-region (Morrone, 2006). Climate in the region is extremely arid; mean annual temperature and rainfall are about 12.5° C and 241 mm, respectively. Evaporation prevails over water contributions, whereby the water level tends to fall slowly (Ostera and Dapeña, 2003; Ciocco and Scheibler, 2008).

Sampling

Five sectors were defined along a spatial gradient stretching from the headwaters of the Carilauquen “stream” to its outlet into the Llanquanelo lake, with the following designations: (i) headwaters (HD), (ii) higher middle reach (HMR); (iii) central middle reach (CMR); (iv) lower middle reach (LMR); (v) outlet-lake (OL; Fig. 1). The sampling area was between 35°38'42” and 35°39'22” S, and between 69°09'44” and 69°16'05”W. Benthos samplings were carried out seasonally over a complete annual cycle, between summer 2000 and spring 2001. Two non-integrated replicate samples were taken at each sampling site using a homemade Petersen dredge (extraction area: 352 cm² per replicate).

Conductivity ($\mu\text{S cm}^{-1}$; Hanna conductivity meter HI 9033), pH (Hanna pH meter HI 9025), transparency (m; Secchi disk), water and air temperature (°C, mercury thermometer) and depth (m, calibrated stick) were measured at each sampling site.

At the extremes of the spatial gradient (HD and OL) and in one of the middle reaches (LMR), complementary seasonal records of SO_4^{2-} , Cl^- , Na^+ , K^+ , Ca^{+2} , Mg^{+2} , HCO_3^- and dissolved oxygen (Winkler method) were made to increase the number of variables to be considered in the multivariate analyses performed to correlate environmental parameters with species density. HCO_3^- , Ca^{+2} and Mg^{+2} were measured through volumetric methods; K^+ and Ca^{+2} by photometry and SO_4^{2-} and Cl^- by Benzidine and Mohr methods, respectively.

All collected specimens were preserved in 5% formol solution for their later laboratory processing and taxonomic identification. Organisms were identified (only whole samples) at the lowest possible taxonomic level (keys by Wiederholm, 1983; Lopretto and Tell, 1995; Castellanos and Landoni, 1995; Fernández and Domínguez, 2001). Permanent microscope slides were prepared for identification of Chironomidae larvae. Samples and slides were deposited in the Entomology Laboratory of CCT CONICET Mendoza.

