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# INFLUENCE OF REGIONAL FACTORS ON ZOOPLANKTON STRUCTURE IN A SALINE LOWLAND RIVER: THE SALADO RIVER (BUENOS AIRES PROVINCE, ARGENTINA)

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#### ABSTRACT

Knowledge of regional factors influencing zooplankton structure in a semiarid river must include both the main channel and any tributaries in order to identify spatial and temporal patterns along with the main factor that affect the zooplankton community. Accordingly, seasonal samples were taken during 1997–1999 at 15 stations in the Salado River basin, where 172 species were identified (53 protozoans, 88 rotifers and 31 crustaceans). Conductivity and temperature optima and tolerances were calculated for the evident taxa. Different assemblages were recognized by cluster analysis, on the basis of their temperature and conductivity preferences. With respect to the zooplankton assemblages, three zones can be distinguished along the longitudinal axis of the basin: (1) the headwaters (the effluent from large saline shallow lakes), (2) the inter-tributaries, and (3) the lower basin and associated shallow lakes. The spatial distribution of the assemblages was a result of the combined action of factors always promoting the dominance of rotifers. The influence of floodplain waters (backwater ponds, waterlogged depressions, flushing lakes) was attenuated progressively downstream, thus producing disadvantages for the crustaceans. The food availability and high nutrient concentrations related to land use in the headwaters favoured the co-dominance of cladocerans and copepods along with the rotifers in that region. Copyright © 2008 John Wiley & Sons, Ltd.

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#### INTRODUCTION

The dynamics and composition of the zooplankton in lowland rivers depend on local processes. Findings on the dynamics of zooplankton have not been in agreement with the proposals of the river-continuum concept (Vannote *et al.*, 1980): species recruitment is not provided from upstream sources alone, the enrichment of the zooplankton along the river is not necessarily progressive and the lateral dimension of the river (Junk, 1999) must also be considered. The temporal and spatial structural changes in the zooplankton are related to the extant hydrological characteristics (Pace *et al.*, 1992; Basu and Pick, 1996; Baranyi *et al.*, 2002) as well as the morphological features of the basin itself (Picard and Lair, 2005). Flood events induce important changes in zooplankton populations, with a reduction in their density occurring at the beginning followed by a recruitment and fast recuperation of their population when the lentic conditions return. Zooplankton diversity is also influenced by the physical habitat of the river. River heterogeneity interferes strongly with zooplankton dynamics, influencing both predation relationships and growth (Picard and Lair, 2005).

In general, zooplankton density increases downstream, in accordance with the increase in food availability (algae or bacteria) there, with minor exceptions to this principle occurring at headwaters. This generalization, however, can prove unreliable in certain lowland rivers (Lair, 2005). For example, those with slow-flowing upper reaches can manifest much higher plankton densities upstream than downstream (Reckendorfer *et al.*, 1999). In Australian rivers the presence of weirs and locks also promotes an increase in zooplankton density and the development of limnoplankton (i.e. microcrustaceans; Shiel *et al.*, 1982). Some investigations of river zooplankton have included only longitudinal sectors of the main channel and have omitted the headwaters and tributaries (Admiraal *et al.*,

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1994; Gosselain *et al.*, 1998a; Lair, 2005). These sectors are important for determining the structure and changes of zooplankton, in both spatial and temporal terms, under different hydrological conditions as well as for obtaining an explanation of zooplankton function. The shift in rotifer density typically observed at the end of summer certainly results from the increase in water discharge and the decrease in temperature (therefore producing a decrease in food) at that time, whose influences act mainly as forcing variables (Lair, 2005). According to this author, the 'age of water' may possibly limit the increase in density; and if the role of the floodplain is in fact essential during high-flow conditions, the importance of the local processes that have been illustrated by several authors may become the key influence on the functioning of river plankton. The drifting of plankton from adjacent water bodies connected to the river is inevitable and would take place particularly during those periods when large floods occur (Lair, 2005). After occurring progressively along the course of the river, large changes in flow rates at the river-estuary interface induce correspondingly large alterations in both zooplankton densities and their species composition (Lair, 2005). It is generally thought that the brackish species are restricted to the lower sectors and the mouth of these lowland rivers (Kobayashi *et al.*, 1998).

On some occasions, the number of taxa recorded in investigations was related to the sampling design or the extraction methods used (Burger *et al.*, 2002). In every instance the community was found to be dominated by rotifers, with a minor contribution of protozoans and even lower numbers of crustaceans (Winner, 1975; Lair, 2005). The crustacean assemblages were generally dominated by small bosminids, ceriodaphnids and juvenile copepods (Pourriot *et al.*, 1997; Kobayashi *et al.*, 1998). Rotifers are considered more greatly resilient to changes in hydrological conditions than other zooplankton groups (Pourriot *et al.*, 1997; Baranyi *et al.*, 2002; Lair, 2005). Their competition with crustaceans occurred in low-water periods when the cladoceran biomass became significant (Baranyi *et al.*, 2002).

There have been few studies on zooplankton in the arid and semiarid zones of the world (Shiel *et al.*, 1982; Wallace *et al.*, 2005; Shiel *et al.*, 2006). This fact even in spite of the progressive salinization that has occurred in numerous river systems and lakes along with the replacement of freshwater species by halophile or halobiont assemblages that tolerate the new conditions (Shiel, 2002; Schallenberg *et al.*, 2003). In nature, freshwater zooplankton may be exposed to NaCl sporadically, though very few species of freshwater rotifers can tolerate high salt concentrations (Bailey *et al.*, 2004; Sarma *et al.*, 2006). Resting eggs, however, are likely to be able to resist higher levels of salinity (Snell *et al.*, 1991; Bailey *et al.*, 2004). The same behaviour is observed in cladocerans with more tolerance than is seen in diapausing eggs (Sarma *et al.*, 2006). Temperature also has an influence on zooplankton structure and dynamics (Pace *et al.*, 1992).

