PRIMARY RESEARCH PAPER

Patagonian ostracods as indicators of climate-related hydrological variables: implications for paleoenvironmental reconstructions in Southern South America

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Abstract Different precipitation regimes across Patagonia generate an environmental gradient that is expected to reflect upon the solute composition and concentration of lake water through the ensuing differences in water balance. In turn, this hydrochemical gradient could influence the occurrence and distribution of ostracods in the area. A cluster analysis on hydrochemical data of 36 Southern Patagonian

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Departamento de Biodiversidad y Biología Experimental, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Intendente Güiraldes 2160, Ciudad Universitaria—Pabellón II, C1428EGA Buenos Aires, Argentina waterbodies shows that low salinity, bicarbonatedominated waters characterize Andean and ecotonal lakes, located in the wetter part of the precipitation gradient, while their steppe counterparts, which receive a much lower precipitation input, are more saline, enriched in all major anions and sodiumdominated. Kruskal-Wallis tests followed by Mann-Whitney pairwise comparisons show statistically significant differences in the ostracod species each water type hosts, with L. patagonica, E. cecryphalium, P. smaragdina and P. incae being found in the more dilute waters characteristic of Andean and ecotonal lakes and Limnocythere rionegroensis in the mesohaline, evaporatively evolved waters typical of steppe lakes. Other species studied do not appear to have such distinct distributions, having been found throughout the range of conditions studied. These findings promote the use of the aforementioned ostracods as semi-quantitative paleohydrological indicators, which could improve paleoclimatic reconstructions in Patagonia.

Keywords Freshwater Ostracoda · Ecology · Patagonia · Hydrochemistry

Abbreviations

TDS Total dissolved solids T. Alk. Total alkalinity SP Southern Patagonia NP Northern Patagonia

N-CP Northern and Central Patagonia

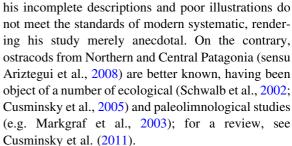


WA Weighted average SD Standard deviation CV Coefficient of variation

Introduction

Ostracods constitute a diverse group of aquatic microcrustaceans which can be found in a wide range of both the marine and the non-marine habitats worldwide. They secrete a calcite bivalve carapace with a high preservation potential, thanks to which they have left an excellent fossil record extended as far as the Ordovician. In addition to their wide geographical and geological range, the marked preferences of some species to particular environmental conditions make ostracods good proxies of environmental change, especially in continental environments (e.g. De Deckker & Forester, 1988; Carbonel et al., 1988; Curry, 1999; De Deckker, 2002). Published ostracodbased paleoenvironmental reconstructions include univariate indicator species approaches, based on fossil occurrences of certain species with known environmental tolerances (e.g. Forester et al., 2005), and more complex multivariate indicator species approaches involving development of transfer functions (e.g. Mezquita et al., 2005).

As with other biological proxies, the use of ostracods for paleoenvironmental reconstruction requires a deep knowledge of their taxonomy and ecology, a requisite usually not met in some remote areas. One of such poorly studied areas is Southern Patagonia, a region of particular interest for Quaternary paleoclimatic research as it is, together with Antarctica, the sole emerged landmass at high latitudes in the Southern Hemisphere (e.g. Zolitschka et al., 2006). During the last few years, a number of multiproxy paleolimnological studies including biological indicators have been carried out in the region (Schäbitz et al., 2003; Haberzettl et al., 2005, 2006; Mayr et al., 2005, 2007; Wille et al., 2007; Fey et al., 2009); however, none of them included ostracods. The only information available for Southern Patagonia ostracod fauna is the study of the German naturalist Daday (1902), who studied the aquatic invertebrates of Santa Cruz Province over a century ago. Daday described seven ostracod species but unfortunately



Recent unpublished studies (Massaferro et al., 2010; Maidana et al., 2010; Ramón Mercau et al., 2010) show the great potential of ostracods for paleoenvironmental reconstructions in Southern Patagonia, which could be extended if more precise taxonomical and ecological information was available. The present contribution aims to advance the use of ostracods as proxies of environmental change in the area by analyzing the hydrochemistry of modern assemblages host waters, using both the limnological data gathered in the course of the present investigation for Southern Patagonia and that available in the literature for Northern and Central Patagonia. As part of this approach, we explored the relationships between water chemistry and geographical location of the lakes under study; this information constitutes, to the best our knowledge, the first of its kind to be published for the area. A few Patagonian waterbodies with no limnological variables measured were also considered in this study for the sake of species list completion, as some of the ostracods found in them are reported for the first time for this region.

Study area

The Patagonian region is the southernmost portion of South America, extending between the Río Colorado River at 35°S approximately and the Cape Horn at 56°S (Fig. 1). This latitudinal range falls within the area of influence of the westerlies, which have been the main forcing of the climate of Patagonia as it reached its present geographical position in the late Miocene (Compagnucci, 2011). Were their flux unimpeded, the westerlies would be solely responsible for precipitation patterns over the Patagonian region through the advection of moist air from the Pacific Ocean. However, the Andean Cordillera acts as a barrier for wind flow, causing abundant orographic precipitation over Western Patagonia due to uplift of



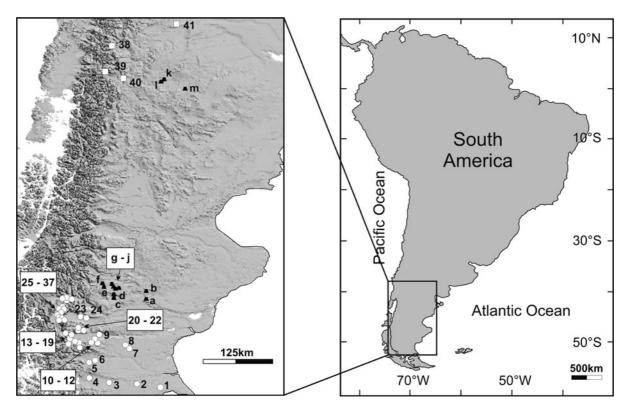


Fig. 1 Map of the studied area. White dots The SP waterbodies, white boxes the NP waterbodies and black triangles the N-CP waterbodies. Site codes are as follows: 1 L. Azul, 2 L. Potrok Aike, 3 L. El Morro, 4 L. Huergo, 5 L. Esperanza, 6 L. Salada, 7 L. San Ignacio, 8 L. Nueva, 9 L. Rincón, 10 Arroyo I, 11 L. Alta, 12 L. Sarmiento, 13 L. Cachorro I, 14 L. Cachorro II, 15 L. Roca, 16 L. Las Mellizas, 17 L. Cerro Frías I, 18 L. Cerro Frías II, 19 Punta Banderas, 20 L. Ernesto, 21 Sosiego I, 22 Sosiego II, 23 L. Agustín, 24 L. El Toro, 25 L. Pajonales, 26 L. Capri, 27 L.