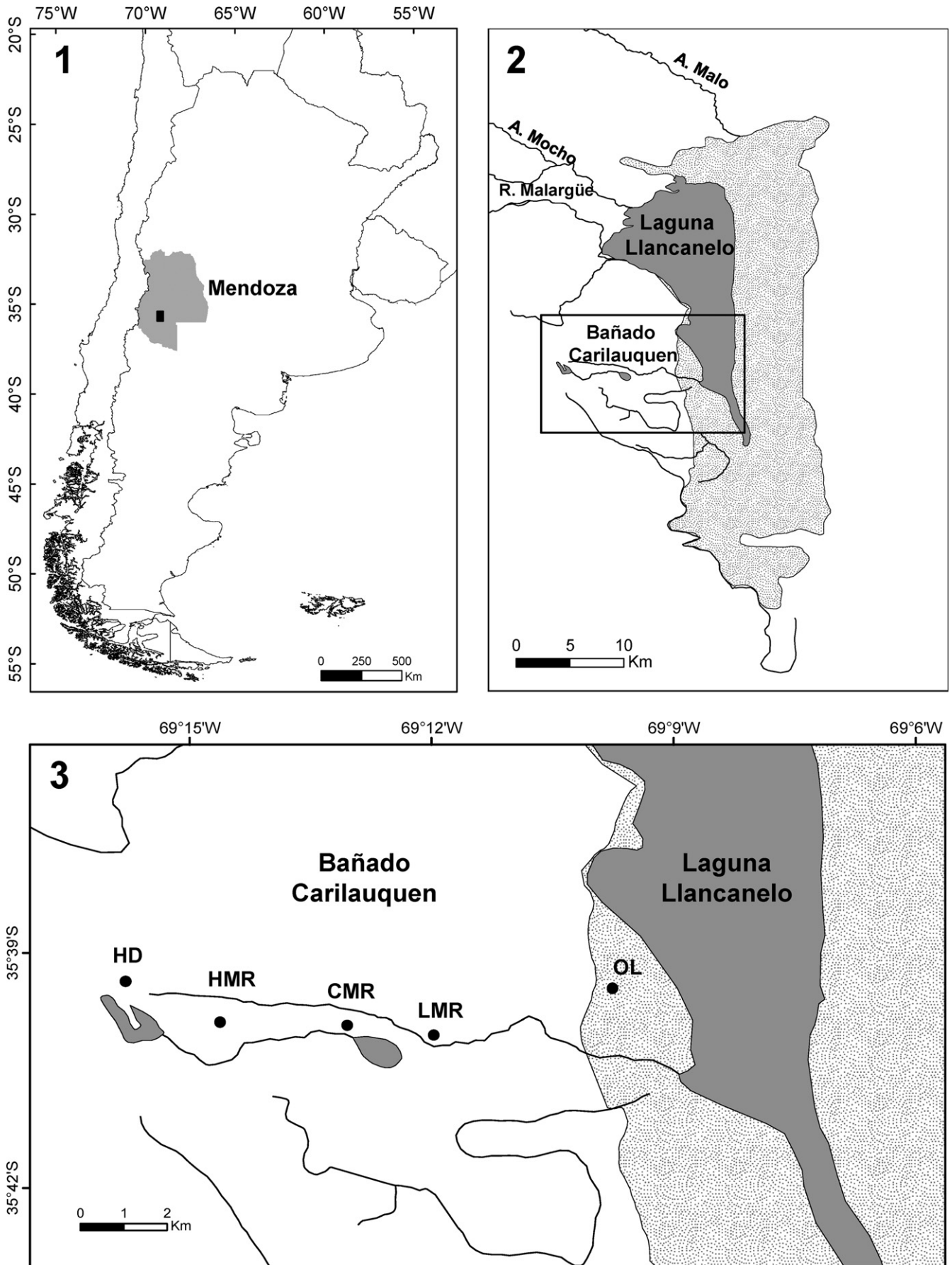


Fig. 1. Study area maps. (1) Location of Mendoza Province; (2) Location of Bañado Carilauquen; (3) Sampling sites (HD: headwaters; HMR: higher middle reach; CMR: central middle reach; LMR: lower middle reach; OL: outlet-lake).

Data analysis

Qualitative composition of benthic communities

In order to compare taxonomic richness among sampling sites and observe how macroinvertebrate communities were distributed along the BC, Sorensen's Cluster Analysis was applied, using the unweighted pair group method (UPGMA; software MVSP version 3.11, Multi-Variate Statistical Package 2000). A matrix of presence and absence of invertebrates was used for this analysis, considering all four seasons of the year pooled together.

Community structure and spatial-temporal variation

Variations in densities of abundant taxa were statistically analyzed with generalized linear models (GENSTAT program, version 4.2, 2005), to examine the effect of sampling sites (SS), seasons (SE) and the interaction (SS*SE). Because the data were discrete (density of taxa), a logarithmic regression was used, assuming a Poisson distribution. Detailed procedures for this type of analysis can be found in *Crawley (1993)* and *McConway et al. (1999)*. No estimate was made for *H. parchappii* because its densities did not fit the model, exhibiting a very high residual deviance.

Influence of physicochemical variables on community distribution

To explore the relationship between species and environmental variables, a Canonical Correspondence Analysis (CCA) was applied to data from sampling sites located at the extremes of the spatial gradient and in one of the middle reaches (HD, LMR and OL). Data on species density and environmental variables (excepting pH) were transformed by applying $\log(x+1)$. Prior to the CCA, in an exploratory fashion, a non-parametric correlation analysis (Spearman) was performed among environmental variables to ascertain whether there was a high level of correlation between them. Only those correlations showing $\rho \geq 0.60$ ($p < 0.05$) were considered to be significant. In both the non-parametric test and the CCA, the data matrix used was that corresponding to environmental variables recorded at the HD, LMR and OL in the different climate seasons. MVSP software, version 3.11, Multi-Variate Statistical Package 2000, was used for the CCA.

Table 1

Mean environmental records per sampling site and season of the year at Bañado Carilauquen (values in parenthesis: standard deviation). References: electrical conductivity at 25 °C ($\mu\text{S cm}^{-1}$), water temperature (°C), air temperature (°C), pH, transparency (m), depth (m).

Site/Parameter	Conductivity	Water Temp.	Air Temp.	pH	Transparency	Depth
HD summer	953.00 (1.41)	13.55 (0.21)	17.20 (2.12)	7.40 (0.28)	1.60 (0.57)	1.60 (0.57)
HMR summer	1169.50 (304.76)	24.85 (0.92)	21.65 (2.62)	8.50 (0.57)	0.28 (0.04)	0.28 (0.04)
CMR summer	1055.00 (1.41)	22.20 (4.81)	30.40 (0.57)	7.60 (0.71)	0.20 (0.00)	0.20 (0.00)
LMR summer	1233.00 (22.63)	24.20 (0.42)	24.20 (4.53)	8.15 (0.78)	0.45 (0.21)	0.45 (0.21)
OL summer	8415.00 (586.90)	24.05 (1.77)	20.70 (2.26)	8.20 (0.00)	0.50 (0.14)	0.50 (0.14)
HD autumn	941.50 (9.19)	13.80 (0.71)	7.15 (1.48)	6.95 (0.21)	1.60 (0.57)	1.60 (0.57)
HMR autumn	1226.50 (416.49)	10.35 (1.48)	9.00 (0.00)	7.03 (0.03)	0.28 (0.04)	0.28 (0.04)
CMR autumn	1241.00 (292.74)	8.55 (2.90)	7.00 (4.24)	7.59 (0.45)	0.20 (0.00)	0.20 (0.00)
LMR autumn	1389.50 (116.67)	9.30 (2.26)	8.95 (1.48)	7.04 (0.78)	0.45 (0.21)	0.45 (0.21)
OL autumn	16795.00 (3853.73)	8.45 (1.34)	5.85 (0.07)	6.74 (0.33)	0.50 (0.14)	0.50 (0.14)
HD winter	922.00 (11.31)	11.00 (0.99)	9.25 (1.06)	7.35 (0.35)	1.60 (0.57)	1.60 (0.57)
HMR winter	1450.00 (70.71)	6.20 (1.27)	9.50 (0.71)	7.45 (0.36)	0.25 (0.07)	0.25 (0.07)
CMR winter	1150.00 (70.71)	6.85 (0.78)	9.00 (0.00)	7.26 (0.21)	0.23 (0.11)	0.23 (0.11)
LMR winter	1200.00 (0.00)	6.90 (1.56)	9.10 (1.27)	7.34 (0.01)	0.45 (0.21)	0.45 (0.21)
OL winter	10420.00 (876.81)	5.65 (0.21)	8.50 (0.71)	6.65 (0.07)	0.50 (0.14)	0.75 (0.49)
HD spring	1050.00 (70.71)	15.10 (0.28)	7.75 (0.35)	7.75 (0.07)	1.60 (0.57)	1.60 (0.57)
HMR spring	1600.00*	16.30*	8.00*	7.60*	0.20*	0.20*
CMR spring	1300.00 (141.42)	11.05 (2.62)	9.05 (0.35)	7.36 (0.35)	0.15 (0.07)	0.15 (0.07)
LMR spring	1300.00 (0.00)	13.85 (2.05)	10.10 (0.28)	7.37 (0.33)	0.35 (0.07)	0.35 (0.07)
OL spring	9250.00 (70.71)	12.10 (1.41)	11.10 (0.14)	7.39 (0.30)	0.55 (0.07)	0.80 (0.28)

