



Zooplankton-population dynamics in the Salado-River basin (Buenos Aires, Argentina) in relation to hydraulic works and resulting wetland function

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Abstract

The construction of drainage canals in the upper stretch of the Salado River has caused the input of salty waters into the basin, with unexplored consequences on zooplankton dynamics and reproduction. To determine the consequences of those anthropic interventions, zooplankton samples were taken under four hydrologic conditions (high water, mean flows, low flows, very low flows) in the canals and the river watercourse. Environmental variables were measured in situ (pH, temperature, conductivity, turbidity, flow velocity, water level, dissolved-oxygen concentration) and in the laboratory (chlorophyll *a*, nutrients). A total of 166 zooplankton taxa was identified, among which rotifers and ciliates were the most diverse and abundant. A redundancy analysis indicated temperature, conductivity, and water discharge to be the main constraints to zooplankton development. Accordingly, abundance peaks were recorded during mean and low flows in the spring and summer, and minimum values during high water (autumn–winter floodings). The dominant species, *Brachionus plicatilis* s.l., recorded outstanding densities at ca. 34,800 ind L⁻¹—that figure representing a worldwide novelty—during low flows in the canals and at the river downstream site. The wetlands and shallow lakes in the study area acted as sources of inocula for the river, increasing the total abundance of zooplankton, gravid females, nauplii, copepodites, juveniles, and total number of eggs being carried at the second river site downstream from the canals' discharges. The presence of diverse habitats coupled with the alternation of hydrologic conditions have resulted in the development of a very rich, complex zooplankton community.

Keywords Zooplankton · Lowland river · Drainage channels · *Brachionus plicatilis* · Egg ratio

Introduction

In temperate river systems, plankton dynamics are recognized to be mostly determined by seasonal variation in the physicochemical parameters and hydrologic regime (Thomaz et al. 2007; Schöll et al. 2012). In addition, flow velocity is another major restriction to zooplankton owing to advective losses, while increases in water discharge may also impair retention and growth (Pace et al. 1992). These limiting influences are advantageous for small-bodied organisms,

whose rapid somatic growth rates and short life cycles can successfully compensate for the shorter residence times of fluvial ecosystems (Viroux 1997). As a consequence, the majority of lowland rivers have similar zooplankton communities (Kobayashi et al. 1998). Thus, ciliates and rotifers become the best adapted groups to lotic conditions, although nauplii and some small cladocerans have been cited as well (José de Paggi and Paggi 2007).

Among the prominent representatives of zooplankton, rotifers and cladocerans have evolved into parthenogenesis as an efficient reproductive method, with short generation times (from several days to weeks). In addition, these zooplankton groups produce resting eggs and ephippia that survive adverse conditions (e.g. drying out of the habitat), and also aid in dispersal (Lair 2006).

In contrast, copepods have obligatory sexual reproduction, and their life cycle may extend from weeks to months (Lehman 1988). For this reason, copepods may require more stable environments (i.e., shallow lakes, backwater,

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storage zones) to facilitate mating (Lair 2006). Therefore, lentic environments within the river's floodplain enhance the growth and reproduction of plankton, thus acting as major sources of inoculum for rivers (Shiel et al. 1982; Górski et al. 2013; Furst et al. 2014). In addition, flow discharge and hydrologic regime are fundamental aspects in water exchange between river and adjacent water bodies, through establishing an efficient route of dispersion (Picard and Lair 2005; Simões et al. 2013). River rearrangements, however, alter these hydrodynamics along floodplain connectivity, thus threatening plankton biodiversity (Chaparro et al. 2019).

Most zooplankton studies in lowland rivers have been based on adult organisms, and only a small number have considered larval stages such as nauplii (Zimmermann-Timm et al. 2007; Wahl et al. 2008). Fewer have included gravid females (Vásquez and Rey 1989; Casper and Thorp 2007), and still fewer have documented egg ratios and the number of eggs in the gravid females of rivers and floodplain environments (Saunders and Lewis 1989; Hillbricht-Ilkowska 1999; Chaparro et al. 2011).

Previous studies on the Salado River had identified the dominant zooplankton species along the river course, and the influence of hydrologic regime on plankton development (Neschuk et al. 2002; Claps et al. 2009; Gabelone et al. 2014). Those investigations, however, were not focussed on the zooplankton of the upper basin and its major tributaries—that is, the saline canalizations of the sandy pampas. In addition, those canals pass through diverse wetlands and shallow lakes within the study area before discharging into the Salado River proper. In consequence, those water discharges, being mainly governed by the ongoing hydrologic condition, affect the water characteristics of the Salado-River water. Therefore, small water bodies like the aforementioned canals are essential ecosystems because of their influence on larger watercourses, despite their having been overlooked by traditional research (Biggs et al. 2017). Accordingly, little is known about the ecologic functioning of artificial canals in the pampas plain.

On the basis of these considerations, we proposed the hypothesis that the transfer of the drainage canals into the Salado River influenced the zooplankton's structure and dynamics. Moreover, we hypothesized that the impact of those transfers would be mostly governed by particular hydrologic conditions as well as by the presence of wetlands and lentic environments within the study area. Accordingly, the objectives of this work were: (a) to analyze the structure and dynamics of the zooplankton community, and its reproduction stages in the study area, and (b) to recognize zooplankton responses to changes in the physicochemical variables during different hydrologic conditions, and (c) to assess the influence of the canals' discharges into the

zooplankton community in the Salado River downstream from that input.

Materials and methods

Study area

The Salado River is the main lowland river within the 'pampas'—a wide plain dominated by natural pastures along with sparse trees and shrubs—and that watershed is one of the most productive agricultural regions in the Argentina (Gonzalez and Fernandez 2007). The natural drainage network of the basin is poorly developed owing to low topographic slope (0.107 m km^{-1} to the East), and low geomorphologic energy (Palmer et al. 2002). In consequence, evaporation and infiltration became predominant, with temporary storage of water excesses in land depressions and groundwater (Forte Lay et al. 2007). In addition, there is a regional climatic phenomenon where various consecutive wet years are followed by dry ones, hence producing extended floodings and droughts that alternate in an irregular pattern (Iriondo and Kröhling 2007).

The upper stretch of the Salado River receives allochthonous discharges from the sandy-pampas region—a previously endorheic zone covering $66,000 \text{ km}^2$ —by means of a drainage system of artificial canals. These canalizations were constructed and connected within the Salado basin after the extreme floodings during 1987 through 1988 (Ludueña 2006). Moreover, the region is characterized by a close linkage between ground- and surface-water processes, and the occurrence of saline groundwater is mostly attributable to continental evaporite deposits (Palmer et al. 2002). As a consequence of the artificial canalizations, the hydrologic regime has become altered, with saline water being introduced into the basin. The altitude in the region is about 50 m asl. , and the mean annual precipitation is 850 mm . The climate is temperate and humid; however, a negative water balance between November and February occurs, and the water accumulated in land depressions evaporates producing soil salinization (Ludueña 2006). All these particular features greatly affect human activities, and the economic exploitation of the land in the region, that is, extensive cattle breeding along with crop and pasture rotation (Ghersa et al. 2002).

Sampling design

The sampling stations selected in the study area were (Fig. 1): the Mercante Canal (Canal 1), where all the canalizations in the sandy pampas converge (250 km in length); the Vinculación Canal (Canal 2), which links the wetland

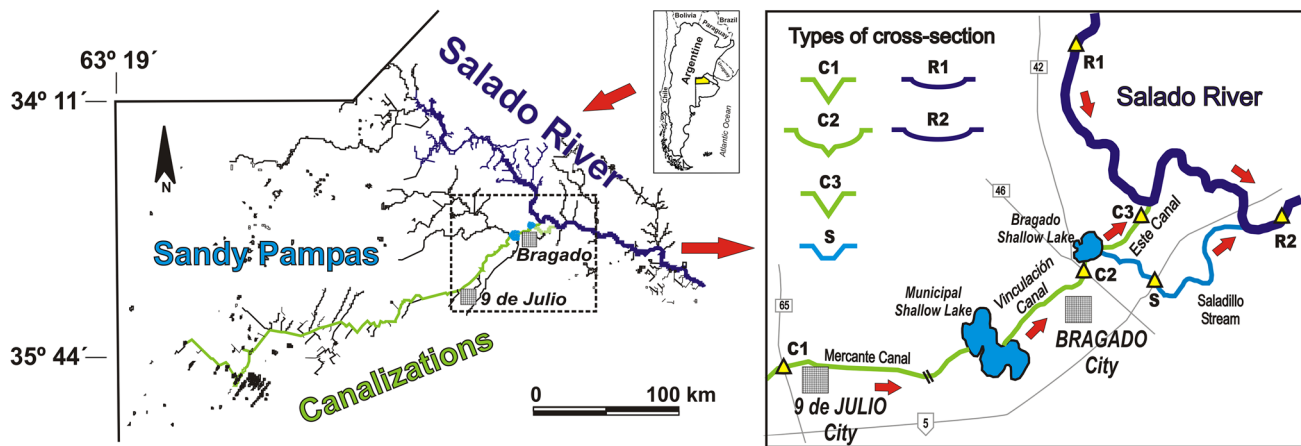


Fig. 1 Map of the Salado-River watershed (left panel) illustrating the sampling sites along with the recent canalizations within the sandy pampas, and the location of the study area (dotted box enlarged in the right). The inset indicates the location of the sandy pampas within Argentina. In the right panel, a schematic drawing depicting the posi-

tioning of the sampling stations (triangles) and the location of the canals and the two shallow lakes is shown. There, a representation of the cross-section of the sampling sites is included (upper left). *References of sampling sites:* C1 (Canal 1), C2 (Canal 2), C3 (Canal 3), S (stream), R1 (River 1), and R2 (River 2)

between the Municipal and the Bragado shallow lakes; the Este Canal (Canal 3); and the Saladillo Stream (Stream)—these latter two being effluents from the Bragado shallow lake that discharge into the Salado River. In the river, we placed an upstream (River 1) and a downstream (River 2) site in relation to the discharge of the aforementioned system of drainage canals. The samples were taken under four different hydrologic conditions, hereafter referred to as: *A*, high water (autumn, May 2007); *B*, mean flows (late summer, March 2008); *C*, low flows (spring, November 2008); and *D*, very low flows in the tributaries but with mean flows in the river proper (late winter, September 2009). The Este Canal Station (Canal 3) was added and then sampled during low-water conditions.

