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Article

Relationship between the zoo- and phytoplankton biomasses in a saline lowland river (Argentina): a short-time-scale analysis

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With 10 figures and 6 tables

Abstract: Short-time-scale (days) lotic investigations during low-discharge conditions are appropriate for elucidating trophic relationships within plankton. The objectives of this study were to determine the successional changes in the zooplankton biomass, the relationship of that biomass to physical parameters and palatable phytoplankton species, and to evaluate the observational time scale. Plankton samples were taken thrice weekly at two sampling stations in the Salado River lower sector (Buenos Aires province, Argentina). Since almost one-third of the country's agricultural and cattle productions come from the Salado-River basin with their resulting impacts (nutrients, suspended material) in the basin, limnological research has been conducted there during recent decades. To estimate grazing, we employed three models and also the relationship between the zoo- and nanoplankton biomasses. The seasonal temperature and conductivity changes indicated three clearly different periods and were the main parameters driving the seasonal succession of the zooplankton. During the first period, the total zooplankton biomass was less than in the other two, with the tintinnids predominating. Later, the rotifers became prevalent with a predomination by *Brachionus plicatilis* and *Keratella tropica*. The grazing pressure of the r-strategy dominated zooplankters was highly variable. Zooplankter-species replacement by those of different grazing efficiencies promoted changes in the phytoplankton structure and nanoplankton biomass. A top-down effect on the total phytoplankton biomass by the zooplankton was not detected, though an abundance diminution for certain palatable algae was observed. The biomass of the nanoplankton species was significantly related to the total zooplankton biomass, with the highest rotifer values being associated with an exponential decrease in the nanoplankton biomass.

Key words: plankton, biomass, pampean lowland river, Argentina.

Introduction

The potamozooplankton in the majority of lowland rivers have a similar community structure (Pace et al. 1992, Kobayashi et al. 1998, Lair 2006). This characteristic feature is related to the common hydraulic conditions present that favor the development of small organisms having low individual body weights and short generation times, such as ciliates and rotifers. These latter organisms exhibit a high abundance at low discharge rates and can restore populations rapidly after floods (Rossetti et al. 2009). Other population-influencing conditions are salinity, seasonal changes in temperature, and the particular geomorphologic features of the basin (i.e., the presence of associated lakes) or of the main course (i.e., constituent dead zones, flushing lakes). In rivers with a high turbidity, this condition exerts an essential influence on

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planktonic structure by: (1) promoting a dominance of rotifers, especially in turbulence produced by hydraulic modifications and dredging of a river, (2) acting negatively on crustacean development (Lair 2006). Nevertheless, Kobayashi (1997) found that rotifers also predominated in low-turbidity rivers. Basu & Pick (1996) pointed out that rotifers were dominant in several rivers in Canada with different uses of the surrounding land. The low density of crustaceans in the plankton of rivers may not be related simply to the presence of particles since the dominance of rotifers has been reported in rivers with considerable differences in turbidity, conductivity, flow velocity, macrophyte profiles, the type and density of zooplankton, and the nutrient concentration (Lair 2006, Burdis & Hoxmeier 2011). During low water discharge, biotic interactions (e. g., zooplankton grazing and predation, invertebrate and fish predation on zooplankton) can be considered essential drivers of a river's planktonic structure (Gosselain et al. 1998b, Lair et al. 1999, Thorp & Casper 2003, Lair 2005, Picard & Lair 2005, Rossetti et al. 2009). It is also possible to determine the typical lotic composition in response to the limited incorporation of inocula from associated lentic water bodies (Ferrari et al. 2006).

Since small-scale occurrences present informative opportunities for detecting fine changes in species dominance and very short successional events, samplings must be made at shorter intervals, especially under low-flow conditions (Ferrari et al. 1989, Bonecker et al. 2002, Ferrari et al. 2006, Kiss et al. 2009, Harris & Heatwait 2012).

In the Salado-River basin, several plankton investigations have been carried out during the last decades. The plankton associated with a backwater pond has been investigated monthly in the lower sector (Gabellone et al. 2001, Solari et al. 2002). An input of organisms from that backwater pond 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 a seasonal characterization of rotifer assemblages throughout the entire basin and emphasized that the nature and distribution of the species present were determined by conductivity and nutrient availability as well as by an input from adjoining ponds and waterlogged depressions. The rotifer assemblages recorded were similar to those present in Australian rivers (Kobayashi et al. 1998, Shiel et al. 1982, Shiel 1985, Shiel et al. 2006). During a seasonal investigation, Claps et al. (2009) distinguished different zones within the longitudinal axis of the basin according to the zooplankton assemblages present: (1) the headwaters, (2) an intertributary zone (i. e., the tributaries plus the middle sector), and (3) the lower basin. They found that the species with spatial and temporal dominance exhibited a wide tolerance to the high salinity values of this lowland river, and represented all-habitat species within the assemblages. As an initial finding in this type of short-time-scale sampling, Bazzuri et al. (2010) reported that the Salado-River phytoplankton showed significant seasonal variations with respect to composition and species abundance in response to environmental physical variables such as conductivity, temperature, and hydrologic fluctuations – namely, an evident modification in phytoplankton structure occurred from late summer (predominance of *Planctonema lauterbornii* and species of *Chrooccocus* and *Merismopedia*) to winter (e.g., *Binuclearia* sp., *Microcystis firma*). We consider that the performance of an intensive sampling investigation on a lowland river containing a diversity of plankton would facilitate an understanding of the system's complexity, characterize very short successional events, and assess the impact of hydraulic modifications on the plankton community. We assume here that the succession of changes in phytoplankton structure and biomass have a direct effect on the corresponding zooplankton structure and biomass. The effects of grazing zooplankters on the total phytoplankton biomass depend specifically on the contribution of the palatable nanoplankton algae within that biomass and vary according to the grazing efficiencies of zooplankton species. Since the effects of zooplankton grazers on the total phytoplankton biomass depend specifically on the contribution of the nanoplankton, the nanoplankton participation within the total phytoplankton biomass will necessarily determine the extent to which such grazing is possible and therefore the overall resulting impact of that predation on the total phytoplankton population.

The main objectives of this study were: a) a determination of the changes in the biomasses of the most abundant zooplankters during short time periods (days), b) the relationship between the zooplankton biomass and the palatable phytoplankton species, c) the relationship between the structural changes in the zooplankton and the variations detected in the physical parameters along with the possibility that those interactions may have synergistic effects on the phytoplankton, and d) a comparison of some of the results of this investigation with those obtained previously at both sampling sites in order to evaluate the observational time scale.

Study area

The Salado – the major river within the Buenos Aires province and the southernmost tributary of the La-Plata-River basin – is a typical lowland river 571 km in length with a low mean slope of 0.107 m km^{-1} and a catchment of approximately 150,000 km^2. The Salado basin is located in dry, temperate floodplains and includes a large number of shallow lakes with different degrees of connectedness, occupying 1,000 km^2 under normal conditions of river flow. The Salado's regime is quite variable with flows reaching no more than 100 m^3 s^{-1} in dry periods, but increasing to as much as 1,500 m^3 s^{-1} (recurrence of 10 years) during floodings (mainly in autumn), along with consequent variations in the conductivity and transport of dissolved and particulate materials (Gabellone et al. 2005). The climate is humid and temperate with a mean annual precipitation of 899 mm (Gabellone et al. 2001, Gabellone et al. 2008, Solari et al. 2002).

The study area comprises the lower stretch of the river at two different sampling sites, El Destino (ED) and Guerrero (G), located 108 and 92 km from the mouth, respectively (Fig. 1). This portion of the river includes a series of interconnected depressions, such as the La Tigra flushing lake and the San Miguel backwater pond, the latter being connected to the river by a short channel. The upstream site, ED (35° 57′ S; 58° 01′ W), is located 462 km from the source and constitutes the beginning of the river's lower basin. The other sampling site, G (35° 59′ S; 57° 51′ W), is located downstream at an old bridge, La Postrera, whose removal and replacement were carried out during the present study. During the period of observation, both bridge construction and dredging were performed.

In addition to the La Tigra and San Miguel bodies, the river also receives discharges from other connected ponds along the San Miguel Stream – those being the Camarones Grande and Chica and the San Lorenzo shallow lakes (Solari et al. 2002). Almost one-third of the agricultural and cattle productivity of the country is located in the Salado-River basin. The mouth of the Salado is a RAMSAR conservation site (Ramsar Convention Bureau 2004), and the basin has been altered