In Argentina, zooplankton investigations on saline rivers have been performed in the provinces of Santa Fe (José de Paggi and Paggi, 1998) and Buenos Aires (Modenutti, 1998; Neschuk *et al.*, 2002; Solari *et al.*, 2002). In the first of these studies, a comparison of the zooplankton structure was performed in three environments (two rivers with different salinity and a shallow lake). The dominant species in the river with the higher salinity (2,960–6,300  $\mu$ S cm<sup>-1</sup>) were *Brachionus plicatilis*, *B. caudatus* and *B. angularis*. The replacement of *B. plicatilis* by *B. caudatus* occurred when the chloride concentration became less than 500 mg L<sup>-1</sup>. In the Buenos Aires province, an investigation of the rotifer assemblages was performed in the Samborombón River basin (Modenutti, 1998). These assemblages were related to seasonal changes in temperature and conductivity. The highest density values were recorded in the main channel, principally in the middle sector, but high number of species were also observed in the tributaries (Modenutti, 1998).

In the Salado River of the Buenos Aires province, plankton investigations associated with a backwater pond have been carried out in the lower sector (Solari *et al.*, 2002). An input of organisms from the backwater pond (94 ha) was detected in the river, and the zooplankton structure downstream from this lentic environment was similar to that recorded in the pond itself. Neschuk *et al.* (2002) carried out an investigation of rotifer assemblages in the entire basin and emphasized that the different rotifer species were present in regions determined by conductivity and nutrient availability as well as in adjoining ponds and waterlogged depressions.

The objective of this study was to characterize the spatial and seasonal patterns of zooplankton composition and abundance along the entire basin and in its tributaries. The latter were included in order to investigate their influence on the spatial distribution of the zooplankton species. Another objective was to identify the effects of temperature and conductivity on the dominant species, whose parameters could be considered as key determinants of the variation in the zooplankton assemblages present.

## STUDY AREA

The Salado River, the southernmost tributary of the Rio de la Plata Basin, is a typical lowland river and the major autochthonous one of the Buenos Aires province. The Salado's length is approximately 571 km, its slope is low (mean: 0.107 m km<sup>-1</sup>) and its catchment is approximately 150,000 km<sup>2</sup>. The regime of the Salado River is quite variable: its flow reaches not more than  $100 \text{ m}^3 \text{ s}^{-1}$  in dry periods but increases up to as much as  $1,500 \text{ m}^3 \text{ s}^{-1}$  during flood periods, with consequent variations in conductivity and transport of dissolved and particulate materials. The flooding of large areas during weeks or months is one of the most important characteristics of the Pampean Plain. The annual mean rainfall for the whole catchment was 1,057 mm in 1997, 921 mm in 1998 and 749 mm in 1999. The seasonal rainfall has an autumn-to-spring maximum and a winter minimum. The mean annual rainfall (1911–1996) was 870 mm and the mean annual temperature (1911–1996) 14°C (mean temperatures for summer: 22.3°C, autumn: 15.6°C, winter: 9.3°C and spring: 15.8°C). The concentration of chlorophyll a, as an estimation of phytoplankton biomass, was at a maximum  $(599 \text{ mg m}^{-3})$  through the spring and summer in the headwaters of the basin (St. 4), but at a minimum (2.5 mg m<sup>-3</sup>) through the autumn and winter in a tributary (St. 2; Gabellone *et al.*, 2005). The Salado basin is divided into two distinct geographic regions in terms of land use, whose areas produce clear differences in the water chemistry. The basin includes one of the most important agricultural regions of the country; and as a consequence the concentrations of total phosphorus and nitrates plus nitrites are the highest in this portion (the headwater sector), though these values decrease markedly towards the river mouth in response to the low nutrient input of the middle-sector subcatchments. The concentrations of nitrates plus nitrites were  $4,350 \ \mu g \ L^{-1}$  (St. 1) and  $4,179 \ \mu g \ L^{-1}$  (St. 4) in spring 1997. The highest total-phosphorus concentration  $(2,237 \ \mu g \ L^{-1}; St. 4)$  was detected in summer 1997. The lowest total-phosphorus concentrations were recorded in the lower basin (St. 9), but there the same trend was maintained as in the headwater stations, with total-phosphorus values lower than 600  $\mu$ g L<sup>-1</sup> (Gabellone *et al.*, 2005).

The headwaters of the river, consisting in the effluent from large shallow lakes, are of variable volume depending on the season and weather conditions. The Salado Stream (St. 1), an order-one tributary, discharges into the Mar Chiquita Lake (a flood-valley lake); and the main river channel that interconnects two flushing lakes (Gómez and Carpincho) begins from this location. These latter two shallow lakes occupy more than 150 km<sup>2</sup>. All of these lakes presented high salinity readings (more than  $8,000 \,\mu\text{S cm}^{-1}$  during high-water periods), and values of total dissolved solids of 10,636 mg L<sup>-1</sup> were recorded in the summer as a result of evaporation (Ringuelet *et al.*, 1967). Between these lakes, the mean river flow is less than  $30 \,\text{m}^3 \,\text{s}^{-1}$ . The headwater sector is characterized by the presence of sedimentary aquifers of high sodium-chloride concentrations, which originated during the Pleistocene epoch. The effects of this feature are manifested in the presence of saline streams and shallow lakes that determine the salt balance of the Salado River. The Saladillo-Stream catchment receives the Jauretche and the Mercante, the República de Italia canals, whose sources drain the western internal basin (characterized by the presence of sandy dunes). In this endorheic zone, the regional groundwater salinities are in excess of 2,000 mg L<sup>-1</sup> of total dissolved solids. In the lower basin, however, the salinity is reduced during flood periods by the influx of runoff water.