Analytical procedures

At each sampling site, temperature, turbidity, pH, and conductivity were measured with a multiple sensor Horiba U-10, dissolved-oxygen concentration (DO) with YSI oximeter, and light penetration with a Secchi disk. Flow velocity was detected by means of a current meter and the hydrometric level determined as well. A submersible centrifugal pump was used for sample extraction, and water samples were collected in 1-L polyethylene bottles for chemical analysis. For chlorophyll *a* estimations, water samples were drawn through Whatman GF/C filters into a suction flask connected to a manual vacuum pump. In the laboratory, dissolved reactive phosphorus (DRP), total phosphorus, $N-NO_3^-$ plus $N-NO_2^-$, $N-NH_4^+$, chlorophyll *a*, total suspended solids,

and particulate organic matter were determined by the methods described in APHA (2012).

Zooplankton samples were collected subsurface in the main channel, where 50 L were pumped and passed through a 35- μ m-mesh net. One fraction was fixed in 4% (v/v) aqueous formaldehyde and was used for quantification and identification of the species. The other fraction was preserved in 45% (w/v) sucrose solution (Haney and Hall 1972) and was used in the observation and quantification of fragile zooplankton structures, such as eggs and embryos. The zooplankton organisms were counted in (1-mL) Sedgwick–Rafter and (10-mL) Bogorov chambers under a binocular microscope and stereo microscope, respectively. Repeated subsamples were counted until a coefficient of variation < 20% in the total abundance of the dominant species was reached. The reproductive stages of rotifers, copepods, cladocerans, and ostracods were counted separately—i.e., males, females, gravid females, nauplii, copepodites, cladocerans embryos, and juveniles. In addition, the total number of eggs carried by each female was counted, and the egg-ratio index—i.e., the total number of eggs carried by gravid females divided by the total abundance of those gravid females—calculated for each species at each sampling site during the survey.

Statistical determinations

Before analysis, the physicochemical data were standardized and species abundance was Hellinger transformed (Legendre and Gallagher 2001), that is, applying quadratic root to species relative abundance. A multivariate analysis was

carried out in order to determine the relationships among the environmental variables and species abundance, as such including the results from all four surveys. From a total of 166 taxa, the species with a relative abundance of < 5% and a relative frequency < 10% were discarded, thus resulting in 61 taxa for further analysis. A Redundancy Analysis (RDA) was carried out by means of the program CANOCO 4.0. In order to avoid multicollinearity, variables with an inflation factor > 10 were discarded (ter Braak and Smilauer 1998). At that moment, manual selection of environmental variables was selected, and each variable was analyzed using Monte Carlo Test, with 499 non-restricted permutations under full model. Only significant variables ($p < 0.05$) were added to the resulting model. In addition, a cluster analysis was performed by applying Bray–Curtis similarity and completeness of linkage to a basic matrix of species abundance with its reproductive data differentiated. A significant test based on 999 simulations was also realized by means of the program PRIMER v5 (Clarke and Gorley 2001).

Results

The water of the Salado River and its tributaries was alkaline with variations in conductivity depending on sampling site and hydrologic condition. Table 1 lists the range of values for the main physicochemical variables measured at each sampling site. The zooplankton underwent a seasonal development, recording abundance peaks during mean and low flows, in coincidence with the reproductively favorable spring–summer period. In general, total zooplankton abundance was higher at canal sites than at river sites. Under most of the hydrologic conditions (high water, mean and

low flows), increases in total zooplankton abundance and its main components were recorded in the river downstream site, below the canals' discharge (Fig. 2).

During high water, a progressive decrease in conductivity, total abundance of zooplankton, main taxonomic groups, and dominant species was observed along the tributary system, from higher values at Canal 1 to gradually lower ones at Canal 2, and finally, the stream sampling site. Minimum abundances were recorded in the river, with a slight increment in ciliates, cladocerans, and copepods at the river downstream (River 2). During mean flows, the abundance peaks of total zooplankton were recorded at Canal 2 and the river downstream, which taxa consisted mostly of ciliates and rotifers. The ciliates were quite abundant in the tributaries, especially *Epistylis* spp., *Stentor* spp., and *Vorticella* spp. at Canal 1 and the Stream sampling sites. Moreover, predator ciliates like *Prorodon* spp. and suctoria species showed remarkable densities at those sites.

In low flows, the highest zooplankton abundance also was recorded at Canal 2, where rotifers numbered at 42,600 ind L⁻¹, and *Brachionus plicatilis* s.l. was the dominant species at a mean density of 34,800 ind L⁻¹ (at values ranging between 13,800 and 55,800 ind L⁻¹). Whereas *B. plicatilis* s.l. was quite abundant in Canal 1 and Canal 2, *Brachionus angularis* was the dominant species at Stream, Canal 3, and the river sampling sites; though both rotifer species increased their density at the river downstream over that recorded at the upstream site. During low flows, the rotifers contributed up to 94% of total zooplankton abundance.

In very low flows, Canal 1 and Stream sampling sites contained minimum zooplankton abundances in conjunction with stagnant waters and basal flows. In contrast, notable densities were recorded in river sites where a

Table 1 Mean values and standard deviations (in parentheses) of the physicochemical variables and chlorophyll *a* recorded at each sampling site during the four hydrologic conditions surveyed (i.e., high water, mean flows, low flows, and very low flows)

Variables / Sites	Canal 1	Canal 2	Canal 3	Stream	River 2	River 1
Water temperature (°C)	19.2 (7.3)	19.4 (7.7)	21.7 (5.9)	20.8 (6.2)	19.5 (6.1)	20.5 (8.6)
Conductivity (mS cm ⁻¹)	16.7 (6.3)	10.9 (6.2)	9 (11.2)	7.8 (6.1)	8.3 (4.3)	5.2 (1)
pH	8.6 (0.2)	8.7 (0.3)	8.9 (0.4)	8.5 (0.2)	8.8 (0.2)	9.1 (0.3)
Turbidity (NTU)	161 (45.4)	182.5 (71)	163 (84.6)	123.5 (62)	218 (119)	412 (281)
Dissolved-oxygen concentration (mg L ⁻¹)	9.3 (4.1)	9.8 (2.9)	8.2 (2.6)	9.4 (4.2)	11.9 (3.5)	12.6 (3.7)
Secchi disk (cm)	34.3 (10.2)	26.3 (6)	41 (21.2)	25.9 (11.6)	29 (15.9)	18.4 (12.8)
Flow velocity (m s ⁻¹)	0.4 (0.3)	0.4 (0.5)	0.027 (0.03)	0.2 (0.1)	0.65 (0.7)	0.31 (0.2)
Total suspended solids (mg L ⁻¹)	125 (58)	100 (62)	59.6 (61.7)	52.4 (27.5)	123 (67)	227 (176)
Particulate organic matter (mg L ⁻¹)	58.2 (32.6)	47.6 (34)	28 (24)	27.5 (11.7)	55.6 (26.6)	94 (67)
Nitrites + Nitrates (µg L ⁻¹)	143 (142)	80.3 (59)	149 (16.8)	283 (203)	111 (42)	176 (84)
Ammonium (µg L ⁻¹)	316 (559)	40 (36)	7.2 (7.3)	4,483 (2,957)	44 (30.6)	69.6 (70.8)
Total phosphorus (µg L ⁻¹)	728 (277)	811 (199)	495 (143)	2,081 (1,262)	1,154 (451)	2,023 (1,061)
Dissolved reactive phosphorus (µg L ⁻¹)	65.2 (41)	128 (159)	52.7 (55.6)	840 (478.5)	375 (305)	815 (434)
Chlorophyll <i>a</i> (mg m ⁻³)	158 (125)	143.6 (83)	85.9 (78)	73.4 (43.3)	207 (130)	260 (151)