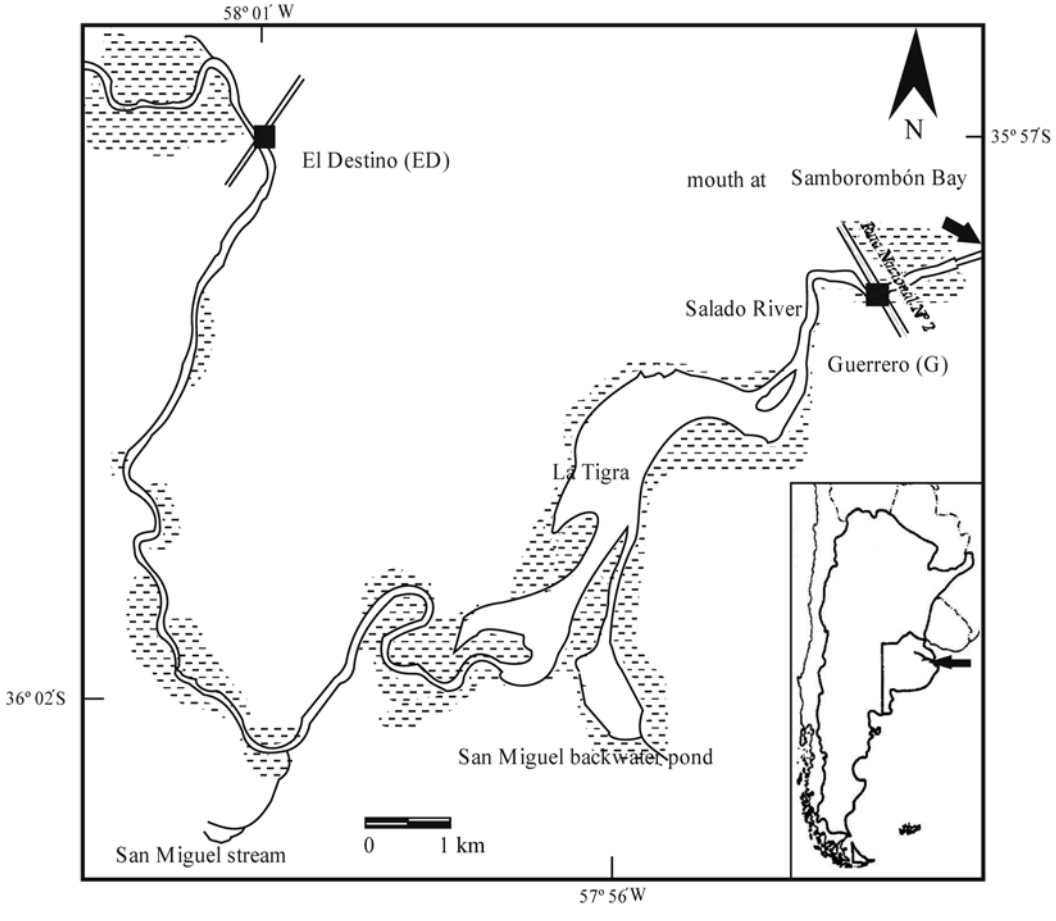

Fig. 1. The main drainage system and locations of the sampling stations in the Salado-River basin.

there by hydraulic modifications to improve the drainage of the agricultural zones. At the present time, policies of management and monitoring are absent for this river system.

Methods

Sampling and laboratory methods

Zooplankton samples were usually taken with a suction pump three times a week – from 22 March to 5 July of 2004 (Autumn to Winter) – and numbered 42 in all for each site. Three 10-L samples, taken at equal intervals along the line extending from bank to bank, were pooled and passed through a 25-mm-diameter hose into a 35-µm mesh net. The material retained was preserved in a 4 % (v/v) aqueous formaldehyde solution. At each sampling point along the river, in-situ measurements of environmental physical variables (temperature, pH, conductivity, dissolved-oxygen concentration (DO), and turbidity) were obtained with a Horiba U-10 multimeter and the mean values for the data were subsequently calculated. 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 subsamples were then enumerated while taking into account that the coefficient of variation was lower than 20 %. Ciliate-cell volumes were calculated through the use of geometric formulae (Karayanni et al. 2004) based on an individual's size and shape. Tintinnid-cell volumes were considered as half the lorica volume (Beers & Stewart 1969).

Biomass estimations employed the conversion of cell volumes to dry weights (DW) by the factor 0.279 pg of DW μm^{-3} (Park & Marshall 2000), while the values for rotifers were estimated from the volume measurements by means of geometric approximations (Ruttner Kolisko 1977) on each sampling date (with n = 10 to n = 30 for each taxon sampled). The measured volume was converted to dry weight assuming a specific gravity of 1.0 and a ratio of dry to wet weight of 10 % (McCauley 1984). The DWs of cladocerans, larval, juvenile stages and adults of copepods were estimated on each sampling date from the length-weight regressions available for morphologically similar species (Dumont et al. 1975). The phytoplankton biovolume was calculated according to the formula proposed by Hillebrand et al. (1999) and converted to dry weight after Jepessen et al. (1999). In addition, with the exception of cyanobacteria and diatoms, the edible and inedible nanoplankton were distinguished on the basis of grazing-resistant shapes and adaptations (e. g., the presence of spines, mucilage, cell number of colonies or coenobia). The models proposed by Knoechel & Holtby (1986), Lampert (1988), and Keckeis et al. (2003) were applied to determine the phytoplankton-clearance rates of grazers. Zooplankton grazing was also estimated by the relationship between the biomasses of the grazer zooplankton (µg DW L^{-1}), the total phytoplankton (µg DW L^{-1}), and the palatable phytoplankton (< 20 µm) for each sampling date. At high grazing pressure, this rate can exceed 100 %, indicating a complete depletion of the food algae.

The concentrations of total suspended solids (SS) were measured (method 2540D, APHA 1995) and the total phosphorus (TP) was determined by the ascorbic-acid assay after digestion with acidic persulfate (method 4500-PB, APHA 1995).

Statistical analysis

The rates of change in the temperature and conductivity for each period were estimated by dividing the difference between the values for two consecutive sampling dates by the quantity of days lapsed between each measurement. Upon taking into account all the sampling dates during each period, the sum of those values gives the rate of change in the temperature (°C d^{-1}) and conductivity (µS d^{-1}) for each period.

Simple- and multiple-regression analyses (the stepwise method) were employed to analyze the relationship between the zooplankton biomass and the total phosphorus, suspended solids, environmental physical variables, and the biomasses of the nanoplankton (< 20 µm) and the total phytoplankton.

The differences between environmental variables (conductivity, pH, temperature, turbidity, TP, SS, DO), and the biomass of the most abundant zooplankton species in the samples of the two sectors (El Destino and Guerrero) from different periods were tested by Analysis of Similarities (ANOSIM). The Euclidean distance was used as the similarity index for normalized environmental variables and 10,000 permutations run to calculate the significance level of the sample statistic R. The ANOSIM-test results were then supported by an analysis of multidimensional-scaling (MDS) ordination. A similarity matrix of zooplankton abundance with log (x +1)-transformed data was constructed by means of the Bray-Curtis similarity index. The percent contribution of each taxon to patterns of dissimilarity was examined by Similarity-Percentage (SIMPER) analysis, and those taxa contributing at least 10 % dissimilarity were considered significant differentiators. The MDS, SIMPER, and ANOSIM analysis were performed through the use of the PRIMER v. 5.2.9 (2001).

Multivariate-ordination techniques from the CANOCO program (version 4.5) were used to investigate the relationship between species composition and environmental variables over the length of the total study period with the environmental variables being standardized (Pielou 1984, Ter Braak 1986). Because the lengths of the gradients of explanatory variables were short, the method of redundancy analysis (RDA) was selected over the canonical-correspondence analysis, as suggested by ter Braak & Smilauer (2002). Only the environmental parameters with variance-inflation factors < 10 were retained in the analysis because a greater value would indicate a multicolinearity among the variables (ter Braak & Verdonschot 1995). The statistical significance of the variation in the parameters and the overall significance of the ordination were tested with the Monte Carlo permutation test (499 unrestricted permutations; $p < 0.01$).

Results

Physical and chemical characteristics

During the sampling period coinciding with seasonal temperature variations, significant changes occurred in the local rainfall in this and other basin sectors that affected the discharge directly and the conductivity indirectly. These changes permitted the recognition of three clearly different periods influencing the zooplankton community. Initially, the mean conductivity

Table 1. Mean, minimum, maximum, and standard-deviation values of specific physicochemical parameters along with zooplankton biomasses recorded (µg DW L–1) in the sampling stations during the three established periods.

	1st period Mean (minimum–maximum)	SD	2nd period Mean (minimum–maximum)	SD	3rd period Mean (minimum–maximum)	SD
El Destino (ED)						
pH	8.2 (7.7–8.4)	0.21	8.2 (8.0–8.4)	0.09	8.3 (8.2–8.4)	0.07
Conductivity (µS cm^{-1})	10960.4 (583.0–12570.0)	210.80	7140.1 (5830.0–8040.0)	82.50	6307.0 (5590.0–6920.0)	37.10
Turbidity (NTU)	233.0 (167.0–311.7)	44.00	242.6 (157.7–356.3)	57.70	322.9 (148.7–663.3)	129.00
Dissolved oxygen (mg L^{-1})	4.8 (2.8–7.2)	1.29	7.1 (5.2–12.0)	2.00	8.4 (5.9–17.8)	3.09
Temperature (°C)	21.6 (15.7–25.8)	3.36	13.0 (10.9–17.0)	2.20	10.7 (8.3–13.1)	1.30
Suspended solids(g L^{-1})	0.11 (0.07–0.14)	0.02	0.10 (0.06–0.15)	0.03	0.14 (0.10–0.18)	0.02
Total phosphorus (µg L^{-1})	763.9 (571.8–1152.9)	183.33	820.8 (403.6–1091.7)	211.30	867.8 (480.0–1229.3)	241.80
Total zooplankton biomass	91.7 (14.4–235.6)	63.18	154.1 (62.1–319.5)	68.70	100.4 (50.3–179.9)	34.10
Ciliate biomass	42.0 (0.7–193.5)	48.41	19.3 (0.0–67.6)	21.30	0.004 (0.0–0.06)	0.01
Rotifer biomass	47.8 (10.3–112.1)	27.92	128.7 (32.2–299.2)	69.30	72.4 (34.0–128.1)	24.90
Crustacean biomass	1.9 (0.0–13.4)	3.54	6.1 (0.0–21.7)	7.30	28.0 (6.2–51.8)	16.80
n	14		14		14	
Guerrero (G)						
pH	8.4 (7.8–8.5)	0.18	8.3 (8.2–8.5)	0.09	8.3 (8.2–8.4)	0.07
Conductivity(µS cm^{-1})	11317.0 (6770.0–12200.0)	1338.29	7082.0 (5957.0–8030.0)	79.03	6302.0 (5670.0–6930.0)	36.90
Turbidity (NTU)	265.7 (113.0–370.0)	59.79	234.2 (175.3–408.7)	60.06	209.6 (131.7–251.7)	33.30
Dissolved oxygen (mg L^{-1})	6.8 (2.8–10.5)	2.29	9.5 (6.6–19.1)	3.00	10.4 (7.4–18.9)	3.50
Temperature (°C)	21 (14.2–27.5)	4.87	12.4 (8.7–15.4)	1.920	10.6 (8.2–13.6)	1.40
Suspended solids (g L^{-1})	0.12 (0.08–0.19)	0.03	0.08 (0.07–0.10)	0.01	0.09 (0.07–0.12)	0.12
Total phosphorus (µg L^{-1})	779.3 (541.2–1229.0)	213.76	753.1 (434.1–984.7)	185.15	717.0 (449.0–1321.1)	214.80
Total zooplankton biomass	73.4 (7.5–240.3)	68.70	126.1 (25.2–357.7)	88.50	123.6 (47.1–244.2)	49.30
Ciliate biomass	57.1 (0.1–225.6)	69.21	6.3 (0.0–26.1)	7.54	0.05 (0.0–0.45)	0.12
Rotifer biomass	16.0 (2.7–37.8)	11.21	118.1 (22.4–350.0)	89.36	109.59 (41.9–190.8)	41.30
Crustacean biomass	0.3 (0.0–2.3)	0.66	1.7 (0.0–7.8)	2.68	13.9 (3.4–53.4)	13.80
n	14		14		14	

