



Changes in the zooplankton and limnological variables of a temporary hypo-mesosaline wetland of the central region of Argentina during its drying

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Abstract. Many aspects of the ecology of temporary wetlands are known in other countries, but not in Argentina. Although many conclusions about the functioning of temporary ecosystems can be adapted to those of Argentina, the presence in them of many neotropical endemic taxa makes their application may be limited. The aims of this work were to analyze the variation in the environmental variables and zooplankton of a temporary lake of the central region of Argentina and to test the hypothesis that specific richness and abundance decrease whereas biomass increases due to increased salinity accompanying drying. Water and zooplankton samples were taken from December 2005 (salinity = 10.4 g.L⁻¹) until August 2006 (salinity = 23.1 g.L⁻¹), before it became dry. The lake was hypereutrophic and had reduced transparency. We recorded 16 taxa and verified the decrease in taxonomic richness and replacement, with the appearance of halophilic crustaceans towards the end of the study. Contrary to our expectations, the density increased towards the end. Rotifers predominated, accounting for 96% of total density and contributing over 47% of total biomass. This makes the lake studied more similar to other shallow lakes of La Pampa but with lower salinity, permanent, with fishes and very low proportion of inorganic suspended solids.

Key words: shallow lakes, temporary wetlands, zooplankton, *Daphnia menucoensis*, rotifers, La Pampa

Resumen. Cambios en las variables limnológicas y el zooplancton durante el secado de un humedal temporario hipo-mesosalino de la región central de Argentina. Muchos aspectos de la ecología de los humedales temporarios en otros continentes es conocida, pero en Argentina no ha ocurrido lo mismo. Si bien algunas conclusiones sobre el funcionamiento de ecosistemas temporarios son adaptables a los ecosistemas argentinos, la presencia en éstos de muchos taxones endémicos neotropicales hace que su aplicación pueda ser limitada. El objetivo de esta contribución fue analizar la variación de las variables ambientales y el zooplancton que ocurrió durante la desecación de una laguna en el centro de Argentina y testear la hipótesis de que la diversidad y la abundancia disminuyen pero la biomasa aumenta debido al aumento de la salinidad que acompaña a la desecación. Se tomaron muestras de agua y zooplancton desde diciembre de 2005 (salinidad = 10,4 g.L⁻¹) hasta agosto de 2006 (salinidad = 23,1 g.L⁻¹), antes de la desecación. Su condición fue hipertrófica con reducida transparencia. Se registraron 16 taxa y se verificó la disminución de la riqueza y el reemplazo taxonómico, con la aparición de crustáceos halófilos hacia el final del estudio. Contrariamente a lo esperado, la densidad aumentó hacia el final. Predominaron los rotíferos, que representaron el 96% de la densidad total y aportaron más del 47% de la biomasa total, lo que hace que el lago estudiado sea más parecido a lagos someros de La Pampa de menor salinidad, permanentes, con fauna íctica y muy baja proporción de sólidos suspendidos inorgánicos.

Palabras clave: lagos someros, humedales temporarios, zooplancton, *Daphnia menucoensis*, rotíferos, La Pampa

Introduction

Temporary wetlands are ecosystems that contain water during periods that can vary from a few months to several years (Schwartz & Jenkins 2000). They are generally developed in shallow depressions, are widely distributed in the world, and can have from a few square meters to hundreds of hectares (Williams 1987 and 2002, Schwartz & Jenkins 2000).

Some authors have studied several aspects of the cycles that alternate between the wet and dry phases and their influence on the biota of both temporary and seasonal environments of Australia (Williams *et al.* 1998, Bayly 2001, Roshier *et al.* 2001), North America (Smith *et al.* 2003, Wallace *et al.* 2005) and Europe (Mura & Brecciaroli 2003, Frisch *et al.* 2006). However, in Argentina, although they are very frequent, their ecology has received little attention, especially in the semiarid central-west region of the country. At present, the few studies about these ecosystems have been carried out in relation with the conservation of some wetlands of importance for certain bird species (Canevari *et al.* 1998), but there is little information about the ecology of the invertebrates that inhabit them during the wet phases.

Although many conclusions about the functioning of other temporary ecosystems of the world may be applicable to those of Argentina, generalizations are hampered by the great diversity of landscapes where temporary water bodies occur (Fahd *et al.* 2000). In addition, the biodiversity of South American aquatic environments is not adequately known (Lévêque *et al.* 2005) and the species assemblages differ from those of other continents, especially regarding crustaceans, which show some endemic taxa to the Neotropical region (Paggi 1998, Adamowicz *et al.* 2004, Echaniz *et al.* 2005 and 2006, Vignatti *et al.* 2007), and about which there is little ecological knowledge.

The importance of studying the ecology of these environments is increased by the high rate at which they are disappearing due to human action, generally to be transformed in agricultural fields (Belk 1998, Williams 2002, Jenkins *et al.* 2003, Eitam *et al.* 2004), with the consequent loss of some species (Simovich 1998, Boix *et al.* 2002), which significantly affects regional biodiversity (Waterkeyn *et al.* 2008).