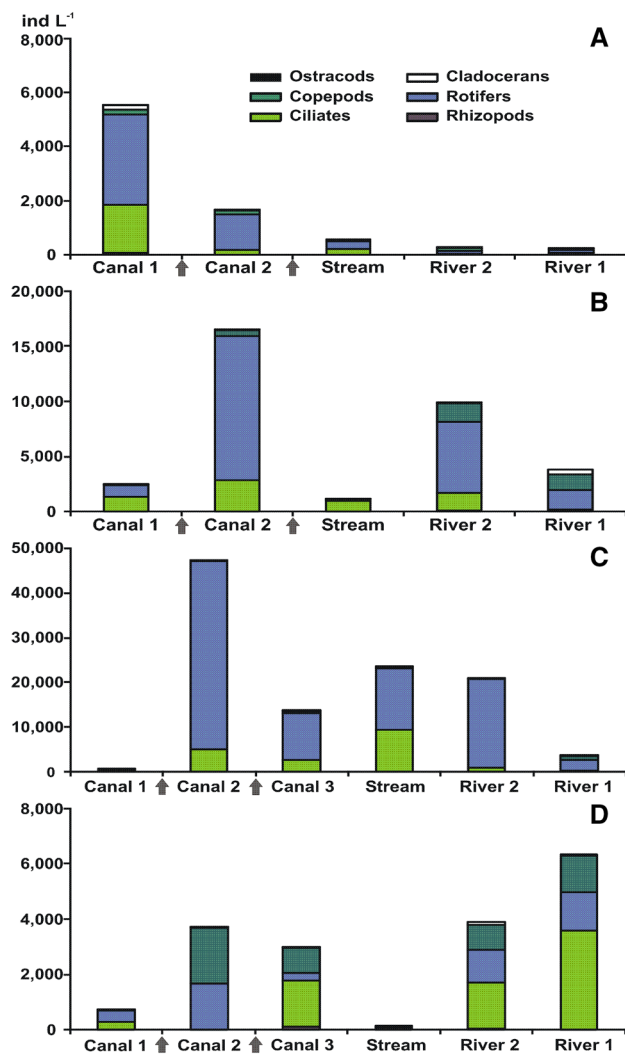


Fig. 2 In the graph of each panel, the total abundance (ind L^{-1}) of zooplankton main groups (bars) is plotted on the *ordinate* for each of the sampling sites designated on the *abscissa* under each of the following hydrologic conditions hereafter referred as: Panel A, high water; Panel B, mean flows; Panel C, low flows; Panel D, very low flows in the tributaries (Canal 1, Canal 2, Canal 3 and Stream), with mean flows throughout the Salado River upstream (River 1) and downstream (River 2) sampling sites. The arrows mark the location of the respective Municipal and Bragado shallow lakes. The bar colors indicate the different zooplankton groups at each sampling site with the corresponding bar colors depicting the abundances of those groups

mean-flow condition prevailed. There, ciliates were the dominant group, followed by the rotifers *Brachionus urceolaris* and *B. pterodinoides*. In general, copepods, cladocerans, and rhizopods present at the river upstream site were displaced by rotifers and ciliates at downstream, after the canals' discharge.

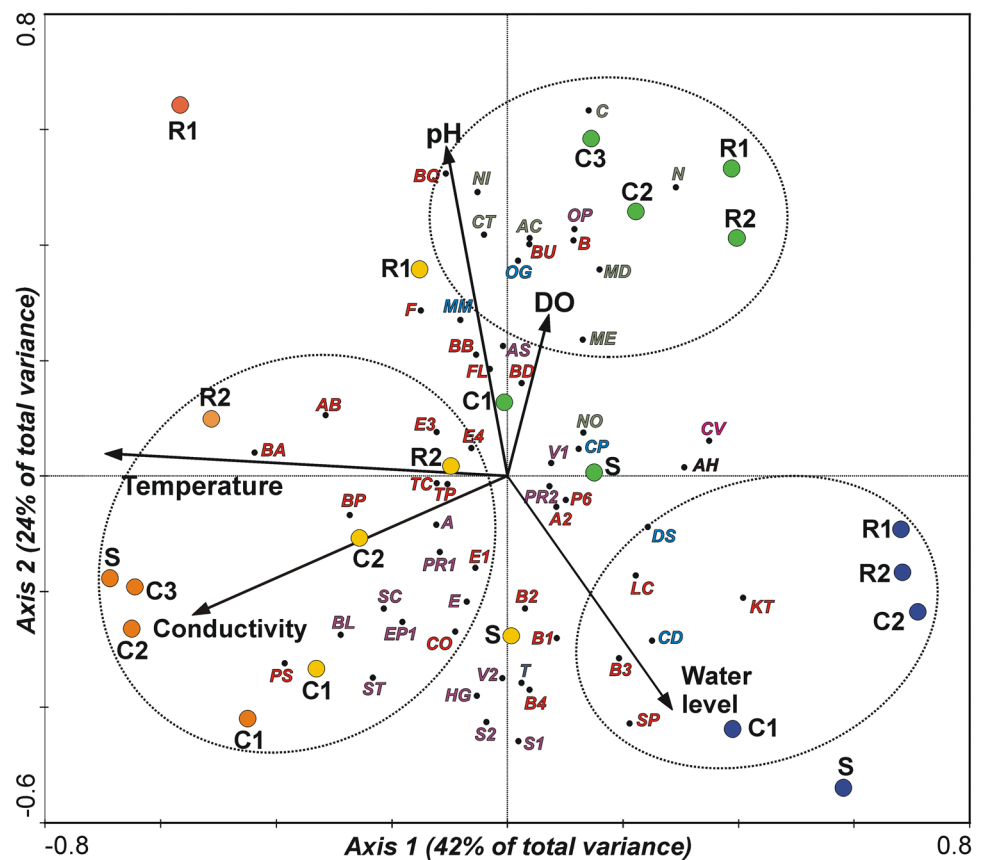
Statistical analysis

The model fitting from the RDA procedure explained 66% of the total variance with the sum of Axis 1 and 2 (Fig. 3). According to the Monte-Carlo test, the entire model was significant when the environmental variables: temperature ($p < 0.002$), conductivity ($p < 0.008$), DO ($p < 0.01$), pH ($p < 0.002$), and water level ($p < 0.036$) were included. Among them, temperature and conductivity were negatively correlated with Axis 1, the same as water level with Axis 2. The DO and pH were positively correlated with Axis 2. The acronyms for the zooplankton species used in the resulting triplot of the model are itemized in Table 2. Most ciliates were related to higher conductivities (*Stentor* spp., *Blepharisma* sp., *Strombilidium caudatum*, *Strombidium* sp1, *Vorticella* sp2, *Enchelys* sp., *Epistylis* sp1, *Prorodon* sp1). The dominant rotifers *Brachionus angularis*, *B. plicatilis*, *Asplanchna brightwellii*, and *Pompholyx sulcata* were associated with higher temperatures and conductivity values during mean and low flows. Other species clustered under higher values of pH and DO—e. g., *B. urceolaris*, *B. pterodinoides*, and *B. quadridentatus*, the cladocerans *Moina micrura* and *Ovalona glabra*, and most copepods (*Microcyclops dubitabilis*, *Metacyclops mendocinus*, *Acanthocyclops robustus*, *Nitokra* sp., *Cletocamptus tertius*, nauplii, and copepodites). The cladocerans *Ceriodaphnia dubia* and *Daphnia spinulata* were associated with higher values of water level, as were the rotifers *Keratella tropica* and *Synchaeta pectinata* that correspond to the high water survey.

Rotifers, cladocerans, ostracods, and copepods in reproduction

The presence of gravid females of rotifers and crustaceans was associated with total abundance of those two groups. Moreover, most zooplankton species in reproduction were found in Canal 2 (i.e., 25 taxa), and there—followed by the river downstream sampling site—the abundance peaks of gravid females and total number of eggs carried by females were likewise present. Gravid rotifer females were observed in all the sampling sites and under all the hydrologic conditions, although those females were conspicuously abundant at Canal 2 and the river downstream during mean and low flows (Fig. 4). Accordingly, the dominant species *B. plicatilis* s.l. exhibited abundance peaks in low flows particularly at Canal 2 ($12,400 \text{ ind L}^{-1}$) but secondarily at the river downstream site (Fig. 5). The highest values of: egg ratio (2 eggs on average per gravid female), total number of eggs per gravid female (9 eggs), and resting eggs in progress were recorded at the river downstream during low flows. In addition, *B. plicatilis* s.l. increased the abundance of gravid females and egg ratios at the river downstream with respect

Fig. 3 Redundancy analysis (RDA) triplot with Axis 1 and 2: variables (radial arrows), sampling sites (circles), and zooplankton species abundances (triangles) with the acronyms of Table 2. *Indications:* DO (dissolved-oxygen concentration), blue dotted ovals (high water), yellow dotted ovals (mean flows), orange dotted ovals (low flows), green dotted ovals (very low flows at the tributary canals with mean flows at the Salado-River), C1 (Canal 1), C2 (Canal 2), C3 (Canal 3), S (stream), R1 (River 1), and R2 (River 2). The color code for the species' names is: purple (ciliates), red (rotifers), magenta (ostracod), blue (cladocerans), pale green (copepods), and black (rhizopods)



to the corresponding parameters at the river upstream site during the four hydrologic conditions (Table 3). *Brachionus angularis* also showed notable densities of gravid females in low flows, particularly at the river downstream (7500 gravid females L^{-1}), hence exceeding by one order of magnitude the abundance of the reproductive females there over the values recorded at the river upstream site. During mean flows, that species furthermore showed major abundances of gravid females at Canal 2 (540 ind L^{-1}) and in river sites. In contrast, the gravid females of *K. tropica* were particularly abundant at Canal 1 (541 ind L^{-1}) during high water, followed by Canal 2 and Stream sampling sites.

Gravid females, embryos, and juveniles of cladocerans—such as *Ovalona glabra*, *Coronatella poppei*, *Moina micrura*, and *Ceriodaphnia dubia*—were mostly distributed between the two river sites, particularly at the river upstream site (Fig. 6). In contrast, *D. spinulata* had substantial densities of gravid females at Canal 1 during high water, whereas only one species of ostracod had gravid females at that same site during low flows. Copepods' gravid females were mostly distributed at river sites, although such females were abundant (Fig. 7) at Canal 2 (during mean flows) and Canal 1 (at high water). Copepodites were relevant in the river during mean-flows and at Canal 3 and Canal 2 during low and very low flows, respectively. Finally, the highest densities of the

nauplii occurred at Canal 2 during very low flows (1530 ind L^{-1}), followed by Canal 3 and those of the river.