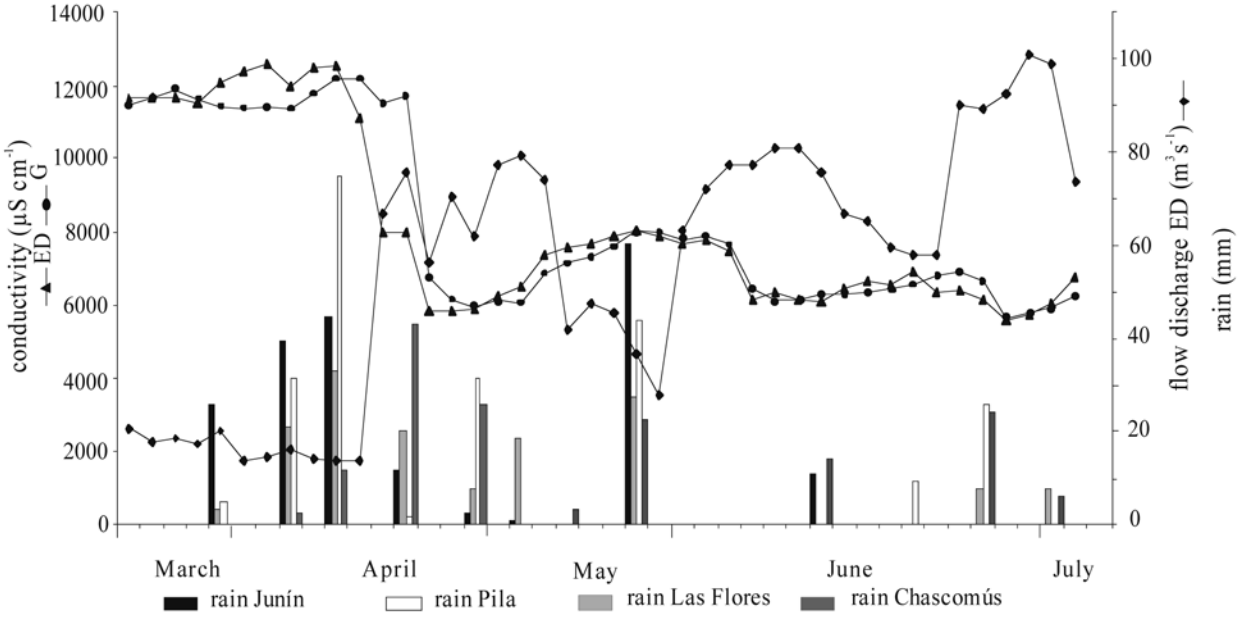

Fig. 2. Rainfall records at selected sites (Junín, Las Flores, Pilar, Chascomús) within the Salado-River basin, conductivity values at both the present sampling sites, and flow discharges corresponding to ED.

values were the highest while the mean temperature was above 20 °C, but later decreased to values of 10 °C (Table 1, Fig. 2). In the first period, the DO was less than in the other two. These changes were more evident at ED. In general, during the first period, the values of the physical and chemical parameters were the lowest at ED. The maxima for the TP concentration were recoded in the third period and the minima in the second (Table 1). The turbidity and SS decreased slightly at G throughout the periods but increased at ED (Table 1). The pH values were always alkaline, without significant differences among the three periods at either site.

According to the ANOSIM (significant global R of 0.4, significance level = 0.1 %), and SIMPER analyses, the environmental variables manifested some differences among the three periods. In both sectors, the differences between the second and third periods were not significant. At ED, turbidity and temperature were responsible for the differences between the first and the third periods. At G, those differences were significant between the first and second periods mainly as a result of the differing temperatures and DO. Turbidity, TP, and DO were responsible for the differences between the first and third periods. Moreover, the differences recorded between each period at both sampling sectors were not significant (first period: R = 0.09, significance level = 3.4 %; second period: R = 0.08, significance level = 5.7 %; third period: R = 0.15, significance level = 0.9 %). An MDS analysis supported the ANOSIM results, pointing to the differences between the first third as opposed to either of the others at both sampling sectors (Fig. 3).

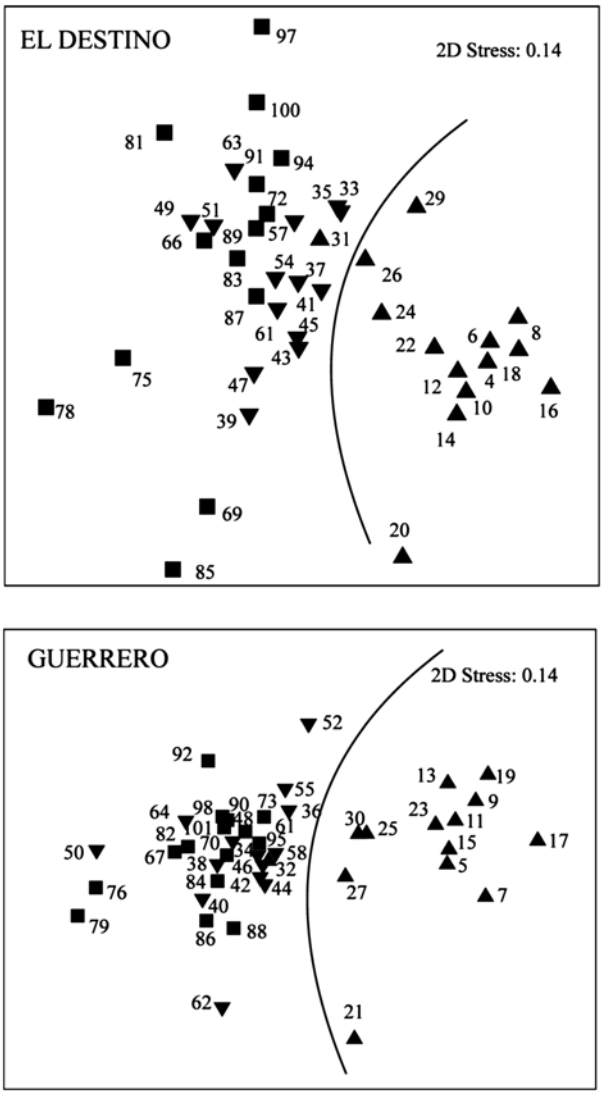

Fig. 3. MDS plot of environmental parameters for the three periods: triangles, first; inverted triangles, second; squares, third.

Zooplankton structure and dynamics

In the zooplankton, 48 taxa were identified (Table 2). The highest species richness (SR) was recorded in May and June, while the corresponding minima were registered in June and in May, and at two later dates in June. The minimum SR value recorded at ED coincided with the maximum zooplankton biomass. At ED and G, the rotifers were dominant (mainly Brachionidae species), while ciliates codominated. In spite of differences throughout the study (Fig. 4), the overall mean SR was similar at both sites (at ED, 12 species and at G, 11.5 species).

The total zooplankton biomass was the highest at ED, with that maximum corresponding to a greater contribution of the crustaceans. The ciliates and rotifers had similar mean-biomass values at both sites (Table 1). The rotifers were present on all sampling occasions with biomass values higher than 10 µg DW L^{-1}. At ED, the maximum total zooplankton biomass was detected in June (Fig. 4), with a predominance of *Brachionus plicatilis* followed by *Keratella tropica*, but with values lower than those of *B. plicatilis* by an order of magnitude. On this occasion, the rotifer biomass represented nearly the total value for the zooplankton. A second, previous biomass peak (April) had coincided with a low SR (Fig. 4) and involved a predominance of tintinnid ciliates. At G, a biomass maximum higher than 300 µg DW L^{-1} (in June) also coincided with an SR minimum, whereas the other peaks were detected in coincidence with high SR values (in April and June). The minimum in both sectors

Table 2. The percentage of the main zooplankton species present in the total number sampled and their frequency at the indicated sampling stations during the three established periods.