Since the precipitations in the east of the province of La Pampa, in the central region of Argentina, are lower than evapotranspiration (Casagrande *et al.* 2006) and there are numerous arheic basins, temporary wetlands are frequent. They

are specially fed by precipitations and their salinity and water level are highly variable.

In spite of the abundance of this type of ecosystems in the province, there is only one study about the diversity of crustaceans and rotifers, and the changes in some physico-chemical variables during the period from the filling until the drying of a shallow wetland (Echaniz & Vignatti 2010). In addition, this lake was a subsaline one (salinity < 3g.L⁻¹) according to Hammer (1986) classification.

On the other hand, it is known that there is an inverse relationship between the total salt concentration and zooplankton richness and abundance in limnic water bodies (Hammer 1986, Green 1993, Greenwald & Hurlbert 1993, Williams 1998, Hall & Burns 2003, Derry *et al.* 2003, Ivanova & Kazantseva 2006) due to the increased environmental stress (Herbst 2001), and that high salinity lakes tend to have higher zooplankton biomass than low salinity ones (Evans *et al.* 1996).

Therefore, the aim of this contribution was to analyze the variation in the environmental variables and the changes in the zooplankton diversity, abundance and biomass of a temporary lake of the north of La Pampa province during its drying period, when it changes from hyposaline (3-20 g.L⁻¹) to mesosaline conditions (20-50 g.L⁻¹) (Hammer 1986), and to test the hypothesis that due to the increased environmental stress produced by increased salinity, species richness and abundance decreased while the zooplankton biomass increases.

Materials and methods

Study area

Aime Lake is a temporary shallow lake situated in the north of La Pampa province (35° 28' S, 64° 15' W) (Fig. 1), in a region characterized by a plain with soft hills in the ecotone between the Pampa Plains and Thorny Forest phytogeographic provinces (Cabrera 1976). The land use of its basin is mainly agriculture of cereals and oil crops and extensive livestock breeding. Aime Lake has a regular shape, with few accidents, and lacks macrophytes and ichthyic fauna.

It is fed mainly by precipitations, being the annual mean of the region close to 700 mm (Casagrande *et al.* 2006), with maximum values in December and March (Cano 1980). However, potential evapotranspiration is about 800 mm (Ponce de León 1998). It is located in an arheic basin and loses water by evapotranspiration or infiltration and suffers great fluctuations in its level. The predominant direction of winds in the region is N-NE and S-SW, with annual mean speeds ranging

from 2.8 to 4.2 m.s⁻¹ and with strong seasonality, as they are more intense in late winter (Cano 1980).

The lake was filled by precipitations in December 2004 and reached a maximum depth of

0.8 m. During the study, the lake had a maximum length and width of 1360 and 640 m respectively, a maximum depth of 0.42 m and a maximum area of 61.2 ha.

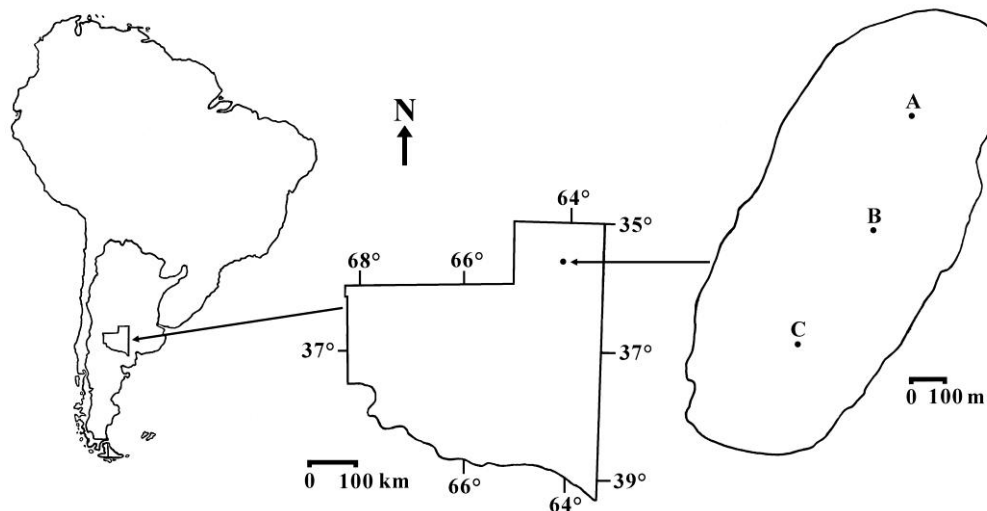


Figure 1. Geographical ubication in South America and in La Pampa province and sketch of Aime temporary lake. A, B, and C: Sampling sites.

Field and laboratory work

Samples were taken between December 2005 and August 2006, about 15th of each month at noon, in three sites located along its main axis (Fig. 1). The following variables were determined in each site: water temperature, concentration of dissolved oxygen (oximeter Lutron® OD 5510), water transparency (Secchi disk), and pH (digital pH meter Corning® PS 15), and water samples were collected and frozen until their analysis in the laboratory.