HD: headwaters, HMR: higher middle reach, CMR: central middle reach, LMR: lower middle reach, OL: outlet-lake.

* HMR spring: only data.

Results

Environmental features

The waters of the Bañado Carilauquen ranged from hard to very hard according to the classification of the US Environmental Protection Agency (EPA, 1986), with mean conductivity records fluctuating between $922 \mu\text{S cm}^{-1}$ (SD: 11.3; HD, winter) and $16795 \mu\text{S cm}^{-1}$ (SD: 3853.73; OL, autumn) (Table 1; seawater = $56000 \mu\text{S cm}^{-1}$). A growing conductivity gradient was detected, starting in the less saline waters of the headwaters (mean for all four seasons together: $966.63 \mu\text{S cm}^{-1}$; SD: 59.44) and ending in the extremely saline and hard waters of the outlet-lake (mean for all four seasons together: $11220 \mu\text{S cm}^{-1}$; SD: 3834).

The pH was in general neutral, with annual mean for all five sampled reaches oscillating between 7.24 and 7.65, a mean maximum record per site and sampling date of 8.5 (SD: 0.57; HMR summer) and a minimum mean of 6.65 (SD: 0.07; OL winter). Mean annual water temperature for the five sampling sites fluctuated between 12.7 and 14.6 °C, with a maximum mean per site and sampling date of 24.85 (SD: 0.92; HMR, summer) and a minimum mean of 5.65 (SD: 0.21; OL, winter). Mean annual depth of the different reaches varied between 1.6 m (HD) and 0.19 m (CMR); water transparency records corresponded to clear waters (Table 1).

The increasing conductivity gradient described above corresponded, from the headwaters (minimum values) to the outlet-lake (maximum values), with an increased concentration of the great majority of ions recorded for the HD, LMR, and OL (Table 2).

Macroinvertebrate assemblages

Qualitative composition of benthic communities

The macroinvertebrate community at the Bañado Carilauquen was composed of 36 taxa (Table 3). Overall, the watershed outlet showed the lowest richness values of the BC. The benthic community displayed higher taxonomic richness at the HD (18 taxa), followed by LMR (17 taxa), HMR (14 taxa), and CMR and OL (12 taxa).

Table 2

Mean ion and dissolved oxygen concentrations (in mg l⁻¹) at the extremes of the spatial gradient and in one of the middle reaches in Bañado Carilauquen (all season of the year together; values in parenthesis: standard deviation).

Parameters/Site	HD: headwaters	LMR: lower middle reach	OL: outlet-lake
HCO ₃	162.67 (45.92)	128.10 (40.00)	109.67 (31.98)
Cl ⁻	20.34 (8.62)	674.68 (1268.63)	3723.01 (506.81)
SO ₄ ²⁻	375.93 (54.78)	740.78 (243.08)	1832.10 (283.55)
Na ⁺	16.34 (3.63)	42.50 (33.32)	1865.59 (818.78)
K ⁺	3.18 (0.62)	6.73 (2.15)	102.51 (26.80)
Ca ⁺⁺	177.35 (16.84)	248.35 (35.49)	896.35 (237.18)
Mg ⁺⁺	7.35 (0.81)	11.93 (2.17)	154.48 (45.32)
O ₂	6.41 (0.90)	6.53 (0.78)	6.51 (0.87)

Table 3

Benthic macroinvertebrate taxa in the Bañado Carilauquen.

Ephemeroptera
<i>Caenis</i> sp
Trichoptera
<i>Metrichia</i> sp
<i>Oxyethira</i> sp
Odonata
<i>Rhionaeshna absoluta</i>
<i>Ischnura fluviatilis</i>
Coleoptera
<i>Liodesus</i> sp
<i>Tropisternus setiger</i>
<i>Lancetes biremis</i>
<i>Berosus</i> sp
<i>Haliplus</i> sp
Bembidiina Gen. sp
Staphylinidae Gen. sp
<i>Stenopelmus minutus</i>
Hemiptera
<i>Sigara jensenhaarupi</i>
Diptera
<i>Cricotopus</i> sp
<i>Chironomus</i> sp
<i>Pseudochironomus</i> sp
<i>Dicrotendipes</i> sp
<i>Djalmabatista</i> sp
<i>Tanypus</i> sp
<i>Paratanytarsus</i> sp
<i>Polypedilum</i> sp
Dolichopodidae Gen. Sp
Tabanidae Gen. sp
Ephydriidae Gen. sp
<i>Dasyhelea</i> sp
Gastropoda
<i>Heleobia parchappii</i>
<i>Heleobia hatcheri</i>
<i>Chilina mendozana</i>
<i>Lymnaea viator</i>
<i>Biomphalaria peregrina</i>
Amphipoda
<i>Hyaella curvispina</i>
Oligochaeta
Oligochaeta Gen. sp
Hirudinea
Hirudinea Gen. sp
Turbellaria
Dugesidae Gen. sp
Nematoda
Nematoda Gen. sp

With respect to faunal composition along the longitudinal gradient of the BC, the similarity detected between the headwaters and middle sectors was low (48% and 37% of similarity), but considerable between HMR and CMR sites (64% of similarity). In turn, composition of the outlet macrofauna was the least similar to that in the rest of the Bañado (only 29% of similarity) (Fig. 2).