#### MATERIALS AND METHODS

Seasonal samples were obtained during the period from March 1997 to May 1999 in 15 locations (Figure 1) from the headwater sectors to the mouth of Salado River (Junín 1: St. 3, Junín 2: St. 4, Achupallas: St. 5, Ruta 30: St. 6, Roque Pérez: St. 7, Gorchs: St. 8, Belgrano: St. 9, Destino: St. 10, and La Postrera: St. 11) and from its main tributaries (Salado: St. 1, Piñeiro: St. 2, Saladillo: St. 4-5r, Saladillo-Vallimanca: St. 6-7r, Las Flores: St. 7-8r, and an artificial channel, Canal 16: St. 7-8c). An additional sampling was made during two different flow conditions (October 1997 and January 1998) in other sampling stations from where the Salado River (St. 8) receives the discharges of the Saladillo Vallimanca Stream (St. 6-7r), Canal 16 (St. 7-8c) and the Las Flores Stream (St. 7-8r) downstream to St. 7 (Figure 2).

The sites were visited initially in March 1997 and then quarterly on a seasonal basis through to the autumn of 1999. Each sampling took place over three consecutive days. On the first four occasions, 14 stations were sampled. During the period from May 1998 to June 1999, two tributaries were also included because they bring in water from



Figure 1. Map of the area and location of the sampling stations

sub-basins on the lower slopes of mountains (St. 7–8c [Canal 16] and 7–8r [Las Flores Stream]). The incorporation of these sites improves the interpretation of the results.

Different zones can be distinguished within the basin on the basis of geological, soil and agricultural influences as well as ecological characteristics. These selected zones involve different limnological parameters, such as concentration-flow relationships, and have been described in detail by Gabellone *et al.* (2003, 2005, 2008).

Temperature ( $^{\circ}$ C) and conductivity were measured with a Horiba U10 multimeter. Chloride concentration was determined according to the method 4500-Cl B recommended by APHA (1995).



Figure 2. Confluence sector where the Salado river (St. 8) receives the discharges of the Saladillo Vallimanca stream (St. 6-7r), Canal 16 (St. 7-8c), and the Las Flores stream (St. 7-8r) downstream at St. 7

Sampling ocassion	mean T (°C)	mean cond.( $\mu$ S cm <sup>-1</sup> )	$T^{\circ}$ groups	cond. groups
Mar-97	21.0	5708	Ι	Ι
Jul-97	7.6	4216	II	II
Oct-97	20.1	6352	Ι	Ι
Jan-98	24.7	4437	III	II
May-98	15.7	1971	IV	III
Oct-98	22.0	3520	Ι	IV
Feb-99	24.9	4813	III	II
May-99	14.0	3149	IV	IV

Table I. Groups of samples determined according to their optimal temperature and conductivity ranges

Zooplankton samples were collected from each station at mid-channel by means of a suction pump. A volume of 1001 was pumped from a depth of 0.50 m below the surface and passed through a 25-mm-diameter hose into a 35 µm mesh net. The material retained was preserved in a 4% aqueous formaldehyde solution. Protozoans and rotifers were counted in (1 ml) Sedgwick–Rafter chambers and crustaceans in (10 ml) Bogorov chambers. The samples were first mixed with a magnetic stirrer and repeated sub-samples then enumerated. The coefficient of variation (maximum 20%) was used for abundance comparisons between dominant species in paired samples. Protozoans were identified with reference to Curds (1982), Curds *et al.*, (1983), Foissner *et al.* (1999), among others. Rotifer identification was based on Koste (1978), Segers (1995), De Smet (1996) and Nogrady and Segers (2002). Crustaceans, with the exception of juvenile copepods, were identified to the level of genus or species based on Ringuelet (1958), Olivier (1962), Paggi (1978, 1994), Dumont and Pensaert (1983), Reid (1985), Bayly (1992), Smirnov (1996), Sinev (2001, 2004), Benzi (2005) among others.

The Olmstead–Tukey diagram was applied for analysing the frequency of occurrence and mean abundance of each species (Sokal and Rohlf, 1979; López-López and Serna-Hernández, 1999). An average was calculated on both axes, resulting in four categories: frequent and abundant (dominant) species; abundant and non-frequent (occasional) species; non-frequent and non-abundant (rare) species and frequent and non-abundant (common) species.

The density of the main rotifer species was log-transformed for regression analysis versus conductivity and chloride concentration.

Conductivity and temperature optima as well as tolerances were assessed for certain taxa (comprising five rotifers, two protozoans and two crustaceans) taking into account their frequency and density. We used abundance-weighted averaging to calculate taxon-specific conductivity and temperature optima and tolerances (ter Braak, 1985, 1995; Potapova and Charles, 2003).