Two quantitative samples of 20 L were taken at each site for zooplankton analysis. Because of the shallow depth, these samples were taken with graduated containers that integrated the water column, and water was filtered through a 40 microns pore size net. A qualitative sample was also taken with a similar net. All the samples were anesthetized with CO₂ and kept refrigerated until fixation with formaldehyde 4%. The total dissolved solids concentration (TDS) was determined by means of the gravimetric method with drying at 104°C. The chlorophyll-*a* concentration (Chl-*a*) was established by extraction with aqueous acetone and spectrophotometry (APHA 1992, Arar 1997), the total phosphorus (TP) by the ascorbic acid method after digestion with acidic persulfate (APHA 1992) and the Kjeldahl total nitrogen (TN) (sum of free-

ammonia and organic nitrogen compounds) by the digestion method with sulfuric acid and colorimetric determination with Nessler reagent (EPA 1993 a). The suspended solids content was determined by means of fiberglass filters Microclar FFG047WPH, dried at 103 - 105°C until constant weight and later ignited at 550 °C (EPA 1993 b).

Counts to determine the abundance of microzooplankton (rotifers and nauplii) (Kalff 2002) of each sample were carried out in Sedgewick-Rafter chambers under an optical microscope with 40-100 X magnification taking aliquots with a micropipette of 1 ml. Macrozooplankton (cladocerans and copepods) (Kalff 2002) were counted in Bogorov chambers under a stereomicroscope with 20X magnification, taking aliquots with a Russell subsampler of 5 ml. The number of aliquots was determined with Cassie's equation (Downing & Rigler 1984).

To determine zooplankton biomass, we measured at least 30 individuals of each species with a Carl Zeiss ocular micrometer and used formulas that related total length with dry weight in the case of crustaceans (Dumont *et al.* 1975, Rosen 1981, McCauley 1984, Culver *et al.* 1985 and Kobayashi 1997) or with geometric forms in the case of rotifers (Ruttner Kolisko 1977).

To explore the relationships between the environmental factors and the zooplankton features we calculated non-parametric Spearman's correlation coefficients (r_s) and also carried out a principal component analysis (PCA) (Pérez 2004, Mangeaud 2004) without data transformation. To test physical, chemical and biological differences between sampling sites we carried out nonparametric Kruskal-Wallis analysis of variance (H) (Sokal & Rohlf 1995, Zar 1996) and since spatial variations were not significant ($p < 0.05$), we used mean values. Alpha dominance diversity index was estimated, and to determine the replacement of species throughout the study period we calculated Whittaker's beta diversity index in temporal sense (Magurran 2004). We used Past version 1.94b (Hammer *et al.* 2001) and Infostat (Di Rienzo *et al.* 2010) softwares.

Results

The lake was very shallow, and at the beginning of the study, the maximum depth was 0.41 m. It remained relatively stable until May, when it increased slightly because of local precipitation and then it decreased until it dried out, after the sampling carried out in August (Fig. 2).

The total dissolved solids concentration in water was very variable and ranged between 8.97 g.L^{-1} in March to 23.1 g.L^{-1} in August. A slight decrease was observed in May, in coincidence with increasing depth (Fig. 2 and Table I) and a high correlation with depth was found ($r_s = -0.82$; $p = 0.0072$). In contrast, the pH showed little variation along the period studied (Table I).

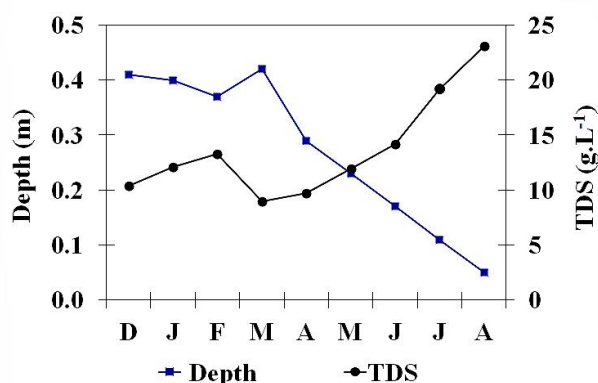


Figure 2. Monthly variation in the maximal depth and total dissolved solids concentration (TDS) in Aime temporary lake during the period December 2005-August 2006.

The water temperature followed a seasonal pattern, with a maximum over 28°C in December and a minimum close to 9°C in June (Table I). The

dissolved oxygen concentration was relatively high (mean = $9.27 \text{ mg.L}^{-1} \pm 1.25$) and remained relatively stable (Table I).

Water transparency was very low during all the period studied (mean = $0.05 \text{ m} \pm 0.03$) (Table I). It was maximum at the beginning and then decreased towards the end of the study (Fig. 3). Phytoplankton chlorophyll-*a* mean concentration was relatively high ($247.2 \text{ mg.m}^{-3} \pm 231$), but was very low (15.8 mg.m^{-3}) at the beginning of the study and then increased to be maximum in July (679.6 mg.m^{-3}) (Fig. 3). We found a significant correlation of chlorophyll-*a* concentration with water transparency ($r_s = -0.84$; $p = 0.0046$).