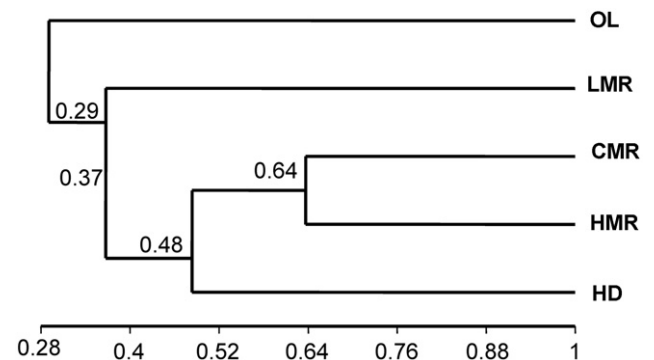


Fig. 2. Sorensen's coefficient diagram showing similarity between benthic communities along the Bañado Carilauquen. Ref.: HD: headwaters; HMR: higher middle reach; CMR: central middle reach; LMR: lower middle reach; OL: outlet-lake.

Community structure and spatial-seasonal variation

The zoobenthic community had a total density of 66 326 individuals/m² over the annual cycle at all five sampling sites. The taxon with highest density was Insecta (35 940 ind/m²), and Diptera was dominant within it, with a total density of 33 572 ind/m². Mollusca (22 408) and Amphipoda (5411) were next in decreasing order, whereas taxa with lower density were Dugesiidae sp. (1179), Hirudinea sp. (609), Oligochaeta sp. (453) and Nematoda sp. (326). Among aquatic insects, *Chironomus* sp. (11150 ind/m²) and *Dasyhelea* sp. (7541 ind/m²) were the dominant taxa. A decline in total density was also observed from the headwaters (19894 ind/m²) toward the outlet (10139 ind/m²) of the wetland system. In intermediate sectors, although the HMR recorded the lowest total density (7653 ind/m²), LMR and CMR exhibited high densities: 16 775 and 11 867 ind/m², respectively.

Total density of taxa showed significant differences among sampling sites and seasons; interactions between site and season were observed for *Lymnaea viator* and *Chironomus* sp. only (Table 4).

While *Chironomus* sp. was found at all sampling sites and its density increased from the HMR toward the OL, *Cricotopus* sp. and *Dicrotendipes* sp. were detected only at the HD, *Dasyhelea* sp. was present in the HMR and LMR (Table 5). Trichopterans were found only at the headwaters of the Bañado. Among coleopterans, *Liodesus* sp. occurred in the middle reaches of the BC, with maximum abundances in summer in the CMR and LMR. While the gastropod *H. parchappii* presented high densities and frequency of appearance at all sampling sites, *Ch. mendozana* was present only at the headwaters where *H. hatcheri* also predominated. Seasonal and annual mean densities of each taxon by site are shown in Table 5.

Table 4
Percentage of variation in abundance of each taxa that each significant variable explains: sampling site (SS), season (SE) and sampling site*season interaction (SS*SE) in Bañado Carilauquen: NS: not significant.

Taxa	SS	SE	SS*SE
<i>H. curvispina</i>	47.92 **	7.91 *	NS
<i>H. hatcheri</i>	63.30 **	14.67 *	NS
<i>L. viator</i>	34.88 **	12.54 **	14.14 **
<i>B. peregrina</i>	29.64 **	49.65 **	NS
<i>Ch. mendozana</i>	65.48 **	16.47 *	NS
<i>Oligochaeta</i>	47.46 **	18.04 *	NS
Hirudinea	52.19 **	NS	NS
Dugesidae	38.08 **	20.49 *	NS
Nematoda	43.24 **	37.84 **	NS
<i>Cricotopus</i> sp	46.35 **	37.91 **	NS
<i>Metrichia</i> sp	56.71 **	22.29 *	NS
<i>Oxyethira</i> sp	63.51 **	27.84 **	NS
<i>Liodessus</i> sp	35.24 **	42.96 **	NS
<i>Dicrotendipes</i> sp	32.83 **	44.78 **	NS
<i>Djalmabatista</i> sp	39.11 **	32.71 **	NS
<i>Pseudochironomus</i> sp	39.50 **	31.22 **	NS
<i>Tanypus</i> sp	39.05 **	20.83 *	NS
<i>Paratanytarsus</i> sp	51.90 **	41.17 **	NS
<i>Chironomus</i> sp	30.96 **	47.49 **	15.24 *
<i>Dasyhelea</i> sp	66.00 **	29.13 **	NS

* $p > 0.001$; ** $p < 0.001$.

Influence of physicochemical variables on community distribution

The variables Ca^{+2} , Mg^{+2} , K^+ , Na^+ , Cl^- and SO_4^{-2} were excluded from the canonical correspondence analysis because they were significantly correlated with conductivity ($p < 0.0001$); depth was likewise neglected because of its correlation with transparency ($p < 0.0001$). The first three axes of the ordination explained 53.4% of the accumulated variance. Eigenvalues obtained were CCA1: 0.633, CCA2: 0.399 and CCA3: 0.284. Species-environment correlation values ranged between 1 and 0.98.