Two cluster analyses were carried out through the use of the complete linkage and the Pearson correlations (Kovach, 1990). The matrices were made according to the conformed sample groups over four ranges of conductivity and temperature (Table I) and the mean species density for each group obtained. The basic matrix of temperature included 67 species, while the one for conductivity included 77, because of the importance of some species in defining clustering groups, even in spite of their low abundance.

To determine spatial distribution of the zooplankton assemblages, the first step was to carry out the nonhierarchical-clustering procedure (k means) for grouping species and sites maximizing the variability among groups. The second step was the identification of indicator species corresponding to the different groups from the sampling sites through the indicator-value index (INDVAL) proposed by Dufrêne and Legendre (1997). The species present in four groups at IndVal indices higher than 10 were considered to be all-habitat.

### RESULTS

During the sampling period, 172 species (Table II) were identified (53 protozoans, 88 rotifers and 31 crustaceans). The mean species richness of the entire basin fluctuated between 17 (March 1996 and October 1998) and 30 species (January 1998 and May 1998). These maxima corresponded to periods characterized by regular

Table II. List of species found in the zooplankton of Salado river basin

Protozoa	Rotifera		Arthropoda
Ciliophora	Anuraeopsis fissa	L. lunaris	Crustacea
Acineta flava	Ascomorpha saltans	L. nana	Ostracoda
A. tuberosa	Asplanchna sp.	L. papuana	Cypridopsis sp.
Askenasia sp.	A. brightwelli	L. pyriformis	<i>Ilyocypris</i> sp.
Aspidisca sp.	A. girodi	L. signifera	Cladocera
Carchesium sp.	Brachionus angularis	Lecane sp.	Alona glabra
Chilodonella uncinata	B. bidentatus	Lepadella acuminata	Alona intermedia
Codonaria fimbriata	B. budapestinensis	L. ovalis	A. monacantha
Codonella cratera	B. calyciflorus	L. patella	Alona cf. setigera
Coleps hirtus	B. caudatus	Lophocharis salpina	Alona sp. <sub>1</sub>
Cotnurnia sp.	B.aimiaiatus	Monommata sp.	Alonella cl. excisa
Diainium nasutum	B. havanaensis	Mytilina mucronata	Bosmina huaronensis
Epistylis plicatilis	B. nilsoni B. selis stilis	M. ventralis	Certoaaphnia ci. aubia
Epistylis sp.	B. pilcaniis B. standingidae	Notnoica acuminata	C. reticulata
Euplotes patella Foliouling holtoni	B. preroainoiaes	N. squamula	Chyaorus sphaericus
Foliculina bolloni Haltoria oraș din ella	B. quaariaeniaius B. muhana	Notommata sp.	Daphnia spinulaia Magnathrin latiographia
Halophma simplar	D. rubens B. satanious	Platylas quaaricornis Polyarthra yulgaris	Macroinrix taticornis Moing eugeniae
Lacrymaria salinarum	B. urocolaris	Pompholyx sulcata	Moina eageniae M. micrura
Litopotus fasciola	B. urceotaris B. variabilis	Progles sp	Plaurorus of aduncus
Metacineta sp	B. Variabilis Bdelloid	Proglides sp.	Pleurorus sp.
Meracineia sp. Mesodinium sp	Bdelloida	Rotaria nentunia	Pseudochydorus alohosus
Stentor roeseli	Colurella colurus	Synchaeta pectinata	Scanholeberis spinifera
Paramecium caudatum	C uncinata	Testudinella patina	Dianhanosoma hirgei
Podophrva sp.	Cephalodella sp.1	<i>Testudinella</i> sp.	Copepoda
Prorodon sp.	Cephalodella sp.2	Trichocerca cylindrica	Boeckella gracilis
Pyxicola sp.	Cephalodella sp.2	T. pusilla	Notodiaptomus incompositus
Spirostomum sp.	$Cephalodella \text{ sp.}_{4}$	T similis	Acanthocyclops robustus
Strombilidium sp.	Conochilus sp.	T. rattus	Diacyclops michaelseni
Systylis hoffi	Dicranophorus claviger	T stylata	Tropocyclops prasinus
Thuricola sp.	Dicranophorus sp.	Trichocerca sp. <sub>1</sub>	Paracyclops fimbriatus
Tintinnidium fluviatile	Encentrum sp.	Trichocerca sp. <sub>2</sub>	Metacyclops mendocinus
Tokophrya lemnarum	<i>Epiphanes</i> sp.	Trichocerca sp.3	Thermocyclops brehmi
T. quadripartita	Euchlanis dilatata	Trichocerca sp. <sub>4</sub>	Microcyclops alius
T. pyrum	Filinia longiseta	-	Cletocamptus deitersi
Tintinnopsis sp.	F. passa		
Vaginicola sp.	Gastropus sp.		
Vorticella campanula	Hexarthra fennica		
V. convallaria	Keratella americana		
<i>Vorticella</i> sp.	K. cochlearis		
Zoothamnium sp.	K. lenzi		
Rhizopoda	K. tropica		
Arcella dentata	Lecane arcula		
A. discoides	L. brasiliensis		
A. hemisphaerica	Lecane bulla		
Centropyxis aculeata	L. candida		
C. ecornis	L. closterocerca		
Cyclopyxis sp.	L. crepiaa L. doginiona		
Cyphoderia ampulla	L. decipiens		
Dijjiugia acuminata Diffugia aramen	L. namata L. hastata		
Dijjiugia gramen Diffugia sp	L. nasiana I. hornomann:		
Dijjiugia sp. Fualizha acanthonhona	L. nornemanni L. inopinata		
Eugryphia acanthophora E laguis	L. mopinaia L. laonting		
L. idevis Trinama sp	L. ieonina I luna		
Inneniu sp.	L. 111111		

decreases in conductivity values throughout the entire basin, with the exception of May 1998, when all the sampling stations showed a similar number of species. With respect to spatial distribution, the minima in species richness were always recorded at headwaters (Salado Stream: mean 16 species), while the maximum was at the Saladillo Vallimanca Stream, with a mean of 31 species. The middle sector (St. 5-7) and low basin (St. 9-11) showed similar species richness (means: 25 and 26 species, respectively).