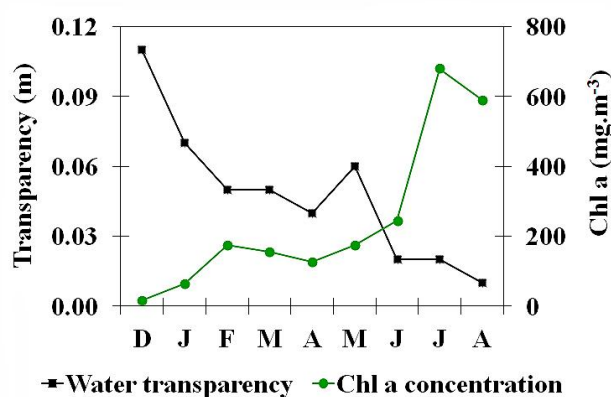


Figure 3. Monthly variation in water transparency and chlorophyll-*a* concentration in Aime temporary lake during the period December 2005-August 2006.

The mean total suspended solids concentration was $931.5 \text{ mg.L}^{-1} \pm 1155.5$, among which those of inorganic origin represented almost 70 % of the total. The levels of both fractions were relatively low between December and May, and then increased to a maximum in August (2911.1 mg.L^{-1} and 866.7 mg.L^{-1} inorganic and organic solids respectively) (Fig. 4).

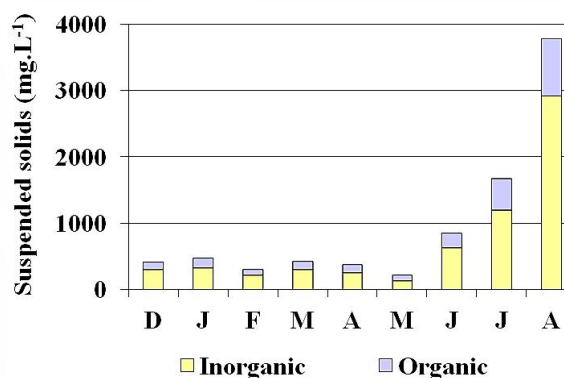


Figure 4. Monthly variation in organic and inorganic suspended solids concentration in Aime temporary lake during the period December 2005-August 2006.

The nutrients concentration was high (Table I), being that of total phosphorus of 16.06 mg.L^{-1} (± 6.73), and that of total nitrogen of 28.11 mg.L^{-1} (± 10.03). The correlation between the concentrations

of both nutrients was high ($r_s = 0.85$; $p = 0.004$), but a significant correlation was found only between chlorophyll-*a* and total nitrogen ($r_s = 0.73$; $p = 0.0261$).

Table I. Limnological variables recorded in Aime temporary lake between December 2005 and August 2006.

	n	Mean	S.D.	Min.	Max.
Temperature ($^{\circ}\text{C}$)	9	28.01	6.41	9.4	28.10
Water transparency (m)	9	0.05	0.03	0.01	0.11
Total dissolved solids (g.L^{-1})	9	13.65	4.65	8.97	23.08
pH	9	9.13	0.21	8.87	9.38
Chlorophyll <i>a</i> (mg.m^{-3})	9	247.18	230.6	15.79	679.64
TP (mg.L^{-1})	9	16.06	6.73	8.75	25.83
TN (mg.L^{-1})	9	28.11	10.03	13.13	39.4
Dissolved oxygen (mg.L^{-1})	9	9.27	1.95	7.1	13.6
Total suspended solids (mg.L^{-1})	9	931.47	1155.5	207.86	3777.8
Inorganic suspended solids (mg.L^{-1})	9	685.53	895.9	290.5	2911.1
Organic suspended solids (mg.L^{-1})	9	245.96	260.9	108.2	866.7

We recorded 16 taxa: 3 cladocerans, 5 copepods and 8 rotifers (Table II). Among crustaceans, *Cletocamptus deitersi* and *Metacyclops mendocinus* were the most frequent species. In contrast, others were recorded on a few occasions at the beginning (*Moina micrura* and *Boeckella gracilis*) or at the end of the study (*Daphnia menucoensis* and *Boeckella poopoensis*). Among rotifers, the most frequent ones were *Brachionus plicatilis* and *B. dimidiatus*, whereas others such as *Filinia* sp. and *Keratella tropica* were recorded only on one occasion (Table II).

Maximum diversity (10 taxa) was recorded in December and then decreased until its minimum (5 taxa) in August (Table II) and a significant correlation was found only between the species number and the lake depth ($r_s = 0.71$; $p = 0.0333$). The Whittaker beta diversity index showed that the highest replacements of species was between December and January (0.33) and between July and August (0.23).

The mean total zooplankton abundance was 11763.6 (± 12156.8) ind.L^{-1} , with a minimum of 2065.3 ind.L^{-1} in March and two peaks: one in

February (34883.4 ind.L^{-1}) and another one in August (29499.3 ind.L^{-1}) (Fig. 5). We found a significant correlation between the total abundance and the lake depth ($r_s = 0.75$; $p = 0.0199$), total dissolved solids ($r_s = 0.82$; $p = 0.0072$), chlorophyll *a* concentration ($r_s = 0.78$; $p = 0.0125$) and water temperature ($r_s = 0.70$; $p = 0.0347$).

