Diversity of aquatic insects and other associated macroinvertebrates in an arid wetland (Mendoza Province, Argentina)

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Diversidad de insectos acuáticos y otros macroinvertebrados asociados en un humedal de zonas áridas (Provincia de Mendoza, Argentina)

■ **ABSTRACT.** The goal of this work was to expand the evaluation of diversity of aquatic insects and associated macroinvertebrates along the Bañado Carilauquen using hand net for water column and Petersen dredge for benthos. Additionally, we explored seasonal and spatial differences and similarities of macroinvertebrate assemblages' qualitative composition. Samplings were conducted seasonally in five reaches of the Bañado Carilauquen, from headwaters to outlet. A total of 47 taxa were identified; 37 of them were insects, mainly Coleoptera, Diptera and Hemiptera, in this order. Macroinvertebrate composition was more conditioned by the spatial than the seasonal variable at the ends of the gradient. Three faunal groupings were detected: headwaters, middle reach and outlet. The highest richness detected at headwaters was correspondent with the lowest conductivity levels at the Bañado Carilauquen. The least diverse and most different faunal composition was recorded at outlet (highest conductivity levels). In the middle reach, richness levels were higher than expected in relation to conductivity, possibly because of the occasional presence of transient species.

KEY WORDS: Macrofauna. Lentic habitats. Inventory. Spatial and seasonal variations. Ramsar site.

■ **RESUMEN.** El objetivo del trabajo fue expandir la evaluación de la diversidad de insectos acuáticos y macroinvertebrados asociados a lo largo del Bañado Carilauquen, usando red de mano para la columna de agua y draga de Petersen para el bentos. Adicionalmente, se exploraron diferencias y similitudes espacio-temporales en la composición cualitativa de los ensambles de invertebrados. Se realizaron muestreos estacionales en cinco tramos del Bañado Carilauquen, desde la cabecera hasta la desembocadura. Se identificaron 47 taxa; 37 fueron insectos, principalmente Coleoptera, Diptera y Hemiptera, en ese orden. La composición de macroinvertebrados estuvo mejor condicionada por la variable espacial que por la temporal, en los extremos del gradiente espacial estudiado. Fueron detectados tres grupos faunísticos: cabecera, tramo medio y desembocadura. La mayor

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riqueza detectada en la cabecera se correspondió con los valores más bajos de conductividad del Bañado Carilauquen. La menor diversidad y la mayor diferencia en la composición faunística fueron observadas en la desembocadura (mayores niveles de conductividad). En el tramo medio, la riqueza fue mayor a la esperada según niveles de conductividad, debido posiblemente, a la presencia de especies transitorias.

PALABRAS CLAVE: Macrofauna. Hábitats lénticos. Inventario. Variaciones espacio-temporales. Sitio Ramsar.

INTRODUCTION

Most of the scientific information about Argentine wetlands comes from the temperate-warm and humid northern and central eastern areas of the country where the main watersheds are concentrated, particularly the La Plata river basin (Canevari *et al*., 1999). Conversely, in the arid/semiarid areas comprising most of Argentina (from the NW, across the Central West, to extra-Andean Patagonia in the South), wetlands are comparatively scarce and knowledge of their biological attributes is fragmentary and geographically heterogeneous.

At a world scale, the relevance of reliable surface water in arid environments has long been recognised, not only in terms of animal and human uses, but also for the high ecological and biogeographic value characterising this type of water bodies (Timms, 2007; Moreno *et al*., 2010). Natural saline aquatic ecosystems are among conservation priorities at global scale due to their importance to human development in arid and semiarid regions and because of their ecological fragility to environmental threats such as surface inflow diversions, global climate change, groundwater withdrawal, secondary salinization, mining, biological disturbances, pollution and other human activities (Williams, 2002; Timms, 2005). In fact, Box *et al*. (2008) highlighted the importance of having surveys of biological diversity in aquatic environments of arid/ semiarid regions to provide a baseline for comparison against future surveys, and which can be used to document changes in habitat quality and availability, as well as in species richness and diversity.

Invertebrate macrofauna has been reported as one of the most recommended taxa to include in faunal inventories and be used as a biological indicator of the environmental status of wetlands across the world (Kratzer & Batzer, 2007; Oertli *et al*., 2008). Insects are frequently the dominant taxocenosis among aquatic macroinvertebrates (Boix *et al*., 2007; Solimini *et al*., 2008). Hemiptera, Odonata, Coleoptera and Diptera are among the most frequent insect orders in lentic environments (Fontanarrosa *et al*., 2004; Martinoy *et al*., 2006; Peralta *et al*., 2007).

