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Luis B. Epele<sup>a</sup> & María Laura Miserendino<sup>a</sup>

<sup>a</sup> Centro de Investigación Esquel de Montaña y Estepa Patagónica (CONICET-UNPSJB), Esquel, Argentina

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## Temporal dynamics of invertebrate and aquatic plant communities at three intermittent ponds in livestock grazed Patagonian wetlands

Luis B. Epele and María Laura Miserendino

Centro de Investigación Esquel de Montaña y Estepa Patagónica (CONICET-UNPSJB), Esquel, Argentina

### ABSTRACT

Ponds are recognized worldwide as biodiversity hotspots; nevertheless in Patagonia studies are still needed that reveal the composition and status of their communities. This paper analyses the temporal patterns of aquatic invertebrates and assesses the environmental factors that best predict the variation in community structure at three small intermittent ponds, subjected to ranching practices (summer stocking) in the Patagonian steppe. Variables identified as important in structuring community assemblages were related to environmental conditions (rainfall and water temperature), chemical features (conductivity and pH) and biotic factors (macrophyte coverage). During the connected phase only a small number of invertebrate species were present, in contrast to the 11 taxa that were frequent and abundant during the isolated period (*Eucyclops chilensis*, *Hyaella curvispina* and *Rhionaeschna* sp. were dominant). In this sequence the submersed *Myriophyllum quitense* and *Lilaeopsis macloviana* played a crucial role offering habitat and food resources. The present study provides valuable information that can contribute to minimizing the environmental damage and the development of strategies for the conservation of Patagonian wetlands.

### ARTICLE HISTORY

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Invertebrates; steppe; dynamics; temporary ponds; macrophytes

### Introduction

Ponds are recognized worldwide as biodiversity hotspots (Céréghino et al. 2014) and play a significant role in the provision of ecosystem services. The richness of their wildlife, the number of rare species, their role in geochemical cycles (Downing et al. 2008) and their iconic status in many societies (Jeffries 2011) are features that have led to a remarkable renaissance of studies on pond ecology in the last decade.

Temporary ponds are habitats that generally exhibit a great abiotic variability (Oertli et al. 2009) sustaining populations of freshwater invertebrates that often display high levels of biodiversity and endemism (Díaz-Paniagua et al. 2010). These communities comprise an important part of animal production within wetlands (Oertli 1993), and are tightly integrated into the structure and functioning of their habitats (e.g. organic matter processing, nutrient retention, food resources for vertebrates such as amphibians, fish or

birds) (Wissinger 1999). Their community composition and dynamics are determined primarily by the hydrological regimen (Williams 2006). For this reason, temporal study of invertebrates requires at least monthly visits to appropriately cover the seasonal variation (Florencio et al. 2013).

Wetlands in Patagonia are locally named *mallines*, an aboriginal (Mapuche) word that means swampy area or lowland area where water accumulates. These environments provide habitat for several terrestrial and aquatic endemic species (Perotti et al. 2005) and are important suppliers of water and forage to the livestock in semi-arid and arid areas (Gaitán et al. 2011). Freshwater invertebrates constitute a diverse group of species that react strongly and often predictably to human influences (Cairns and Prall 1993). As a result, they have been widely used not only as bioindicators to assess the ecological status of ponds (e.g. Sharma and Rawat 2009) but also to analyse the consequences of different land use practices in these environments. However, to use aquatic invertebrates from Patagonian ponds as bioindicators it is necessary to carry out baseline studies that reveal the composition and status of their communities.

The colonization sequences of species seem to be ruled by different factors according to the spatial and temporal dimensions of their particular environments (Florencio et al. 2013). The study of Jara et al. (2013) focusing on the predatory insect community revealed that Patagonian temporary wetlands with short (< 6 months) and intermediate (between 6 and 9 months) hydroperiods have a seasonal colonization pattern beginning in early spring. The initial colonization sequence seems to be strongly related to the dispersal abilities of the taxa (Bilton et al. 2001), whereas the further changes that take place in the community composition and structure are mainly ruled by the changes occurring in the condition of the habitat (Cañedo-Argüelles and Rieradevall 2011).

In contrast to the large volume of studies in river and lake ecology in Patagonia, knowledge of wetlands is incipient and fragmentary. The ecological role and the value of ponds in the Patagonian landscape have not been established and scientific information on the associated species of aquatic plants and invertebrates is relatively scarce (e.g. Burrioni et al. 2011; Epele and Archangelsky 2012; Kutschker et al. 2014). Very little research has addressed the dynamics of pond communities using a temporal approach. In this work we hypothesize that the increasing environmental harshness that occurs – with higher precipitation, which connects ponds, and lower temperatures, which partially freeze them – will produce a strong disturbance in the ponds' conditions, creating an early successional state. Therefore, generalist organisms will colonize the available habitats, modifying their conditions, allowing the colonization of specialist species.

The present work was conducted in three ponds (Mallín Crespo) located in the Patagonian steppe. As occurs in most wetlands in the area, livestock management is limited to summer months, coinciding with the time of year in which the water table decreases and produces the isolation of ponds. The main aims of the study were: to analyse the temporal succession of invertebrate assemblages during the connection and isolation phases; and to identify the main environmental factors that govern the variation in composition, density, biomass and functional structure of aquatic invertebrates in the three ponds in the Patagonian steppe. The accomplishment of these goals will contribute to better understanding of the functioning and dynamic of temporary ponds as well to suggest actions for management and conservation of grazed wetlands.

## Material and methods

### *Study area*

The Patagonian climate is generally dry, cold and windy. The strong west–east rainfall gradient has resulted in two main phytogeographical provinces: Sub-Antarctic Forest and the Patagonian Steppe (Tell et al. 1997). In the steppe, precipitation is concentrated in winter and ranges from 300 mm in the west to < 150 mm in the east, increasing slowly towards the Atlantic coast (Barros et al. 1979). The low precipitation has resulted in xerophytic and cushion vegetations forms.

Compared with other territories, the human colonization process in Patagonia is relatively recent, nevertheless significant human-induced changes have occurred since the arrival of the first settlers (between 1880 and 1920). The predominant land use in this area has been grazing by sheep, which has resulted in an increase of the desertification process. After more than a century, this activity has resulted in low-productivity lands, forcing the landowners to change the extensive livestock practices for intensive use of more productive areas such as pastures on wetlands (Perotti et al. 2005).