		1st		2nd		3rd				1st		2nd		3rd	
	% samples (n = 84)	ED	G	ED	G	ED	G		% samples (n = 84)	ED	G	ED	G	ED	G
Arcella hemisphaerica	12	0	29	7	7	21	7	*Cephalodella* sp. 2	2	0	0	0	0	14	0
Fabrea salina	4	14	7	0	0	0	0	*Colurella* sp.	10	21	14	0	7	7	7
Codonella cratera	42	43	100	29	43	7	29	*Conochilus unicornis*	2	7	0	0	7	0	0
Difflugia sp.	6	14	0	7	0	14	0	*Filinia longiseta*	49	100	100	36	43	7	7
Epistylis sp.	18	7	14	29	21	21	14	*Keratella americana*	4	0	0	7	0	7	7
Holophrya sp.	25	14	7	36	36	29	29	*K. tropica*	99	100	93	100	100	100	100
Paramecium sp.	19	0	0	14	7	43	50	*K. serrulata*	5	0	0	0	0	0	29
Systylis hoffi	1	0	0	7	0	0	0	*Lecane luna*	7	7	0	21	0	0	14
Stentor sp.	2	0	0	0	0	14	0	*Lecane* sp.	7	7	0	14	7	7	7
Tintinnidium fluviatile	58	100	93	79	79	0	0	*Lepadella ovalis*	7	0	7	7	0	14	14
Tintinnopsis fimbriata	17	21	36	0	21	7	14	*Notholca acuminata*	14	0	0	14	14	14	43
Tokophyra sp.	4	7	14	0	0	0	0	*N. squamula*	7	0	0	0	7	21	14
Vorticella campanula	33	50	64	14	29	29	14	*Pompholyx sulcata*	17	21	7	0	7	29	36
Zoothamnium sp.	2	0	0	0	0	14	0	*Polyarthra vulgaris*	24	50	21	43	29	0	0
Asplanchna brightwellii	79	57	71	93	71	93	86	*Proales* sp.	24	7	21	43	57	7	7
A. girodi	13	7	0	29	21	7	14	*Proalides* sp.	42	21	14	71	64	36	43
Brachionus angularis	55	100	100	57	50	7	14	*Squatinella rostrum*	2	0	0	7	0	0	7
B. caudatus	49	50	29	57	57	50	50	*Synchaeta pectinata*	4	0	0	7	0	7	7
B. havanaensis	11	36	14	14	0	0	0	*Testudinella patina*	4	0	7	0	0	14	0
B. plicatilis	100	100	100	100	100	100	100	*Trichocerca pusilla*	36	21	29	50	50	21	43
B. pterodinoides	12	14	14	21	14	7	0	*Bosmina huaronensis*	27	0	0	0	7	79	79
B. quadridentatus	19	7	0	7	7	43	50	*Acanthocyclops robustus*	5	0	0	7	0	7	14
B. urceolaris	12	14	0	21	7	14	14	*Notodiaptomus incompositus*	6	0	0	0	0	29	7
Bdelloids	62	57	57	64	86	36	71	*Cletocamptus deitersi*	81	71	57	93	64	100	100
Cephalodella sp. 1	1	0	0	0	0	7	0								

was recorded in March at the very beginning of the study (Fig. 4).

At ED, the ciliates passed through a maximum in April, whereas at G this group showed two peaks during consecutive days (April 12 and 13 with the higher value on the latter). *Tintinnidium fluviatile* was the dominant tintinnid at ED, whereas this species maintained constant values at G, with *Codonella cratera* being the predominant ciliate there (Table 3). In the beginning of June, the ciliate abundance diminished markedly, showing insignificant biomass values (lower than 1 µg DW L^{-1} (Fig. 4).

The crustaceans always developed biomass values lower than 60 µg DW L^{-1}, with a reduced or absent contribution at ED until the beginning of June. The maximum for this group occurred in June in both sectors. At the site nearer the mouth (G), the mean biomass was lower, having only two peaks (June): In the first one, and for this sole occasion, *Notodiaptomus incompositus* (44.5 µg DW L^{-1}) and *Bosmina huaronensis* (6.9 µg DW L^{-1}) were responsible for the peak in comparison with the biomass values recorded in the upstream sector for the second (at only 12.0 µg DW L^{-1}). At ED, *Cletocamptus deitersi* was the crustacean with the highest frequency, but only *B. huaronensis* and *B. huaronensis* along with *N. incompositus* were responsible for the maximum in biomass (Fig. 4).

In the third period, the total biomass diminished markedly at ED. This is in spite of the increase in the crustacean component in response to the decrease in the biomass of the rotifers and the corresponding decline in predation by the *Asplanchna* species. At G, the total biomass in the second and third periods was similar as a result of the contribution of the crustaceans (Table 1).

The most significant contribution in biomass of *K. tropica* was recorded at G. *Cletocamptus deitersi* developed a maximum biomass at ED during the second and third periods. Certain species manifested marked differences between the two sectors. The biomass of *A. brightwellii* was only greater at ED than at G in the first period. During that same period, the biomass of *B. plicatilis* at ED became four times greater than that recorded at G, but during the second period the value was slightly higher at ED, with the opposite pattern occurring during the third period. In the first period, the ciliates predominated at a high abun-

Table 3. Mean of biomass (µg dry weight L^{-1}) of selected zooplankton species at the sampling stations during the three established periods (standard deviation in italic, minimum and maximum values in brackets.

	El Destino			Guerrero		
	1st	2nd	3rd	1st	2nd	3rd
Asplanchna brightwellii	3.57 *6.58* (0–21.7)	10.83 *13.21* (0.00–42.00)	2.46 (0.00–9.10)	2.09 *2.67* (0.00–6.99)	11.99 *19.6* (0.00–71.5)	2.41 *2.45* (0.00–7.7)
Brachionus angularis	1.98 *1.92* (0.04–7.02)	0.28 *0.33* (0.00–1.51)	0.00	1.14 *0.64* (0.11–2.23)	0.19 *0.29* (0.00–0.99)	0.004 *0.009* (0.00–0.3)
B. caudatus	0.20 *0.31* (0.00–0.98)	0.36 *0.69* (0.00–2.43)	0.05 *0.06* (0.00–0.15)	0.09 *0.19* (0.00–0.53)	0.12 *0.19* (0.00–0.69)	0.12 *0.15* (0.00–0.44)
B. plicatilis	36.20 *20.01* (7.9–72.5)	111.61 *72.22* (29.62–287.29)	68.35 *23.00* (32.12–119.87)	10.34 *7.21* (1.23–2.46)	94.20 *85.70* (14.57–323.27)	94.94 *38.27* (35.96–167.95)
Filinia longiseta	1.09 *0.97* (0.01–2.65)	0.02 *3.67* (0.00–0.11)	0.00	0.35 *0 39* (0.01–1.25)	0.03 *0.05* (0.00–0.15)	0.002 *0.008* (0.00–0.03)
Keratella tropica	4.63 *5.43* (0.00–13.48)	2.75 *3.67* (0.99–15.21)	1.51 *0.48* (0.27–2.21)	2.07 *3.81* (0.00–13.19)	11.41 *7.17* (3.77–23.52)	12.12 *4.53* (5.25–2.17)
Polyarthra vulgaris	0.14 *0.22* (0.00–0.65)	0.52 *1.13* (0.00–4.22)	0.00	0.01 *0.02* (0.00–0.07)	0.01 *0.02* (0.00–0.04)	0.00
Trichocerca pusilla	0.03 *0.08* (0.00–0.29)	0.08 *0.12* (0.00–0.37)	0.01 *0.02* (0.00–0.05)	0.021 *0.05* (0.00–0.16)	0.06 *0.09* (0.00–0.32)	0.01 *0.01* (0.00–0.05)
Codonella cratera	0.35 *0.74* (0.00–2.79)	0.05 *0.09* (0.00–0.03)	0.004 *0.01* (0.00–0.06)	35.34 *65.17* (0.06–185.04)	0.94 *1.49* (0.00–4.26)	0.06 *0.12* (0.00–0.45)
Tintinnidium fluviatile	40.45 *48.56* (0.22–193.46)	20.98 *20.50* (0.00–67.35)	0.00	21.55 *17.11* (0.00–45.74)	5.38 *6.50* (0.00–35.40)	0.00
Cletocamptus deitersi	0.95 *1.27* (0.00–3.61)	6.38 *7.33* (0.00–22.18)	6.97 *4.35* (2.26–15.54)	0.30 *0.66* (0.00–2.26)	1.59 *2.41* (0.00–7.69)	3.73 *1.76* (1.63–7.93)
Bosmina huaronensis	0.00	0.00	13.27 *13.01* (0.00–44.94)	0.00	0.11 *0.46* (0.00–1.74)	6.21 *4.59* (0.00–15.93)