The Bañado Carilauquen is one of the major components of the endorheic wetland system denominated Laguna Llancanelo, a saline lake located in the south of Mendoza Province, midwestern Argentina. This saline wetland is a Ramsar site since 1995 and simultaneously, its subsoil contains extensive oil reserves that have been exploited since the 1930's. In addition, mining, overgrazing, poaching and pollution, among others, have been mentioned as threats to the area's sustainability (Sosa, 1995; Iglesias & Pérez, 1999). The word "Bañado" is a geographic term and means a wetland under arid conditions. The Bañado Carilauquen, stretching along an increasing salinity gradient from headwaters to outlet, has been characterised as eutrophic and saprobiotic with growing deterioration of water quality and plant cover toward the outlet, including records of hydrocarbon in the middle reaches (Peralta & Fuentes, 2005). It is a shallow (headwaters and outlet-lake) to very shallow water body (middle reaches; Scheibler & Ciocco, 2011), subjected to significant spatial-temporal variations in water level (middle reaches in particular), which is exposed to severe disturbance, especially the middle sector under cattle grazing (Sosa, 1995).

Despite the Bañado Carilauquen's ecological fragility, its economic potential and the importance it holds to conservation, knowledge about the invertebrate organisms of the area is limited to phytobenthos and plankton (Peralta & Fuentes, 2005) and to invertebrate fauna from the littoral benthos (Ciocco & Scheibler, 2008; Scheibler & Ciocco, 2011). A total of 36 taxa, mainly insects, were reported recently for the benthic macroinvertebrate assemblages of the Bañado Carilauquen, together with a decline in richness and density from the headwaters to the outlet (Scheibler & Ciocco, 2011). The goal was to expand the evaluation of diversity of aquatic insects and associated macroinvertebrates along the Bañado Carilauquen using two kinds of samplers. Additionally, we explored seasonal and spatial differences and similarities of macroinvertebrate assemblages qualitative composition from headwaters to outlet.

MATERIAL AND METHODS

Study Area

The Bañado Carilauquen lies West of Laguna Llancanelo, a saline and shallow lake of about 65000 ha located between 35º 30-36º S and 69º-69º 15 W in midwestern Argentina near 1300 m a.s.l. (Fig. 1). The major tributary of the Laguna Llancanelo is the Malargüe River. Various streams also contribute to the system as well as several semi-permanent watercourses, notable among which is the Bañado Carilauquen, which runs for about 10 km from West (headwaters) to East (outlet into lake), draining into the Laguna Llancanelo. Mean depth of the Bañado Carilauquen is around 0.20 m (maximum around 2 m at headwaters and isolated ponds). Waters from the Bañado Carilauquen range from hard to very hard, showing an increasing conductivity gradient from headwaters (around 900 µS cm^{-1}) to outlet-lake (around 17000 µS cm^{-1}). The headwaters and outlet-lake always have water, in contrast to shallow middle reaches which undergo periods of desiccation. Dominant vegetation is composed of hygrophilous macrophytes such as *Schoenoplectus californicus* Mey Steud., *Cortaderia selloana* Schult and *Chara vulgaris* Linnaeus (Méndez, 2005; Peralta & Fuentes, 2005). Climate in the region is extremely arid; mean annual temperature and rainfall are about 12.5 ºC and 241 mm, respectively. Evaporation prevails over water contributions, whereby the water level tends to fall slowly (Ostera & Dapeña, 2003; Ciocco & Scheibler, 2008). From the biogeographic perspective, the Llancanelo watershed system is located in the Andean Region, specifically in the Patagonian Sub-region (Morrone, 2006).

Sampling

For sample collection, five sectors were defined along a spatial gradient stretching from the headwaters of the Bañado Carilauquen to its outlet into the Laguna Llancanelo: i) headwaters (HD); ii) higher middle reach (HMR); iii) central middle reach (CMR); iv) lower middle reach (LMR); v) outlet-lake (OL; Fig. 1).

Qualitative samplings of macro-invertebrate assemblages were performed seasonally over a complete annual cycle (summer 2000 to spring 2001) using two techniques: hand held net for the water column community (900 m mesh size; from near the bottom to the surface, including submerged roots of floating macrophytes; approximately 20 minutes per replicate), and modified Petersen dredge (extraction area: 352 cm^2 per replicate) for the substratum community. Two non-integrated replicate samples were taken from each sampling site with both techniques.