Ten rotifers were dominant, with five species (*B. plicatilis*, *B. angularis*, *B. caudatus*, *K. tropica* and *Filinia longiseta*) showing a high frequency (more than 50% of the total of 119 samples) and density (Figure 3). Eight species (3 protozoans and 5 rotifers) were common. Only five species, four rotifers and one ciliate (*T. fluviatilis*), were occasional, whereas 26 species, consisting of protozoans, rotifers and crustaceans, were rare (Figure 3).

Rotifers were the most abundant group (Figure 4). The crustaceans co-dominated at headwaters in March 1997 (nauplii), in July 1997 (*Acanthocyclops robustus, Daphnia spinulata*, and nauplii), in October 1997 (nauplii), in October 1998 (*Ceriodaphnia* cf. *dubia, Bosmina huaronensis* and *B. gracilis* were dominant along with nauplii) and in February 1999 (*D. spinulata, Moina micrura, Metacyclops mendocinus* and *Thermocyclops brehmi*) (Figure 4). The protozoans were abundant mainly in tributaries and the sampling stations of the lower sector because of the numerical contribution of the tintinnid ciliates (*T. fluviatile* in spring: in both October 1997 and October 1998, and *Codonaria fimbriata* in January 1998) (Figure 4). In spring and summer, the high relative abundance of ciliates at the headwaters and middle sectors was associated with *Paramecium caudatum, Stentor roeselii* and species of the *Vorticella* genus (Figure 4).

Zooplankton-density peaks were recorded in the middle sector of the basin (Saladillo Stream), coinciding with the highest conductivity values (maximum: 4,685 individuals  $L^{-1}$  at 7,390  $\mu$ S cm<sup>-1</sup>, in summer 1999). The minima occurred in other tributaries such as Piñeiro, Canal 16 and Las Flores Stream (minimum of 19 individuals  $L^{-1}$  with 1,600  $\mu$ S cm<sup>-1</sup> in Canal 16, in spring 1998). The mean zooplankton density decreased from the headwaters to the mouth of the river, with the maximum located in the middle sector because of the contribution



Figure 3. Olmstead-Tukey diagram of the Salado river zooplankton species (protists: star rotifers: circle crustaceans: pentagon)



Figure 4. Spatial and temporal variations in relative abundance of the main zooplankton groups (protists: black, rotifers: white, crustaceans: squared)

of two tributaries (the Saladillo and Saladillo Vallimanca streams) (Figure 5). The mean relative contribution of the crustaceans diminished downstream from the headwaters (Figure 5). The abundance of cladocerans and copepods at the headwaters was related to the direct connection of large shallow lakes within the main channel. The protozoans maintained similar mean contributions throughout the entire basin except in the tributaries from the mountains (Las Flores Stream and Canal 16), where they co-dominated. Protozoans were not detected at Salado Stream on all sampling occasions (Figure 5).

The dominant species showed a wide range of conductivity tolerance. Synchaeta pectinata was the one that occurred within a wide conductivity range  $(\pm 2,567 \,\mu\text{S cm}^{-1})$ , a value representing more than 100% of its conductivity optimum (Figure 6a). More restricted ranges were calculated, however, for *B. calyciflorus*  $(\pm 877 \,\mu\text{S cm}^{-1})$ . *Brachionus plicatilis* and *B. angularis* showed the highest conductivity optima, while *P. caudatum* exhibited the lowest one (Figure 6a). The other six species selected have similar optima, falling between 4,447 and 4,954  $\mu$ S cm<sup>-1</sup> (Figure 6a). In contrast, with respect to temperature, the selected species showed more restricted ranges along with optimum temperature levels between 10 and 24°C. Synchaeta pectinata can be considered a winter species, with an optimum of 10.8°C ( $\pm 5.3^{\circ}$ C; Figure 6b). Five species (species g, j, d, i, h) showed a preference for temperature optima close to 20°C, while *K. tropica* and *P. caudatum* preferred a lower temperature (16°C). *Keratella tropica* and *B. plicatilis* were the species with the maximum temperature ranges ( $\pm 5.91$  and  $5.68^{\circ}$ C, respectively), whereas *M. micrura* was the most stenothermal species ( $2.6^{\circ}$ C) (Figure 6b).