A cluster analysis performed on the zooplankton species abundance and the corresponding reproductive data indicated significant differences ($p < 0.05$) at 14 nodes in the dendrogram (Fig. 8). As a result, the river upstream and downstream sampling sites had highest similarity during mean flows with scanty inflows from the tributaries, secondly followed by high waters. In contrast, the river downstream site was significantly related to the canals during mean and low flows, whereas the river upstream site was related to itself in those hydrologic conditions.

Discussion

Zooplankton abundance and environmental variables

According to the RDA, our results suggest that temperature, conductivity, DO, pH, and hydrologic level determined the zooplankton abundance and species composition in the study area. In this regard, temperature and salinity have been considered as structuring parameters of zooplankton community in Australian rivers (Shiel et al. 1982, 2006). Similarly, Ning

Table 2 List of zooplankton species selected for RDA analysis

Ciliates		Rhizopods	
A	<i>Askenasia</i> sp.	AH	<i>Arcella hemisphaerica</i>
AS	<i>Aspidisca</i> sp.	T	<i>Trinema</i> sp.
BL	<i>Blepharisma</i> sp.	Rotifers	
E	<i>Enchelys</i> sp.	AB	<i>Asplanchna brightwellii</i>
EP1	<i>Epistylis</i> sp1	A2	<i>Asplanchna</i> sp2
HG	<i>Halteria grandinella</i>	BA	<i>Brachionus angularis</i>
OP	<i>Opercularia</i> sp.	BB	<i>Brachionus bidentatus</i>
PR1	<i>Prorodon</i> sp1	B1	Bdelloid sp1
PR2	<i>Prorodon</i> sp2	B2	Bdelloid sp2
SC	<i>Strombilidium caudatum</i>	B3	Bdelloid sp3
S1	<i>Stentor</i> sp1	B4	Bdelloid sp4
S2	<i>Stentor</i> sp2	BD	<i>Brachionus dimidiatus</i>
ST	<i>Strombidium</i> sp1	BP	<i>Brachionus plicatilis</i> s.l.
V1	<i>Vorticella</i> sp1	B	<i>Brachionus pterodinooides</i>
V2	<i>Vorticella</i> sp2	BQ	<i>Brachionus quadridentatus</i>
Cladocerans		BU	<i>Brachionus urceolaris</i>
OG	<i>Ovalona glabra</i>	CO	<i>Colurella obtusa</i>
CP	<i>Coronatella poppei</i>		<i>Colurella uncinata</i>
CD	<i>Ceriodaphnia dubia</i>	E1	<i>Encentrum</i> sp1
DS	<i>Daphnia spinulata</i>	E3	<i>Encentrum</i> sp3
MM	<i>Moina micrura</i>	E4	<i>Encentrum</i> sp4
Copepods		FL	<i>Filinia longiseta</i>
AC	<i>Acanthocyclops robustus</i>	F	<i>Filinia pejleri</i>
CT	<i>Cletocamptus tertius</i>	KT	<i>Keratella tropica</i>
C	Copepodites	LC	<i>Lecane closterocerca</i>
NI	<i>Nitokra</i> sp.	P2	<i>Proalides</i> sp1
MD	<i>Microcyclops dubitabilis</i>		<i>Proalides</i> sp2
ME	<i>Metacyclops mendocinus</i>	P6	<i>Proales</i> sp6
N	Nauplii		<i>Proales</i> sp5
NO	<i>Notodiptomus incompositus</i>	PS	<i>Pompholyx sulcata</i>
Ostracods		SP	<i>Synchaeta pectinata</i>
CV	<i>Cypridopsis vidua</i>	TC	<i>Trichocerca capucina</i>
		TP	<i>Trichocerca pusilla</i>

The species with acronyms are arranged in the triplot of Fig. 3; the remaining species are not shown because of the minimal contribution to the model—it being a central distribution

et al. (2013) established that the zooplankton structure in the Ovens, Kiewa, and Murray Rivers was best explained by conductivity, discharge, water residence time, and DO, among others.

The highest zooplankton densities were recorded during low flows, in conjunction with longer water-residence times (Reckendorfer et al. 1999; Vadadi-Fülöp et al. 2009). Accordingly, low-water velocities are widely considered to improve zooplankton development (Sluss et al. 2008; Czerniawski et al. 2013) and also, to structure the community composition (Ning et al., 2013). In contrast, minimum abundance values were recorded during high water, where the plankton was negatively affected by the low autumn temperatures and the dilution effect of flooding (Claps et al. 2009; Kim et al. 2012).

In general, the zooplankton community found was dominated by small filtering organisms such as rotifers and ciliates, and the species assemblages were similar to those cited in other lowland rivers (Kobayashi et al. 1998; Picard and Lair 2005; José de Paggi et al. 2014). In addition, many zooplankters were typical of eutrophic-mesoeutrophic environments (Ghadouani et al. 1998), as previously observed in the basin (Neschuk et al. 2002). The ciliates mainly constituted benthic and periphytic forms that were typical of large rivers (Scherwass and Arndt 2005; Kiss et al. 2009; Pauleto et al. 2009). Most of those organisms were already known to feed on the bacteria present in eutrophic waters with a high content of organic matter (Foissner and Berger 1996; Weisse 2002), while some of the ciliates were also tolerant of high salinities (Foissner et al. 1999). The tributaries had

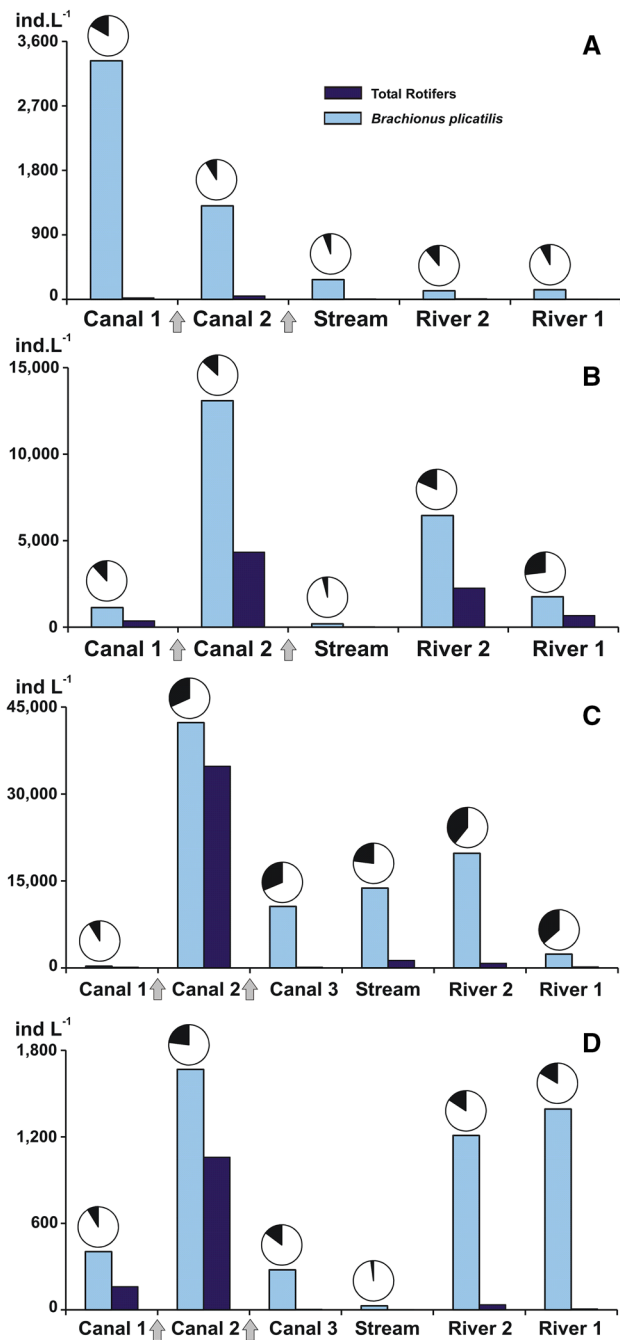


Fig. 4 In the graph of each panel, the total abundance (ind L⁻¹) of rotifers (light-blue bars) and *Brachionus plicatilis* (blue bars) are plotted on the *ordinate* and the relative abundance of females (pie charts) without eggs (white) versus gravid (black) recorded at each sampling site is designated on the *abscissa* and under each of the aforementioned hydrologic conditions (Panels A, B, C, D). The arrows mark the location of the respective Municipal and Bragado shallow lakes

higher ciliate densities than did the river course (Scherwass et al. 2010), although the abundances in the latter were lower than those of other eutrophic rivers (Kiss et al. 2009). In particular, Canal 1 and Stream sampling sites had markedly