Conductivity (µS cm^{-1}; Hanna conductivity meter HI 9033), pH (Hanna pH meter HI 9025), transparency (m; Secchi disk), water temperature (ºC; mercury thermometer) and depth (m; calibrated stick) were measured at each sampling site.

All collected specimens were preserved in 5% formaldehyde solution for their

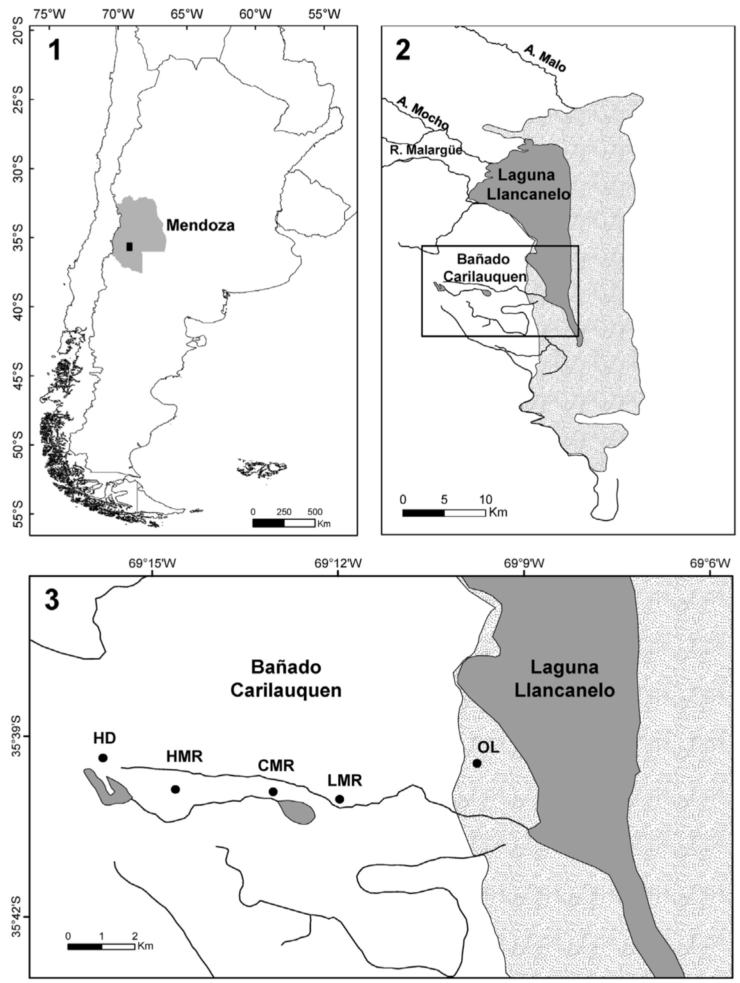

Fig. 1. Study area maps. 1: Location of Mendoza Province; 2: Location of Bañado Carilauquen; 3: Sampling sites (HD: headwaters; HMR: higher middle reach; CMR: central middle reach; LMR: lower middle reach; OL: outlet-lake).

later laboratory processing and taxonomic identification. Organisms were identified at the lowest possible taxonomic level (keys by Wiederholm, 1983; De Castellanos & Landoni, 1995; Lopretto & Tell, 1995; Fernández & 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, Argentina.

Data analysis

In order to qualitatively compare taxonomic richness among sampling sites and seasons, and to observe how macroinvertebrate communities were distributed along the Bañado Carilauquen, a Sorensen's Cluster Analysis was applied, using the unweighted pair group method analysis (UPGMA) (MVSP, 2000). A matrix of presence and absence of each taxon by site and season of the year was used for this analysis.

Principal component analysis (PCA) was used to examine which combinations of environmental variables were more predictive in describing each sampled site using all standardised environmental data by season and site, using INFOSTAT (Di Rienzo *et al.*, 2011).

RESULTS

Environmental variables

Physicochemical values confirmed the hardness of the Bañado Carilauquen waters, starting in the less saline headwaters (mean for all four seasons together: 966 µS cm^{-1}; SD: 59) and ending in the extremely saline waters of the outlet-lake (mean for all four seasons together: 11220 µS cm^{-1}; SD: 3834; Table I). The pH was, in general, neutral; mean annual water temperature for the five sampling sites fluctuated between 12.7 and 14.6 ºC and mean annual depth of the different reaches varied between 1.60 m (HD) and 0.19 m (CMR) (Table I).