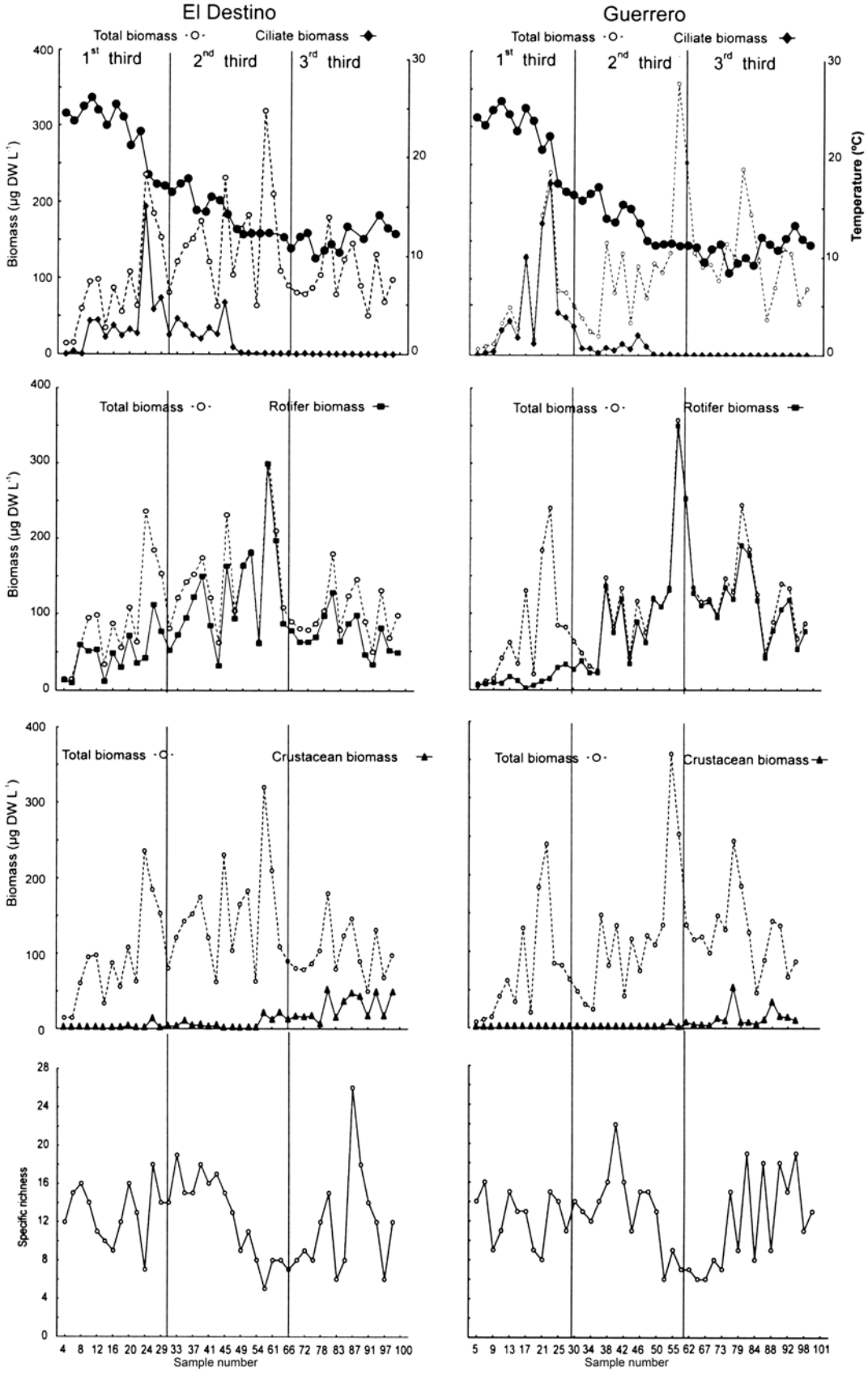

Fig. 4. The total zooplankton, ciliate, rotifer, and crustacean biomasses, temperatures, and species richness at the two sampling stations. The vertical lines indicate the three different constituent periods into which the series of samplings was divided.

dance in both sectors (ED, 3,572; G, 3,341 individuals L^{-1}), whereas the biomass of the ciliates in ED was lower than that of rotifers (Table 1). *Codonella cratera* showed low biomass values at ED in all sampling periods, whereas this species dominated at G in the first. The biomass of *T. fluviatile* and *B. huaronensis* at ED was always double the values recorded at G, whereas the biomass of *C. deitersi* showed the opposite behavior (Table 3).

Brachionus plicatilis and *K. tropica* attained a frequency of 100 % with respect to all the sampling dates and sites. *Brachionus angularis* and *Filinia longiseta* were present in all the samples of the first period, with a clear diminution in the second and a practical disappearance in the third. The predator *A. brightwellii* had a greater presence in the first period, while *T. fluviatile* was the most frequent ciliate in the first and second periods, though absent in the third. *Codonella cratera* was also frequent, with a maximum presence in the first period. The harpacticoid *C. deitersi* (including both immature forms and adults) showed the highest frequency among the crustaceans, with the highest values recorded in the third period in both sectors. *Bosmina huaronensis* was present in only the third period at either site (Table 2). Certain taxa not included in the biomass estimation, such as bdelloids, were frequent with a substantial presence occurring at G during the second and third periods. Other rotifers exhibited a markedly temporal distribution. For example, *Brachionus quadridentatus*, *Notholca acuminata*, and *N. squamula* were more frequent during the third period (winter), whereas *Brachionus havanaensis* prevailed in the first (summer), but was absent in the third (Table 2).

According to the ANOSIM (significant global R, 0.6; significance level, 0.1 %) and SIMPER analyses, the biomass of the most prevalent zooplankters showed significant differences between all of the three periods in both sectors. At ED, *T. fluviatile*, *B. plicatilis*, and *A. brightwellii* were responsible for the difference between the first and second period, whereas at G the same species plus *K. tropica* and *C. cratera* contributed to that dissimilarity. At ED, the biomass of *T. fluviatile*, *C. deitersi*, and *B. huaronensis* was responsible for the differences between the first and third periods (Table 4). Moreover, differences between each period in both sampling sectors were significant (first period, $R = 0.24$ and significance level = 0.1 %; second period, $R = 0.29$ and significance level, 0.2 %; third period, $R = 0.44$ and significance level = 0.1 %). An MDS analysis supported the ANOSIM results, pointing to the differences among the three periods at both sampling sectors (Fig. 5).

According to the RDA results for ED, the first canonical axis and the sum of all canonical axes explained a significant portion of the variance in the zooplankton-biomass data ($p = 0.01$; $p = 0.004$, respectively). The environmental variables that were significantly correlated ($p < 0.05$) with the canonical axes were pH, conductivity, temperature, and DO. Temperature, conductivity and DO were correlated with the first axis ($R = 0.83$, 0.62, and −0.55, respectively), while pH with the second axis ($R = -0.79$). The first two canonical axes explained 98 % of the cumulative variance. The temperature and conductivity defined the first axis, with *T. fluviatile* and the majority of the rotifer species located on the positive end. All these zooplankters presented their highest biomass values during the first period. In the negative sector of the axis, the species were characterized by maxima in biomass coinciding with the highest DO concentration and the lowest temperature and conductivity values registered in the second and third periods (Fig. 6).

In the RDA applied at G, the first two canonical axes explained 97 % of the cumulative variance of the

Table 4. Average dissimilarity between the periods taking in account contributions of main species for each sampling site. The highest values of contributions between groups are highlighted with numbers in bold.

	El Destino			Guerrero		
	1st–2nd	1st–3rd	2nd–3rd	1st–2nd	1st–3rd	2nd–3rd
Tintinnidium fluviatile	**20.4**	**23.4**	**21.2**	**16.6**	**17.8**	**15.6**
Codonella cratera				**16.0**	**13.2**	5.7
Brachionus plicatilis	**14.3**	7.1	6.8	**19.9**	**16.6**	10.1
Keratella tropica	8.4	6.1	2.9	**17.4**	**13.7**	7.2
Asplanchna brightwellii	**15.8**	7.5	13.7	13.0	6.3	**15.9**
Cletocamptus deitersi	13.2	**12.4**	11.8	5.6	9.0	13.1
Bosmina huaronensis		**15.9**	**21.3**		11.5	**19.8**

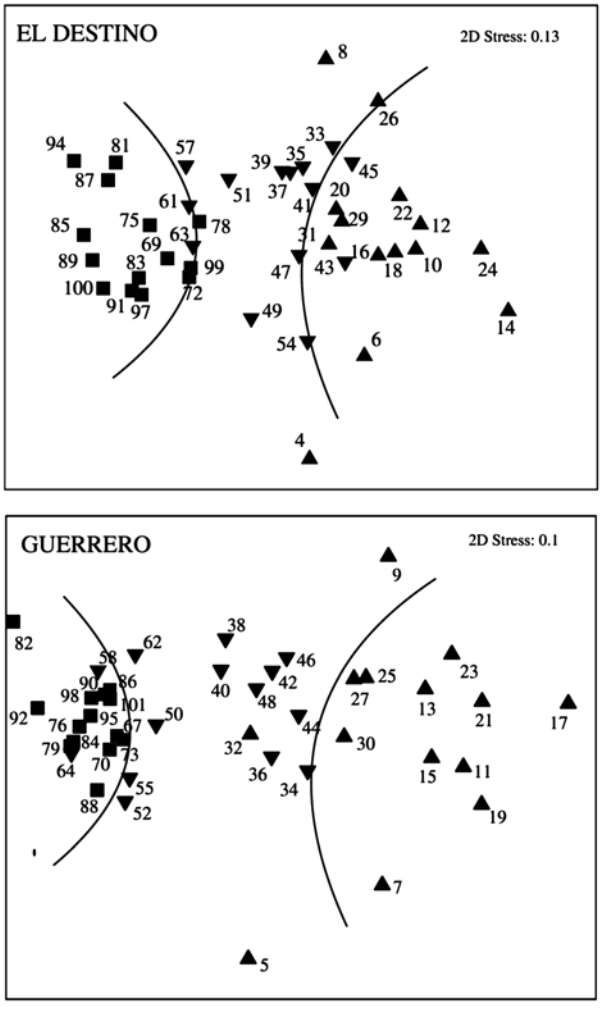

Fig. 5. MDS plot of zooplankton biomasses for the three periods: triangles, first; inverted triangles, second; squares, third.

species-environment relationship. The first canonical axis and the sum of all canonical axes explained a significant portion of the variance in the zooplankton-biomass data ($p = 0.002$; $p = 0.002$, respectively). The environmental variables that were significantly correlated ($p < 0.05$) with the canonical axes were conductivity, temperature, turbidity, and SS. Temperature and conductivity were correlated with the first axis (R = 0.98 and 0.82), while turbidity and SS were correlated with the second axis (R = 0.57, and 0.49, respectively). The general spatial pattern of the species was similar to that observed at ED, except for *K. tropica* and *A. brightwellii*. The rotifers, having a marked increase in biomass during the second and third period, were located in the negative sector of the first axis as exemplified by . Since the copepods were absent on many sampling occasions, the biomass of the group was not significant. The turbidity and SS were the highest in the first period and for this reason were related to the temperature and conductivity within the positive sector of the first axis (Fig. 6).