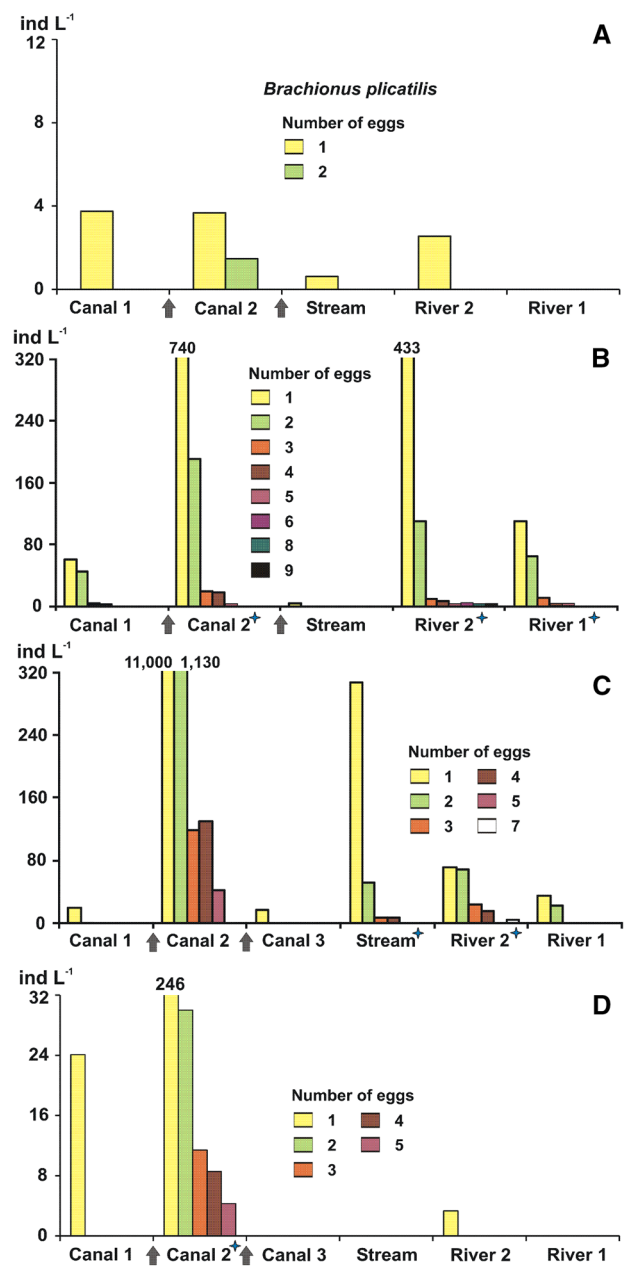


Fig. 5 In the graph of each panel, the total abundance (ind L⁻¹) of gravid females of *Brachionus plicatilis* (bars) is plotted on the *ordinate* for each sampling site indicated on the *abscissa* for each of the aforementioned hydrologic conditions (Panels A, B, C, D). The pluses on the *abscissa* denote the presence of females with resting eggs in progress at those sampling sites. The key to the bar colors representing the number of eggs per female is indicated within the graph of each of the panels. The arrows mark the location of the respective Municipal and Bragado shallow lakes

elevated abundances of *Epistylis* spp., *Stentor* spp., and *Vorticella* spp.—which taxa are recognized as indicators of α - β saprobic conditions (Foissner and Berger 1996)—and also of predator ciliates and suctoria species, whose density values were similar to those in sewage waste-waters (Araújo

Table 3 Total abundance (ind L⁻¹) of zooplankton species in reproduction (bold face), percentage of gravid females (parentheses), egg ratio (curved brackets), and range of number of eggs (square brackets) in gravid females at each sampling site and under each of the following hydrologic conditions: A, high-water (autumn floodings); B, mean flows (late summer); C, low flows (spring); D, very low flows in the tributaries with mean flows in the river (late winter)

	Canal 1	Canal 2	Canal 3	Stream	River 2	River 1
Rotifers						
<i>Anuraeopsis fissa</i>	B	22.3 (29%) {1}				
	C	0.5	6.7 (50%) {1}	12.2		
<i>Ascomorpha ovata</i>	C	1.5	6.7 (50%) {1}	34.1 (8%) {1}	4.7	
<i>Brachionus angularis</i>	B	20.2 (33%) {1}		5	1,281 (37%) {1.1} [1–2, 4] [*]	423.6 (46%) {1.1} [1–3]
	C	37.2 (7%) {1}	9,787 (33%) {1.1} [1–2] [1–3] [*]	11,731 (23%) {1.1} [1–3]	18,485 (41%) {1.2} [1–5] [*]	1,875 (41%) {1} [1–3] [*]
	D		2.7 (53%) {1.4} [1–2]	2.6		
<i>Brachionus bidentatus</i>	A	2.8 (16%) {1}			24.7 (13%) {1}	
	B	156.7 (6%) {1.3} [1–2]		5.8	38.9 (26%) {1}	40.7 (21%) {1}
	C	5		1.4	45 (33%) {1.3} [1–2] [*]	31.5 (35%) {1.2} [1–2] [*]
<i>Brachionus calyciflorus</i>	D	0.5 (100%) {1}	1			4.2 (40%) {1}
	C		0.5 (100%) {1}			
<i>Brachionus caudatus</i>	A	9 (43%) {1}			0.6	
	B	14.2 (63%) {1}			1.6	
	C	0.5				2.5
<i>Brachionus dimidiatus</i>	D	0.5 (100%) {1}			0.6	
<i>B. dimidiatus inermis</i>	A	4	3.3			
	C	0.4 (100%) {2}				
<i>Brachionus plicatilis s.l</i>	A	683 (1%) {1.3} [1–2]		5.6 (11%) {1}	7.6 (34%) {1}	1.3
	B	48 (11%) {1.3} [1–2]		12.4 (30%) {1}	22.50 (26%) {1.3} [1–9] [*]	662 (29%) {1.5} [1–5] [*]
	C	357 (31%) {1.5} [1–4]		1,293 (30%) {1.2} [1–4] [*]	771 (24%) {2} [1–4, 7] [*]	175 (33%) {1.4} [1–2]
	D	129 (15%) {1} [1–2]	116.7 (14%) {1}	0.3	35 (10%) {1}	6
<i>Brachionus pteridinoides</i>	C	34,795 (36%) {1.1} [1–5]	4			
	D	1,059 (30%) {1.3} [1–5] [*]	3.3 (100%) {1}	2.9	12.5 (27%) {1} [1] [*]	20.9
<i>Brachionus quadridentatus</i>	B	1			483 (19%) {1.2} [1–4]	401 (15%) {1.6} [1–3] [*]
	C	13.9		7.5	26 (25%) {1}	37.2 (16%) {1}
	D	74.3 (23%) {1.5} [1–3]		0.6 (50%) {1}	58.3 (89%) {1}	42 (77%) {1.95} [1–3]
<i>Brachionus rotundiformis</i>	B				41 (21%) {1}	13.9 (62%) {1}

Table 3 (continued)

	Canal 1	Canal 2	Canal 3	Stream	River 2	River 1
<i>C</i>	2 (25%) {1}	3.3	130 (28%) {1}		3.4	
<i>D</i>	25.6 (26%) {1}	24.3 (18%) {1.3} [1–2]			16.7 (10%) {1}	14.5 (14%) {1}
<i>Brachionus urceolaris</i>	<i>B</i>	10.7 (19%) {1}			16.4 (2%) {1}	5.5
	<i>D</i>	1			367 (14%) {1.6} [1–2.4]	322 (24%) {1.4} [1–3]*
<i>Colurella uncinata</i>	<i>B</i>	3			14.7 (11%) {1}	
	<i>C</i>	15.2 (3%) {1}	6.7		20.2	
<i>Dicranophorus</i> sp.	<i>C</i>	34		156 (42%) {1.1} [1–2]		
<i>Encentrum</i> sp3	<i>D</i>	1.4			23.3	90.5 (6%) {1}
<i>Encentrum</i> cf. <i>marinium</i>	<i>D</i>	96.8 (2%) {1}		0.9 (33%) {1}		106.5
<i>Euchlanis dilatata</i>	<i>D</i>					
<i>Filinia longiseta</i>	<i>B</i>	15.9			237 (27%) {1} [1–2]	
	<i>D</i>	1.4	59 (8%) {1.1} [1–2]			
<i>Filinia pejeri</i>	<i>B</i>	275 (13%) {1.9} [1, 3–4]			144 (6%) {1}	317 (14%) {1.2} [1–3]
	<i>C</i>	23.4 (56%) {1.8} [1–2]				29.5 (40%) {1.7} [1–3]
	<i>D</i>		29 (21%) {1.2} [1–2]			
<i>Hexarthra fennica</i>	<i>C</i>		6.7 (50%) {1}			
<i>Keratella americana</i>	<i>C</i>	6.1 (8%) {1}				27.1
<i>Keratella tropica</i>	<i>A</i>	3058 (18%) {1}		118 (13%) {1}	67.4 (16%) {1}	68.8 (14%) {1}
	<i>B</i>	10.7			21.3 (31%) {1}	42.7 (39%) {1}
	<i>C</i>	2.6 (100%) {1}	146.7 (2%) {1}	50.3	125.9 (28%) {1}	2.5
	<i>D</i>	559 (12%) {1} [1]*	138 (20%) {1}		48.3 (28%) {1}	6.5 (100%) {1}
<i>Notholca acuminata</i>	<i>A</i>	8.1 (17%) {1}				
<i>Polyarthra dolichoptera</i>	<i>A</i>	3.9		5.9	0.6	1.25 (50%) {1}
	<i>D</i>	14.5 (20%) {1}	4.6 (11%) {1}	2.9		
<i>Pompholyx sulcata</i>	<i>B</i>	17.4 (44%) {1.1} [1–2]			46.3 (21%) {1}	20 (28%) {1}
	<i>C</i>	21.5 (16%) {1}	63.3 (68%) {1.4} [1–2]	63 (28%) {1}	14.3 (41%) {1}	
<i>Proales</i> sp2	<i>B</i>	71.4		4.4 (43%) {1}		
<i>Proales</i> sp4	<i>C</i>	10.4 (100%) {1}				
<i>Proalides</i> sp1	<i>B</i>	9.7		1.2	1235 (3%) {1}	97.5 (3%) {1}
	<i>C</i>	9 (6%) {1}	30	61.2 (9%) {1}	48.3 (11%) {1} [1]	
	<i>D</i>				43 (19%) {1.2} [1–2]*	243 (24%) {1.1} [1–2]*
<i>Proalides</i> sp2	<i>B</i>	1872 (2%) {1}				
<i>Synchaeta pectinata</i>	<i>A</i>	44.6 (3%) {1}		61.4	24.9	3.1
	<i>B</i>	529.5 (1%) {1}		57.9 (3%) {1}	110.3	
<i>Trichocerca capucina</i>	<i>B</i>	3.1			101.5	
<i>Trichocerca pusilla</i>	<i>B</i>	2 (100%) {1}			124.2	36.3