PCA results (Fig. 2) revealed that the first axis explained about 49.20% of the variability of environmental parameters, whereas the second axis explained 38.30% of it. Eigenvectors are given in Table II. HMR, LMR and CMR were associated with lowest depth, high values of pH and highest water temperature values. HD was characterized by highest values of depth and transparency and OL by the highest conductivity registers.

Macroinvertebrate assemblages

In all, 47 taxa were identified among the 80 samples of macroinvertebrates collected with hand net and Petersen dredge at the Bañado Carilauquen; 37 corresponded to insects (mainly Coleoptera, Diptera and Hemiptera, in this order), 5 to gastropods, and the rest of invertebrates to Amphipoda, Oligochaeta, Hirudinea, Turbellaria and Nematoda. Taking into account the total taxonomic richness found along the Bañado Carilauquen, the watershed outlet was observed to have less richness (10 taxa) than all other sampling sites (HD: 25; HMR: 25; CMR: 22; LMR: 24). At the seasonal level, maximum richness (20 taxa) was found in autumn in HMR (Table III).

Thirty of the 47 taxa were sampled with both hand net and Petersen dredge. *Hydrovatus* sp., *Lancetes varius*? Fabricius, *Laccornellus* sp., *Enochrus lampros* Knisch, *Desmopachria mendozana* Steinheil and species of Scirtidae were taxa present in the water column and absent from the benthic communities. Species of Bembidiinae and *Stenopelmus minutus* Hustache were found only in samples extracted from the benthos.

Spatial and seasonal taxonomic richness

A qualitative comparison of taxonomic richness among sampling sites and seasons in the complete vertical profile sampled along the Bañado Carilauquen (Fig. 3) indicated that: i) except for the summer samples from HMR, close and similar to those of

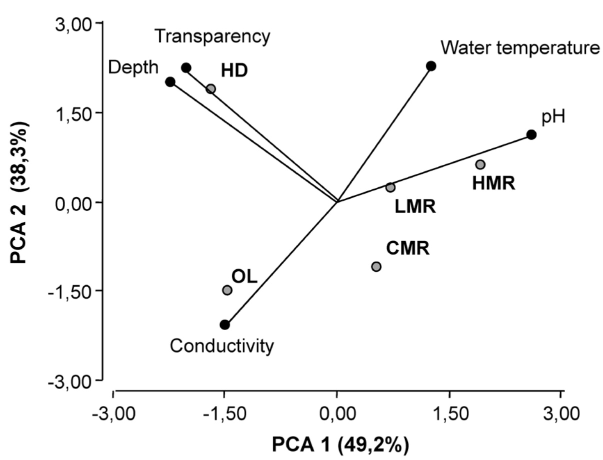

Fig. 2. Biplot of sampled sites and environmental variables resulting from the Principal Component Analysis (PCA).

Table I. Mean environmental records per sampling site and season of the year at Bañado Carilauquen (values in parenthesis: standard deviation, SD). References: Cd.: conductivity (µS cm^{-1}), WT: water temperature (C), pH: potential of hydrogen, Tr.: transparency (m), Dp.: depth (m), HD: headwaters, HMR: higher middle reach, CMR: central middle reach, LMR: lower middle reach, OL: outlet-lake, *: HMR spring: only data.