Phytoplankton biomass

The phytoplankton mean total biomass in the three periods was similar (Fig. 7), reaching values up to 5,500 µg DW L^{-1} in both sectors. One of the peaks occurred at both sites on the same occasion (May). At ED, other maxima were recorded during the first period, whereas at the beginning of the third period the highest total phytoplankton biomass was observed (9,364 µg DW L^{-1}). At G, two peaks were registered in the second period and another in the third, while one minimum was recorded in the second period. Moreover, five other minima were distinguished at the same site: two in the first period, two on consecutive days in the second period, and one in the third period. In general, the species responsible for the total biomass were of larger size than the nanoplanktonic algae, with *Chroococcus limneticus*, *P. lauterbornii*, *Peridinium* sp. and *Microcystis aeruginos*a being dominant in the first period; *Nodularia spumigera*, *P. lauterbornii*, and *Surirella striatula* in the second; and *N. spumigera*, *Peridinium* sp., and *M. aeruginos*a in the third.

The mean total biomass (µg DW L^{-1}) of the nanoplankton was higher at G (617.6; SD 312) than at ED (508.7; SD 355). The same difference was observed throughout the entire sampling period. At G, peaks were recorded on March, April and May, with the last one coinciding with the maximum in total phytoplankton biomass. At ED, the three periods were clearly different, with a notable decrease in the third. The maxima were observed during the first period in March and April, with approximately 1,000 µg DW L^{-1} for each peak. The minima occurred in the second period (May and June), coinciding with a diminution in the total phytoplankton biomass. *Crucigenia quadrata*, *C. rectangularis*, and *Coenochloris planconvexa* were the species with major contributions to the nanoplanktonic total biomass in that first maximum.

The mean SR of the total phytoplankton was similar for both sectors (ED, 61; G, 63 species). At both sites, the minimum occurred during the second period. In ED, the maximum was recorded in April, while at G, four maxima were observed during the first and the second periods. The total biomass and SR of the phytoplankton exhibited the same pattern for both sampling sites, with the presence or absence of *N. spumi-*

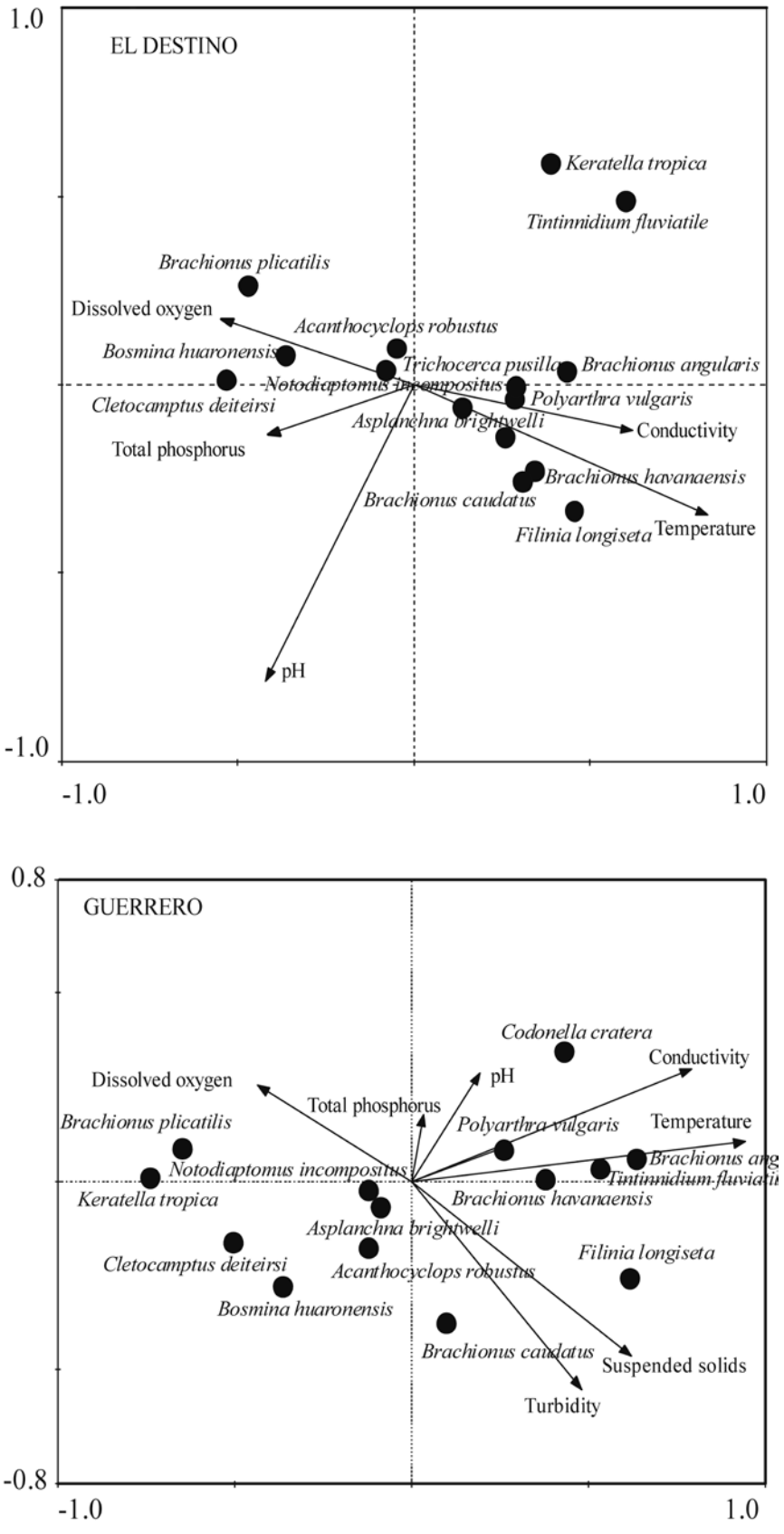

Fig. 6. Results of the redundancy analysis (RDA) between the main species of zooplankton and the environmental variables at both sampling sites.

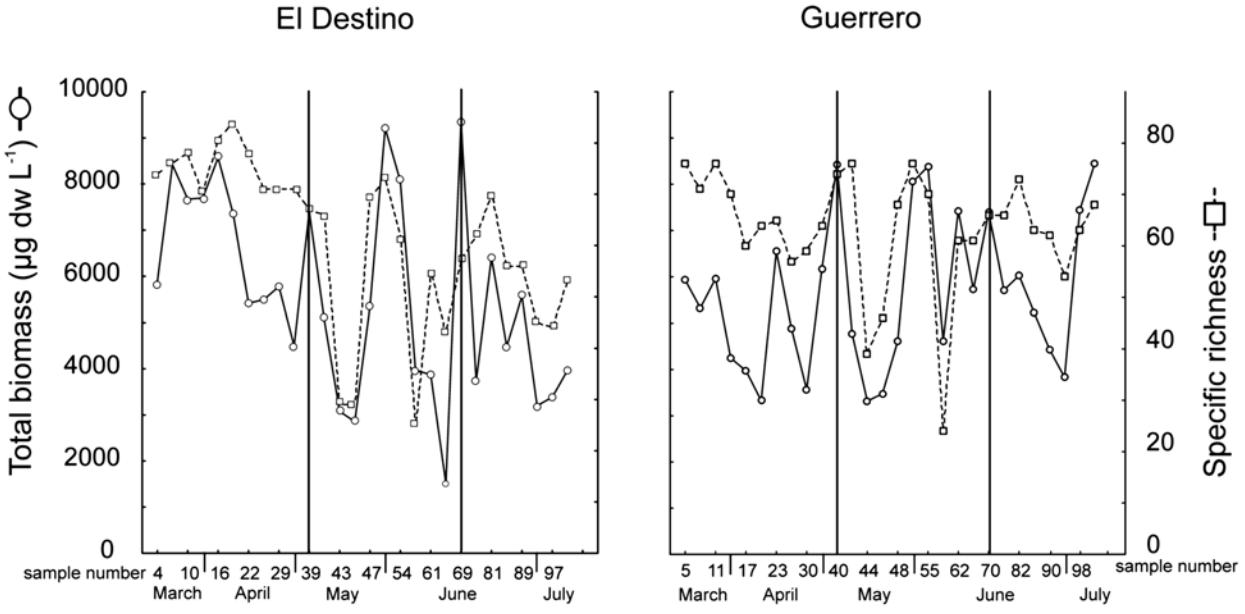

Fig. 7. The total phytoplankton biomass and species richness at the two sampling stations. The vertical lines indicate the three different constituent periods into which the series of samplings were divided.

gera determining the observed differences in both of these variables (Fig. 7).

Relationships between the zoo- and phytoplankton biomasses

At ED, the total zooplankton biomass was negatively related to the temperature and to the pH. The ciliate biomass likewise had an inverse association with the pH, but was positively associated with the conductivity, with the latter also being true at site G. The rotifer biomass exhibited a negative correlation with the temperature plus the suspended solids at ED, but with the temperature alone at G. Moreover, at this latter site, the crustacean biomass was negatively associated with the conductivity, but at ED was positively correlated with the suspended solids (Table 5).

Palatable nanoplankton species were selected for analysis on the basis of having the most significant association with the presence of the rotifer grazers as revealed by the correlation analysis performed. *Scenedesmus nanus* and *Kirchneriella irregularis* were present in both sectors, whereas *Scenedesmus acutus* and *S. intermedius* were absent at G. At this latter site, other nanoplankton species had significant correlations with the total zooplankton biomass (e. g., *Scotelliopsis reticulata*, *Kirchneriella obesa*, *Monoraphidium convolutum*, *S. nanus*, and *Oocystella lacustris*).