The highest density was that of rotifers, which exceeded 90% of the mean total abundance, in particular *B. plicatilis* and *B. dimidiatus* (Table III). The peaks in total abundance were especially produced by these species since the former reached its maximum density (26500 ind.L^{-1}) in August and the latter in February (29890 ind.L^{-1}). Among copepods, the most abundant species was *Metacyclops mendocinus*, followed by *Cletocamptus deitersi* (Table III) which reached 713.3 ind.L^{-1} in May and 439.3 ind.L^{-1} in July respectively. Cladocerans were scarce and *Moina macrocopa* was the most abundant species (Table III), reaching 70 ind.L^{-1} in May.

The high value of the dominance index, which was close to 0.8 in two occasions (Fig. 5), was due to the predominance of *Brachionus*

angularis in January, which had a density of 3050 ind.L⁻¹, i.e. 88% of the total of the community, and to that of *B. plicatilis* in August, which reached an

abundance of 26500 ind.L⁻¹, i.e., 90% of total density.

Table II. List of species recorded in the zooplankton of the Aime temporary lake and their occurrence in the sampling period (December 2005-August 2006). The first row indicates the concentration of total dissolved solids and the last, the richness recorded in each occasion.

	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug
Total dissolved solids (g.L ⁻¹)	10.4	12.1	13.3	8.97	9.74	11.93	14.15	19.18	23.08
Cladocerans									
<i>Daphnia menucoensis</i> Paggi, 1996								—	—
<i>Moina micrura</i> Kurz, 1874	—								
<i>M. macrocopa</i> (Straus, 1820)					—	—	—	—	—
Copepods									
<i>Boeckella gracilis</i> (Daday, 1902)	—	—	—	—	—				
<i>B. poopoensis</i> Marsh, 1906								—	—
<i>Metacyclops mendocinus</i> (Wierzejski,1892)	—	—	—	—	—	—	—	—	—
<i>Microcyclops anceps</i> (Richard, 1897)		—	—						
<i>Cletocamptus deitersi</i> (Richard, 1897)	—	—	—	—	—	—	—	—	—
Rotifers									
<i>Brachionus plicatilis</i> Müller, 1786	—	—	—	—	—	—	—	—	—
<i>B. angularis</i> Gosse, 1851	—	—	—	—	—	—			
<i>B. dimidiatus</i> Bryce, 1931		—	—	—	—	—	—	—	—
<i>B. pterodinooides</i> Rousselet, 1913				—	—	—	—	—	—
<i>Filinia</i> sp.	—								
<i>Keratella tropica</i> (Apstein, 1907)	—								
<i>Asplanchna</i> sp.	—	—	—	—	—	—			
<i>Hexarthra fennica</i> (Levander, 1892)	—		—						
Species number	10	8	9	8	7	6	6	8	5

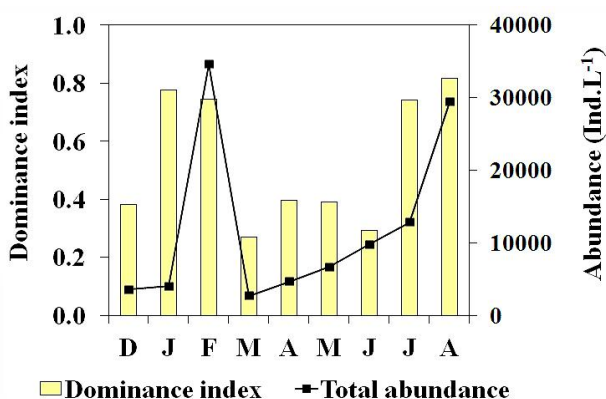


Figure 5. Monthly variation of the zooplanktonic abundance and dominance index of Aime temporary lake during the period December 2005-August 2006.

The mean zooplankton biomass was 4344.4 (± 2539.4) $\mu\text{g.L}^{-1}$ with a minimum of 523.6 $\mu\text{g.L}^{-1}$ in January and a maximum of 8551.6 $\mu\text{g.L}^{-1}$ in July (Fig. 6). Although copepods contributed the highest mean biomass along the study (1840.4 $\mu\text{g.L}^{-1} \pm 1523$), particularly by the contribution of *Metacyclops mendocinus* accounting more of the 72% of the taxonomic group (Table III), rotifers were the ones that contributed most in three occasions (Fig. 6). *Asplanchna* sp. reached 3424 $\mu\text{g.L}^{-1}$ in February and *B. plicatilis* 4084.8 $\mu\text{g.L}^{-1}$ and 6095 $\mu\text{g.L}^{-1}$ in July and August respectively. The cladocerans only contributed significantly in July (2761.6 $\mu\text{g.L}^{-1}$), when their biomass accounted 32.3% of total, by the contribution of *D. menucoensis*.

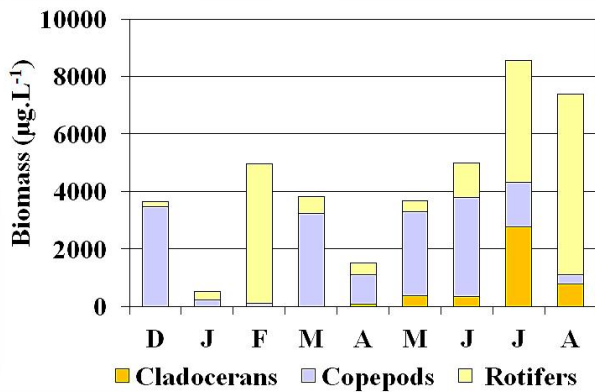


Figure 6. Monthly variation of the zooplanktonic biomass in Aime temporary lake during the period December 2005-August 2006.