low level winds and very dry conditions over Eastern Patagonia through forced subsidence of the air masses (Garreaud et al., 2009). As a result of this rain shadow effect, the Argentinean Patagonia exhibits a strong precipitation gradient ranging from 2,000 mm/y or higher at the West, at the base of the Andes, to <200 mm/y at the East (Paruelo et al., 1998). The scarcity of meteorological stations in the area and the fragmentary nature of their records represent a major shortcoming when attempting to characterize the climate of Patagonia. Mean annual precipitation isolines presented by Paruelo et al. (1998)—based on a variety of sources, including both the meteorological records and the climate databases—and those presented by Tonello et al., (2009)—based on gridded monthly precipitation estimates (Leemans and Cramer, 1991 in Tonello et al., 2009)—differ somewhat,

Madre, 28 L. Hija, 29 L. Nieta, 30 L. Torres, 31 L. Azul II, 32 Las Lolas I, 33 Las Lolas II, 34 L. Verde, 35 L. Cóndor, 36 L. Huemul, 37 L. del Desierto, 38 Lahuen-Co, 39 La Angostura, 40 L. Los Juncos, 41 La Herradura. a L. Honda, b L.1, c L. Cardiel, d Spring creek pool 1, e Marrón Grande, f Marrón Chica, g L. Strobel, h L. Encadenadas, i L.6 lake, j L.6 spring, k L. Carilaufquen Grande N Bay, l L. Carilaufquen Grande, m L. Ñeluan. Location of N–CP waterbodies obtained from Cusminsky et al. (2005)

but both agree that between 50° and 52°S approximately the 200- and 400-mm isolines exhibit a pronounced curve towards the southeast, related to the lesser height of the Andean cordillera and the weakening of low level westerlies during austral winter at these latitudes (Garreaud et al., 2009). According to these authors, most precipitation throughout the Patagonian region falls during winter, especially towards the east.

These precipitation patterns are among the main determinants of the marked contrast between Western and Eastern Patagonia, allowing the recognition of two distinct subregions: Andean Patagonia and Patagonian Steppe, divided by an ecotone of Subandean grassland (Paruelo et al., 1998). Precipitation and evapotranspiration are the most important factors affecting waterbodies at both the subregions. As the former is much



higher in Andean Patagonia and the latter is intense throughout the region, steppe waterbodies in general differ considerably in their hydrological balance with respect to Andean lakes. Limnological studies carried out at a regional scale in permanent and temporary lakes in Northern Patagonia lakes (Díaz et al., 2000; Perotti et al., 2005; Rogora et al., 2008) found that waterbodies from Andean settings have lower total salinity and nutrient concentrations than those located at the steppe, as well as different solute composition.

Materials and methods

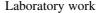
Field work

Surface sediments were sampled from 37 waterbodies (one stream, two moors and several temporary and permanent lakes; Fig. 1) located between 49° and 52°S and 69° and 73°W in Santa Cruz Province, Argentina. The samples were taken during three field trips carried out in January 2009, April 2010 and April 2011 as part of the Southern Patagonia Interdisciplinary Project (PIPA). This dataset is referred to as Southern Patagonia (SP) samples.

In addition, four sediment samples were obtained from Northern Patagonia (NP) during the same period: one from a small stream (Lahuen-Co, Neuquén Province); one from a temporary pond (La Angostura, Río Negro Province) and two from permanent ponds (La Herradura, Neuquén Province and Los Juncos, Río Negro Province) (Fig. 1).

All the sediment samples were obtained by scooping superficial sediments in a metal container attached to a handle, or else by sweeping through them with a plastic bag. Sediment samples were cold stored in plastic bags for routine ostracod analysis.

Water samples were taken from all but one (Arroyo I) of the SP sites for chemical analysis. Water temperature, pH, conductivity, dissolved oxygen and total dissolved solids (TDS) were measured in situ with a Hanna HI 9828 Multiparameter Portable Meter. From each lake, a single surface sample was collected in a pre-washed plastic bottle and stored at 4°C for successive chemical analyses, which were performed at the CNR-ISE (Institute of Ecosystem Study, Verbania Pallanza, Italy).



Chemical analysis

Water samples were analysed for the major chemical variables at CNR Institute of Ecosystem Study hydrochemical laboratory. The following variables were considered: pH, conductivity, alkalinity (acidimetric titration, Gran's method), ammonium, total nitrogen, total phosphorus and reactive silica (spectrophotometry), major anions (SO₄⁻², NO₃⁻, Cl⁻) and cations (Ca⁺², Mg⁺², Na⁺, K⁺) (ion chromatography) and total organic carbon (TOC, high temperature catalytic oxidation, IR detection). Details on the analytical methods used can be found in Tartari & Mosello (1997). To check analytical quality for each analysis, a comparison between the sum of anions and cations, and between measured and calculated conductivity was performed. The ionic balance error was below 10% for all the samples, which were therefore included in the following statistical analysis.

Further quality assurance measures were adopted in the laboratory, such as the use of control charts and the analysis of synthetic samples on a regular basis. Participation in several inter-laboratory comparisons on surface water analysis allowed a further quality check of the results.

Ostracod analysis

Sediment samples were washed under tap water on a 75-µm pore diameter sieve and dried by thermostatic stove at 40°C. The more aggregated samples were treated with 10% H₂O₂ overnight in order to facilitate the sieving. Five grams of sediment were examined under stereomicroscope and any ostracods found were picked out with a brush and placed in a micropaleontological slide. As the aim of this investigation was to generate information for paleoenvironmental reconstruction purposes, identification was based on caparaces and valves only, as the sole body parts capable of overcoming the taphonomic barrier. Adult ostracods were determined at specific level based on specialized bibliography (Purper & Würdig, 1974; Martens & Behen, 1994; Cusminsky & Whatley, 1996; ; Rossetti & Martens, 1998; Meisch, 2000; Cusminsky et al., 2005) and by comparison with holotypes and paratypes deposited at La Plata Natural Sciences Museum (Argentina): Limnocythere patagonica Cusminsky



& Whatley, 1996 (MLP 184–188); *Ilyocypris ramirezi* Cusminsky & Whatley, 1996 (MLP 189–192); *Eucypris virgata* Cusminsky & Whatley, 1996 (MLP 206–210); *Eucypris cecryphalium* Cusminsky & Whatley, 2005 (MLP-Mi 1,386–1,392) and *Kapcypridopsis megapodus* Cusminsky & Whatley, 2005 (MLP-Mi 1,395–1,400).