Table 3 (continued)

	Canal 1	Canal 2	Canal 3	Stream	River 2	River 1
Copepods						
<i>Acanthocyclops robustus</i>	A 35.1 (29%)	2.7 (5%)		1	0.12	
	B	5.5 (58%)		0.4	100 (38%)	312.9 (12%)
	C	1.5	16 (21%)	3		20.9 (40%)
	D	28.6 (20%)	13.5 (3%)	0.3	28.3 (29%)	44.4 (39%)
<i>Cletocamptus tertius</i>	A 0.3	0.1 (100%)				0.26
	B 1	76.4 (10%)		0.8 (100%)		13.1 (46%)
	C 0.1	0.3	2.7		2	21.6 (2%)
	D 13.1 (12%)	10.3 (17%)		0.6	9 (37%)	38 (5%)
<i>Nitokra</i> sp.	A 6.4 (39%)	1.9			0.4	0.26
	B	20.9 (18%)			11.6	17.7
<i>Metacyclops mendocinus</i>	A 20 (21%)	6.1 (20%)		2.3 (23%)	0.27	
	B	1.6		0.4	5.5 (35%)	41.2 (3%)
	C 0.2	5.5	67	57.4 (3%)		
<i>Microcyclops dubitabilis</i>	B	7 (46%)		0.8	37.2 (5%)	15.2 (20%)
	D	32.9			52 (1%)	39.9 (1%)
<i>Notodiaptomus incompus</i>	B	1.5 (26%)			1.3	
<i>Paracyclops fimbriatus</i>	D		0.4		9.7 (7%)	7.7 (5%)
Cladocerans						
<i>Ovalona glabra</i>	B	3.2 (100%) {2}			7.1 (29%) {2}	51 (19%) {1.4} [1-2]
	C				1.2	203.2 (6%) {1}
	D				56.3 (11%) {1.26}	2
<i>Coronatella poppei</i>	A 2.6	6 (19%) {1.5} [1-2]		0.9 (29%) {1}	0.6	12.9 (8%) {1}
	C					
	D			3.1 (9%) {1}	23.3	2.6
<i>Ceriodaphnia dubia</i>	A 7.9	17.9 (3%) {5} [5]		7.2		11.8 (5%) {1}
<i>Daphnia obtusa</i>	D					0.6
<i>Daphnia spinulata</i>	A 148 (3%) {2.7} [2-4]*	12.6 (9%) {2} [2]*			1.14	300 (3%) {2.1} [1-2, 4]
<i>Moina micrura</i>	B				63.8	
<i>Simocephalus</i> sp.	D				3.7 (9%) {15}	
Ostracod						
<i>Heterocypris incongruens</i>	C 1.6 (6%) {7}					

The asterisks denote the presence of resting eggs

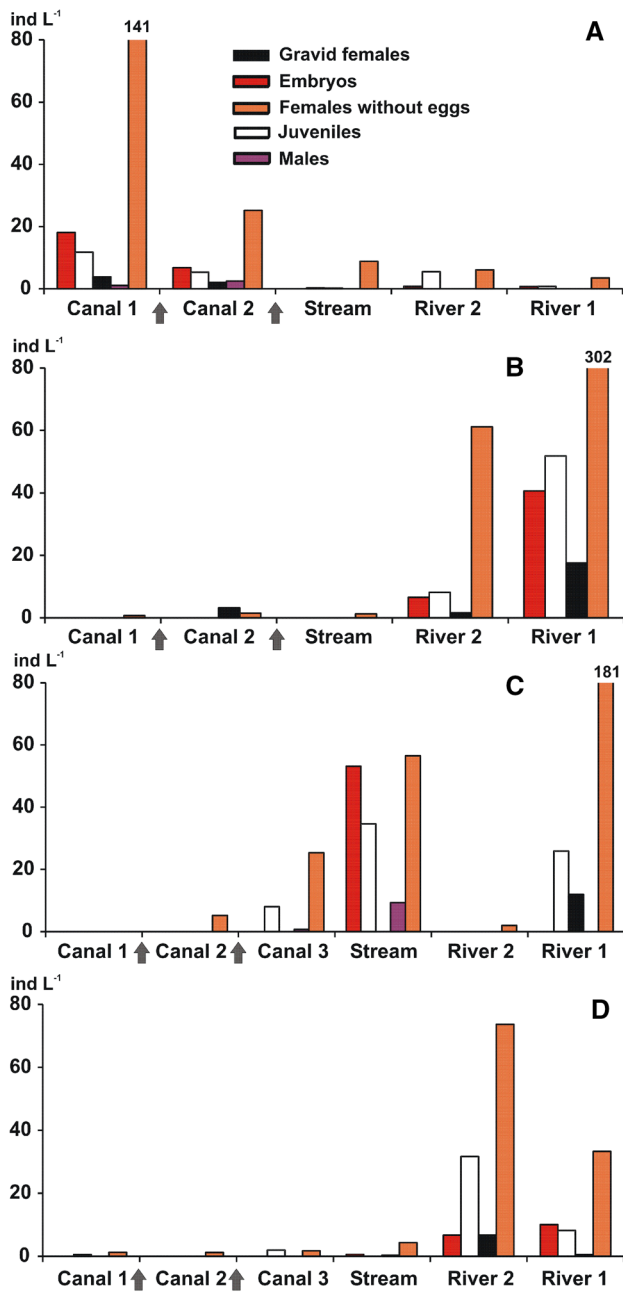


Fig. 6 In the graph of each panel, the total abundance (ind L^{-1}) of cladocerans gravid females, females without eggs, males, embryos, and juveniles, as indicated by the bar colors, is plotted on the *ordinate* for each sampling site designated on the *abscissa* for each of the aforementioned hydrologic conditions (Panels A, B, C, D). The arrows mark the location of the respective Municipal and Bragado shallow lakes

dos Santos et al 2014; Foissner 2016). This particular species assemblage could be related to the highly nutrient-rich waters found at those two sites, with an abundance of ammonia along with low DO levels, such as is recorded in septic outflows (Bazzuri et al. 2018). Accordingly, the Stream sampling site is downstream from the effluent of

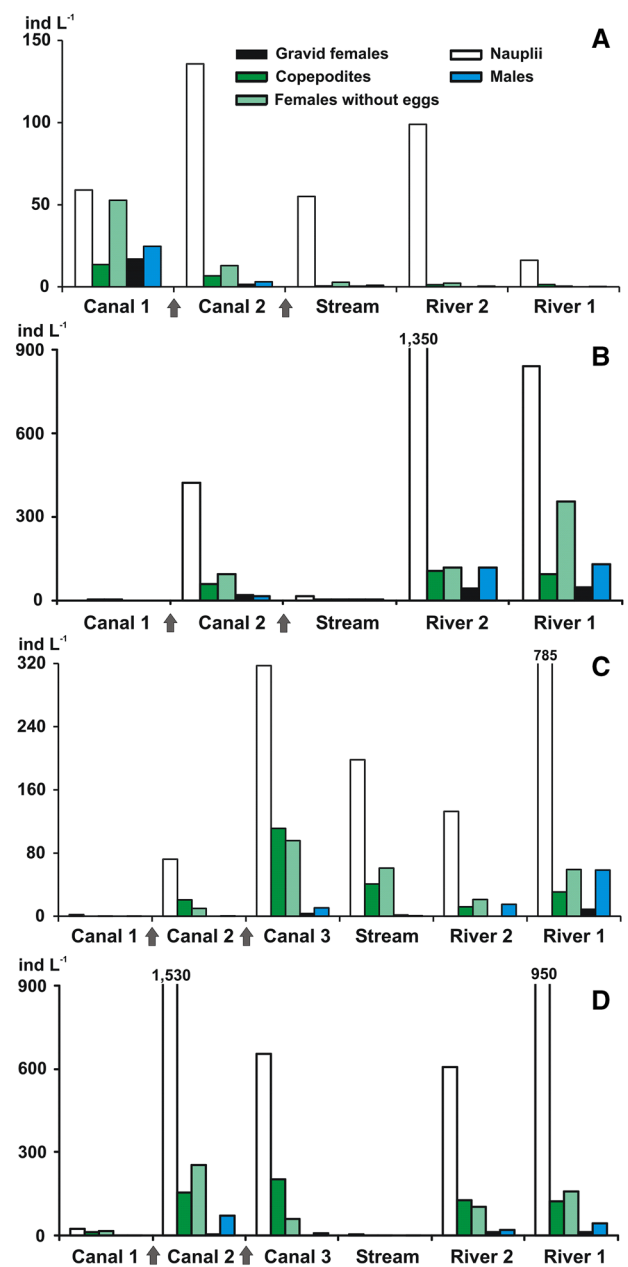


Fig. 7 In the graph of each panel, the total abundance (ind L^{-1}) of copepod gravid females, females without eggs, males, nauplii, and copepodites, as indicated by the bar colors, is plotted on the *ordinate* for each sampling site designated on the *abscissa* for each of the aforementioned hydrologic conditions (Panels A, B, C, D). The arrows mark the location of the respective Municipal and Bragado shallow lakes

the Bragado–City wastewater-treatment plant, and Canal 1 receives urban outflows from the city 9 de Julio.