The first component of the PCA explained 51.1% of the variance and was positively correlated with physical variables such as transparency, temperature and depth, and negatively correlated with the dissolved and suspended solids concentrations (Fig. 7). The PCA indicated that species richness was positively influenced by the depth of the lake and water transparency, but negatively influenced by the dissolved solids, chlorophyll *a* and suspended solids concentrations (Fig. 7).

Considering the taxonomic groups, the PCA showed that cladocerans abundance had a negative

relation with the depth, transparency and temperature, but was not affected by dissolved solids and chlorophyll *a* concentrations. However, PCA indicated the positive influence of the latter variables on their biomass. In the case of copepods, both abundance and biomass were scarcely affected by environmental variables, but that of the rotifers appeared to have been positively influenced by the dissolved solids and chlorophyll *a* concentrations and negatively by the depth, transparency and temperature (Fig. 7).

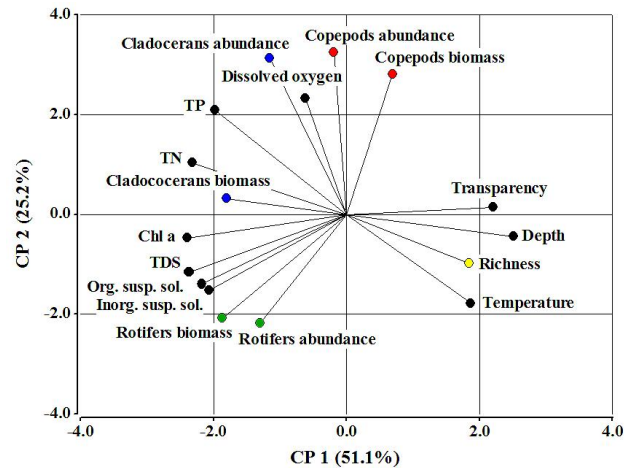


Figure 7. Biplot of the Principal Component Analysis. TP: total phosphorous. TN: total Kjeldahl nitrogen. Chl *a*: chlorophyll *a*. TDS: total dissolved solids. Org. susp. sol.: organic suspended solids. Inorg. susp. sol.: inorganic suspended solids.

Table III. Mean and standard deviation of the abundance and biomass of the taxa registered in the zooplankton of Aime temporary lake between December 2005 and August 2006.

	Abundance (ind.L ⁻¹)		Biomass (µg.L ⁻¹)	
	Mean	S.D.	Mean	S.D.
<i>Daphnia menucoensis</i>	4.96	11.04	394.29	925.10
<i>Moina micrura</i>	0.70	2.11	1.61	4.84
<i>M. macrocopa</i>	14.85	26.07	85.04	152.04
<i>Boeckella gracilis</i>	53.70	157.25	348.96	1033.36
<i>B. poopoensis</i>	0.41	0.81	2.98	5.93
<i>Metacyclops mendocinus</i>	269.03	276.18	1330.82	1428.38
<i>Microcyclops anceps</i>	9.25	25.21	9.90	26.98
<i>Cletocamptus deitersi</i>	102.52	140.25	125.75	220.49
<i>Brachionus plicatilis</i>	8765.53	400.00	1327.37	2209.85

Table III (Cont.)

<i>B. angularis</i>	1161.09	0.00	11.27	14.10
<i>B. dimidiatus</i>	9583.98	140.00	124.94	191.01
<i>B. pterodinoides</i>	1083.19	0.00	87.48	151.62
<i>Filinia sp.</i>	31.67	0.00	0.63	1.90
<i>Keratella tropica</i>	3.33	0.00	0.04	0.12
<i>Asplanchna</i>	260.87	0.00	495.56	1110.31
<i>Hexarthra fennica</i>	36.38	110.00	0.74	1.95

Discussion

The province of La Pampa is located in a region characterized by the predominance of arid and semiarid conditions, which increase towards the west due to the existence of a decreasing gradient of precipitations (Casagrande *et al.* 2006). These precipitations are always lower than potential evapotranspiration (Ponce de León 1998). This makes the water bodies of the region to remain dry for several years until they are filled by precipitations, generally torrential ones, which take place during the warmer months (Cano 1980) and retain water during variable periods.

Unlike recorded during the same period in other environments of the province which showed stability in most of the environmental variables (Echaniz *et al.* 2008 and 2009), Aime Lake showed a marked decrease in the water level until it dried out. During that process there was an increase in the concentration of dissolved solids which made it shift from a hyposaline condition at the beginning of our study to a mesosaline condition (*sensu* Hammer 1986) just before drying.

Aime is a lake with high turbidity caused by the great amounts of suspended solids in the water. The high amounts of suspended solids of inorganic origin could be due to the resuspension of sediments from the bottom by effect of the wind, a phenomenon particularly important in shallow lakes (Markensten & Pierson 2003, de Vicente *et al.* 2006, Borell Lövestedt & Bengtsson 2008). In the case of the studied lake, this was favored by the fact that it is located in a plain, very exposed to frequent winds (Cano 1980), with a relatively flat bottom and absence of macrophytes that could reduce the waves (Moss *et al.* 1996). Moreover, the highest amount of suspended solids was recorded in July and August, months during which the most intense winds are recorded (Cano 1980).