Numerical methods and statistical analysis

A cluster analysis (Bray-Curtis similarity measure, paired group linking algorithm) was performed on the 36 Southern Patagonia waterbodies sampled with chemical data available, taking into account the following variables: Ca^{+2} ($\mu\text{eq/l}$), Mg^{+2} ($\mu\text{eq/l}$), K^{+} ($\mu\text{eq/l}$), Na^{+} ($\mu\text{eq/l}$), SO_{4}^{-2} ($\mu\text{eq/l}$), Cl^{-} ($\mu\text{eq/l}$), total alkalinity (T. Alk.) (µeq/l), TN (mg/l), TOC (mg/l), TP (µg/l) and pH. Further analysis of these and other limnological variables is under way and will be presented elsewhere (Michela Rogora, personal communication). The water type of the SP waterbodies, as well as that of the Northern and Central Patagonia waterbodies studied by Schwalb et al. (2002) and Cusminsky et al. (2005), was determined with the AquaChem[©] software. Trilinear ion (Piper) plots were drawn in order to graphically summarize water type of selected sites.

Schwalb et al. (2002) and Cusminsky et al. (2005) reported ostracod assemblage composition and several limnological variables of 17 Northern and Central Patagonia waterbodies, herein referred to as the N-CP dataset. We selected 13 of those sites (Fig. 1), leaving out those without hydrochemical data available and one sample bearing a single species determined up to genus level only. T. Alk. $(HCO_3^- + CO_3^{-2})$ and TDS contents were estimated based on the concentrations of the other major ions using the AquaChem[©] software. This information, along with the data gathered in the course of this investigation, was used to compile a Patagonian ostracod database including assemblages' composition and their host waters hydrochemistry. The salinity scale chosen is that of the Venice Symposium (1958, in Neale, 1988), which is suitable for ostracod analysis.

The diversity of the ostracod assemblages studied was summarized by a series of indices: the species richness *S*, equitability and Simpson's index (Krebs, 1989). Equitability is calculated as:

$$\frac{H}{\ln(S)} = \frac{-\sum \left[\frac{ni}{N}\ln\left(\frac{ni}{N}\right)\right]}{\ln(S)},\tag{1}$$

where ni is the proportion of individuals of species i, N is the total number of individuals and H is the Shannon–Wiener index. This estimate measures the evenness with which individuals are divided among the taxa present; assemblages strongly dominated by one species have very low values (0 is assigned to monospecific assemblages). Simpson's index, 1 - D, is calculated as:

$$1 - \sum \left(\frac{ni}{N}\right)^2 \tag{2}$$

and is a nonparametric measure of diversity which takes into account both the species richness and the evenness. It ranges between 0, when a single species is present, to almost 1 for assemblages with many species accounting for similar numbers of individuals.

Ostracod species in this database with at least four recordings with relative abundance $\geq 3\%$ were compared with respect to their hydrochemical preferences. In particular, ecological data for L. rionegroensis used in this study was obtained entirely from bibliographical sources, as it was not found in SP sediment samples. Following Curry (1999) and Forester et al. (2005), ostracod host water composition was characterized by the natural logarithm of calcium concentration relative to T. Alk. and the common logarithm of TDS. The former index is a measure of the relative enrichment of water in either of these major ions, which depends on the initial solute composition and its hydrochemical evolution. By plotting ln ([T. Alk.]/[Ca⁺²]) against log (TDS) a solute composition field is defined which reflects the importance of evaporation in the resulting hydrochemistry. Our aim was to compare the location of each species along this solute space in order to establish their preferences. Their statistical significance was evaluated by means of two Kruskal-Wallis tests, each performed on the TDS or ln ([T. Alk.]/[Ca⁺²]) values multiplied by the relative abundance of each species at each site where they occurred. These were followed by Mann-Whitney pairwise comparisons in lieu of post hoc tests. The species optima were estimated by calculating the weighted average [WA(sp)] of the value of the environmental variable X (TDS or $\ln ([T. Alk.]/[Ca^{+2}])$) weighting X by the abundance of the species in question and adding across all the samples where it was present:



$$WA(sp) = \frac{\sum X * \frac{ni}{N}}{\sum \frac{ni}{N}}.$$
 (3)

In turn, the species tolerances were estimated by calculating an amount analogue to a standard deviation (SD); namely, as the square root of the weighted mean of the squared differences between the species WA and the actual values of *X* in the corresponding samples (Lepš & Šmilauer, 2003):

$$SD = \sqrt{\frac{\sum (X - WA(sp))^2 * \frac{ni}{N}}{\sum \frac{ni}{N}}}.$$
 (4)

In order to compare the magnitude of such dispersion between the different species, the coefficient of variation (CV) was also calculated.

The cluster analysis on the SP waterbodies and the nonparametric tests on the species' hydrochemical values were performed with the PAST software version 1.81 (Hammer et al., 2001).

Results

Southern Patagonia waterbodies characterization

The majority of the SP lakes analysed (Fig. 2a) have calcium bicarbonate-dominated waters. Seven

waterbodies are dominated by an anion other than bicarbonate: sodium chloride is the most abundant salt at steppe lakes San Ignacio, Nueva, Salada and Potrok Aike, while the Andean lakes Azul II, Ernesto and Rincón have sulphate dominated waters. As for the cations, calcium is dominant or codominant in most lakes. Sodium is the main cation present in eight waterbodies, of which lakes Agustín, El Morro, Huergo and Sarmiento, all of them located in steppe settings, can be considered soda lakes (sodium bicarbonate-dominated waters) albeit with codominant ionic species.

Except at the six most saline lakes of the SP dataset (Potrok Aike, Salada, Nueva, San Ignacio, El Morro and Huergo), the Na $^+$ to Cl $^-$ ratio in lake water is well above the corresponding ratio in seawater (0.858), indicating a weathering contribution to Na $^+$ concentration. For its part, the ${\rm SO_4}^{-2}$ to Cl $^-$ ratio in lake water is above the ratio in marine water (0.103) in all but six lakes (Las Lolas II, Pajonales, Huergo, Nueva, Potrok Aike and San Ignacio), four of which are the same as the previously mentioned exceptions. As atmospheric deposition of ${\rm SO_4}^{-2}$ on the lakes can be ruled out at this remote location, these high values can be attributed to weathering of soils and rocks with sulphur minerals within their drainage basin.