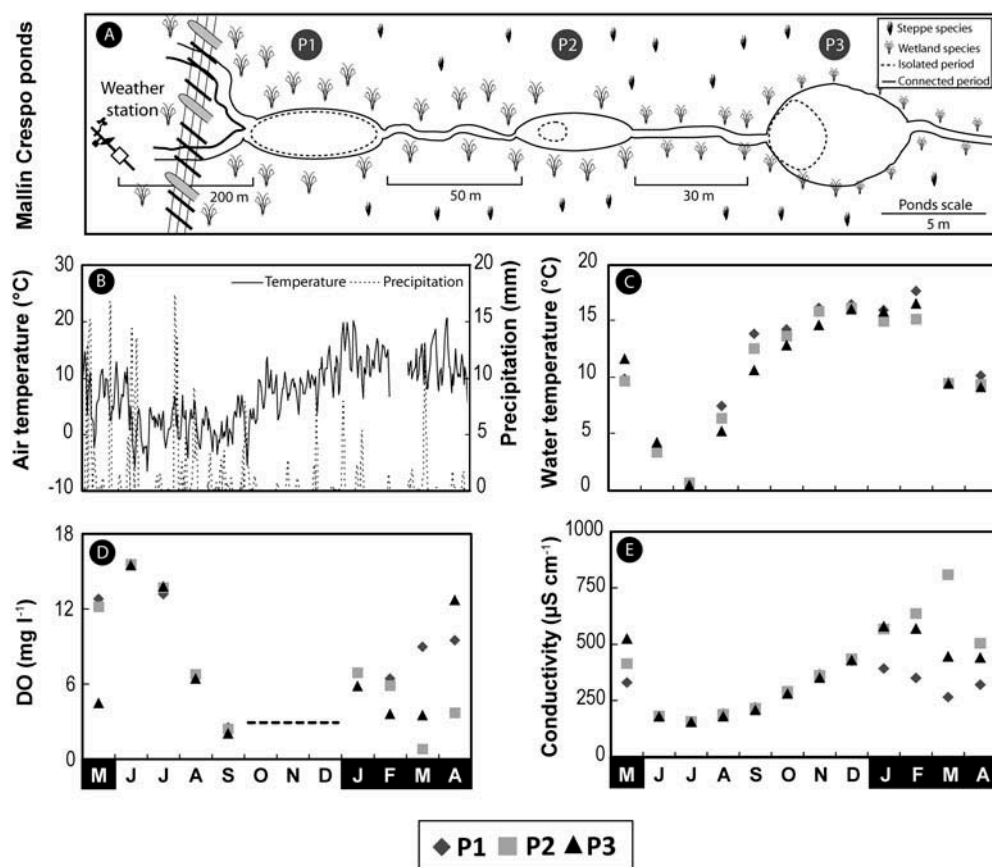
The study was conducted monthly (May 2008–April 2009) at three ponds (P1, P2 and P3) located in a small watershed (1284 ha), which flows into the middle part of the Genoa River (Ciari 2009). The selected ponds (the only ponds existing in this particular wetland) are representative of other small aquatic environments in the steppe with the same grazing practices (Figure 1A). The wetland under study is locally named ‘Mallín Crespo’ (44.18° S, 70.55° W, 808 m above sea level) and is used to feed livestock (mainly sheep); to date there are no laws that protect it or that limit livestock land use.

Based on the classification of temporary waters of Williams (2006), the study site has an intermittent flood regimen. During the study period the water table was near the surface, resulting in ponds always being present. However, the annual rainfall during the 2009 winter and subsequent years was very low, and at present the studied ponds have become ephemeral. Regarding the land-use of the wetland, between November 2008 and January 2009, 1760 sheep (1100 adults and 660 lambs), were stocked at the studied area.

### *Environmental characterization and sampling*

Data for precipitation, air temperature, speed and direction of wind were documented hourly during the study period by a weather station (Davis, Wizard III) that was installed for that purpose by the Instituto Nacional de Tecnología Agropecuaria. During the study morphometric and physicochemical measurements were taken once per month and pond ( $n = 12$  per pond). Measurements included: length (measuring tape), pond area and depth (calibrated stick). Water temperature, specific conductance ( $\mu\text{S}\cdot\text{cm}^{-1}$ ), total dissolved solids, pH and dissolved oxygen ( $\text{mg O}_2\cdot\text{l}^{-1}$ ), were measured 10 cm below the water surface with a Hach sensION156 multiparameter probe. For better comparisons, the sites were visited approximately at the same time of the sampling day (between 10 and 12 a.m.).

Nutrient contents and total suspended solids measurements were obtained only at P1, for this purpose, one monthly water sample was collected below the surface and kept at 4°C before analysis. In the laboratory, total nitrogen, total phosphorus, total oxidized nitrogen ( $\text{NO}_3^-$  plus  $\text{NO}_2^-$ ), ammonia ( $\text{NH}_4^+$ ) and soluble reactive phosphate



**Figure 1.** (A) Location of the sampling sites (P1, P2 and P3) at Mallín Crespo (Chubut Province, Patagonia, Argentina) during connected (June–December) and hydrologically isolated (January–May) periods. The three ponds are in the same scale. (B) Daily rain (dashed line) and mean daily air temperature (solid line), from May 2008 to April 2009. (C–E) Physicochemical variables sampled monthly and once per pond. Dashed line (D), indicates unavailable data.

were analysed following the methods of the APHA (1994). Total suspended solids were measured gravimetrically.

The percentage cover of aquatic plants was estimated visually (Galatowitsch et al. 2000) and divided into seven categories (<1%, 1–5%, 6–25%, 26–50%, 51–75%, 75–99%, and 100%) (Daubenmire 1959). Samples of aquatic plants were collected and stored in plastic bags for further identification using general and regional taxonomic books (Correa 1978–1999).

### *Invertebrate analysis*

Aquatic invertebrates were sampled using a D-frame net (800-μm mesh). The net was swept vertically four times from the margins to the middle part of each pond. The net was swept from the bottom to the surface, removing invertebrates associated with the water column and aquatic plants (epibenthic and nektonic invertebrates). Contents of

the four sweeps were pooled into one composite sample per month and pond. Considering the area of the D-frame and the distance covered in the water (the maximum depth of each pond), density of invertebrates was expressed as individuals  $\text{m}^{-3}$ . Samples were fixed in the field in 4% formalin. At the laboratory the samples were sorted under  $\times 5$  magnification and invertebrates were stored in 70% ethyl alcohol. Organisms were identified using a stereomicroscope (Leica MZ6) to the lowest possible taxonomic level (Domínguez and Fernández 2009) and counted.

Detritus, also collected with the D-frame net, was divided into fine particulate organic matter (800–1000  $\mu\text{m}$ ; FPOM) and coarse particulate organic matter ( $>1000 \mu\text{m}$ ; CPOM) using a set of sieves. An additional fraction was 'macrophyte biomass parts', which was obtained manually from the samples. All fractions were dried (110°C for 4 h) and weighed with an electronic balance to  $\pm 0.5 \text{ mg}$ .

For most taxa, available length–mass relationships were used to estimate the biomass of individuals [ $\text{g dry mass (DM) m}^{-3}$ ] (Benke et al. 1999; Miserendino 2001). New length–mass regressions were obtained for the following taxa *Rhionaeschna* sp., *Cyanallagma interruptum*, *Ectemnostega quadrata*, *Tropisternus setiger* and *Lancetes* sp. Complete descriptions of the methodology and instruments used can be found in Epele and Miserendino (2011).

All aquatic invertebrates (adults and larvae) were assigned to functional feeding groups using available literature (Merritt et al. 2008), previous knowledge of mouthpart morphology and feeding behaviour, and also through analysis of gut contents.

### Data analysis

Single non-parametric correlations tests (Spearman rank) were used to explore the relationships among community attributes (richness, density and biomass) and environmental variables (STATISTICA for Windows 6.0).

To assess whether the measured variables changed over time and, in particular, whether they changed when ponds were isolated, the sampling design used a structure of repeated measures, with three replicates (ponds) and 12 repeated measures (months). We used general linear models with time (month) as a fixed effect. The lack of independence or pseudoreplication associated with the collection of multiple measurements and samples from the same sites over time was modelled through a covariance matrix (class: compose symmetry structure). When data sets showed over-dispersion we used a variance function (class: VarIdent), hence we modelled the heterogeneity of variance. The hypothesis of equality between months before and after the isolation of ponds was assessed using *a priori* contrast. Selection among models was performed using likelihood ratios. Statistical analyses were achieved using InfoStat software, Version 2011 (Di Rienzo et al. 2011).

To assess the relationships between aquatic invertebrate assemblages and environmental variables, a Redundancy Analysis (RDA) was performed using CANOCO (ter Braak and Smilauer 1999). RDA was chosen because previous inspection of the data revealed a linear model rather than a unimodal response in the biotic variables (ter Braak and Smilauer 1998). This technique of direct gradient analysis allows the part of the variation in community composition that can be explained by a particular set of environmental variables to be studied. It is especially useful for temporal series of data, with a small

**Table 1.** Nutrients and total suspended solids measured monthly (May 2008 to April 2009) in a Patagonian wetland, Chubut, (Argentina).