The density of the three dominant zooplankton species (rotifers) was related to both conductivity and chloride concentration. Nevertheless, the latter parameter was the better predictor of density for all species. *Brachionus plicatilis* was the species showing the best fit with chloride concentration; whereas the corresponding fit for *B. angularis* was poor (p > 0.05; Figure 7). The various species showed similar spatial gradients, with the



Figure 5. Pie chart of the mean abundance of the zooplankton groups included in the Salado basin scheme (protists: black, rotifers: white, crustaceans: squared)



Figure 6. Calculated conductivity (a) and temperature (b) optima and tolerance ranges for selected species of the Salado river zooplankton (a: *Paramecium caudatum*, b: *Synchaeta pectinata*, c: *Brachionus calyciflorus*, d: *Tintinnidium fluviatile*, e: *Keratella tropica*, f: *Brachionus caudatus*, g: *Metacyclops mendocinus*, h: *Moina micrura*, i: *Filinia longiseta*, j: *Brachionus angularis* and k: *Brachionus plicatilis*)

maximum density in the Saladillo Stream being characterized by the highest conductivity values and chloride levels. Nevertheless, these species were either absent or exhibited low abundances in streams associated with the lowest conductivities, such as Piñeiro, Las Flores, and Canal 16 (Figure 7).

A comparison of two summer periods, one with low waters (February 1999, St. 9,  $35 \text{ m}^3 \text{ s}^{-1}$ ) and the other with an average flow rate (January 1998, St. 9,  $107 \text{ m}^3 \text{ s}^{-1}$ ), revealed that the maximum density was obtained in the first (mean values 3,022 vs. 1,349 ind. L<sup>-1</sup>, respectively) (Figure 8). In contrast, a clear decrease in zooplankton density (mean value 702 ind. L<sup>-1</sup>) was recorded during a high-water period in May 1998 (481 m<sup>3</sup> s<sup>-1</sup>). The Saladillo (St. 4-5r) and Saladillo Vallimanca (St. 6-7r) streams were the tributaries with the highest contribution of organisms. Marked differences in abundance were recorded in the middle and lower sectors of the basin, whereas the variations were insignificant at the headwaters (Figure 8).



Figure 7. Regression analysis between conductivity, chloride concentration and population density of three dominant rotifers



Figure 8. Comparison of zooplankton density recorded during three different discharge conditions (mean discharge: January 1998, high water: May 1998: low water: February 1999)

A detailed density-variation analysis was performed on two occasions at the place where the Salado River receives simultaneously the discharges of the Saladillo Vallimanca Stream, Canal 16 and the Las Flores Stream downstream from St. 7 (Figure 2). In a low-water condition (October 1997, St. 5,  $15 \text{ m}^3 \text{ s}^{-1}$ ), the samples obtained on both riverbanks downstream from the confluence of the head and subcatchment waters showed marked differences in conductivity values (4,350 µS cm<sup>-1</sup>: St. 8a, right bank, and 7,630 µS cm<sup>-1</sup>: St. 8b, left bank) (Figure 9a). Nevertheless, during a mean-flow condition (January 1998, St. 5,  $102 \text{ m}^3 \text{ s}^{-1}$ ), the conductivity



Figure 9. Differences in conductivity, zooplankton density and the contribution of the main zooplankton groups (protozoans: black, rotifers: white, crustaceans: squared) recorded at both riverbanks within the confluence sector, where the Salado river receives the discharges of the Saladillo Vallimanca stream, Canal 16, and Las Flores stream during low-water (a) and mean-discharge (b) periods

differences at these two downstream sites were minor  $(4,500 \,\mu\text{S cm}^{-1}: \text{St. 8a, right bank, and 3,480 }\mu\text{S cm}^{-1}: \text{St. 8b, left bank})$  (Figure 9b). During the former condition (low-water, high conductivity differences), the density of zooplankton at each bank was similar for the two water sources. The right bank (Figure 9a) pertained to the subcatchment Saladillo-Vallimanca (St. 6-7r), but the left bank corresponded to the main channel upstream (St. 7), with the presence of benthic copepods because of the shallow depth (<1 m). In contrast, during the latter condition (mean-flow, minor conductivity differences), the zooplankton density on both banks showed intermediate values between the minimum of the main course (St. 7) and the maximum of the subcatchment sites (St. 6-7r). The proportion of the zooplankton groups for the four sites was comparable (Figure 9b).

### Multivariate analysis

The zooplankton species showed a clear seasonal pattern. Six clusters were defined (Figure 10). The summer assemblage included protozoans (*C. fimbriata*, *D. gramen*, *C. ampulla*), rotifers (*B. dimidiatus*, *B. urceolaris*, *B. quadridentatus*, *Colurella colurus*, *F. longiseta*, *F. passa*, *Trichocerca pusilla*, *T. tigris*, *T. stylata*) and crustaceans (*M. micrura*, *M. mendocinus*, *T. brehmi*). Some species (*B. plicatilis*, *B. budapestinensis*, *B. angularis* and *Alona* sp.) preferred summer and spring temperatures (above 20°C), while other notable zooplankton members thrived during the temperatures of spring to those of summer (*B. calyciflorus*, *T. fluviatile*, among others). The winter assemblage is clearly defined and included protozoans (*Vorticella* sp.<sub>2</sub>), rotifers (*B. pterodinoides*, *N. acuminata*, *N. squamula*, *H. fennica*) and crustaceans (*A. monacantha*, *D. spinulata* and *N. incompositus*). *Keratella tropica*, *K. cochlearis*, *S. pectinata*, *Acanthocyclops robustus* and *Diacyclops michaelseni* manifested the highest densities in winter, but were not restricted to this season. Some species (*Systylis hoffi*, *Ascomorpha saltans*, *Asplanchna girodi*, *Lecane arcula*, *bdelloids*, *C.* cf. *dubia*) characterized the fall period. The last group represented



Figure 10. Zooplankton assemblages of the Salado river basin as defined by cluster analysis and arranged according to their thermal preference

the assemblages that were not prevalent at low temperatures (*Euglypha acanthophora*, *Proalides* sp., *Proales* sp., *Lecane bulla* and *P. vulgaris*; Figure 10).