The cluster analysis performed yielded results consistent with these hydrochemical differences

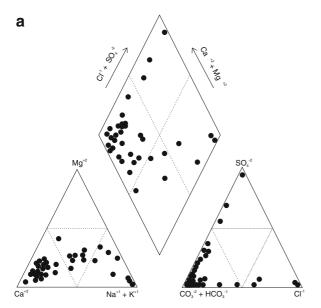
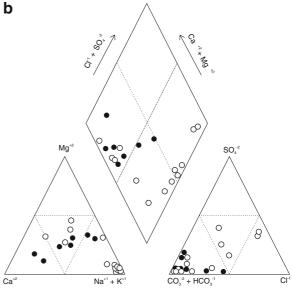


Fig. 2 a Ionic composition of SP waterbodies. b Ionic composition of Patagonian ostracod host waters. N-CP sites are represented by *empty circles*, while SP sites are represented by



filled circles. Part of the data on ostracod host waters ionic composition is taken from Cusminsky et al. (2005)



(Fig. 3). The resulting dendrogram (cophenetic correlation coefficient: 0.91) allowed recognition of five groups, while two lakes (Ernesto and Nueva) were considered outliers. Lake Ernesto has a very high SO_4^{-2} content relative to other ions, while L. Nueva presents the highest values in T. Alk., Cl^- , SO_4^{-2} , Na^+ and K^+ among the sampled waterbodies.

Lakes Salada and San Ignacio (Cluster V) are set apart from the rest on account of being dominated by sodium chloride and having the highest ionic content within the dataset upon exclusion of outlier Lake Nueva. Lakes Potrok Aike, El Morro and Huergo, which form Cluster III, have a similar solute composition to the

Cluster V pair but their salinity is an order of magnitude lower (Table 1). Except for L. Huergo, lakes in these two clusters have extremely high TP values (>1,000 μ g/l) and are located in the Patagonian steppe (Fig. 1).

Cluster I (Table 1) comprises 13 waterbodies with well-buffered waters (median T. Alk. content = 2,948 μ q/l; median pH 8.14) of moderate solute content. Total phosphorus concentration is medium to high in most lakes (median value = 49 μ g/l), while total nitrogen content is above 2 mg/l in all the waterbodies. Members of this cluster are located in ecotonal and Andean settings except for L. Azul, which is located in the steppe (Fig. 1).

Fig. 3 Cluster analysis of Southern Patagonian waterbodies based on hydrochemical characteristics. Site codes are as follows: LAGU L. Agustín, LALT L. Alta, LAZU L. Azul, LAZUII L. Azul II, LBAN Punta Banderas, LCACI L. Cachorro I, LCACII L. Cachorro II, *LCAP* L. Capri, LCFI L. Cerro Frías I, LCFII L. Cerro Frías II, *LCON* L. Cóndor, LDES L. Desierto, LUER L. Huergo, LTOR L. Toro, LERN L. Ernesto, LESP L. Esperanza, LHIJ L. Hija, LHUE L. Huemul, LIGN L. San Ignacio, LOLI L. Las Lolas I. LOLII L. Las Lolas II. LMAD L. Madre, LMEL L. Las Mellizas, LMOR L. El Morro, LNIE L. Nieta, LNUE L. Nueva, LPAJ L. Pajonales, LPTA L. Potrok Aike, LRIN L. Rincón, LROC L. Roca, LSAL L. Salada, LSAR L. Sarmiento, LRES L. Torres, LVER L. Verde, LSOSI Sosiego I, LSOSII Sosiego II

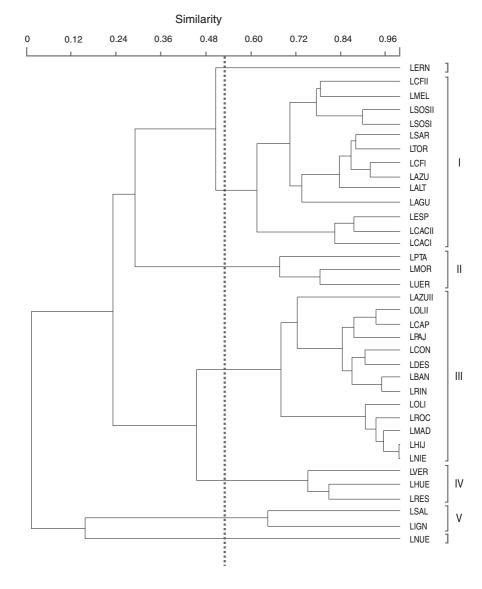




Table 1 Descriptive statistics of hydrochemical values used for the cluster analysis of Southern Patagonia lakes (see Fig. 3)

	-								=		
	Ca ⁺² (μeq/l)	Mg ⁺² (μeq/l)	Na ⁺¹ (μeq/l)	K ⁺¹ (μeq/l)	T. Alk. (meq/l)	Cl ⁻¹ (μeq/l)	SO ₄ ⁻² (μeq/l)	TP (μg/l)	TN (mg/l)	TOC (mg/l)	pН
Cluster I											
Minimum	679	350	259	25	1,401	25	30	5	0.22	2.22	6.70
Median	1,208	796	1091	63	2,948	147	221	49	0.60	7.22	8.14
Maximum	2,844	1,258	3,852	203	4,100	722	1,457	398	2.34	20.34	9.94
Cluster II											
Average	1,818	5,389	12,348	930	10,417	9,588	711	929	3.32	54.19	8.71
Cluster III											
Minimum	254	47	38	5	174	9	0	1	0.06	0.38	6.37
Median	347	77	78	10	425	16	96	4	0.11	1.51	7.35
Maximum	654	138	151	16	741	27	246	16	0.66	10.51	8.85
Cluster IV											
Average	115	17	28	8	123	7	40	5	0.11	0.70	7.28
Cluster V											
Average	4,034	18,422	449,453	16,573	77,000	40,4120	30,085	1,879	10.68	134.15	8.81

The parameters informed depend on whether group size is ≥ 3

For its part, 13 lakes grouped in Cluster III (Table 1) have a somewhat similar composition to the alkaline waterbodies that make up Cluster I, although more dilute and oligotrophic. All the members of this cluster excepting L. Rincón are located in Andean settings (Fig. 1). Andean lakes Verde, Huemul and Torres (Cluster IV), in turn, have similar characteristics to the lakes in Cluster III, especially with regards to nutrient content, but they have the lowest salinity values of the dataset.

Ostracod species occurrence

Ostracods were found in the four NP waterbodies sampled for this study and in six of the SP waterbodies (lakes Cerro Frías I, El Toro, Alta, Pajonales, Sosiego I and the creek Arroyo I) (Fig. 4). The majority of the individuals which were collected alive, as inferred by the presence of soft parts remains, were adults. A notable exception is the darwinulid *Penthesilenula incae*: in our study, the four samples in which this species was present included individuals with two to five (usually three) larvae retained within the caparace, including the Pajonales pond, whose surface was partially frozen at the moment of sampling (April 2010). In general, total counts were low in both (SP and NP) the set of samples: abundances >300

individuals were only recorded at lakes Alta and Cerro Frías I (SP) and the stream Lahuen-Co (NP).