	M	J	J	A	S	O	N	D	J	F	M	A
TN ( $\mu\text{g l}^{-1}$ )	363	356	347	281	275	277	346	353	327	389	–	232
$\text{NO}_2^- + \text{NO}_3^-$ ( $\mu\text{g l}^{-1}$ )	<3	<3	<3	<3	<3	<3	<3	<3	<3	<3	–	<3
$\text{NH}_4^+$ ( $\mu\text{g l}^{-1}$ )	8	5	<5	9	6	5	6	<5	6	9	–	13
TP ( $\mu\text{g l}^{-1}$ )	63	30	24	24	33	41	31	36	45	35	–	16
SRP ( $\mu\text{g l}^{-1}$ )	6	4	<2	2	5	5	<2	<2	<2	2	–	<2
TSS ( $\text{mg l}^{-1}$ )	85.8	14.9	19.4	28.2	21.8	37.5	109.8	130.8	79.7	32	–	63.9
TN/TP	5.8	11.9	14.5	11.7	8.3	6.8	11.2	9.8	7.3	11.1	–	14.5

TN, total nitrogen;  $\text{NO}_3^-$ , nitrates;  $\text{NH}_4^+$ , ammonia; TP, total phosphorus; SRP, soluble reactive phosphate; TSS, total suspended solids; –, not available. The black bars indicate the isolated months.

number of samples but a high number of species (Verdonschot and ter Braak 1994). The RDA analysis included invertebrate taxa of the three studied ponds (56 taxa) and 14 environmental variables (see Table 1) but excluded nutrients and total suspended solids because they were measured only at P1. Variables that were strongly intercorrelated with others (those with an inflation factor > 20) in the initial analysis were excluded (total dissolved solids, salinity, dissolved oxygen, FPOM, CPOM, macrophytes biomass). The forward selection option provided by CANOCO was applied and those variables with  $p < 0.05$  (Monte Carlo permutation test with 999 permutations) were kept for the analysis. The final RDA model was run using a set of independent and significant environmental variables (ter Braak and Smilauer 1998).

## Results

### Seasonal patterns of environmental features

During the study period, air temperature ranged between  $-11.3$  and  $28.9^\circ\text{C}$  and the mean annual value was  $6.7^\circ\text{C}$  (Figure 1B). Total annual rainfall at Mallín Crespo was  $303.6 \text{ mm year}^{-1}$ , although  $\sim 67\%$  of the annual precipitation (200 mm) occurred from May to August. We considered it to be a humid year because the annual rainfall exceeded the average of the last 12 years ( $260 \text{ mm year}^{-1}$ ). Water temperature displayed a great seasonal variation; however, mean annual values were fairly similar among ponds (Figure 1C). The lowest value of dissolved oxygen,  $0.8 \text{ mg l}^{-1}$  was found in March at P2, and the highest value was recorded during June at P1 ( $15.6 \text{ mg l}^{-1}$ ) (Figure 1D). Oxygen meter malfunctioning prevented the recording of oxygen data from October to December. During the study period, pH values varied from circum-neutral to alkaline (7–8.3) whereas water conductivity increased at all ponds during the isolation phase coincidentally with sheep stocking. This pattern was more marked at P2 and P3 (Figure 1E). Environmental variation at ponds during hydrological phases showed significant differences for: pond volume, conductivity and pH (Mann–Whitney  $U$ -test,  $p < 0.001$ ).

Nutrient values showed little variation throughout the study, with total nitrogen ranging from 232 (April) to  $389 \mu\text{g l}^{-1}$  (February) and total phosphorus from 16 (April) to  $63 \mu\text{g l}^{-1}$  (May). Ammonia and nitrate values were also within the expected values. Also, the total nitrogen : total phosphorus ratio was always  $< 14$ , suggesting that ponds were limited by nitrogen. Two peaks of total suspended solids were observed, one in November ( $110 \text{ mg l}^{-1}$ ) and another in December ( $131 \text{ mg l}^{-1}$ ), which coincided with the stocking months (Table 1).



### Aquatic plants and particulate organic matter dynamics

We recorded a total of 19 species of aquatic plants from 10 families, mostly native or endemic. Species richness ranged from three (June) to 12 (December) (Table 2). Global richness (all ponds pooled) of macrophytes increased significantly towards the warmer months ( $r_{\text{air temp}} = 0.63$ , Spearman  $p < 0.02$ ; 33%), and did not differ between connected and isolated phases (Mann–Whitney  $U$ -test,  $p > 0.05$ ). The submerged *Myriophyllum quitense*, *Lilaeopsis macloviana* and *Chara* sp. were the more persistent species (present during >10 months).

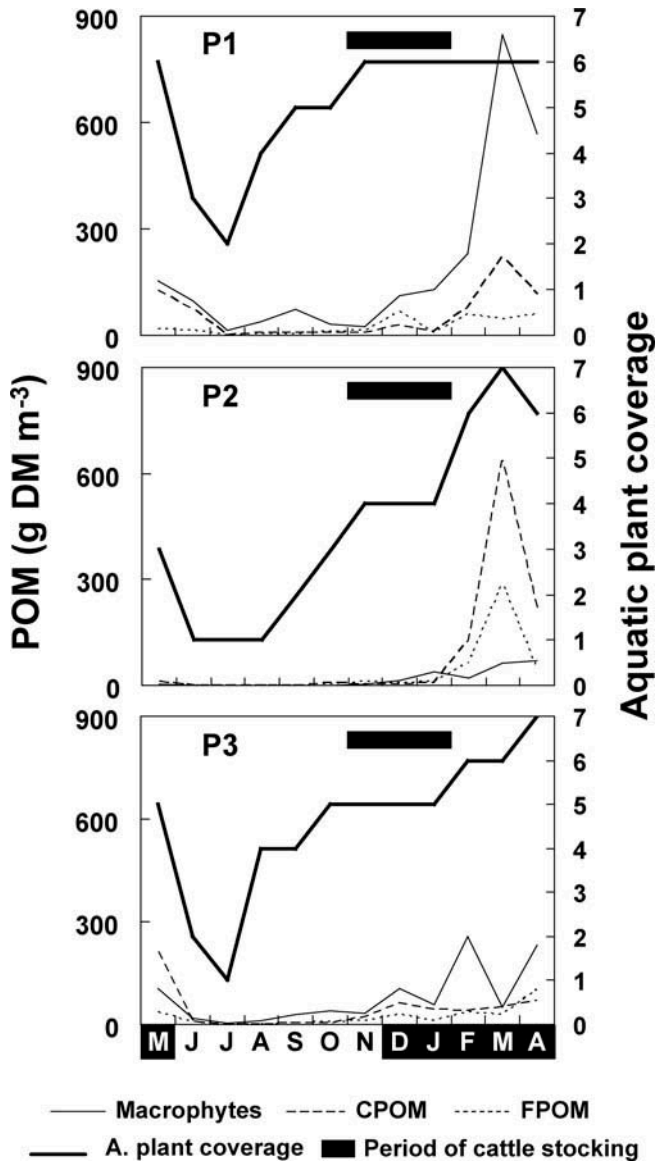
As expected, aquatic plant coverage markedly increased (50%) during spring and summer, and decreased (52%) when ponds became partially frozen (June–July) (Figure 2). The analysis of POM revealed that the ‘macrophytes biomass’ (mostly *M. quitense*) was the dominant fraction at P1 (maximum 847 g DM m<sup>-3</sup>) and P3 (maximum 257 g DM m<sup>-3</sup>). However, CPOM prevailed at P2, reaching a biomass of 637 g DM m<sup>-3</sup> in March. At this pond *Cladophora* sp. was the dominant primary producer. FPOM biomass was 287.8 g DM m<sup>-3</sup> at P2 in this month (Figure 2).