Like the ciliates, the rotifers exhibited extremely elevated densities during low flows, as had been found in other lowland rivers (Kobayashi et al. 1998; Rossetti et al. 2009). In particular, rotifers attained abundances of $42,600 \text{ ind L}^{-1}$

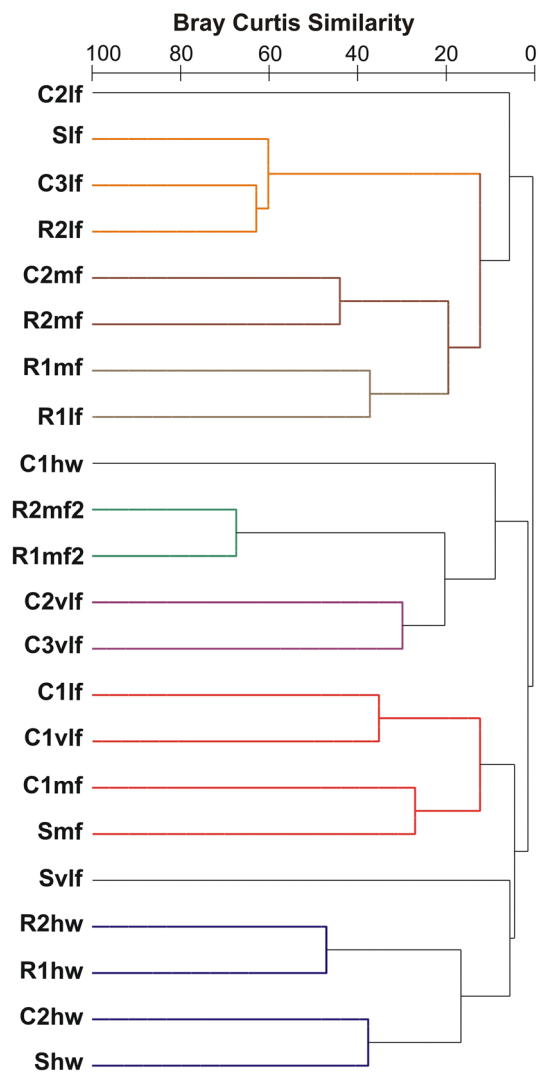


Fig. 8 Cluster analysis (indicating the Bray Curtis Similarity) of the zooplankton species abundance differentiated by reproductive stages (i.e., females, males, gravid females, juveniles, nauplii, and copepodites) at each sampling site—C1 (Canal 1), C2 (Canal 2), C3 (Canal 3), S (stream), R1 (River 1), and R2 (River 2)—during the surveys: high water (hw), mean flows (mf), low flows (lf), very low flows (vlf) in the tributaries with mean flows (mf2) in the river. The colored bold face denotes significant groupings ($p < 0.05$)

at Canal 2, which value represented a novelty for the basin as well as worldwide. Thus, the highest rotifer density ever recorded previously had been reported to be 18,000 ind L^{-1} in a channelized section of the Great Ouse River, UK (Bass et al. 1997). Other conspicuous abundances of that group were recorded by Holst et al. (2002) in the Elbe River (at 10,000 ind L^{-1}) during the favorable season as well as by Lair (2006) in the Loire River (at 4,000 ind L^{-1})—there during a short drought. Therefore, the rotifers are recognized in general as developing notable populations in eutrophic environments given their efficient reproduction capabilities and short life cycles (Ghadouani et al. 1998; Reckendorfer et al.

1999). In addition, the dominance of rotifers in lotic environments has also been associated with hydrologic conditions as well as with the local hydromorphologic profile that governs the water-residence time (Viroux 1997; Zimmermann-Timm et al. 2007). Accordingly, the Canal 2 sampling site is a channelized wetland that links two shallow lakes, whose outflows also contributed to increases in the abundances of the group in the river's downstream site. Likewise, Górski et al. (2013) found that the outflows of wetlands definitely contributed considerable numbers of rotifers within the Waikato-River basin.

The dominant species (*Brachionus plicatilis s.l.*, *B. angularis*, *Keratella tropica*) are known to prefer eutrophic environments and tolerate a wide range of salinities (Marneffe et al. 1996; Ghadouani et al. 1998). In the passage from more eutrophic environments (canals) to less eutrophic ones (Salado River) during the autumn high-water condition, *K. tropica* in particular decreased in abundance (Claps et al. 2009). In contrast, the soft-bodied species were prevalent in the canals that drained the shallow lakes, with many being indicators of eutrophic conditions and were typically limnetic, epiphytic, or epibenthic, having been commonly observed in lentic environments within river floodplains (Lair 2006; Zimmermann-Timm et al. 2007; Schöll et al. 2012).

Brachionus plicatilis s.l. was dominant in most of the sampling sites, with abundance peaks in Canal 2 during low flows (38,400 ind L^{-1}) with warm water temperatures (29 °C) and high conductivities (19 mS cm^{-1}). The species is recognized as being tolerant to high salinities (Shiel et al. 2006) and is well documented in the Salado River as well as in the La Pampa province, particularly during the spring and summer seasons in conjunction with high conductivities (Neschuk et al. 2002; Claps et al. 2009; Echaniz and Vignatti 2011). Even so, the extraordinarily high density of *B. plicatilis s.l.* recorded in this research is a worldwide maximum. In this regard, Holst et al. (2002) recorded 12,000 ind L^{-1} of the species in the Elbe River estuary, where the salt content of the marine waters likely favored its development. In contrast, *B. angularis* was the dominant species at the sampling sites Canal 3, Stream, and the river downstream (18,500 ind L^{-1}) in the present work during low flows and in the spring season, mostly favored by the warm water temperatures, as had been observed in the Meuse River (Marneffe et al. 1996). Accordingly, the RDA demonstrated that the species was related to higher temperatures and conductivities, as had been reported for the Oder River (Czerniawski et al. 2013).

The copepods found in this survey were ubiquitous, most being typical of lentic or lotic environments, although certain ones are known to be endemic to the neotropical region (e.g., *Notodiaptomus incompositus*, *Metacyclops mendocinus*; José de Paggi and Paggi 2007; Silva 2008). The nauplii were the most abundant members of this group, attaining

notable densities in the spring and summer seasons, particularly at Canal 2 and the river sites as in other lotic environments (Casper and Thorp 2007; Rossetti et al. 2009). The cyclopoids predominated, with *Acanthocyclops robustus* being the most conspicuous species, as had been found in European rivers (Marneffe et al. 1996; Vadadi-Fülöp et al. 2009). The harpacticoid *Cletocamptus tertius*—likewise typical of brackish environments—had extremely high abundances during the mean flows in the summer season (Echaniz et al. 2005; Gabellone et al. 2014).

Small-sized cladocerans were dominant, with abundance peaks in the canals during high water; although those species were at lower densities than the ones cited in other lowland rivers (Shiel et al. 1982). In high water, the increased hydrologic connectivity could have favored the passage of cladocerans from the connected lentic environments into the canals, as had been observed in other rivers during autumn floodings (Pourriot et al. 1997). On such occasions, *Daphnia spinulata* predominated, which species was typical of saline waters in the pampa region (Claps et al. 2009). In the river, cladocerans were represented by chydorids that mainly developed during mean flows, as had been previously observed in the basin (Neschuk et al. 2002).

Zooplankton reproduction

According to our results, the wetlands and shallow lakes present in the study area acted as a major resource for inocula, thus incorporating zooplankton eggs, larval stages, and gravid females into the Salado River downstream site. A similar functioning of connected lentic environments within river-floodplain systems had been observed in other lowland rivers (Wahl et al. 2008; Burdis and Hoxmeier 2011).

The egg ratios of rotifers, cladocerans, and copepods were very low during high water, which could be explained by the low water temperatures and the higher water velocities. As stated earlier, both parameters constitute limiting conditions for zooplankton development (Baranyi et al. 2002), such that an inverse relationship has been recorded between egg ratios and flow velocities (Saunders and Lewis 1989). Furthermore, the scarcity of available food resulting from the dilution of phytoplankton during high water has been recognized as negatively affecting zooplankton reproduction (Wahl et al. 2008). In contrast, higher egg ratios were reached during the spring and summer seasons, with that period being accompanied by mean to low flows in conjunction with warm water temperatures (i.e., 24–33 °C). *Brachionus plicatilis s.l.* recorded the highest egg ratio (= 2) at the river downstream site during low flows, and on that occasion the mean number of eggs per gravid female of the species was 0.49. This latter value was lower than the 0.99 found by Chaparro et al. (2011) in a floodplain lake within

the Paraná River, but higher than those cited by Hillbricht-Ilkowska (1999) at 0.4 eggs per gravid rotifer female in the Krutynia-River basin, Poland.

The distribution of the rotifer gravid females was likewise related to the spring–summer period and the hydrologic conditions of mean and low flows. Rotifers, for their part, have been found to be capable of producing huge populations under favorable conditions, reaching densities comparable to those of lentic environments (Holst et al. 2002). In this work, the presence of resting eggs reached peak densities during low flows, as had occurred in the Paraná-River floodplain (Chaparro et al. 2011). Thus, the development of resistant eggs is generally induced by an external trigger, such as an abrupt change in the environmental conditions or demographic changes (Lehman 1988; Schröder 2001)—analogous to the exponential growth of *B. plicatilis s.l.* and *B. angularis* observed in low flows.