SP assemblages exhibited from low (e.g. 1-D=0 for L. Pajonales; 0.113 for stream Arroyo I) to medium (e.g. 1-D=0.699 for L. Cerro Frías I; 0.679 for L. El Toro) diversity values, with species richness ranging between 1 and 8 (Table 2). These relatively low figures reflect the presence of a dominant species in most of the waterbodies: equitability ranged from 0.768 for both Cerro Frías I and El Toro to 0.327 for stream Arroyo I, being 0 in L. Pajonales. Only L. Huergo exhibited a high equitability value of 0.846, but yielded a medium diversity estimate (1-D=0.648) because of its low species richness. For their part, three out of the four NP samples comprised only one species.

Kapcypridopsis megapodus and Eucypris fontana Graf, 1931 were the most frequent species, both having been found in five sites (at streams Arroyo I and Lahuen-Co the former; at lakes El Morro and Alta the latter and both at lakes Cerro Frías I, El Toro and Huergo). K. megapodus also stands out for being the only species found in both the NP and the SP set of samples. The following species were recorded in only one site: Isocypris beauchampi Paris, 1920; Darwinula stevensoni Brady & Robertson, 1870; Potamocypris smaragdina Vávra, 1891; Chlamydotheca incisa



Table 2 Percentage relative abundance of ostracod species found in SP and NP waterbodies

Species/ site	Southern Patagonia									Northern Patagonia			
	LCFI (p.l.)	LTOR (p.l.)	LUER (p.l.)	LMOR (p.l.)	LALT (t.p.)	LSOSI (s.)	ARRI (p.p.)	LPAJ (p.p.)	LAHU (s.)	LHER (t.p.)	LANG (t.p.)	LJUN (p.p.)	
I. ram.	51	3		3			6						
P. inc.	8	14				87		100					
L. pat.	9	53		80	1								
E. vir.	3		7	11	68								
E. fon.	13	6	47	6	25								
E. cec.	4	11	33		6								
K. meg.	7	8	13				94		8				
I. bea.	5												
C. indet.		6											
D. ste.									17				
P. sma.						13							
H. sp									75				
E. sp											100		
C. inc.										100			
C. pub.												100	

LCFI Cerro Frías I, LTOR L. El Toro, LUER L. Huergo, LMOR L. El Morro, LALT L. Alta, LSOSI El Sosiego I, ARRI Arroyo I, LPAJ L. Pajonales, LAHU Lahuen-Co, LHER La Herradura, LANG La Angostura, LJUN Los Juncos, p.l. permanent lake, t.p. temporary pond, s. stream, p.p. permanent pond, I. ram. Ilyocypris ramirezi, P.inc. Penthesilenula incae, L.pat. Limnocythere patagonica, E.vir. Eucypris virgata, E. fon. Eucypris fontana, E. cec. Eucypris cecryphalium, K. meg. Kapcypridopsis megapodus, I. bea. Isocypris beauchampi, C. indet. Candoninae indet., D. ste. Darwinula stevensoni, P. sma. Potamocypris smaragdina, H. sp Heterocypris sp., E. sp Eucypris sp., C. inc. Chlamydotheca incisa, C. pub. Cypris pubera

Claus, 1892; *Cypris pubera* Müller, 1776, *Eucypris* sp., *Heterocypris* sp. and Candoninae indet.

Ostracod hydrochemical affinities

The species with at least four recordings in the compiled Patagonian ostracod database (SP and N–CP samples) were *Limnocythere patagonica*, *L. rionegroensis*, *Ilyocypris ramirezi*, *P. smaragdina*, *E. fontana*, *E. virgata*, *E. cecryphalium* and *Penthesilenula incae* Delachaux, 1928. Their host waters vary considerably with regards to TDS content, spanning three orders of magnitude from limnetic (fresh)—such as lakes Pajonales (TDS = 35 mg/l) and Cerro Frías I (TDS = 390 mg/l)—to polyhaline (Lake Cari-laufquen Grande N Bay; estimated TDS = 23,760 mg/).

Eucypris virgata, E. fontana and I. ramirezi were widely distributed throughout these environments, the former and the latter being present in all the range of salinities considered (Fig. 5). Accordingly, the estimated tolerances (SD) of these three species were

quite wide with respect to their WA TDS host water content, as reflected by their CV values, all >1.

For their part, *L. patagonica*, *E. cecryphalium*, *P. smaragdina* and *Penthesilenula incae* were only found in waters of relatively low salinity. *L. rionegroensis*, on the contrary, was absent from limnetic environments; moreover, its host waters' WA TDS content at least doubles that of the other species (Table 3). *L. rionegroensis*' preference for more saline waters is statistically significant (Kruskal–Wallis test on species' scores: H = 21.43; P = 0.003; Mann–Whitney tests: $P \le 0.014$ for all seven pairwise comparisons against *L. rionegroensis*). *E. cecryphalium*, *P. smaragdina*, *P. incae*, *L. patagonica* and *L. rionegroensis* showed relatively low TDS variation tolerances, as estimated by the SD method; these species' CV were <1.

The analysed species also differ in the ionic composition of their host waters (Fig. 6). *E. cecryphalium*, *P. smaragdina*, *P. incae* and *L. patagonica* were found almost exclusively in Na–Ca–Mg, bicarbonate-dominated waters, while *L. rionegroensis* was present only in



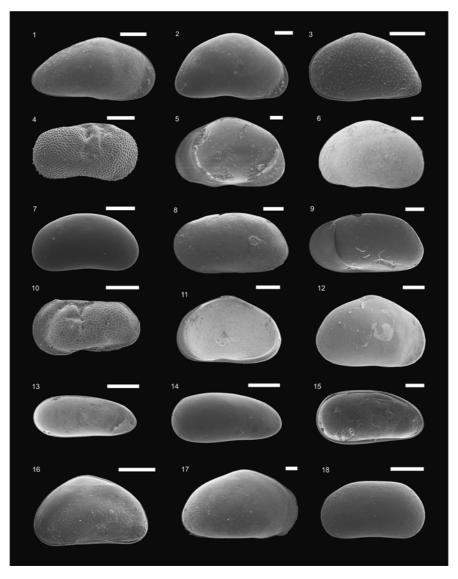


Fig. 4 Freshwater Patagonian ostracod species. *Scale bar* 200 μm. c caparace, ex external view, in internal view, lv left valve, rv right valve, L maximum length, H maximum height. I Eucypris virgata, rv, ex; L=1.01 mm, H=0.51 mm; Cerro Frías I. 2 Eucypris fontana, rv, ex; L=1.24 mm, H=0.71 mm; El Toro. 3 Eucypris cecryphalium, lv, ex; L=0.63 mm, H=0.39 mm; Cerro Frías I. 4 Ilyocypris ramirezi, rv, ex; L=0.76 mm, H=0.40 mm; Cerro Frías I. 5 Eucypris sp, lv, ex; L=1.71 mm, H=1.09 mm; V. La Angostura. 6 Eucypris sp, rv, in; L=1.69 mm, H=1.06 mm; V. La Angostura. 7 Kapcypridopsis megapodum, lv, ex; L=0.73 mm, H=0.38 mm; El Toro. 8 Isocypris beauchampi, lv, ex; L=1.22 mm, H=0.59 mm; El Toro. 9

sodium and chlorine—sulphate-dominated waters. *I. ramirezi*, *E. fontana* and *E. virgata* were found in both the water types, although the former was found in