Physicochemical variables which significantly correlated with axes 1 and 2 were: conductivity, transparency, bicarbonate, pH, air temperature and water temperature (Fig. 3). Sites were strongly associated with physiochemical variables (Fig. 3). Likewise, occurrence of invertebrate taxa at the sites was related to physical and chemical parameters (Fig. 4).

Discussion

Box et al. (2008) highlighted the importance, in aquatic environments of arid/semiarid regions, of having surveys of biological diversity to provide a baseline to compare against future surveys, and which can be used to document changes in habitat quality and availability, as well as in species richness and diversity. We are herewith reporting the first macroinvertebrate inventory for this RAMSAR area. Taxonomic diversity at the BC (total: 36 taxa) is significantly lower in family and species richness than in lentic environments of the Pampean region (i.e. temporary pools and permanent ponds in Buenos Aires Province, 85 taxa; Fontanarrosa et al., 2004) or in the La Plata basin (i.e., lakes on floodplains of the Paraná River: 152 morphospecies; Poi de Neiff and Neiff, 2006), regions with rainfall and temperature regimes significantly higher than those in the semidesert climate of the Central West of Argentina (Bonetto and Hurtado, 1999; Gómez and Toresani, 1999). Compared to other arid and semiarid Andean water bodies, taxonomic richness at the BC is lower than that recorded in lotic environments of Patagonia (Miserendino and Pizzolón, 2000, 2004), probably due to the high salinity and pronounced variability in water permanence in this

Table 5
Seasonal and annual mean densities of taxa by sampling site. References of Bañado Carilauquen: HD: headwaters, HMR: higher middle reach, CMR: central middle reach, LMR: lower middle reach, OL: outlet-lake, sum: summer, aut: autumn, win: winter, spr: spring, yr: annual. Values without decimals.

Taxa/sites	HD sum	HD aut	HD win	HD spr	HD yr	HD	HMR sum	HMR aut	HMR win	HMR spr	HMR yr	HMR	CMR sum	CMR aut	CMR win	CMR spr	CMR yr	CMR	LMR sum	LMR aut	LMR win	LMR spr	LMR yr	LMR	OL sum	OL aut	OL win	OL spr	OL yr	
<i>Metrichia</i> sp	256	0	0	0	0	92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Oxyethira</i> sp	0	0	0	0	0	37	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Liodessus</i> sp	0	0	0	0	0	0	0	0	0	0	0	0	126	0	0	0	14	35	0	0	0	0	0	0	0	0	0	0	0	
<i>Cricotopus</i> sp	2301	0	0	0	0	586	0	0	0	0	0	0	68	0	0	0	0	17	0	0	0	0	0	0	0	0	0	0	0	
<i>Dicrotendipes</i> sp	199	0	0	0	0	50	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Djalmabatista</i> sp	0	0	0	0	0	0	0	29	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Pseudochironomus</i> sp	0	0	0	0	0	0	0	7	0	0	4	0	159	0	0	0	0	40	0	0	0	0	0	0	0	0	0	0	0	
<i>Tanypus</i> sp	0	0	0	0	0	2	250	242	338	0	237	0	0	0	0	0	0	0	1450	0	0	0	45	374	0	0	0	0	0	
<i>Paratanytarsus</i> sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1805	53	0	0	464	0	0	0	0	0	0	
<i>Chironomus</i> sp	0	7	7	7	5	7	276	198	409	0	252	0	2912	36	654	170	943	11	1788	46	14	47	474	2728	0	7	0	684	0	
<i>Dasyhelea</i> sp	1875	483	107	0	0	616	0	0	0	0	0	0	0	0	0	0	0	0	29	0	0	0	7	0	0	0	0	0	0	
<i>H. curvispina</i>	0	185	270	0	114	0	85	0	0	0	24	0	0	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Dugesidae sp	100	21	71	21	53	14	14	28	29	14	22	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	
Hirudinea sp	0	7	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Oligochaeta sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Nematoda sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>H. parctappii</i>	312	710	213	185	355	1093	0	85	511	410	0	241	43	270	426	245	156	142	994	582	469	653	227	824	284	497	0	0	0	
<i>H. hatcheri</i>	57	28	57	36	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Ch. mendozana</i>	256	454	57	1278	511	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>L. viator</i>	0	0	28	0	7	43	142	57	142	89	0	43	383	131	114	71	78	0	14	0	0	0	0	0	0	0	0	0	0	
<i>B. peregrina</i>	0	0	0	0	0	0	0	0	0	28	4	85	21	0	0	0	0	0	0	0	0	14	4	0	0	0	0	0	0	0