Aime Lake is hypertrophic (OECD 1982) and its concentrations of chlorophyll *a* and nutrients found are frequent in La Pampa (Table IV), but they are among the highest ever recorded for Argentina, even higher than those measured in the province of Buenos Aires (Quirós *et al.* 2002, Sosnovsky & Quirós 2006, Torremorell *et al.* 2007). The high concentration of nutrients could be favored by the scarce depth, which in turn favors polymixis, removal of sediments and resolubilization of nutrients, and its consequent internal eutrophication (Nagid *et al.* 2001, Smolders *et al.* 2006), since the amount of phosphorus resolubilized in shallow lakes could be five to ten times higher than in deep lakes (Kalff 2002). Another factor that could contribute to the high trophic state could be the livestock breeding activities carried out in its basin since it has been demonstrated that the inputs of phosphorus caused by the runoff of manure during storms is a factor with high impact in the eutrophication of a water body (Carpenter *et al.* 1998, Bremigan *et al.* 2008, Russell *et al.* 2008). In addition, it should be taken into consideration that since Aime is located in an arheic basin, therefore the outputs of water take place only by evaporation, which leads to processes of concentration. These processes were verified during this study, since the concentrations of both nutrients increased as from April as depth decreased. This was in turn likely related to the increase in the concentration of chlorophyll *a*, in spite of the lower temperatures of autumn and winter months.

Despite the lack of fishes, the chlorophyll *a* concentrations of Aime Lake were almost double than those recorded in two very different shallow lakes of La Pampa, Don Tomás and Bajo de Giuliani (Table IV), characterized by ichthyic fauna and the dominance of *Odontesthes bonariensis*, a zooplanktivorous species (Echaniz *et al.* 2008 and 2009). This fish, with its top down effect, allows the

development of a high phytoplankton biomass (Quirós *et al.* 2002, Scheffer 1998, Scheffer & Jeppesen 2007). The chlorophyll-*a* concentrations recorded in Aime lake were also almost 10 - 12 times higher than those recorded in Prato and San José, two nearby shallow lakes, but similar to Aime, given the absence of fishes (Table IV).

The Aime Lake species richness was the same as that verified in Bajo de Giuliani (Echaniz *et al.* 2009), other Pampean shallow lake of similar salinity, but two times higher than that of Prato and San José (Echaniz & Vignatti 2011) (Table IV), because the dissolved solids concentration of these lakes was almost twice that of Aime. On the other hand, the diversity was considerably lower than that recorded in Don Tomás (Echaniz *et al.* 2008) and El Guanaco (Echaniz & Vignatti 2010), two shallow lakes with salinities 10 times lower than that of Aime (Table IV). A negative effect of increasing salinity verified during the study could have produced the decline in the zooplankton diversity observed, due mainly to a decrease in the number of species of rotifers. This relation has been observed by other authors; for example Williams (1998) found that although other factors such as the hydrological patterns (degree of permanence of water) affect species richness, salinity is a major determinant of the structure of biological communities (composition and species richness) in saline lakes. The same negative relationship between salinity and diversity found in Aime lake, was observed by De Los Ríos (2005) in a study covering 26 shallow lakes of Chile in a wide salinity gradient and by Waterkeyn *et al.* (2008) in a high number of Mediterranean temporary water bodies.

Another difference between Aime Lake and other environments of the province of La Pampa with more stable environmental characteristics was the replacement of species, especially among crustaceans, which was higher in summer (December-January) and winter (July-August). The importance of the increase in salinity as a modulatory factor of species richness of an aquatic environment (Herbst 2001) was evidenced both in the decrease in species richness and in the fact that some less tolerant crustaceans (*M. micrura* and *B. gracilis*) were recorded at the beginning of the study, when this variable was at lower levels. This is similar to that reported by Mura & Brecciaroli (2003) in temporary water bodies of Oasis of Palo (Italy), where they observed that when environmental conditions become harsher by the increase in temperature and evaporation, the less tolerant species disappeared from the pool resulting in a reduction in diversity. In contrast, in Aime

Lake, at the end of the study, when the total dissolved solids were higher than 19 g.L⁻¹, autochthonous halophilic species, such as *D. menucoensis* (Paggi 1996, Adamowicz *et al.* 2004, Echaniz *et al.* 2006) and *Boeckella pooensis* (Menu Marque *et al.* 2000), were recorded.

The appearance of relatively large and halotolerant cladocerans as *D. menucoensis* and *M. macrocopa* caused that the biomass of that group was greater by the end of the study, despite its low abundance. Their presence in this lake could be due to the absence of zooplanktivorous fishes, since in other environments of La Pampa in which ichthyic fauna has been recorded, these species are absent or present sporadically (Echaniz *et al.* 2009 and 2010). In contrast, the prevalence of *M. mendocinus* among copepods made that the abundance and biomass of that group was little affected by environmental variables, since it is a relatively tolerant species both to salinity and to changes in water temperature (Echaniz *et al.* 2006).