Isocypris beauchampi, rv, in; $L=1.22~\rm mm$, $H=0.63~\rm mm$; El Toro. 10 Limnocythere patagonica, lv, ex; $L=0.65~\rm mm$, $H=0.34~\rm mm$; El Toro. 11 Heterocypris sp, rv, in; $L=0.97~\rm mm$, $H=0.60~\rm mm$; Lahuen-Co. 12 Heterocypris sp, rv, ex; $L=0.91~\rm mm$, $H=0.59~\rm mm$; Lahuen-Co. 13 Darwinula stevensoni, lv, in; $L=0.64~\rm mm$, $H=0.27~\rm mm$; Lahuen-Co. 14 Penthesilenula incae, rv, ex; $L=0.70~\rm mm$, $H=0.32~\rm mm$; Cerro Frías I. 15 Penthesilenula incae, lv, in; $L=1.14~\rm mm$, $H=0.55~\rm mm$; El Toro. 16 Potamocypris smaragdina, c, ex; $L=0.63~\rm mm$, $H=0.36~\rm mm$; Cerro Frías I. 17 Cypris pubera, rv, ex; $L=1.98~\rm mm$, $H=1.20~\rm mm$; Los Juncos. 18 Candoninae indet. lv, ex; $L=0.63~\rm mm$, $H=0.34~\rm mm$; El Toro

greater relative abundances in low salinity, bicarbonated waters. In spite of the Kruskal–Wallis test's failure to assess these differences with respect to evaporative



Fig. 5 Box plot depicting salinity (expressed as the logarithm of TDS in mg/l) of selected Patagonian ostracod species' host waters. Some TDS values used were estimated based on information published by Cusminsky et al. (2005)

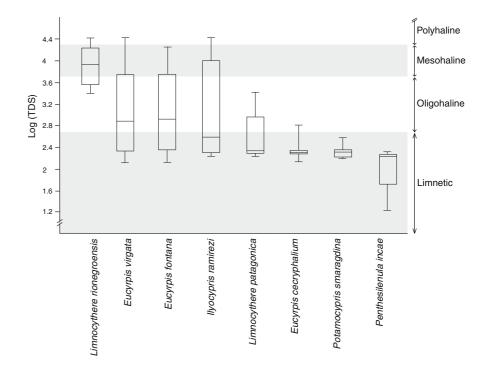


Table 3 Weighted average (WA), tolerance (SD) and CV of TDS and ln ([T. Alk.]/[Ca⁺²]) for host waters of selected Patagonian ostracod species

	L. rionegroensis	E .virgata	E. fontana	I. ramirezi	L. patagonica	E. cecryphalium	P. smaragdina	P. incae		
TDS (mg/l)										
WA	9,873	4,361	3,025	1,422	526	295	295	102		
SD	7,864	5,812	5,108	4,580	86	187	187	80		
CV	0.80	1.33	1.69	3.22	0.16	0.63	0.22	0.78		
ln ([T. Alk.]/[Ca ⁺²])										
WA	4.73	4.21	3.81	2.67	2.36	2.57	2.07	1.46		
SD	0.69	1.80	1.31	0.86	0.49	0.31	0.46	0.20		
CV	0.15	0.43	0.34	0.32	0.21	0.12	0.22	0.14		

enrichment as statistically significant overall (H = 11.62; P = 0.11), the Mann–Whitney tests show that L. rionegroensis is more abundant in bicarbonate-enriched host waters ($P \le 0.05$ for all seven pairwise comparisons against L. rionegroensis).

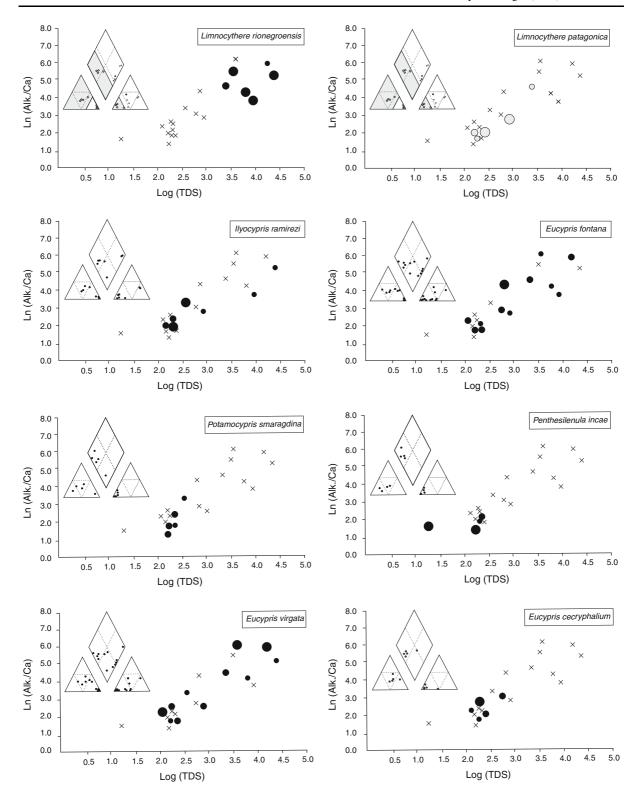
Discussion

Southern Patagonia lakes hydrochemistry

The grouping of the sampled lakes according to their water chemistry (Fig. 3) conforms to a pattern which

could reflect their different hydrological regimes. The lakes grouped in Clusters I, III and IV, as well as outlier L. Ernesto, have an hydrochemistry indicative of a positive hydrological balance, namely diluted (within the limnetic salinity range, except for L. Ernesto which has a slightly higher TDS content), calcium bicarbonate-dominated waters (Kalff, 2001). Furthermore, the ionic ratios analysed suggest a strong influence of weathering in water solute composition, which could be indicative of significant runoff input (Rogora et al., 2008). For their part, the lakes in Clusters II and V and the outlier L. Nueva have more concentrated waters (oligohaline or polyhaline) with







■ Fig. 6 Distribution of selected Patagonian ostracods' ocurrences across the range of values of ln ([T. Alk.]/[Ca⁺²]) against log TDS. Hydrochemistry of the sites where the species were found is shown with a trilinear plot (inset ion abundances as in Fig. 2). Those sites in which the particular species is found are shown as circles, while the rest of the sites within the dataset are represented by a cross. Relative abundance of the species at the site is represented as follows: big circle >50%, medium circle 10% < x ≤ 50%, small circle <10%. L. rionegroensis/patagonica graphs: the former is represented by black circles and the latter by grey circles (division in the inset). Data partially obtained from Cusminsky et al. (2005)
</p>

predominance of sodium and chloride (together with bicarbonate, in the case of the lakes in Cluster II) in similar proportions among the major elements, which points to water losses by evaporation greater than water input.