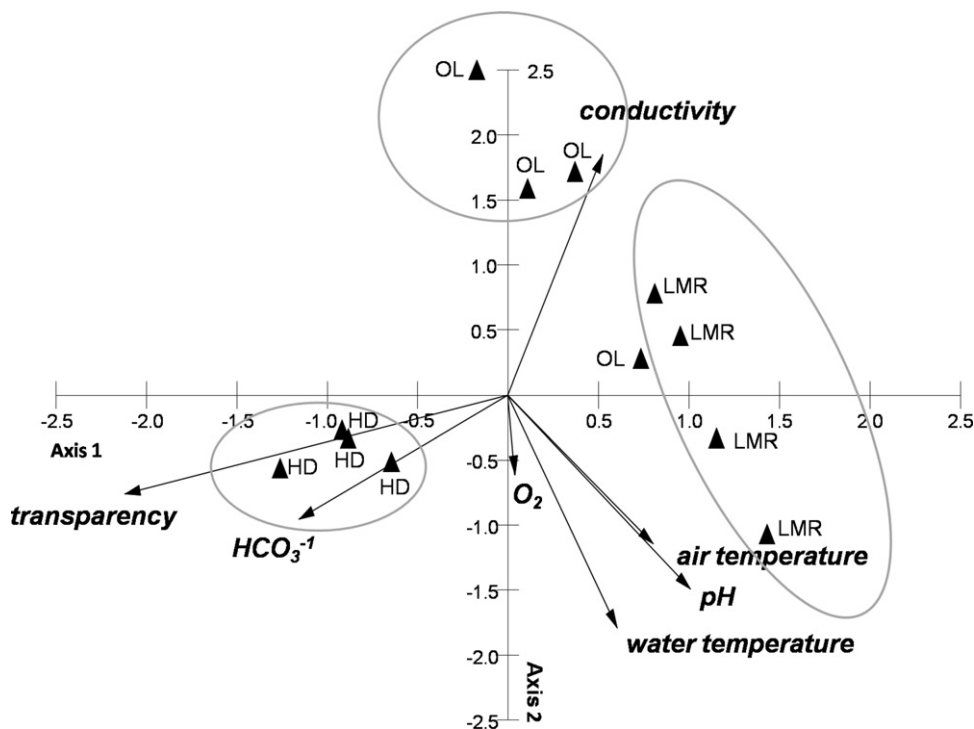


Fig. 3. Canonical correspondence analysis ordination plot for sampling sites and environmental variables of Bañado Carilauquen.

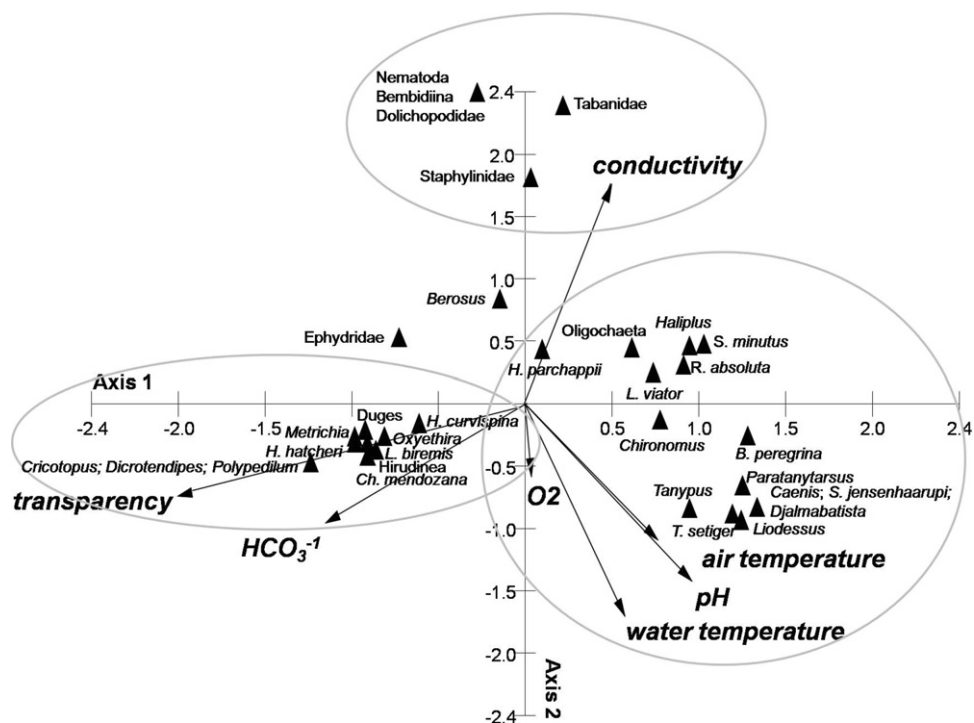


Fig. 4. Canonical correspondence analysis ordination diagram showing the relationship between species and environmental variables of Bañado Carilauquen. Ref: HD: headwaters; LMR: lower middle reach; OL: outlet-lake.

disturbed inland lake. Further studies, including manipulative experiments, are needed to understand, at different space scales, the synergy effect of factors modelling macroinvertebrate diversity in lentic and running waters from the arid northern Andean-Patagonian region with contrasting environmental conditions.

The fact that macroinvertebrate communities have displayed maximum levels of diversity at the headwaters (18 taxa), where

the lowest levels of conductivity were detected, suggests that the less saline waters of the higher reaches offer more favourable conditions for existence of multiple taxa. Conversely, the less diverse faunal composition of the Bañado outlet indicates these harder waters of the lower end of the gradient support fewer macroinvertebrate taxa. Consistent with other studies on running or lentic waters, high salinity levels, together with natural

hydrological variability, may act as an abiotic stressor for macroinvertebrate assemblages, with high conductivity values coinciding in general with significant drops in taxonomic richness (Williams et al., 1990; Vidal Abarca et al., 2004; Piscart et al., 2005; Timms, 2007; Waterkeyn et al., 2008; Carver et al., 2009; Moreno et al., 2009).

With regard to spatial heterogeneity due to water permanence, favourable and stable water conditions such as those of the headwaters would generate higher availability of suitable microhabitats for most of the species. In fact, a marked spatial distribution has been reported for the littoral vegetation of the Bañado Carilauquen, with a conspicuous decline in cover and species diversity towards the outlet (Peralta and Fuentes, 2001). The presence of aquatic macrophytes reduces predation (Agostinho et al., 2003), provides food and refuge, generates oxygenated environments and increases the number of spaces available to swimmer species of the orders Coleoptera (one of the dominant taxa at the BC) and Hemiptera (also present at the BC) (Bazzanti et al., 2009).