**Table 2.** Floristic composition, presence/absence, origin, habit and taxa richness of aquatic plants in three ponds, sampled monthly between May 2008 and April 2009 (Chubut, Patagonia, Argentina).

Taxa	Ori.	Hab	M	J	J	A	S	O	N	D	J	F	M	A
<b>Bryophyta spp.</b>		E	■	■	■	■	■	■	■	■	■	■	■	■
<b>Characeae</b>			■	■	■	■	■	■	■	■	■	■	■	■
<i>Chara</i> sp.	S		■	■	■	■	■	■	■	■	■	■	■	■
<b>Cladophoraceae</b>			■	■	■	■	■	■	■	■	■	■	■	■
<i>Cladophora</i> sp.	S		■	■	■	■	■	■	■	■	■	■	■	■
<b>Apiaceae</b>			■	■	■	■	■	■	■	■	■	■	■	■
<i>Lilaeopsis macloviana</i> (Gand.) A.W. Hill	N	S	■	■	■	■	■	■	■	■	■	■	■	■
<b>Brassicaceae</b>			■	■	■	■	■	■	■	■	■	■	■	■
<i>Cardamine variabilis</i> Phil.	En	E	■	■	■	■	■	■	■	■	■	■	■	■
<b>Campanulaceae</b>			■	■	■	■	■	■	■	■	■	■	■	■
<i>Lobelia oligophylla</i> (Wedd.) Lammers	N	E	■	■	■	■	■	■	■	■	■	■	■	■
<b>Cyperaceae</b>			■	■	■	■	■	■	■	■	■	■	■	■
<i>Carex nebularum</i> Phil.	N	E	■	■	■	■	■	■	■	■	■	■	■	■
<i>Eleocharis pseudoalbibracteata</i> S. González & Guagl.	N	E	■	■	■	■	■	■	■	■	■	■	■	■
<i>Phylloscirpus acaulis</i> (Phil.) Goetgh. & D.A. Simpson	N	E	■	■	■	■	■	■	■	■	■	■	■	■
<b>Haloragaceae</b>			■	■	■	■	■	■	■	■	■	■	■	■
<i>Myriophyllum quitense</i> Kunth	N	S	■	■	■	■	■	■	■	■	■	■	■	■
<b>Juncaceae</b>			■	■	■	■	■	■	■	■	■	■	■	■
<i>Juncus balticus</i> Willd.	N	E	■	■	■	■	■	■	■	■	■	■	■	■
<i>Juncus scheuchzerioides</i> Gaudich.	N	E	■	■	■	■	■	■	■	■	■	■	■	■
<i>Juncus stipulatus</i> Nees & Meyen	N	E	■	■	■	■	■	■	■	■	■	■	■	■
<b>Poaceae</b>			■	■	■	■	■	■	■	■	■	■	■	■
<i>Poa pratensis</i> L.	Ex	E	■	■	■	■	■	■	■	■	■	■	■	■
<b>Phrymaceae</b>			■	■	■	■	■	■	■	■	■	■	■	■
<i>Mimulus glabratus</i> Kunth	N	E	■	■	■	■	■	■	■	■	■	■	■	■
<b>Ranunculaceae</b>			■	■	■	■	■	■	■	■	■	■	■	■
<i>Caltha sagittata</i> Cav.	N	E	■	■	■	■	■	■	■	■	■	■	■	■
<i>Ranunculus flagelliformis</i> Sm.	N	F	■	■	■	■	■	■	■	■	■	■	■	■
<i>Ranunculus hydrophilus</i> Gaudich.	En	S	■	■	■	■	■	■	■	■	■	■	■	■
<i>Ranunculus trichophyllus</i> Chaix	N	S	■	■	■	■	■	■	■	■	■	■	■	■
<b>Taxa richness</b>			9	3	4	6	7	7	11	12	10	6	8	10

Floristic origin: N, native; En, endemic; Ex, exotic. Floristic habit: E, emergent; F, floating-leaved; S, submersed. Black bars indicate the presence of aquatic plant species. Black months indicate isolated period.

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**Figure 2.** Seasonal variation of particulate organic matter (POM, dashed lines) and aquatic plant coverage (solid line) at three ponds on a Patagonian steppe wetland (Argentina) during the study period (May 2008 to April 2009). Categories of aquatic plant coverage explained in methodology. Livestock stocking period is indicated in the figure (black bar).

### **Seasonal pattern of attributes of invertebrate communities**

Altogether, 56 taxa of invertebrates were identified. The main group were insects, constituting a total of 71% of the taxa richness. The most frequently recorded (>8 months) organisms belonged to *Aulodrilus limnobius*, *Ostracoda* sp. and *Paratrichocladius* sp. (Table 3). Diptera and Coleoptera were the best represented orders with 19 and 12 taxa, respectively.

**Table 3.** Mean isolated (January–May) and connected (June–December) densities (individuals m<sup>-3</sup>) and frequency (between brackets) of aquatic invertebrate taxa in three ponds of Mallín Crespo, Chubut, Argentina (May 2008 to April 2009).