Site	Summer					Autumn					Winter					Spring				
	Cd.	WT	pH	Tr.	Dp.	Cd.	WT	pH	Tr.	Dp.	Cd.	WT	pH	Tr.	Dp.	Cd.	WT	pH	Tr.	Dp.
HD	953 (1.4)	13.5 (0.2)	7.4 (0.3)	1.6 (0.6)	1.6 (0.6)	941.5 (9.2)	13.8 (0.7)	7.0 (0.2)	1.6 (0.7)	1.6 (0.7)	922 (11.3)	11 (1)	7.4 (0.4)	1.6 (0.6)	1.6 (0.6)	1050 (70.1)	15.1 (0.3)	7.8 (0.1)	1.6 (0.6)	1.6 (0.6)
HMR	1169.5 (304.8)	24.9 (0.9)	8.5 (0.6)	0.3 (0)	0.3 (0)	1226.5 (416.5)	10.4 (1.5)	7 (0)	0.3 (0.1)	0.3 (0.1)	1450 (70.7)	6.2 (1.3)	7.5 (0.4)	0.3 (0.1)	0.3 (0.1)	1600*	16.3*	7.6*	0.2*	0.2*
CMR	1055 (1.4)	22.2 (4.8)	7.6 (0.7)	0.2 (0)	0.2 (0)	1241 (292.7)	8.6 (2.9)	7.6 (0.5)	0.2 (0)	0.2 (0)	1150 (70.7)	6.9 (0.8)	7.3 (0.2)	0.2 (0.1)	0.2 (0.1)	1300 (141.4)	11.1 (2.6)	7.4 (0.4)	0.2 (0.1)	0.2 (0.1)
LMR	1233 (22.6)	24.2 (0.4)	8.2 (0.8)	0.5 (0.2)	0.5 (0.2)	1389.5 (116.7)	9.3 (2.3)	7 (0.8)	0.5 (0.2)	0.5 (0.2)	1200 (0)	6.9 (1.6)	7.3 (0)	0.5 (0.2)	0.5 (0.2)	1300 (0)	13.9 (2.1)	7.4 (0.3)	0.4 (0.1)	0.4 (0.1)
OL	8415 (586.9)	24.1 (1.7)	8.2 (0)	0.5 (0.1)	0.5 (0.1)	16795 (3853.7)	8.5 (1.3)	6.7 (0.3)	0.5 (0.1)	0.5 (0.1)	10420 (876.8)	5.65 (0.21)	6.7 (0.1)	0.5 (0.1)	0.8 (0.5)	9250 (70.7)	12.10 (1.41)	7.4 (0.3)	0.6 (0.1)	0.8 (0.3)

Table II. Eigenvalues for the first (PCA1) and the second (PCA2) principal components.

Variables/ Variance	**PCA 1** (49.20%)	**PCA 2** (38.30%)
pH	0.59	0.25
Conductivity	-0.33	-0.47
Water temperature	0.29	0.51
Transparency	-0.45	0.50
Depth	-0.50	0.45

Table III. Taxa registered using hand net (1) and Petersen dredge (2) by season and sampling site at Bañado Carilauquen. References: HD: headwaters, HMR: higher middle reach, CMR: central middle reach, LMR: lower middle reach, OL: outlet-lake.

	SUMMER					AUTUMN					WINTER					SPRING				
Taxa/site	HD	HMR	CMR	LMR	OL	HD	HMR	CMR	LMR	OL	HD	HMR	CMR	LMR	OL	HD	HMR	CMR	LMR	OL
INSECTA																				
EPHEMEROPTERA																				
CAENIDAE																				
Caenis sp				1.2												1				
TRICHOPTERA																				
HYDROPTILIDAE																				
Metrichia sp	1.2	1				1.2					2					1				
Oxyethira sp											2					1.2				
ODONATA																				
AESHNIDAE																				
Rioaeshna absoluta								1	1.2				1	1			2		1	
COENAGRIONIDAE																				
Ischnura fluviatilis							2													
COLEOPTERA																				
DYTISCIDAE																				
Liodessus sp			2	2		1	1					2		1			1	1.2	1.2	
Lancetes biremis						1.2	1	1	1					1			1		1	
Hydrovatus sp						1	1	1	1			1								
Lancetes varius?	1																			
Laccornellus sp									1											
Desmopachria mendozana																	1			
HYDROPHILIDAE																				
Tropisternus setiger				2			1	1				1								
Berosus sp	1						1.2		1.2			1.2		1	2		1	1	1	
Enochrus lampros		1																		
HALIPLIDAE																				
Haliplus sp								1	1				1	1.2					1	
CARABIDAE																				
Bembidiina															2					
STAPHYLINIDAE															2					1.2
CURCULIONIDAE																				
Stenopelmus minutus														2						
SCIRTIDAE							1													
HEMIPTERA																				