Similarly, the highest densities of the cladocerans' gravid females were recorded in the river sites during low flows, as had been reported for the Orinoco River (Vásquez and Rey 1989). Likewise, Casper and Thorp (2007) had recorded a higher proportion of gravid females of that taxon in areas with low-flow velocities and standing waters. Conversely, *Daphnia spinulata* exhibited gravid females at the Canal 1 and Canal 2 during high water, probably attributable to the hydrologic connectivity between the river and the adjacent lentic environments (Hillbricht-Ilkowska 1999).

The copepods reproduced in the shallow lakes and wetlands of the study area, since their effluents (recorded at the sampling sites Stream, Canal 2 and Canal 3) exhibited large amounts of nauplii during the favorable season. Similar situations had been recorded in the lake outlets of Algonquin Provincial Park, Canada (Walks and Cyr 2004) and in the outflows of wetlands of the Waikato-River floodplain in New Zealand (Górski et al. 2013). At the river upstream sampling site, the presence of a backwater and the natural configuration of the river margins could have favored the occurrence of gravid females and nauplii there during the spring and summer seasons. Similarly, Picard and Lair (2005) had found copepod reproduction was enhanced by habitat heterogeneity and the availability of low-flow areas within the middle Loire River.

Zooplankton dynamics and the function of river-drainage canals

During high water, hydrologic connectivity between lentic and lotic environments of the study area resulted in the presence of similar zooplanktonic communities throughout the sampling sites. This process of habitat homogenization and reduction of the spatial variability during floodings is a common feature in other lowland rivers of the region; such as the

Paraná River, where that parameter is strongly governed by the hydrologic regime (Thomaz et al. 2007). Conversely, the canals recorded the highest values of species richness during the high water condition (On-line Resource 1), probably attributable to the addition of species from the wetlands and the shallow lakes that those watercourses drain.

In diametric contrast, a clear differentiation was noted in the structure of the zooplankton community throughout the sampling sites during very low flows. Thus, when the hydrologic connectivity became reduced, the local conditions prevailed, and changes in the zooplankton community were detected (Schöll et al. 2012; Simões et al. 2013). In addition, droughts are recognized as disturbances of planktonic communities (Lake 2003) because low connectivity impedes the exchange between portions of the landscape and produces habitat fragmentation (Ward et al. 1999).

According to the *intermediate-disturbance hypothesis* (Connell 1978) the diversity of communities will be the greatest when a disturbance at an intermediate level of frequency and intensity occurs. Ward et al. (1999) applied that concept to the functioning of large rivers and proposed that the diversity would be maximum during intermediate hydrologic connectivity between the river and the corresponding floodplain. Accordingly, in the river sampling sites the highest zooplankton species richness was recorded during mean flows as well as the total abundance of the zooplankton and the reproduction of the species (Fig. 9). Moreover, in view of the expanded *serial-discontinuity-concept* model (Ward and Stanford 1995), the Salado River should be considered as an integrated river-floodplain system, where the intermediate levels of natural disturbance—i.e., the alternation of dry and wet cycles in the region—are precursors of habitat heterogeneity that promote plankton diversity and higher species richness. According to our results, the occurrence of floodings and droughts in succession—i.e., high water, followed by very low flows—constituted a driving force that conditioned the zooplankton community, with that effect being marked because of the presence of canals and lentic environments within the study area. Accordingly, Ning et al. (2013) considered that extreme hydrologic conditions governed the biotic communities in rivers, having an influence, however, highly dependent on the structural characteristics of the system, such as the effects of anthropically produced flow modifications like the system of drainage canals studied here. In contrast, Furst et al. (2014) found that zooplankton community within the River Murray showed highest abundances during high flows, as the Flood Pulse Concept proposes, mostly influenced by the Chowilla Floodplain (Australia).

The discharges from the canals increased the total abundance of the dominant groups of zooplankton and enhanced the species richness in the river downstream site. Accordingly, similar increments from the tributaries had been

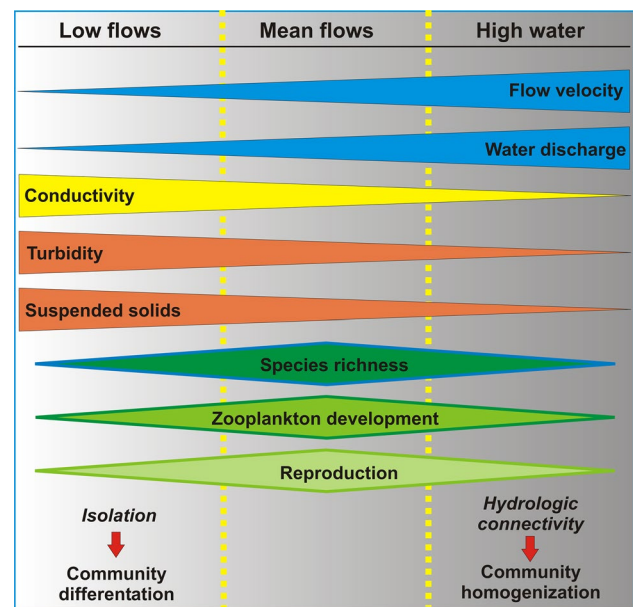


Fig. 9 Schematic representation of the dynamics of zooplankton development (dark green), of the species richness (medium green) and zooplankton reproduction (light green) within the context of key influential environmental parameters. The schema is divided into three hydrologic sectors: low flows (left), mean flows (middle), and high water (right) illustrated in the upper blue profile along with the analogous one of water discharge (lower blue) in the Salado River. The figure depicts how the biologic indices are maximized under conditions of mean flows and discharges (blue) along with medium conductivities (yellow) plus suspended solids and the consequent turbidity (orange). High water also facilitates hydrologic connectivity and the resulting biologic-community homogenization (lower right); while, conversely, low flows promote the isolation of taxa along with community differentiation (lower left). Within the context of this diagram, the two models of *intermediate disturbance* and *serial discontinuity* can be seen to enable a balance between the opposing conditions that generate community homogenization *versus* community differentiation so as to achieve an equilibrium that, along with mean flows, would likewise represent a beneficial ecodynamic overall

previously observed in the Salado basin as well as in other lowland rivers (Neschuk et al. 2002; Zimmermann-Timm et al. 2007; Scherwass et al. 2010), but the input of offspring and reproductive stages of the different taxa that occurred there and were recorded in this study represents a new finding. This influence of the discharges from the tributaries into the Salado River was shown by means of cluster analysis, where the species abundance and its reproductive stages of the river downstream site became significantly related to those of the canals during mean and low flows. Instead, the upstream site was detected by the analysis as being related to itself under those hydrologic conditions. In contrast, the influence of the tributaries was of minor effect during high water as a result of dilution and during very low flows because the inflow from the tributary system became too scanty. The hydrologic condition and the degree of connectivity between the canals and the interconnected lentic

environments of the study area, would thus appear to influence markedly the zooplankton structure in the river downstream site (River 2), through the discharges from the tributaries. Thus, hydrologic connectivity across river-floodplain systems has come to be considered one of the main driving forces for plankton diversity—as such, however, frequently governed by seasonal flow and flood pulses (Górski et al. 2013; Furst et al. 2014; Chaparro et al. 2019). As a consequence, the zooplankton structure in the present work was found to be determined by the upstream community and by the colonization pressure exerted by the tributary discharges mostly during mean and low flows, which influences acting in concert regulated the assemblages of the species found in the river downstream site.

The canals are anthropic modifications in the drainage network of the Salado River, whose array constitutes a trapezoidal cross-sectional area, particularly with respect to the Mercante and Este Canals (Canal 1 and Canal 3 sampling sites, respectively; cf. Fig. 1). Most of the man-made canals follow linear field boundaries, often turning in right angles, and exhibit little relationship to the landscape contours (Biggs et al. 2017). These characteristics impede the development along the canals' margins of the associated communities—i.e., the macrophytes and organisms in the epiphyton, benthos, and epipelon—hence disabling the presence of buffer zones to cope with the input from terrestrial ecosystems through runoff. The steep margins are meant to increase discharge and current velocity, but in contradistinction, this feature instead facilitates the drift of plankton and also impairs zooplankton reproduction (Rossetti et al. 2009; Kim et al. 2012). Consequently, these particular geomorphologic aspects have affected the characteristics of those lotic environments, such as the maximum amplitude recorded in values of the physicochemical parameters and biological descriptors throughout samplings. Unlike natural watercourses, drainage canals lack morphologic features that promote spatial heterogeneity, differential current velocities, or storage areas (i.e., backwaters, stagnant water areas) to encourage plankton development (Walks 2007; Withers and Jarvie 2008). Therefore, such deficiencies could explain the lower zooplankton abundances found at Canal 1 and Canal 3, than at Canal 2, which latter site constitutes the channelization of a wetland between two shallow lakes.

Conclusion

This research represents the first description of the zooplankton reproduction and larval stages in the Salado-River basin, while the exceedingly high abundance of *B. plicatilis* s.l. found here constitutes a novel datum in the region as well as worldwide. In addition, the information gathered in this investigation is relevant in view of the new

canalizations scheduled in the region, such as the direct discharge of the Mercante Canal (Canal 1) into the Salado River. In such a circumstance, the zooplankton diversity and the community structure would be disrupted in the river downstream, because of the avoidance of the wetlands and shallow lakes present in the study area. Those features reduce salts and produce a large number of zooplankton organisms and offspring, with that input always boosting the river productivity. Within this context, we consider that the maintenance of the river connections with the tributaries and the wetlands is essential because those interconnected lentic environments ensure the integrity of the zooplankton dynamics and the ecologic functioning of those taxa in the basin.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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