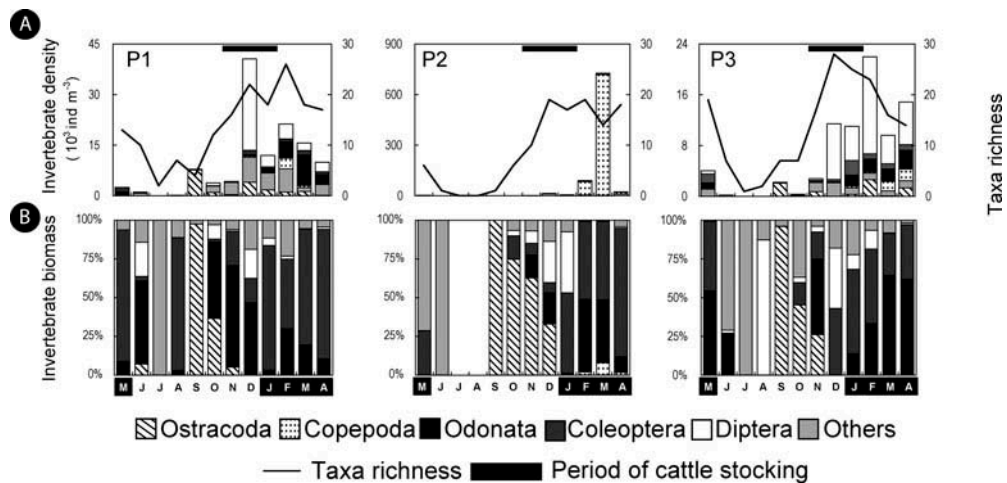
Taxa	CO	FFG	P <sub>1</sub>		P <sub>2</sub>		P <sub>3</sub>	
			I	C	I	C	I	C
<b>Annelidae</b>								
<i>Aulodrilus limnobius</i> Bretscher	Aul	CR	783 (3)	630 (7)	324 (3)	106 (3)	74 (2)	85 (7)
<i>Chaetogaster diaphanus</i> (Gruithuisen)	Cha	CR	982 (4)	777 (2)	1872 (3)	105 (2)	72 (2)	273 (2)
<i>Helobdella michaelseni</i> Blanchard	HeM	P	52 (2)	24 (1)	240 (3)	2 (1)	79 (1)	16 (3)
<i>Helobdella simplex</i> (Moore)	HeS	P		16 (1)			79 (1)	4 (1)
<i>Helobdella</i> sp.2	He2	P	128 (4)	2 (1)	197 (1)		10 (1)	14 (3)
<b>Mollusca</b>								
<i>Lymnaea</i> sp.	Lym	Sh	41 (1)	493 (5)		21 (2)	189 (2)	55 (3)
<i>Biomphalaria</i> sp.	Bio	Sh	15 (1)	4 (1)				1 (1)
<b>Sphaeriidae</b>	Sph	CF	976 (3)	20 (2)	135 (1)		16 (1)	
<b>ARTHROPODA</b>								
<b>Acari</b>								
	Aca	CR	31 (1)		52 (2)		10 (1)	
<b>Crustacea</b>								
Ostracoda	Ost	CF	852 (4)	1855 (5)	535 (4)	1675 (4)	874 (4)	425 (4)
<i>Acanthocyclops</i> sp.	Act	P	28 (1)	2 (1)	925 (3)		283 (4)	6 (2)
<i>Eucyclops chilensis</i> Löffler	Euc	CF	795 (4)	57 (1)	15.10 <sup>4</sup> (3)	2 (1)	469 (4)	33 (2)
<i>Paracyclops chiltoni</i> (Thomson)	Pcy	CF	19 (1)		1577 (3)			
<i>Tropocyclops prasinus meridionalis</i> (Kiefer)	Tpm	CF			1393 (1)			
Harpacticoida	Har	CR	19 (1)		1720 (3)		39 (2)	
<i>Hyalella curvispina</i> Shoemaker	Hya	Sc	68 (3)		498 (3)	2 (1)	330 (5)	
<b>Hexapoda</b>								
<b>Plecoptera</b>								
<i>Potamoperla myrmidon</i> (Mabille)	Pot	Sh		2 (1)				
<b>Odonata</b>								
<i>Rhionaeschna</i> sp.	Rhi	P	596 (5)	28 (4)	578 (4)	2 (1)	969 (5)	3 (1)
<i>Cyanallagma interruptum</i> (Selys)	Cya	P	3063 (5)	49 (4)	290 (2)	5 (2)	922 (5)	10 (3)
<b>Coleoptera</b>								
<i>Lancetes</i> sp.	Lan		234 (5)	102 (3)	13 (1)	32 (3)	245 (4)	36 (3)
<i>Lancetes flavipes</i> Zimmermann	LFl	P	6 (1)					
<i>Lancetes nigriceps</i> (Erichson)	LNi	P	175 (4)	2 (1)	208 (2)		26 (2)	1 (1)
<i>Lancetes varius</i> (Fabricius)	LVa	P	258 (4)		73 (2)		90 (2)	1 (1)
<i>Rhantus signatus</i> (Fabricius)	Rha	P		16 (1)	194 (2)	2 (1)	51 (3)	4 (1)
<i>Liodessus patagonicus</i> (Zimmermann)	Lio	P	31 (2)	18 (2)	222 (2)	2 (1)	9 (1)	
<i>Haliplus subseriatus</i> (Zimmermann)	Hal	CR			9 (1)			
<i>Gymnochthebius</i> sp.	Gym	Sh		4 (1)	222 (2)			7 (1)
<i>Tropisternus setiger</i> (Germar)*	Tro	CR	214 (4)	77 (2)	648 (3)	3 (1)	411 (4)	30 (2)
<i>Enochrus</i> sp.	Eno	CR				2 (1)		2 (1)
<i>Enochrus vicinus</i> Solier	EVi	P-H	59 (2)				371 (2)	
<i>Enochrus darwini</i> (Knisch)	EDa	P-H	28 (1)		13 (1)		47 (2)	
<b>Hemiptera</b>								
<i>Ectemnostega quadrata</i> (Signoret)	Ect	P-H	164 (4)	8 (1)	7 (1)	3 (2)	158 (3)	20 (1)
<i>Notonecta vereertbruggheni</i> (Hungerford)	Not	P	10 (1)				13 (1)	
<b>Trichoptera</b>								
<i>Verger</i> sp. 1	Ve1	Sc		10 (2)				5 (2)
<i>Verger</i> sp. 2	Ve2	Sc	16 (1)					
<i>Oxyethira bidentata</i> (Mosely)	Oxy	CR					9 (1)	1 (1)
<i>Parasericostoma ovale</i> (Schmid)	POv	Sc	47 (1)	2 (1)				
<b>Diptera</b>								
<i>Chironomus gr. decorus</i>	CDe	CR			259 (2)		635 (2)	
Chironomidae sp.	Chi	CR						2 (1)
<i>Paratanytarsus</i> sp.	Par	CR	910 (4)	204 (2)	632 (3)	6 (1)	2682 (5)	188 (3)
<i>Paratrichocladus</i> sp.	PTr	CR	1054 (5)	1422 (5)	290 (3)	199 (3)	1250 (4)	558 (5)
<i>Parachironomus</i> sp.	Pch	CR	398 (4)	1302 (1)	698 (2)	132 (1)	1332 (4)	349 (1)
Podonominae sp.	Po1	CR		5 (1)		2 (1)		8 (1)
Podonominae sp. 2	Po2	CR		64 (1)		9 (2)		19 (2)
<i>Corynoneura</i> sp.	Cor	CR	112 (2)	979 (2)	52 (1)	16 (1)	217 (3)	122 (2)
<i>Tanytarsus</i> sp.	Tan	CF	31 (1)	33 (1)	39 (1)	3 (1)	100 (3)	

(Continued)

**Table 3.** (Continued).

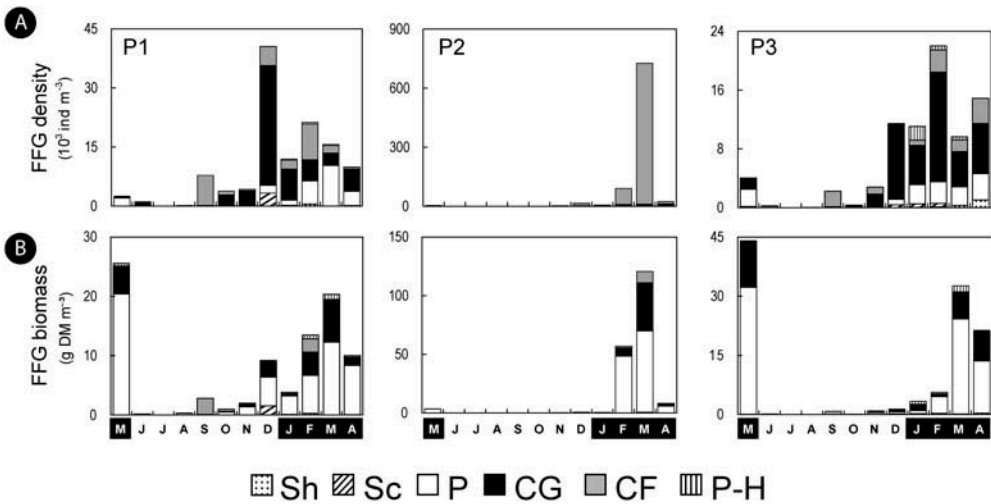
Taxa	CO	FFG	P <sub>1</sub>		P <sub>2</sub>		P <sub>3</sub>	
			I	C	I	C	I	C
<i>Alotanypus</i> sp.	Alo	P	46 (2)	8 (1)	151 (2)		202 (5)	4 (1)
<i>Ablabesmyia</i> sp.	Abl	P			7 (1)		9 (1)	4 (1)
<i>Paramerina</i> sp.	Pme	P	31 (1)		7 (1)		10 (1)	43 (1)
Psychodidae	Psy	CR		8 (3)	9 (1)			
Empididae	Emp	P			177 (1)		24 (2)	
Ephydriidae	Eph	CR		2 (1)			8 (1)	
Stratiomyidae	Str	CR		2 (1)				1 (1)
<i>Gigantodax</i> sp.	Gig	CF		10 (2)				3 (2)
Ceratopogonidae sp. 1	Ce1	P		10 (2)				1 (1)
Ceratopogonidae sp. 2	Ce2	P				2 (1)	9 (1)	1 (1)

CO, Code used for ordination; I, isolated; C, connected. Functional feeding groups (FFG): Sh, shredders; Sc, scrapers; P, predators; CG, collector-gatherers; CF, collector-filterers; P-H: piercers herbivores. \* Larvae: Predator.