Five main groups were defined according to their conductivity-tolerance ranges (Figure 11). Some species (*K. tropica, Pompholyx sulcata*, three *Lecane* species, *P. vulgaris*) preferred conductivity values lower than 2,000  $\mu$ S cm<sup>-1</sup>, although they were nevertheless present under other conductivity conditions. Seventeen species formed the assemblage that was associated with conductivity values between 3,000 and 4,000  $\mu$ S cm<sup>-1</sup> (*A. girodi, T. fluviatile, Trichocerca* spp., *K. americana, Proales sp., Proalides sp., B. huaronensis, C. cf. dubia,* among others). The members (24 species) of the 4,000 to 5,000  $\mu$ S cm<sup>-1</sup> interval clearly preferred, including: *Vorticella* sp., *Difflugia gramen, Brachionus rubens, B. dimidiatus, B. urceolaris, F. longiseta, Filinia passa, Trichocerca tigris, T. pusilla, T. stylata, M. micrura, A. robustus and M. mendocinus*. The assemblage formed by the species that were found at conductivity values higher than 5,000  $\mu$ S cm<sup>-1</sup> consists in *Testudinella patina, Gastropus* sp. and *Epiphanes* sp. *Brachionus plicatilis* and *B. angularis* were characterized by their low density in a conductivity ranges (Figure 11).

Six site groups were identified by the results of the k-means process (Figure 12). The most important reallocation concerned group 6 with five sampling stations. For other k values this group was associated with group 3 (the middle-basin stations) as well as with group 4 (the headwaters in the main channel). Group 2 was very particular and was formed by tributaries with lowest salinity values. Group 5 showed affinity with the sites of group 6, while the Salado Stream (Group 1) did so with group 4, located at the headwaters (Figure 12).

Different assemblages for the defined site groups were obtained through the use of the indicator value (IndVal) of zooplankton species along with the k-means method (Figure 12). The assemblage of group 1 contained rotifer species with high indicator values, such as *A. fissa* (99), *A. brightwelli* (98) and *H. fennica* (90). These species can be considered exclusive to this particular affluent within the headwaters. The assemblage of group 4, which represented main-channel downstream shallow lakes, was formed by cladocerans and copepods, with IndVal



Figure 11. Zooplankton assemblages of the Salado river basin as defined by cluster analysis and arranged according to their conductivity preference



Figure 12. Site-cluster groups obtained by the k-means method with their associated indicator species and indicator values in parentheses. The all-habitat species were included in the group when presenting the highest indicator value

indices higher than 70. The species association of group 2 included mainly tychoplanktonic species with IndVal indices lower than 60. The assemblage of group 5, which represented a sector of the tributary from the sand-dune area having high salinity, comprised species with similar IndVal indices. Group 3, within the middle basin downstream from this affluent and characterized by an increase in alluvial deposits, contained littoral crustaceans and rotifers in the assemblage. The species assemblage of group 6 (the low basin and the main sub-basin: *Saladillo Vallimanca*) was composed of rotifers and protozoans with high IndVal indices, with many members also being considered all-habitat (e.g. *K. tropica* and *B. caudatus*), with the highest IndVal indices in these sampling stations. The rest of the all-habitat species always showed the highest IndVal indices at stations of the main channel, with the

#### DISCUSSION

sole exception of *C. colurus*, which is having a high IndVal index in group 2 (Figure 12).

The species composition was comparable to the majority of lowland rivers (Kim and Joo, 2000). We found the greatest similarity with respect to the rotifer assemblages recorded in the Australian rivers (Kobayashi *et al.*, 1998; Shiel *et al.*, 1982; Shiel, 1985; Shiel *et al.*, 2006).

The spatial distribution of the zooplankton was similar to those reported by Basu and Pick (1997) and Viroux (1997), with maximum densities in the middle sector of the basin, where density peaks of phytoplankton occurred. In the sampling period, the phytoplankton assemblages were generally dominated by nannoplanktonic chlorophytes (species of *Monoraphidium* and *Chlamydomonas*) and cryptomonads. The algal maximum was recorded at Ruta 30 (St. 6) in spring 1998, with about 311,000 individuals ml<sup>-1</sup> and the minimum at Piñeiro Stream (St. 2) in autumn 1998, with about 1,200 individuals ml<sup>-1</sup> (Neschuk, 2001). The total zooplankton abundance was similar to that in other large river systems, such as the Spree (Walz and Welker, 1998) and the Meuse (Gosselain *et al.*, 1998a, 1998b).

Different zones can be distinguished within the longitudinal axis of the basin according to the zooplankton assemblages: (1) the headwaters, (2) an inter-tributaries zone (the tributaries plus the middle sector) and (3) the lower basin. In the first zone, the crustaceans, with either the exclusive presence or the dominance of species of large size, were in a majority along with certain rotifers. The calanoids and cyclopoids are also brought into the main channel from lakes as nauplii or copepodids (Shiel, 1985). In the inter-tributaries zone, the maximum density of zooplankton was recorded with a predominance of rotifers and a decrease in the richness and abundance of crustaceans, with *B. plicatilis* and *K. tropica* being the most frequent species. In summer, *B. angularis, B. dimidiatus* and *B. urceolaris*—with the notable inclusion of *F. longiseta*—figured prominently, though *B. caudatus* co-dominated at intermediate temperatures.

At sectors of tributaries characterized by shallowness (group 2), the addition of benthic organisms, mainly rotifers and protozoans, were evident (Figure 12).