In contrast, at the outlet-lake, though never lacking water, the water volume varies significantly and the littoral vegetation becomes conspicuously less abundant, restricted only to the submerged macrophyte species *Salicornia ambigua* and associated with filamentous chlorophytes (Peralta and Fuentes, 2001). This, along with the high water salinity at the lower end of the BC, may be the underlying mechanism reducing macroinvertebrate richness to a few species tolerant of extreme environmental conditions. On the other hand, at intermediate sites, where unstable environments prevail, taxonomic diversity may be modulated by the temporary presence of transient taxa adapted to changing environmental conditions, which would account for the absence of well-defined richness and abundance patterns in the middle reaches.

The qualitative composition of macroinvertebrate assemblages at the Bañado was largely dominated by aquatic insects (72%, particularly by Diptera and Coleoptera), which is in keeping with reports for other saline water bodies from arid/semiarid regions (Williams et al., 1990; Davis et al., 1993; Juárez and Ibañez, 2003; Pinder et al., 2004, among others).

The decreasing HD-OL gradient of insect density and of the whole group of macroinvertebrates is consistent with the progressive increase in conductivity from the headwaters to the outlet, and with the progressive decrease in taxonomic richness toward the lake. The exclusive presence (*Oxhyetira* sp., *Metrichia* sp., *Polypedilum* sp., *Cricotopus* sp., *L. biremis*) and/or high abundance (*Cricotopus* sp., *Dicrotendipes* sp.) of several more sensitive or less tolerant insects at the headwaters again suggests the existence of comparatively more favourable and stable conditions at the headwaters than in the rest of the BC. Caddisfly (*Oxyethira* and *Metrichia*, Hydroptilidae) larvae, as a group, are largely intolerant of poorly oxygenated water (Winterbourn, 1981), mainly have low or moderate tolerance values and are sensitive to pollution (Bouchard, 1984). The diving beetle *L. biremis* has also been reported for waters with abundant plant cover in Andean and sub-Andean environments (Muzón et al., 2005). Among molluscs, the exclusive and abundant presence of *Ch. mendozana* at the headwaters is consistent with the favourable and stable conditions of the site. For example, it has been reported that the genus *Chilina* occurs in transparent water (Castellanos and Gaillard, 1981) and it has been suggested that *Ch. mendozana* does not tolerate water with conductivity levels $> 1000 \mu\text{S cm}^{-1}$ (Ciocco and Scheibler, 2008). Likewise, the higher relative abundance of *Hyalella curvispina* (an amphipod of wide distribution in Argentina in different types of environments, even disturbed ones) at the headwaters of the Bañado may also respond to its association with the presence of macrophytes

(Casset et al., 2001), favoured at the headwaters because of water stability.

Contrasting with what occurs at the headwaters, lowest density and richness levels were recorded at the other end of the gradient (OL). The only relatively dominant taxa at the outlet were *Chironomus* sp. and the snail *H. parchappii*. The former was found at all sampling sites throughout the year, with densities notably increasing towards the lower reaches, and particularly at the OL. *Chironomus* is one of the most known taxa which is broadly tolerant of critical water conditions, including polysaprobic water with relevant anoxia levels and severe pollution (Hellawell, 1986; Paggi, 1999; Mandaville, 2002). Furthermore, several species of *Chironomus* are halophilous (Pinder and Reiss, 1983), which is in line with the higher abundance of this taxon in waters with mean conductivity levels $> 16000 \mu\text{S cm}^{-1}$, such as those at the outlet and lake of the BC. One more attribute that helps *Chironomus* species survive in these restrictive environments is their capacity as collector-gatherers, the main feeding behaviour shown by invertebrates of desert streams (Fisher, 1986). *H. parchappii* was similarly found at all sites throughout the year. This Cochliopid freshwater snail is known to be able to develop populations not only in the estuary waters of the Atlantic littoral (mean salinity between 26 560 and 35 940 $\mu\text{S cm}^{-1}$; De Francesco and Isla, 2004), but also in continental waters with mean salinity between 1250 and 11 250 $\mu\text{S cm}^{-1}$ such as those of the Bañado (Ciocco and Scheibler, 2008). Nematoda (exclusive to OL) and Oligochaeta (only in HMR and OL) worms are taxa that, as reported by studies conducted in the La Plata River, can show great tolerance of high levels of conductivity, pollution and concentration of heavy metals (Paggi et al., 2006).

In the intermediate sectors, in addition to *Chironomus* sp. and *H. parchappii*, *Tanytus* sp. (HMR and LMR), *Paratanytus* sp. (LMR) and *Djalmabatista* sp. (LMR), *Dasyhelea* sp. (CMR) and *Liodessus* were also abundant. These are aquatic insects with broader tolerances of salinity and hydrological changes than those from the headwaters, but at the same time less tolerant than *Chironomus* of the critical conditions of the outlet (Spinelli and Wirth, 1993; Mandaville, 2002; Paggi, 2003; Pavé and Marchese, 2005; Alarie et al., 2007; Bazzanti et al., 2009).