**Figure 3.** Seasonal variation of total taxa richness (A), mean density (A), and relative contribution of biomass (B) of most abundant groups of aquatic invertebrates at three ponds in a Patagonian wetland (Mallín Crespo) during the study period (May 2008 to April 2009). Livestock stocking period is indicated by the black bar.

The seasonal pattern of total richness was similar for all ponds, with maximum values during the summer months and minimum during the winter ones, although values were slightly lower at P2 than at P1 and P3. Maximum richness occurred at P3 during December (28 taxa) (Figure 3(a)). During July only two taxa were recorded, *Potamoperla myrmidon* (P1 and P3) and *Aulodrilus limnobius* (P1). After that period, colonization by some invertebrates was fast. The first colonizers were: *Cyanallagma interruptum* (Odonata), *Lancetes nigriceps* (Coleoptera), *Verger* sp. (Trichoptera), *Paratrichocladius* sp. (Chironomidae), *Lymnaea* sp. and Sphaeriidae (Mollusca), all recorded during late winter (August). The midges (*Paratanytarsus* sp., *Paratrichocladius* sp., *Parachironomus* sp., Podonominae sp.2, *Corynoneura* sp., *Tanytarsus* sp., *Alotanypus* sp., *Ablabesmyia* sp., *Paramerina* sp.) reached maximum taxonomic richness during December (connected period), whereas coleopterans and



**Figure 4.** Seasonal patterns of functional feeding groups (FFG), (A) by density ( $10^3$  individuals  $m^{-3}$ ) and (B) by biomass [ $g DM m^{-3}$ ] at three ponds (May 2008 to April 2009) of Mallin Crespo wetland (Argentina). Sh, shredders; Sc, scrapers; P, predators; CG, collector-gatherers; CF, collector-filterers; P-H, piercers herbivores.

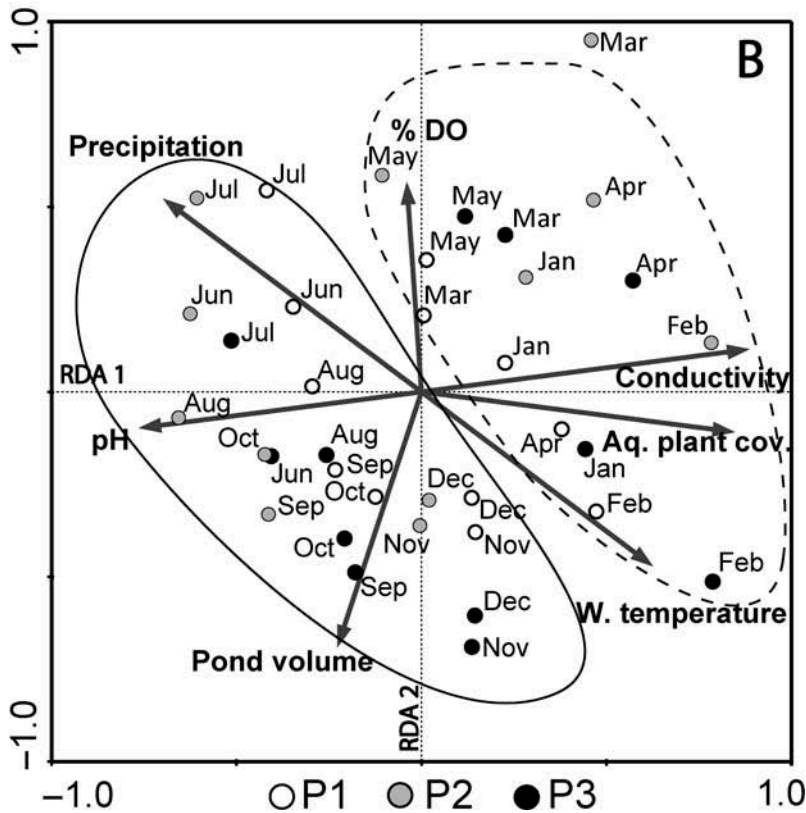
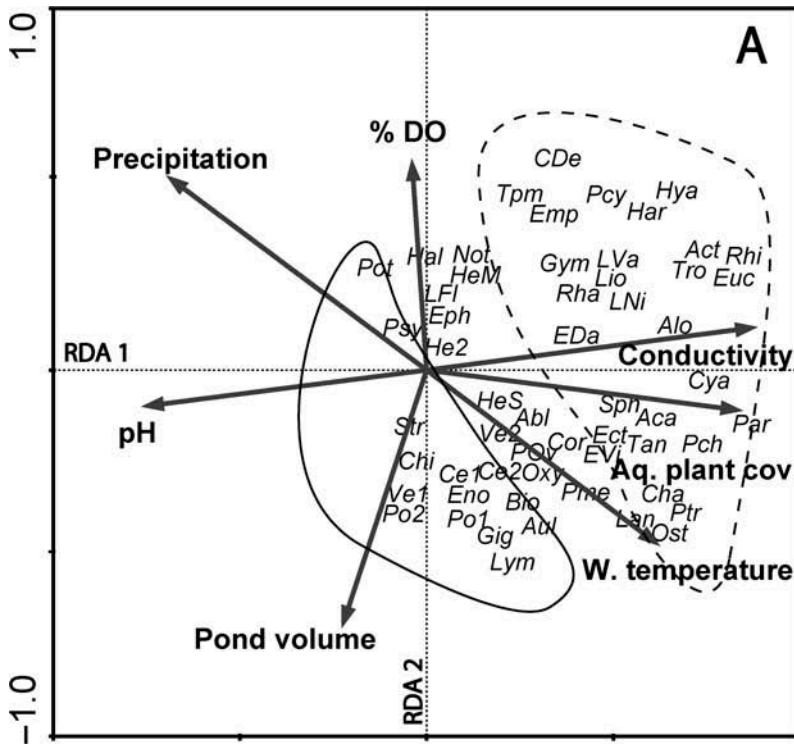
crustaceans were more diverse during late summer (isolated period). *Aulodrilus limnobius* (Oligochaeta) exhibited the longest permanence, occurring during most months.

Seasonal trends in density were quite consistent among ponds, though values and also the dominant groups differed markedly. At P2, maximum density was 15 and 30 times higher than the peaks observed at P1 and P3, respectively (Figure 3). The exceptional value at P2 was explained by the presence of the copepod *Eucyclops chilensis* (mostly in March). Diptera, mostly the chironomids *Paratrichocladius* sp. and *Paratanytarsus* sp., dominated samples at P1 and P3 during December and February, respectively (Table 3). These patterns changed when biomass was analysed throughout the year (Figure 3B), with P1 and P3 being co-dominated by Coleoptera and Odonata, and P2 by Coleoptera and Ostracoda.