At the lower sector, associated with shallow-lake systems, the zooplankton abundance decreased, but their specific richness was similar to the calculated value for the middle sector owing to the incorporation of inocula from the lentic environments. During high-water periods the appearance of lentic species has also been recorded in the lower sector. Solari *et al.* (2002) observed peaks in spring and autumn (1,024 to 1,834 ind.  $L^{-1}$  at discharge values of 90–160 m<sup>3</sup> s<sup>-1</sup>) and a trough in summer (55–153 ind.  $L^{-1}$  at a discharge of 5 m<sup>3</sup> s<sup>-1</sup>). These values were one order of magnitude lower than those recorded in an associated backwater pond (Solari *et al.*, 2002).

Furthermore, the abundance of the zooplankton in the Salado River basin was related to the river discharge, with low densities being recorded during high-water events, in agreement with the observations of Pace *et al.* (1992) and Kim and Joo (2000). The difference in abundance between low-water and high-water periods was more noticeable in the middle and lower sectors of the river. Accordingly, at the headwater section (groups 1 and 4), the differences were either minor or insignificant as a result of the constant addition of zooplankton from the saline shallow lakes. Moreover, the minimal changes in discharge promoted minor variations in zooplankton density. Rotifers dominated in waters of low age, while microcrustacean assemblages appeared in waters of greater age (Shiel, 2002).

Several rotifer species co-dominated because they overcame the problem of competition for resources by taking different-sized food items (Shiel, 2002). After the influence of the discharge from the tributaries of the right margin in the middle and lower sectors (St. 4-5r and St. 6-7r, respectively), the density differences between low- and

high-water periods were marked by the abundance of Brachionidae species such as *K. tropica, B. plicatilis* and *B. angularis*. During occasions of high discharge, the abundant presence of *P. sulcata* and *Proalides* sp. was recorded in the Saladillo Vallimanca Stream. These species were probably incorporated from the shallow lakes, characterized by low salinity (i.e. bicarbonate waters), that are present within this catchment (Gabellone *et al.*, 2008).

Species with high tolerance ranges for conductivity and temperature were more abundant and frequent in the Salado River basin. In agreement with the results of Shiel et al. (2006) in the arid rivers of Australia, the salinity was a significant and independent driver of the composition of the zooplankton assemblages in the Salado River basin. The species with spatial and temporal dominance there exhibited a wide tolerance to the high salinity values of this lowland river, and represented all-habitat species within the assemblages. Congeneric species frequently dominated at different concentrations of the salinity range: the populations of *B. plicatilis* peaked at high salinity (Walker, 1981; Derry et al., 2003; among others). Brachionus dimidiatus preferred lower salinity values, however, and often developed with *B. urceolaris* in the absence of or prior to the maxima of *B. plicatilis* (Iltis and Riou-Duwat, 1971). Brachionius calyciflorus flourished within a narrow conductivity range among the species analysed: its maximum densities were found on occasions where the maximum mean-conductivity values were consistent with the view of authors who considered this species to be tolerant to salinity (Park and Marshall, 2000; Bailey et al., 2004), and thus not strictly a freshwater organism, as Sarma et al. (2006) noted on the basis of laboratory experiments. The optimum conductivity values of the 11 selected species were close to the mean conductivity of the basin  $(4,221 \pm 2,332 \,\mu\text{S}\,\text{cm}^{-1})$ . Some species, including *Lecanidae*, were restricted to those tributaries with low conductivity values (group 2) or were conductivity-indifferent (L. pyriformis). The temperature responses of the zooplankton species were more obligate, showing narrower temperature ranges in comparison with the conductivity-tolerance limits. The majority of the species can be considered warm stenotherms, whose assessment agrees with results obtained in regional studies of the Darling River (Shiel, 1985). The temperature optimum of B. angularis and B. plicatilis recorded in the Salado River coincided with those reported from a laboratory study (Walz et al., 1989) as well as from a field-population study (Walker, 1981). Tintinnidium fluviatile achieved its peaks in spring and summer in agreement with Foissner et al. (1999).

The spatial distribution of the zooplankton assemblages in the Salado River basin (Figure 12) resulted from combined action of conditions that always promoted the dominance of rotifers (Table III). The influence of the floodplain waters (the backwater ponds, the waterlogged depressions, the flushing lakes) had a gradient attenuation downstream (through an increase in tributary discharge), producing a progressive disadvantage for crustaceans. The food availability (the maximum phytoplankton biomass) and the high nutrient concentrations related to land use (within the agricultural zone) at the headwaters (Gabellone *et al.*, 2005) favoured the co-dominance of cladocerans and copepods along with rotifers.

We believe that it is always necessary to include the main channel and tributaries present in a sub-basin in order to gain a detailed knowledge of the regional conditions affecting a semiarid river and thus identify patterns and parameters that both determine and influence its resident zooplankton communities.

Processes	Factors
Structure	
Transport	Inflow of tributaries (natural and artificial) with different degrees of salinity, Discharge fluctuations.
Inocula and resting eggs	Time of salinity change. Association with lentic environments
Food availability	Different trophic states (nutrient concentrations). Land use
Species behaviour	-
Life cycle	Generation time, reproduction strategies
Competence	Feeding mechanisms, quality and quantity of planktonic algae
Predation	Size selection and capture technique (visual or chemical attraction)

Table III. Proposed main processes and factors influencing the structure and species behaviour of the zooplankton in the Salado river basin

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