Table III. Continuation

	SUMMER					AUTUMN					WINTER					SPRING				
Taxa/site	HD	HMR	CMR	LMR	OL	HD	HMR	CMR	LMR	OL	HD	HMR	CMR	LMR	OL	HD	HMR	CMR	LMR	OL
CORIXIDAE																				
Sigara jensenhaarupi			1	1		1	1	1						1						
Sigara rubyae														1						
NOTONECTIDAE																				
Notonecta viscerens		1	1				1												1	
BELOSTOMATIDAE																				
Belostoma bifoveolatum		1					1													
DIPTERA																				
CHIRONOMIDAE																				
Cricotopus sp	1.2										2									
Chironomus sp		1.2	1	2	2	2	2		2		2	1.2		2	2	2		2	2	
Pseudochironomus sp			1.2				2					2								
Dicrotendipes sp	2	1	1.2																	
Djalmabatista sp				2			2													
Tanypus sp		1.2		2			2					2				2			2	
Paratanytarsus sp		1		2					2											
Polypedilum sp	2																			
DIXIDAE						1														
CULICIDAE									1					1					1	
DOLICHOPODIDAE															2					
TABANIDAE	1	1	1	1	1					2									1	
EPHYDRIDAE	1					2					2				2			1		
CERATOPOGONIDAE																				
Dasyhelea sp			1.2					2					2					2		
MOLLUSCA																				
CAENOGASTROPODA																				
COCHLIOPIDAE																				
Heleobia parchappii	1.2	1.2	1.2	1.2	1.2	1.2 1.2	1	1.2	1.2	1.2 1.2	1.2	1.2	1.2	1.2	1.2 1.2	1.2	1.2	1.2	1.2	1.2
Heleobia hatcheri	1.2					2		2			1.2									
PULMONATA																				
CHILINIDAE																				
Chilina aff. parchappii	1.2					2	1				1.2					1.2				
LYMNAEIDAE																				
Lymnaea viator	1	1.2	1.2	2		1	1.2	1.2	1.2	2	1.2	1.2	1.2	1.2		1	1.2	1.2	1.2	
PLANORBIDAE																				
Biomphalaria peregrina			1	1			1	1	1				1	1			1.2	1.2	1.2	

Table III. Continuation

	SUMMER					AUTUMN					WINTER					SPRING				
Taxa/site	HD	HMR	CMR	LMR	OL	HD	HMR	CMR	LMR	OL	HD	HMR	CMR	LMR	OL	HD	HMR	CMR	LMR	OL
CRUSTACEA																				
AMPHIPODA																				
HYALELLIDAE																				
Hyalella curvispina	1.2	1	1.2	1.2		1.2					1.2	1.2	1	1	1.2	1	1.2	1		1.2
ANNELIDA																				
OLIGOCHAETA						1.2			12					1.2					1.2	1.2
HIRUDINEA	1.2	1.2				1.2	1.2	1			1.2	1.2	1.2			1.2	1.2			
PLATYHELMINTHES																				
DUGESIIDAE						1.2	1.2		1		1.2		1.2			1		1.2		
NEMATODA															1.2					

the headwaters, the communities sampled in each season of the year at both ends of the gradient (HD and OL) were more similar between them by site than by season of the year, suggesting that faunal composition exhibited little seasonal variation in both headwaters and outlet; ii) the samples from the middle reaches (HMR, CMR and LMR) were similar to one another, forming a third set characterised by an undefined seasonal pattern and uniform spatial similarity in faunal composition. At the temporal and spatial level, the highest similarity in faunal composition of the three main groupings detected corresponded to the headwaters (52%); in turn, composition of the outlet macrofauna was the least similar to that in the rest of the Bañado Carilauquen (only 32% of similarity; Fig. 3).

DISCUSSION

We are reporting the first macroinvertebrate inventory including fauna of benthos and water column from this Ramsar site. The use of hand net besides Petersen dredge for sampling coincided with an increase in macroinvertebrate taxonomic richness at the Bañado Carilauquen (total: 47 taxa) in relation to that reported for samples from the littoral benthos of the same body of water (36 taxa; Scheibler & Ciocco, 2011). This increase can be mostly attributed to the detection of hydrophilous coleopterans in the water column, mainly Dytiscidae and, to a lesser extent, Hydrophilidae and Scirtidae. Despite the mentioned increase, the taxonomic richness detected at the Bañado Carilauquen remained at low levels, which turned out to be lower in family and species richness than that from lentic environments with a wetter and more temperate climate such as the Pampean region (Fontanarrosa *et al.*, 2004) and the La Plata basin (Poi de Neiff & Neiff, 2006), or that from lotic arid and semiarid Andean water bodies of Patagonia (Miserendino & Pizzolón, 2004). The lower taxonomic richness recorded at the Bañado Carilauquen can be attributed to the critical conditions of this perturbed inland lake