Among rotifers, the species replacement was reduced, as the predominant species were *B. plicatilis*, *B. angularis* and *B. dimidiatus* (recorded in almost all sampling occasions), all of which are euryhaline (Fontaneto *et al.* 2006) and have a cosmopolitan distribution (Pejler 1995). The tolerance of *B. plicatilis* to increased concentrations of dissolved solids caused that during the last two months the higher biomass was provided by rotifers, exceeding that of crustaceans.

We verified an increase in total biomass as salinity increased, but an important difference between Aime and other lakes of La Pampa (Echaniz *et al.* 2009 and 2010, Echaniz & Vignatti 2011) is the decrease in copepods biomass with increasing salinity and the relative increase in that of rotifers and, to a lesser extent, in cladocerans by the appearance of halophilic species. Contrary to our expectations, total zooplankton abundance increased as from March, although the increase in salinity was higher during the last months of the study. The zooplankton density was almost four and seven times higher than that recorded during the same period in Prato and San José, the nearby shallow lakes (Echaniz & Vignatti 2011). Other differences between these lakes were that Aime Lake showed a predominance of rotifers and a reduced abundance of crustaceans (lower than 8%), whereas crustaceans represented more than 30 and 42% of total density in Prato and San José lakes respectively (Echaniz & Vignatti 2011). The predominance of rotifers makes Aime more similar to other shallow lakes of La Pampa, but permanent, with lower salinity, ichthyic fauna with zooplanktivorous species that predate on

the larger species and lower concentrations of inorganic suspended solids (Echaniz *et al.* 2008 and 2009).

Since these wetlands are rarely represented in the literature, this study is the first contribution to the knowledge of the zooplankton dynamics and to

the understanding of the role of the major forces acting on the community during the drying of temporary shallow lakes of relatively high salinity in central Argentina, the more frequent aquatic ecosystems in the region.

Table IV. Mean values and standard deviations of the main limnological and biological parameters of other shallow lakes in the province of La Pampa.

	Prato	El Guanaco	San José	Don Tomás	Bajo Giuliani
Type	Temporary	Temporary	Temporary	Permanent	Permanent
Total dissolved solids (g.L ⁻¹)	25.34 (±6.15)	1.21 (±0.71)	22.22 (±5.24)	0.80 (±0.07)	9.82 (±0.36)
Transparency (m)	0.17 (±0.06)	0.25 (±0.10)	0.45 (±0.19)	0.15 (±0.03)	0.18 (±0.03)
pH	9.01 (±0.17)	8.60 (±0.67)	9.13 (±0.19)	8.64 (±0.39)	9.01 (±0.21)
Chlorophyll <i>a</i> (mg.m ⁻³)	30.79 (±27.01)	n/d	20.16 (±27.45)	154.60 (±41.94)	173.74 (±70.28)
Total phosphorous (mg.L ⁻¹)	18.10 (±4.41)	n/d	8.94 (±2.89)	9.71 (±4.91)	10.29 (±2.82)
Total nitrogen (mg.L ⁻¹)	28.62 (±4.31)	n/d	17.20 (±4.12)	11.52 (±2.51)	18.40 (±6.10)
Dissolved oxygen (mg.L ⁻¹)	6.29 (±2.68)	n/d	8.95 (±2.22)	8.45 (±1.31)	10.60 (±1.83)
Inorganic suspended solids (mg.L ⁻¹)	38.03 (±21.07)	n/d	15.99 (±19.22)	3.28 (±2.56)	23.24 (±19.32)
Organic suspended solids (mg.L ⁻¹)	37.52 (±17.27)	n/d	17.96 (±10.72)	51.29 (±13.18)	73.57 (±17.24)
Total richness	6.00	34.00	8.00	20.00	15.00
Total abundance (ind.L ⁻¹)	2823.97 (±4713.94)	5786.17 (±7515.02)	1346.03 (±1759.42)	998.50 (±977.86)	10012.39 (±12044.51)
Total biomass (µg.L ⁻¹)	6614.06 (±4336.94)	n/d	4659.08 (±3417.30)	2914.42 (±2076.48)	2681.03 (±2372.16)
Cladocerans abundance (ind.L ⁻¹)	247.14 (±344.70)	437.68 (±411.36)	134.24 (±121.78)	69.53 (±119.19)	0.72 (±1.43)
Cladocerans biomass (µg.L ⁻¹)	1796.91 (±2274.86)	n/d	1648.08 (±1562.73)	401.98 (±747.95)	2.40 (±5.57)

Table IV (Cont.)

Copepods abundance (ind.L ⁻¹)	373.91 (±213.15)	95.58 (±64.66)	325.12 (±520.60)	309.19 (±293.43)	332.78 (±218.45)
Copepods biomass (µg.L ⁻¹)	4370.29 (±3059.55)	n/d	2761.38 (±3349.08)	2277.82 (±1384.24)	2094.61 (±2620.25)
Rotifers abundance (ind.L ⁻¹)	2202.92 (±4717.21)	5252.92 (±7640.19)	886.67 (±1883.14)	619.78 (±780.72)	9678.89 (±12114.38)
Rotifers biomass (µg.L ⁻¹)	446.86 (±867.95)	n/d	122.60 (±241.50)	234.61 (±420.96)	584.03 (±661.16)

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