Regarding functional feeding groups, collector-filterers were dominant between February and April at P2 (Figure 4A). However, at P1 and P3, collector-gatherers were the most important functional feeding groups in terms of density. Predators followed by collector-gatherers dominated at all ponds when considering biomass data. The peak of invertebrate biomass recorded at P2 was due to *Rhionaeschna* sp., and it was three and four times greater than observed at P3 (*Rhionaeschna* sp.) and P1 (*Lancetes nigriceps*), respectively (Figure 4(b)).

### Species-environment relationships

The RDA analysis (Figure 5A, B) showed a strong and significant relationship between invertebrate temporal distribution and the measured environmental variables (Monte Carlo test,  $p < 0.0001$ ; Table 4). The species environmental correlations



**Table 4.** Results of redundancy analysis (RDA) for three Patagonian ponds during the study period at Mallín Crespo, Patagonia, Argentina.

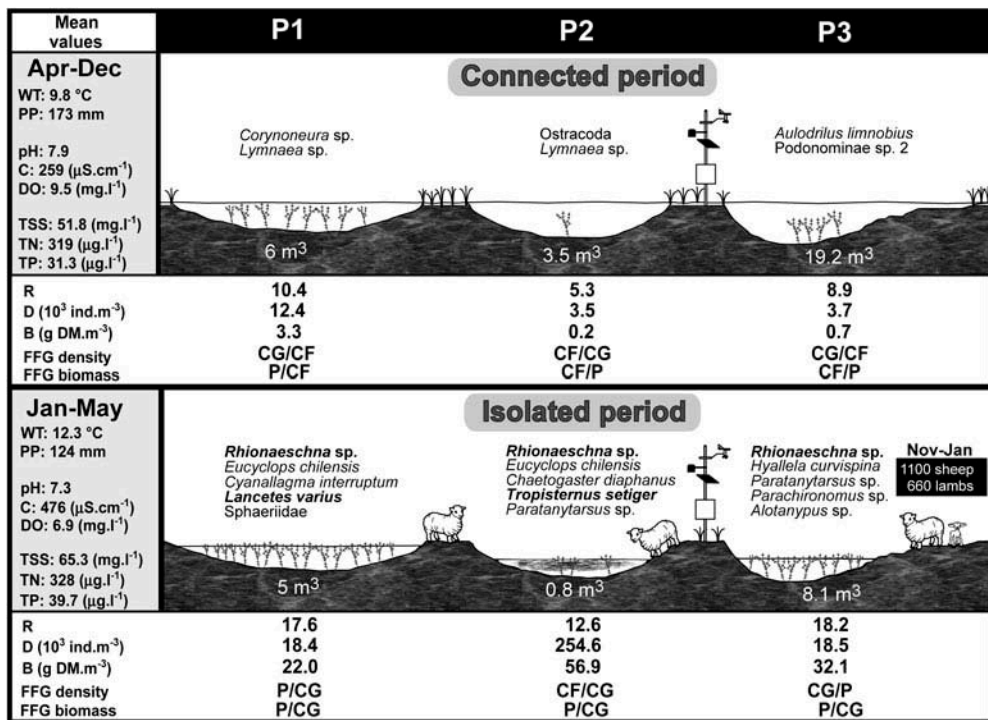
Variable	Axis	
	RDA1	RDA2
Precipitation	-0.62	0.39
Water temperature	0.55	-0.39
Pond volume	-0.19	-0.51
pH	-0.67	-0.07
Water conductivity	0.78	0.09
% Dissolved oxygen	-0.03	0.41
Aquatic plant coverage	0.75	-0.08
Eigenvalues	0.300	0.078
Species–environment correlation	0.90	0.76
Cumulative percentage variance		
of species data	30.0	37.8
of species–environment relation	60.4	76.2

Note:  $p$ -values for Monte Carlo Permutation test: Axis 1:  $F = 11.985$ ,  $p < 0.0001$ . All canonical axes:  $F = 3.94$ ,  $p < 0.0001$ .

Eigenvalues and correlation of standardized environmental variables with the first two RDA axes of each analysis are shown.  $F$ -ratio statistics are listed for the first axis and for all the axes combined.

were: 0.90 and 0.76 for the first and second axes, respectively, suggesting a close relationship with the variables selected. The strongest explanatory factors were physicochemical features, which explained 30.0% of variation in the species data (Table 4). The main environmental gradient (RDA 1) was determined by pH, conductivity, aquatic plant coverage, water temperature and pluvial precipitation (Figure 5A, B). These variables fluctuated strongly along seasons. Samples located on the upper and lower right quadrant corresponded to the warmer months (summer and early autumn, Figure 5B), which, in turn, were coincident with the pond isolation period. Accordingly, during these months precipitation was very low, pH decreased, conductivity displayed the maximum values and aquatic plants increased in coverage. The RDA 2 axis showed an environmental gradient associated with oxygen contents and pond volume. The species colonization sequence was clearly highlighted in the RDA ordination and was linked to the diagonal that crossed from the extreme of the lower left quadrant (higher loads to: *Podonominae* sp.2 and *Lymnaea* sp.) to the upper right quadrant (*Hyalella curvispina* and *Rhionaeschna* sp.). As a result, a total of 28 taxa were clearly linked with the isolation period of ponds (dashed line in Figure 5A), whereas another group (14 taxa, solid line Figure 5A) increased during months when ponds were connected. This period was characterized by lower temperatures, higher precipitation and higher pH values (Table 4). A summary of all variables measured and invertebrate community patterns is shown in Figure 6.

**Figure 5.** Redundancy analysis ordination diagrams for ponds and environmental relationships based on abundance data of aquatic invertebrate taxa during the study period (May 2008 to April 2009) (A) Species–environment bi-plot; (B) Sites–environment bi-plot. Full taxa names are given in Table 3. Solid line indicates the connected period and dashed line the hydrologically isolated one. White circles, P1; grey circles, P2; and black circles, P3.



**Figure 6.** A schematic cross-section of the study wetland (Mallín Crespo) contrasting the condition of the three studied ponds (P1, P2 and P3) during hydrological phases: isolation and connected periods. Distances between ponds, the weather station and sheep are not to scale. Volume (m<sup>3</sup>) is indicated below each pond. Environment variables are: water temperature (WT), precipitation (PP), pH, specific conductivity (C), dissolved oxygen (DO), total suspended solids (TSS), total nitrogen (TN), and total phosphorus (TP). Invertebrate attributes are: taxa richness (R) density (D), biomass (B) and dominant functional feeding groups (FFG). Dominant taxa in terms of density and frequency are listed over each pond. Bold letters are used for taxa that are also dominants in biomass. For both periods first and second dominant FFG are represented. P, predators; CG, collector–gatherers; and CF, collector–filterers.

## Discussion

### *Invertebrate biodiversity and assemblages*

Our study suggests that small intermittent ponds sustain a diverse and abundant invertebrate community and are also habitat for rich macrophyte assemblages, meaning that these small environments constitute reservoirs of biodiversity within the Patagonian steppe. The richness reported in the present contribution (56 taxa) is comparable to that found at ponds in Alpine and Continental regions in Europe (Cérégino et al. 2012), in shallow natural wetlands in North America (Brooks 2000) and farm ponds in Australia (Markwell and Fellows 2008). Nevertheless it is substantially higher than observed in turloughs in Ireland (25 taxa) (Porst et al. 2012), and at constructed ponds in the UK (35 taxa) during long-term research (Jeffries 2011).