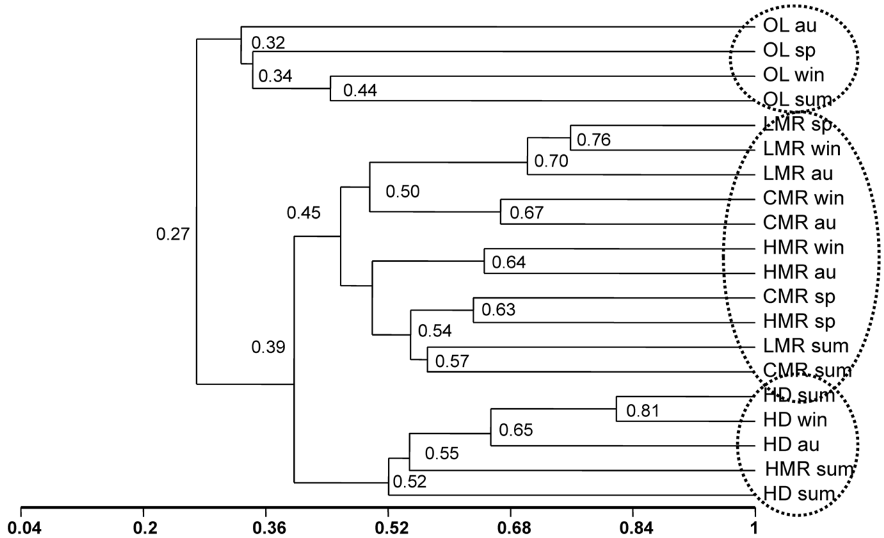

Fig. 3. Sorensen's coefficient diagram showing similarity of macroinvertebrates community composition between spatial and temporal variations along the Bañado Carilauquen. Reference: HD: headwaters; HMR: higher middle reach; CMR: central middle reach; LMR: lower middle reach; OL: outlet-lake; au: autumn; wi: winter; sp: spring and sum: summer.

including hard, eutrophic, polysaprobic and contaminated waters, together with pronounced variability in water permanence and high impact of human activities.

Aquatic insects, mainly Diptera and Coleoptera, were dominant at the Bañado Carilauquen (over 70% of taxonomic richness). Both orders are highly predominant in lentic environments in wetlands under different environmental conditions (Fontanarrosa *et al.*, 2004; Poi de Neiff & Neiff, 2006; Boix *et al.*, 2007; Peralta *et al.*, 2007) and in stressing environments like saline water bodies from arid/semiarid regions (Juárez Flores & Ibañez, 2003; Pinder *et al.*, 2004). The Coleoptera have been mentioned as one of the aquatic insect orders reaching highest diversity in lentic water (Martinoy *et al.*, 2006). They are, in general, very good swimmers that rise from the bottom to the surface of ponds and other shallow water bodies to breathe (White *et al.*, 1984), which makes them dominant components of the water column and regular constituents of the benthos, similarly to our findings at the Bañado Carilauquen. The Diptera, in turn, frequently dominate the composition of aquatic insects due to the high species diversity and density usually shown by the Chironomidae. At the Bañado Carilauquen, chironomids exhibited high taxonomic richness, as was reported, for example, for the arid region of Europe by Moreno *et al.* (2010) (Southeastern Spain, mean annual precipitation < 250 mm) and Trigal Domínguez *et al.* (2010) (North Iberian plateau).

Macroinvertebrate presence/absence matrices as those used in this study have been employed to explore distribution patterns along disturbed spatial gradients (Karr & Chu, 1999). The faunal composition of the macroinvertebrate assemblages studied at the Bañado Carilauquen was more conditioned by spatial variability than by the seasonal component, particularly at the gradient ends. Over 60% of the species found at the Bañado Carilauquen were detected in both hand net and dredge samples. The qualitative composition of macroinvertebrate communities was clearly different along the Bañado Carilauquen, with three distinct faunal sets, one for the headwaters, another one for the middle reaches and a third one for the outlet. The fact that the maximum levels of diversity displayed at the headwaters or in the higher middle reaches where the lowest levels of conductivity were detected, confirms that the less saline waters of the HD and of the higher reaches offer more favourable conditions for existence of multiple taxa as was suggested in other littoral benthos studies of the Bañado Carilauquen (Ciocco & Scheibler, 2008; Scheibler & Ciocco, 2011). In like manner, that the faunal composition toward the outlet turned out the least diverse and most dissimilar from the rest is indicating that the hard waters of the lower end of the studied gradient (outlet-lake) are too stressing and restrictive to support macroinvertebrate assemblages.