Larvae of *Tanytus* inhabit soft sediments in diverse habitat types (shallow, standing and flowing waters) in areas with temperate or warm climate (Wiederholm, 1983). In highly impacted water bodies like the basin of the Matanza-Riachuelo rivers (Buenos Aires Province, Argentina), *Tanytus*, although frequent, was less temporally and spatially constant than *Chironomus* (Paggi, 2003), which suggests that *Tanytus*, albeit tolerant, is so to a lesser extent than *Chironomus*, which is consistent with the pattern of density distribution for both taxa detected for the BC. *Paratanytus* sp., in turn, has been found in ponds from Central Italy with conductivity levels (mean: 884 $\mu\text{S cm}^{-1}$) similar to those of the middle reaches of the BC (Bazzanti et al., 2009). *Djalmabatista* can inhabit lentic environments such as the BC, or lotic ones (Fittkau and Roback, 1983), including from hardly or moderately polluted rivers with conductivities ranging from 631 to 1501 $\mu\text{S cm}^{-1}$ (Pavé and Marchese, 2005) to mixed, well oxygenated, soft water environments (conductivity $< 159 \mu\text{S cm}^{-1}$; Callisto et al., 2005). Also *Dasyhelea* has been recorded in diverse environments, including semi-permanent and permanent waters (Bayly, 1982; Jocqué et al., 2007; Moreno et al., 2009). It has been reported that *Dasyhelea* larvae occurring in shallow waters are often associated with the presence of algae, and that species of this genus can develop in saline environments and resist desiccation (Spinelli and Wirth, 1993). Abundance of this taxon occurring exclusively in summer in the intermediate sectors (CMR) could be attributed to trophic reasons (availability of flowers on whose nectar *Dasyhelea* adults feed). Diving larvae

and adults of the beetle *Liodessus* are frequent in both unstable and permanent environments (Fontanarrosa et al., 2004), can be found even in waters with heavy organic debris (Alarie et al., 2007) and tolerate a wide salinity range (larvae: $< 15625 \mu\text{S cm}^{-1}$; adults: $< 31250 \mu\text{S cm}^{-1}$; *L. affinis*, Matta, 1983).

L. viator, one of the molluscs present exclusively in the middle reaches of the BC, is an aquatic pulmonate snail that breaths atmospheric air, highly resistant to harsh environmental conditions, including extreme cold, thermal waters, high altitude and water stress, and able to tolerate conductivities ranging between 251 and $2420 \mu\text{S cm}^{-1}$ (Castellanos and Landoni, 1981; Ciocco and Scheibler, 2008; Ciocco et al., 2009). *B. peregrina* (the other exclusive, and scarce, snail to the middle reaches) would not tolerate conductivities $> 1000 \mu\text{S cm}^{-1}$ (Ciocco and Scheibler, 2008), and needs shallow water with macrophytes to develop abundant populations (Rumi, 1991).

In addition to oil production and mining, overgrazing and organic pollution in the middle and lower reaches of the Bañado are threats to the area's sustainability (Sosa, 1995; Iglesias and Pérez, 1999). Peralta and Fuentes (2005) characterised the plankton and microbenthos communities of the BC associated with changes in water quality and plant cover from the headwaters toward the outlet, finding records of hydrocarbon in the middle reaches, eutrophic and saprobic waters and increasing deterioration of flora. Consistent with these findings, our results (CCA) detected, on the one hand, that taxa generally recognised as halophiles and/or very tolerant of diverse pollution sources, such as the coleopterans *Berosus* sp. and *Bembidiina* sp., the dipterans *Chironomus* sp., *Dolichopodidae* sp. and *Tabanidae* sp. and the gastropod *H. parchappii*, effectively showed affinity for hard waters like those of the OL. On the other hand, the same analysis allowed detecting that taxa habitually qualified as hardly or moderately intolerant of pollution or restrictive water conditions, such as the trichopterans *Metrichia* sp. and *Oxyethira* sp., the dipterans *Cricotopus* sp., *Polypedilum* sp. and *Dicrotendipes* sp., the coleopteran *L. biremis*, the amphipod *H. curvispina* and the gastropods *H. hatcheri* and *Ch. mendozana* found at the HD, showed preference for soft, transparent water with relatively higher temperature. In addition, Ciocco and Scheibler (2008), exploring the proportion between empty shells and complete snail individuals found in the BC, reported the highest levels of empty shells for the outlet into the lake and the highest registers of complete individuals for the headwaters, which suggests increased mortality toward the outlet proportional to the growing conductivity gradient.

All of the above suggests that the distribution pattern of macroinvertebrates at the BC responds to the HD-OL gradient of conductivity (increasing) and water quality (decreasing). Species with narrower ranges of environmental requirements occur exclusively or with important densities only at the headwaters (relatively less hard, stable, deep, transparent and vegetated water). The middle reaches (unstable, shallower, less vegetated and with moderately hard water) harbour taxa with great capacity to adapt to changing environmental conditions, which translates into lack of similarity patterns in faunal composition and into moderate levels of taxonomic diversity and abundance. Finally, the only taxa found at the outlet-lake (hard and barely vegetated water) are those tolerant of critical environmental conditions, which results in significantly reduced diversity and density.

In saline aquatic environments concurrently affected by conductivity gradients, water quality and spatial-temporal variations in water permanence, macroinvertebrate communities may turn out to be modulated by the synergy effect of more than one factor or by the predominance of one factor over the others (Vidal Abarca et al., 2004; Velasco et al., 2006). Our results suggest that

the spatial conductivity gradient is the major factor modulating the distribution of invertebrate fauna along the Bañado Carilauquen and that, with the exception of the headwaters, hard, eutrophic, polysaprobic and contaminated waters such of those of the Bañado represent critical conditions for the development of macroinvertebrate assemblages.

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