The invertebrate community was dominated by organisms that are typical inhabitants of temporary ponds, such as Chironomidae, Dytiscidae and Hydrophilidae (in terms of



richness), and microcrustacea (mainly *Eucyclops chilensis*, Copepoda) in terms of abundance. Most recorded taxa adapted to tolerate fluctuating environments, due to a variety of physiological features and biological traits (e.g. flexible life cycles, body size, dispersal mechanism) that allow them a successful colonization, dispersion and survival in temporary waters (Williams 2006; Jeffries 2011; Hannigan and Kelly-Quinn 2012). Accordingly, in Mallín Crespo, only a few invertebrates survived the harshest period (*Corynoneura* sp., *Lymnaea* sp., Ostracoda, *Aulodrilus limnobius* and Podonominae sp.2), imposed by winter temperatures and water flow (Figure 6). In late spring, when environmental factors produced pond disconnection, typical species assemblages were usually associated with lentic waters, for example worms (*Chaetogaster diaphanus*), bivalves (Sphaeriidae sp.), copepods (*Eucyclops chilensis*), amphipods (*Hyallela curvispina*), dragonflies (*Rhionaeschna* sp.), damselflies (*Cyanallagma interruptum*) (Jara et al. 2013), or beetles (*Lancetes varius*, *Tropisternus setiger*), (Epele and Archangelsky 2012). These assemblages or associations of invertebrates can be used to characterize different aquatic environments in the Patagonian steppe.

### **Community functional patterns**

The dominance of functional feeding groups at spring pools in intermittent environments seems to change between phases following different successional stages (Williams 2006). A clear replacement of species throughout the connected and isolated stages was observed in our work, and in turn the functional structure of the faunal community differed substantially over time. Consequently the connected period was dominated by collector–gatherers whereas the spring pond stage showed a marked increase in macropredators (*Rhionaeschna* sp., *Cyanallagma interruptum* and *Lancetes varius*), which occurred primarily due to aerial colonization by adult beetles and dragonfly larval development and coincidentally with an extremely high prey offer. During the isolated period, macropredators also dominated the community in terms of biomass. Nevertheless, the probability of interspecific competition occurring is thought to be low, so allowing the coexistence of very similar species (Jara et al. 2012), for example a variety of beetles (e.g. *Lancetes nigriceps*, *Lancetes flavipes*, *Lancetes varius*) which probably fed on the very abundant midge larvae (*Paratanytarsus*, *Paratrichocladius* and *Parachironomus* spp.). In the present study, a total of 16 predatory aquatic insects were recorded, a number substantially higher than recorded by Jara et al. (2013) (three taxa) at temporary ponds in the northwestern Patagonian steppe. However, as the authors anticipated, those ponds with abundant aquatic vegetation and longer hydroperiod could contain greater insect richness.

The scarcity of shredders during the entire study was unexpected (<0.5% of total density and biomass). In an extensive review in North American wetlands, Wissinger (1999) observed that CPOM shredders were rare and so nutrients and energy from detrital resources must enter food webs via FPOM collectors and algal/biofilm grazers. According to Céréghino et al. (2008), during the senescence period, aquatic plants at ponds are a source of food for several organisms supplying CPOM and supporting periphyton communities. Annual plants might also produce abundant fast-decaying detritus that should support dense populations of grazers and FPOM collectors, especially chironomids (in our study the functional group of collector–gatherers:

*Paratanytarsus* sp., *Paratrichocladus* sp. and *Parachironomus* sp.). During late spring (connection phase), only the scrapers *Lymnaea* sp. and *Gymnochthebius* sp. appeared briefly, probably attributable to a higher quality of periphyton associated with macrophytes. Intermittent ponds may also have a significant autotrophic phase produced by planktonic algae that provide a vital food source for early filter-feeders, such as fairy shrimp and other microcrustaceans (Molla et al. 1996). Collector–filterers were present during most months in our study; however, an extremely high peak in density of copepods (*Eucyclops chilensis*) and ostracods occurred during summer (especially at pond P2). These peaks could be explained by the diminution of the pond volume as a result of increased temperature and reduced precipitation.

### ***Invertebrate and environment relationships***

Variables identified as important in structuring community assemblages at the three studied Patagonian ponds were related to changes in environmental conditions (rainfall and water temperature), chemical features (conductivity and pH) and biotic factors such as coverage and biomass of macrophytes. At Mallín Crespo, the abiotic parameters related primarily to hydrology and temperature regulated the dynamics and growth of aquatic plants, whose coverage increased from late winter, reaching maximum values in late summer. Macrophytes seem to influence composition and abundance of invertebrate taxa by providing higher complexity in habitat, good oxygenation, greater stability of sediments and new food resources (e.g. periphyton) (Bazzanti et al. 2010). During July, aquatic plant coverage was very low (< 5%), ponds were connected and partially frozen: the decline in available habitats probably producing a decrease in invertebrate taxonomic richness to only two taxa.

After the winter months, richness and macrophyte coverage significantly increased, when the structurally complex *Myriophyllum quitense* and *Lilaeopsis macloviana* were dominant (mostly at P1 and P3), providing habitat for the aquatic invertebrates. However, P2 was dominated by the filamentous algae *Cladophora* sp., which tends to fulfil all the available space of the shallower ponds reducing existing microhabitats and displaying the lowest invertebrate richness. This also confirms the function of vascular macrophytes in maintaining high invertebrate biodiversity of the Patagonian environments (Epele et al. 2012; Kutschker et al. 2014).

During the connected period, water at the ponds displayed slightly lower pH values than during the isolation phase, probably in response to heavy rains (Brönmark and Hansson 2005). After that, through the isolation period, higher photosynthesis rates at the ponds could alter the carbon dioxide–bicarbonate complex equilibrium, causing an uptake of hydrogen ions and thereby an increase in pH.

As observed in other grazed wetlands (Silver and Vamosi 2012), a marked increase in the level of total suspended solids and in water conductivity occurred as a consequence of sheep stocking, whereas nutrients did not change. Several factors can affect water turbidity, including shallowness, wind exposure, frequent mixing, trampling and bioturbation (Fairchild et al. 2005). Nevertheless, since increases in total suspended solids were not associated with any rainfall event, we consider that turbidity was mostly augmented by trampling of pond shorelines by livestock. Accordingly, during December a group of species tolerant to sedimentation, mostly Chironomidae (*Paratanytarsus* sp.,

*Parachironomus* sp. and *Corynoneura* sp.), accounted for more than 62% of the density (P3). Campbell et al. (2009) stated that agricultural land use, particularly cattle grazing, can markedly influence chironomid communities in farm ponds, and they detected a dominance of midge taxa tolerant of turbid, eutrophic conditions in grazed grassland ponds.

### **Implications for pond conservation**

In the temporal sequence a higher environmental complexity, related to greater coverage of macrophytes during the isolated period, also resulted in a significant increase of richness, density and biomass of invertebrates. However, these environments are threatened, because they are used as water supplies for livestock (Gaitán et al. 2011) and the associated wetlands are used as pasture lands. Conservation actions successfully employed on ponds in other countries that could be applied here are: a selective access of cattle for watering, a supervised grazing management in the surrounding catchment areas, and alternative sources of water supply (e.g. through mechanical drinking infrastructure) (Declerck et al. 2006). These actions may also help to fulfil the needs of local farmers.

Intermittent ponds in the Patagonian steppe appear as fragile environments harbouring rich and diversified aquatic communities of both macrophytes and invertebrates. Compared with other surface waters, ponds still receive little effective protection from legislation or policy (Cérégino et al. 2014) and this is a matter of concern in arid and semi-arid Patagonia, because at present there are no actions for wetlands conservation. Therefore, it would be a priority to establish management guidelines for pond conservation that promote their spatial heterogeneity and that maintain their ecological roles.

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No potential conflict of interest was reported by the authors.

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