In turn, this grouping is related to geographical location of the waterbodies, with the more diluted lakes located at or close to the Andes and the more saline ones located in the Patagonian Steppe (Fig. 1). Among Andean lakes, there are hydrochemical differences among those situated at the northernmost part of the studied area, relative to those located further south. The former, which constitute Clusters III and IV, are more dilute and acidic, while the latter are proportionately more enriched in sodium and magnesium and are included in Cluster I with lakes situated in ecotonal settings. This could be related to the northwest-southeast orientation of precipitation isolines towards the southernmost part of Patagonia. In this respect, it is noteworthy that L. Azul, which is the easternmost sampled site of the dataset, resembles most closely ecotonal lakes with respect to its solute composition. This differentiation of waterbody hydrochemistry roughly coincident with a West-East gradient of decreasing precipitations is in accordance with the findings of other authors relative to climatic control of lake chemistry in Northern Patagonia (Díaz et al., 2000; Perotti et al., 2005; Rogora et al., 2008).

Our results also suggest that bedrock composition is another factor, besides hydrological regime, which could account for variations in solute composition of the waterbodies. In particular, it could account for the high (relative to this dataset) SO_4^{-2} concentration of lakes Ernesto and Agustín, whose hydrochemistry does not suggest evaporative enrichment, and the unusually high TP content of lakes Salada, San Ignacio, Morro and Potrok Aike (Table 1). Zolitschka et al. (2006) propose that the elevated TP values of

Lake Potrok Aike could be related to groundwater and regional geology. Our data lend support to the latter hypothesis, as, although not all the sampled lakes in the vicinity of Potrok Aike show such high TP values, the aforementioned phosphorus-rich lakes are neighbouring to it.

With regards to the representativity of the samples, it must be borne in mind that gathering data at these remote sites presented several difficulties, ranging from the low accessibility of most sites to having to cope with the reluctance or availability of ranch owners and managers who were to grant us access into the private properties were several of the lakes were located. For these reasons, obtaining samples from as many sites as possible to build up a more representative dataset was favoured over repeated sampling of fewer sites.

The seasonality of precipitations in Southern Patagonia means that all sampling was made, in principle, during the dry season (austral summer and early autumn). Some seasonal effects could be expected, though; the intensification in the strength and frequency of the westerlies, coupled with the increase in temperature, cause transpiration losses to peak in spring and early summer (Paruelo et al., 1998). In practice, variability within sites was so high (e.g. conductivity values span a wide range, from about 20 up to 2,000 $\mu\text{S}/$ cm at 20°C) that it effectively overruned the temporary variability involved; the five clusters recognized include waterbodies sampled in January and April.

Recent ostracod ecology

The Southern Patagonian ostracod assemblages recovered exhibited an overall diversity (average 1-D=0.398) comparable to that of the Northern and Central Patagonia assemblages studied by Schwalb et al. (2002) and Cusminsky et al. (2005) (average 1-D=0.353). The higher evenness in the SP assemblages (average equitability = 0.545) when compared to the N-CP ones (average equitability = 0.454) accounts for the similarity in the Simpson's index calculated for both the datasets when considering that the species richness of the later was slightly higher: N-CP assemblages comprised 1-9 species (median S=4), while the SP assemblages included from 1 to 8 species (median S=3).

Regional diversity in terms of species richness in the waterbodies surveyed was lower than that



encountered by Schwalb et al. (2002) and Cusminsky et al. (2005). While our NP sites (labelled 38-41 in Fig. 1) yielded 6 ostracod species, their closest N-CP counterparts (Cari-laufquen area sites, labelled l, m in Fig. 1) contained 10 species. In turn, a total of 15 species were found by the aforementioned authors in waterbodies in the Cardiel area (a-j in Fig. 1), located in Central Patagonia, while a total of 10 species were present in our SP sites. These low values of S in modern ostracod assemblages throughout Patagonia also characterize Quaternary occurrences of these crustaceans (reviewed in Cusminsky et al., 2011). In the Northern Patagonia sedimentary sequence Cari-Laufquen Grande Outcrop only four ostracod species were present, one of them represented by a few individuals in one level. The Maquinchao Outcrop sequence, also located in Northern Patagonia, yielded a total of seven species, with a maximum of six cooccurring in one level. The Holocene ostracod assemblages recovered from the CAR 99-7P core, obtained from lake Cardiel (Central Patagonia), comprised up to four species; a total of six species were present throughout the core. For their part, some of the present authors studied a lacustrine sedimentary core obtained from a maar lake located in Southern Patagonia (Maidana et al. 2010; Massaferro et al. 2010; Ramón Mercau et al. 2010) which yielded six ostracod species as well, with a maximum of five species occurring jointly in one level.

While our results regarding ostracod diversity appear to be in accordance with the published findings for other Patagonian regions, it is surprising that the surveyed Southern Patagonian sites yielded few fertile samples compared with Schwalb et al. (2002) and Cusminsky et al. (2005). This could be partly due to differences in sampling strategy and conditions and the range of environments covered. In the first place, although only six Southern Patagonian ostracod assemblages are reported in this contribution, a few valves were found in as many other locations. These were not included on account of belonging to early stages instars or because of their poor preservation; however, their presence suggests that further and more thorough sampling of these and other lakes would produce better results. Second, sampling procedures were intended to recover other organisms besides ostracods, which inevitably led to a trade-off between the suitability of particular sampling stations for each group. Most of the Northern and Central Patagonian lakes reported by Schwalb et al. (2002) and Cusminsky et al. (2005) had sandy sediments, while in 13 of the Southern Patagonia lakes fine to medium gravels predominated. Preservation of any specimens present in such coarse substrates is expected to be poor due to crushing during collection and handling of the sample. Finally, both datasets did not cover the same range of water types, with some of them being sampled in only one region (Fig. 2); while Schwalb et al. (2002) and Cusminsky et al. (2005) surveyed Steppe and ecotone waterbodies, we obtained most samples from Andean lakes, which differ considerably from them in their hydrochemistry, as already discussed. This bias in sampling was inevitable, as not only is the number of lakes smaller in the Patagonian Steppe than in Andean settings but also some of the steppe waterbodies we visited during the field trips turned out to be dry.