The phytoplankton mean total biomass in the three periods was similar. In general, the peaks of algal biomass that were recorded coincided with values of grazer biomass ranging between 50 and 100 µg DW L^{-1}. At higher values of the grazers, an exponential decrease in the nanoplankton biomass was observed followed by a linear phase. Certain species such *S. nanus* exhibited a minimum biomass when the grazer biomass attained values of 200 µg DW L^{-1}. The relationship between grazer and nanoplankton biomass showed a similar pattern in spite of the different biomass values of the nanoplankton species (Fig. 8). The difference in zooplankton biomass between the two sectors was insignificant in comparison with the wide range exhibited by the phytoplankton. At ED, the rate of increase in zooplankton and phytoplankton total biomass never exceeded 8 %, whereas that of the nanoplankton fraction ranged between 2 and 310 %. At G, these respective rates of increase were lower, having values of 0.1 to 4 % and 1 to 87 %. The highest overall rates, including the increases in total zooplankton plus the nanoplankton at both sampling sites, occurred on different occasions during the second period (Fig. 9a). Moreover, if the separate nanoplankton fractions (5–10 µm and 10–20 µm) are considered, the highest values were detected at ED during the second period (e. g., 5–10 µm at 558 %, and 10–20 µm at 700 %). Another maximum was observed during the

Table 5. Result of analysis by multiple stepwise regression between the biomasses of the total and the main groups of zooplankton and the significant environmental variables (n = 42, ns – not significant; ni – not included; ** $p < 0.01$).

	Total	Ciliates	Rotifers	Crustaceans
El Destino				
pH	(–)**	(–)**		
Temperature	(–)**		(–)**	
Conductivity		(+)**		
Suspended solids			(–)**	(+)**
Guerrero				
pH			ns	
Temperature	ni		(–)**	
Conductivity	ni	(+)**		(–)**
Turbidity	ni			
Suspended solids	ni			

same period but with the small-nanoplankton fraction (5–10 µm at 493 % and 10–20 µm at 352 %). At G, the variations in the rates over time were not notable. The maximum rate for only the 10–20 µm fractions was estimated in the third period (268 %) (Fig. 9a). In both sectors, the ratio of the total zooplankton biomass to the total nanoplankton or total phytoplankton biomass remained relatively constant during the first period. During the second period, at ED two minima were registered coinciding with the maximum grazing rate of the zooplankton there (May and June). At G, a minimum was observed at the end of that second period (June). In both sectors, the contribution of the nanoplankton fractions to the total phytoplankton biomass decreased during the third period, but to a more evident extent at G. In both sectors, the maximum nanoplankton biomass recorded reached ca. 20 % of the total (Fig. 9b).

The grazing percentage calculated according to Lampert (L) (1988) varied little during the entire sampling period and was always lower than 15 %. That same parameter estimated after Knoechel & Holtby (1986) gave a pattern similar to that of L, with comparable or substantially higher values. Finally, the grazing percentage following Keckeis et al. (2003) indicated the highest values during the first period. In general, the grazing rates estimated at G were lower than those at ED, coinciding with the dissimilar dynamics of the two nanoplankton biomasses (Fig. 9c).

Discussion

The zooplankton abundance during the total study period showed a clear alternation in the dominant groups, a condition that was partially reflected by biomass. The rotifers were the prominent group in terms of biomass, abundance, and frequency. At both sampling sectors, the rotifers passed through a maximum in June that was nearly the total value for the zooplankton, with *B. plicatilis* and *K. tropica* being the most prevalent. These species showed wider ranges of temperature tolerance than had been reported from previous studies, where *B. plicatilis* had been observed to be a typical summer species and *K. tropica* a vernal one (Claps et al. 2009). In the present investigation, *B. plicatilis* exhibited biomass peaks < 12 °C, whereas *K. tropica*, as usual, < 17 °C. The crustaceans always had biomass values lower than 60 µg DW L^{-1}, with a reduced or absent contribution at ED until the beginning of June. The scant presence of *B. huaronensis* and its minimal biomass in both river sectors could be related to the high inorganic turbidity recorded during the sampling period in agreement with the suggestion of Kirk & Gilbert (1990) for other cladocerans. The low rate of change in conductivity (Fig. 10) estimated mainly during the second and third periods in this river system, but characterized by marked fluctuations, permitted the highest biomass values of the tycoplanktonic crustacean at a high mean frequency (81–100 %), indicating as well the low water levels during the whole sampling period. Protozoa might be the most influential consumers of phytoplankton (Kobayashi et al. 1998, Kiss et al. 2009). A maximal ciliate biomass at both sampling sites occurred in summer, while the prevalence of that group was low in winter, in agreement with the results obtained by Rossetti et al. (2009) in the Po River. Those authors suggested that the ciliate peaks were caused by the high summer phytoplankton supply. In this study, the peaks coincided with those of the phytoplankton

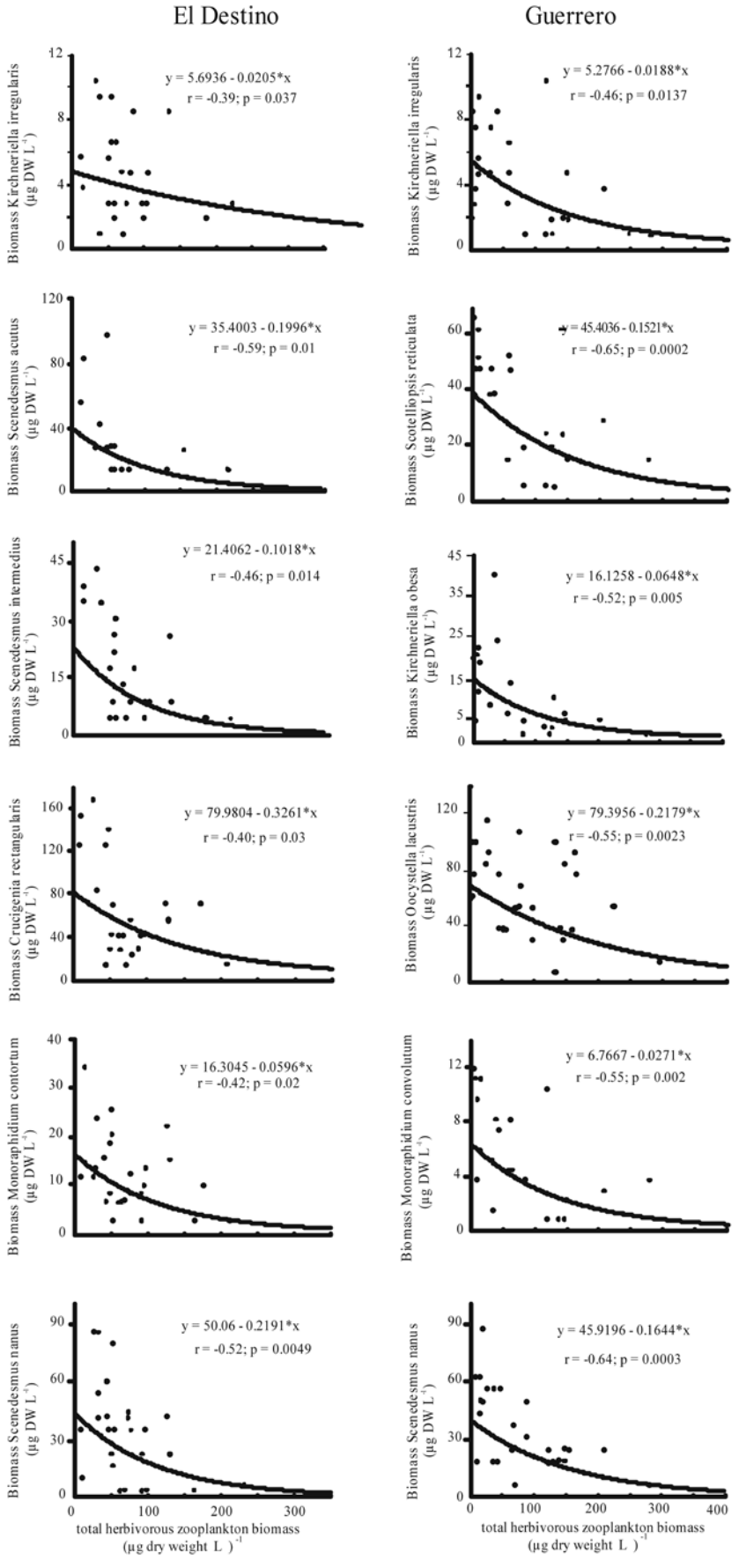

Fig. 8. The relationship between the biomasses of the main species of nanoplankton and the total herbivorous zooplankton as indicated by regression analysis.