It is known that high levels of salinity cause changes in macroinvertebrate assemblage structure when concentration values exceed the species' tolerance range (Kefford *et al*., 2004; Waterkeyn *et al*., 2008). Actually, faunal composition at the headwaters and higher reaches of the Bañado Carilauquen is dominated by taxa with relatively narrow tolerance ranges, whereas the few taxa present all year round in both communities at the outlet, such as *Chironomus* sp., are broadly tolerant of critical water conditions, including very hard and polysaprobic water (Paggi, 1999; Mandaville, 2002). In the middle reaches, where shallow ponds are dominant, taxonomic richness would be modulated by the presence of transient taxa (some of them: *Tropisternus* sp., *Belostoma* sp., *Sigara* sp., *Notonecta* sp., *Haliplus* sp. *Enochrus* sp.) adapted to pronounced changes in environmental conditions (Hall *et al*., 2004). In fact, in the middle reaches of the Bañado Carilauquen there was presence of taxa such as *Tropisternus setiger*, *Haliplus* sp., *Pseudochironomus* sp., *B. peregrine*, species of Culicidae, *Enochrus lampros*, *S. rubyae*, *N. viscerens*, *B. bifoveolatum*, *Tanypus* sp., *Paratanytarsus* sp., *Djalmabatista* sp., *Dasyhelea* sp. and *Liodessus* sp., invertebrates with high tolerance for hydrological shifts (Spinelli & Wirth, 1993; Mandaville, 2002; Paggi, 2003; Pavé & Marchese, 2005; Alarie *et al*., 2007; Ciocco & Scheibler, 2008; Bazzanti *et al*., 2009).

Another factor affecting the macroinvertebrates distribution at the Bañado Carilauquen is water permanence. The headwaters and the outlet-lake always have water; in contrast, the shallow middle reaches are frequently exposed to desiccation periods. Stable water conditions like those at the headwaters coupled with low conductivity values enhance development of littoral vegetation and consequently of macroinvertebrate assemblages due to the increase in food supply, refuge and microhabitats appropriate for the development of invertebrates (Hall *et al*., 2004; Bazzanti *et al*., 2009). In contrast, at the outlet-lake of the Bañado Carilauquen, although it always has water, the hydric volume varies more markedly and littoral vegetation becomes conspicuously less abundant (Peralta & Fuentes, 2001) which, along with the high water salinity, reduces macroinvertebrate richness, both in the benthos and water column, to a few species that are tolerant of extreme environmental conditions.

If the salinity gradient were the sole factor modulating the distribution pattern of macroinvertebrate richness along the Bañado Carilauquen, as strongly suggested by the fact that the soft waters of the headwaters exhibit the highest richness and the hard waters of the outlet the lowest richness, transition reaches (HMR, CMR, LMR) should coincide with intermediate taxonomic richness values and with assemblages dominated by taxa with moderate ranges of tolerance for water hardness. In effect, the dominant taxa in the middle reaches (mainly *Tanypus* sp., *Paratanytarsus* sp., *Djalmabatista* sp., *Dasyhelea* sp. and *Liodessus* sp.) are aquatic insects with broader tolerance of salinity and hydrological shifts than those from the headwaters, but are at the same time less tolerant than *Chironomus* sp., one of the few dominant taxa under the very critical conditions of the outlet (Spinelli & Wirth, 1993; Mandaville, 2002; Paggi, 2003; Pavé & Marchese, 2005; Alarie *et al*., 2007;

Solimini *et al.*, 2008; Bazzanti *et al.*, 2009). Nonetheless, the taxonomic richness detected in the middle reaches was frequently similar to or even higher than that at the headwaters, and did not show a decreasing gradient between higher and lower reaches as would be expected according to the conductivity gradient (total taxonomic richness means for HMR, CMR and LMR hardly varied between 12.75 and 13.50). This relatively higher and more stable taxonomic richness detected in the middle reaches relative to the one expected from the conductivity gradient could be attributed to the semi-permanent condition of intermediate water bodies and to the higher levels of impact and disturbance affecting the middle reaches of the Bañado Carilauquen. In point of fact, it has been hypothesised that high diversity values would be related to intermediate intensities of disturbance (Connel, 1978), which in the case of the Bañado Carilauquen are clearly more conspicuous in the shallow middle reaches due to cattle grazing (Sosa, 1995).

It is a known fact that water quality and water permanence are important factors explaining wetland ecology in arid and semiarid environments, especially in those subject to high levels of evaporation as is the Bañado Carilauquen (McEwan *et al.*, 2006). Community richness would respond to a greater extent to the pattern of water quality under stable hydrological conditions and to a lesser extent to unstable and more disturbed water bodies. However, further studies, including manipulative experiments, are needed to understand, at different space scales, the synergy effect of factors modelling macroinvertebrate richness along contrasting environmental conditions in arid and semiarid inland wetlands.

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