Despite the scarcity of the data, the new ostracod data here presented are valuable because it adds information about poorly known species. For instance, *L. patagonica* has only been cited for two modern lakes in the literature—with a relative abundance >3% in only one of them—while the present authors found this species in three lakes, which allowed for statistical comparison with other species regarding its hydrochemical preferences.

The results obtained suggest that *E. fontana*, *E. virgata* and *I. ramirezi* could be considered eurihaline species, capable of inhabiting waters with a wide range of TDS concentrations. Nonetheless, while both the eucyprids show very similar results with respect to their salinity preferences, *I. ramirezi*'s host water WA TDS content (Table 3) indicates that this species, while tolerant of a wide range of salinity conditions, tends to be more abundant in less saline waters. For their part, *L. rionegroensis*, *L. patagonica*, *E. cecryphalium*, *P. smaragdina* and *P. incae* could be tentatively characterized as stenohaline species.

Furthermore, both the groups of species differ in their preferred host water types. The stenohaline freshwater taxa *L. patagonica*, *E. cecryphalium* and *P. smaragdina* have been found in alkaline (bicarbonate dominated) waters with low (T. Alk.)/Ca⁺² ratios and salinities almost always below 500 mg/l TDS, which implies little evaporative enrichment. On the contrary, the stenohaline *L. rionegronesis* was restricted to sodic waters enriched in chlorine and/or sulphate and/or bicarbonate, with salinities above 2,300 mg/l TDS and mostly within the mesohaline



range, typical of continental waterbodies subject to intense evaporative conditions. The eurihaline species *E. fontana*, *E. virgata* and *I. ramirezi* showed a wider tolerance to water solute composition variation (as reflected by their higher ln ([T. Alk.]/[Ca⁺²]) CV; see Table 3) in addition to their greater salinity ranges.

For the most part, these categorizations agree with those made by Schwalb et al. (2002) and Cusminsky et al. (2005), summarized in Cusminsky et al. (2011). These authors highlight that *I. ramirezi*, *E. fontana* and E. virgata were found in waters of variable solute compositions, and consider that *Penthesilenula incae* and P. smaragdina prefer low salinity waters. However, Cusminsky et al. (2011) conclude that both E. fontana and P. smaragdina prefer waters with low buffer capacity (low alkalinity content). Our results suggest that, even though it can be found at low alkalinity waters such as those were P. smaragdina was recorded, E. fontana is as common in high alkalinity waters (Fig. 5). This discrepancy could be due to the fact that some of the recordings are unique to each database and to the differences in the respective methodologies: the aforementioned authors use the Ca⁺²/pH ratio as an alkalinity measure, while we favoured the $(HCO_3^- + CO_3^{-2})/Ca^{+2}$ ratio. We deemed the latter to be more adequate not only for our objectives—as already mentioned, this index was used by Curry (1999) and Forester et al. (2005) as a water balance estimator-but also for our ostracod host water data: T. Alk. content measurements/estimates were far more variable than Ca⁺² concentration measurements, which ranged between 1,078 and 1,796 µeg/l for the cases analysed.

Further direct comparisons between results are not straightforward due to the different data analysis approaches employed. Schwalb et al. (2002) qualitatively distinguish three types of ostracod host waters taking into account waterbody physicochemical characteristics and isotopic composition both of the waters and the species inhabiting them. These authors sum up these variables in terms of environmental stability and water flow, terming their groups as follows: springs, seeps and streams; permanent ponds and lakes and ephemeral ponds and lakes. Thus, even though most of the hydrochemical data is the same, it is analysed in terms of indicator species with respect to different environmental parameters and techniques than the ones we consider. Consequently, the results presented here can be regarded as complementary to those reported by Schwalb et al. (2002) and Cusminsky et al. (2005).

As for species distribution, some of them were, to the best of our knowledge, previously unknown for the region; this study would be the first to report the occurrence of *Chlamydotheca incisa* and *Isocypris beauchampi* in Patagonia and the southernmost record of *P. incae*. The latter species has been cited for Peru, Bolivia and thermal waters in the Argentinean Altiplano (Laprida et al., 2006) and, as discussed by Rossetti and Martens (1998), it is probably a junior synonym of *P. setosa*, described by Daday (1902) from Santa Cruz Province, Argentina. *Cypris pubera*, which was previously unknown for South America, has been found elsewhere in Argentina (Gabriela Cusminsky, personal communication).

Conclusions

The hydrochemical data on Southern Patagonia lakes presented—which, as far as we are aware, constitutes the first information of its kind for the region—shows that Andean and Steppe lakes differ in their salinity and solute composition. Lakes present diluted, slightly acidic, calcium bicarbonate-dominated waters in the northernmost locations of the mountain range, which turn increasingly more saline and enriched in other major cations towards the south and in ecotonal settings. Waterbodies located at the steppe, in the eastern part of the sampled area, present a contrasting water solute composition, with sodium as the dominant cation and chloride as the dominant or codominant anion, together with salinities as much as three orders of magnitude higher than those of their Andean counterparts. Given that the strong West-East precipitation gradient is one of the main determinants of the differences between both the subregions, it can be concluded that Southern Patagonia lakes' hydrochemistry partially reflects precipitation regimes in the waterbodies' catchment.

In turn, the Patagonian ostracod species studied differ with respect to the solute composition of their host waters. At this stage, only preliminary conclusions can be drawn to this respect, but there is statistically significant evidence that *L. rionegroensis* can be found in more saline and alkaline waters that the other Patagonian ostracod species studied. In particular, this ostracod inhabits mesohaline waters



(WA TDS = 9,870 mg/l) with Na⁺ as the dominant cation and enriched in all major anions, which are typical of (ephemeral) lakes and ponds located in the Patagonian steppe. For their part, *L. patagonica*, *E. cecryphalium*, *P. smaragdina* and *P. incae* are present at low salinity (WA TDS up to 530 mg/l), bicarbonated waters enriched in Ca⁺², Na⁺¹ and Mg⁺², a water type that, according to our findings, is characteristic of lakes situated in ecotonal areas or at low altitudes/easterly locations within the Andean range, were precipitations are less abundant than in fully mountainous settings.

The remaining species studied—*I. ramirezi*, *E. fontana* and *E. Virgata*—exhibit a wider tolerance of both the salinity and the solute composition of their host waters, rendering these species less apt for use as paleohydrological indicators, at least in the context of the present approach.

Overall, the results obtained allow for significant semi-quantitative paleolimnological inferences to be made regarding Southern Patagonian lakes water balance—and hence climatic variations in the region—on the basis of fossil ostracod assemblages recovered from sediment cores, assuming that species—environment relationships have not changed at least during the Quaternary (Birks, 2005).

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