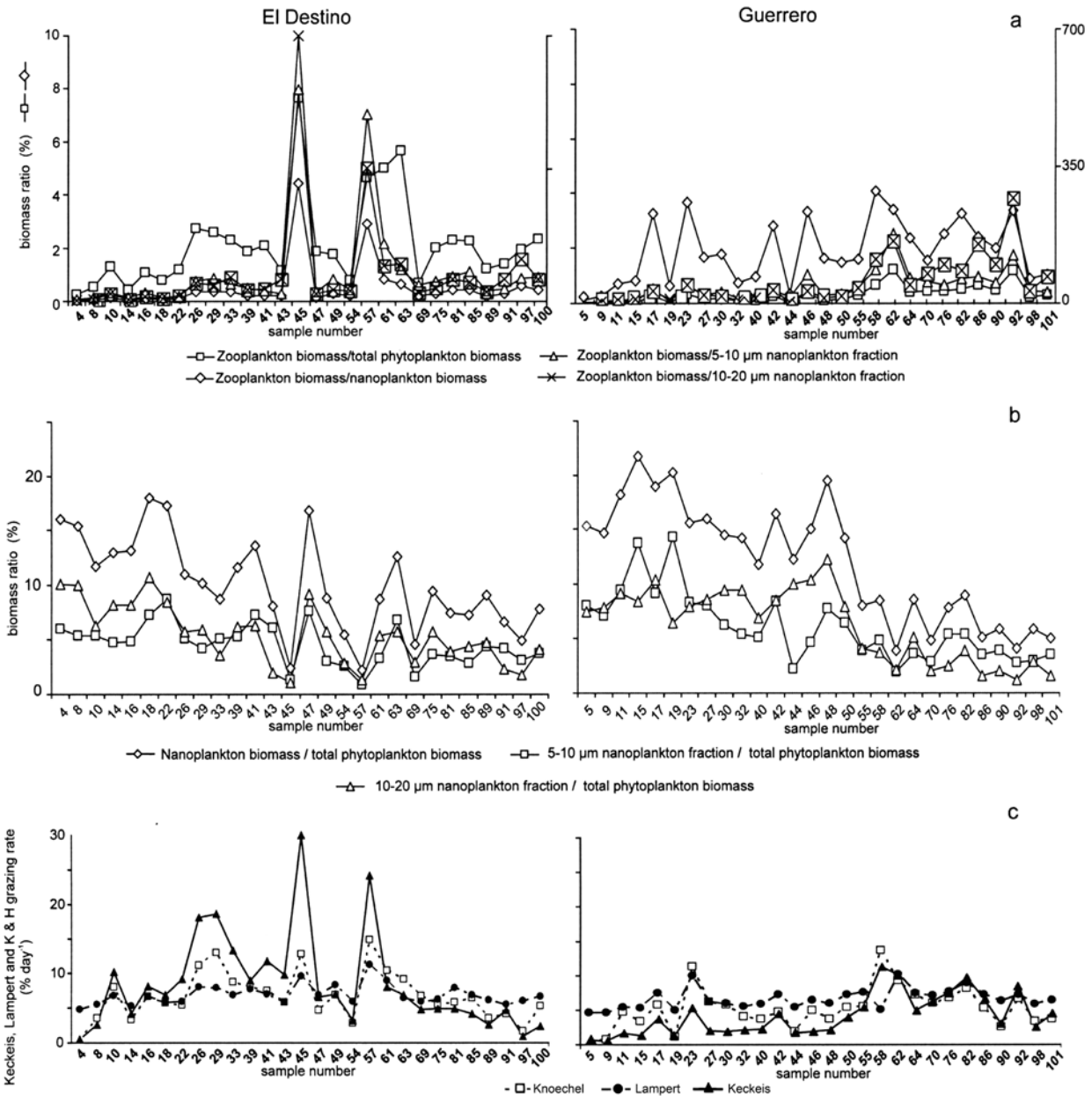

Fig. 9. a) Ratio of the total zooplankton biomasses to the those of the total phytoplankton, the total nanoplankton, and the nanoplankton subclasses; **b)** Contribution of the total nanoplankton and nanoplankton subclasses expressed as a percent of the total phytoplankton biomass; **c)** The grazing rates as calculated after Knoechel & Holby (1986), Lampert (1988), and Keckeis et al. (2003).

abundance, but not with the peaks of nanoplankton biomass.

The zooplankton-biomass values were lower than those cited by Marneffe et al. (1996) for the River Meuse in summer at a low discharge but similar to the values estimated by Gosselain et al. (1998) in the same river under similar conditions.

Both sampling stations registered an independent dynamic for zooplankton species richness, while the biomass remained comparable between the two—that result indicating an emergent propriety on the part of the populations, thus demonstrating mechanisms of effective feedback. Certain species manifested marked differences between the two sectors. The biomasses of

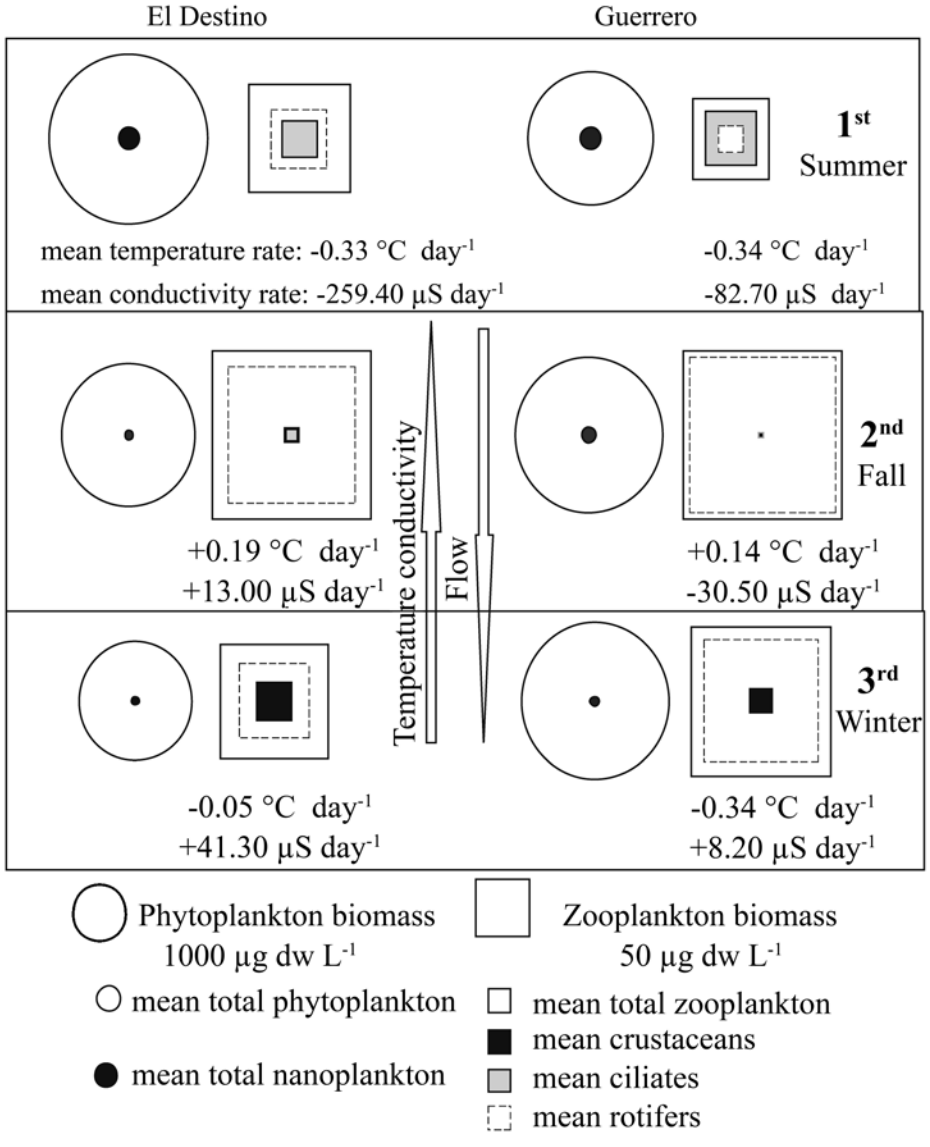

Fig. 10. Conceptual model considering the relationship between the total and nanoplankton biomasses along with the biomasses of the main groups of zooplankton, taking into account the rate of change in the temperature, conductivity, and flow rate for a comparison of both sampling sites.

T. fluviatile, *A. brightwellii*, *B. plicatilis* and *B. huaronensis* were greater at ED than at G, whereas the biomass of *C. deitersi* showed the opposite. One structural difference was the relevant presence and abundance of *C. cratera* at G, whereas at ED this species was infrequent and at a low density when present. Another difference was observed in the third period. At G, the recorded biomasses of the rotifers were higher, while those of the crustaceans lower than the values calculated at ED (Fig. 10). Structural differences in zooplankton should, in general, occur in response to external influences rather than internal population dynamics. The effect of certain parameters (e. g., temperature, conductivity, and DO) on the zooplankton biomass as indicated by RDA (Fig. 6) is in agreement with the conclusions of Lair (2006) among others. In the Salado River, significant differences involving the biotic fractions at both sites were observed, but not as a reflection of the physicochemical parameters according to the results of the dissimilarity analysis (Table 4). However, the temperature and conductivity rates of both sectors were different, being more pronounced at ED where the river is not associated with an upstream flushing lake (La Tigra), as was true at

G (Fig. 10). There the presence of this lake moderated the fluvial condition downstream. Changes in the geomorphologic features of the Salado River during the sampling period produced by dredging and bridge construction were irrelevant to the downstream sampling station (G) in terms of parameters like turbidity and the concentration of suspended solids. In general, the upstream site (ED) manifested the higher concentration of suspended solids and turbidity between the two. This circumstance can also be explained by the presence of La Tigra Lake that influenced the sedimentation rate.

Successional changes in zooplankton are related to seasonal temperature fluctuations, coupled with hydrologic modifications including increases in discharge and the consequent diminutions in conductivity. Temperature and conductivity were the main parameters driving the seasonal succession in this investigation, thus coinciding with the results from the studies of Shiel et al. (1982) and Shiel et al. (2006) in rivers of Australia.

In general, the Salado-River basin exhibited abundant zooplankton throughout its course and in its tributaries. The abundance peaks were always recorded in the medium course and in the tributaries (Claps et al. 2009). This sampling period, occurring during a prolonged low-water condition, disagreed with the usual hydrological expectation for the autumn because this season is characteristically a rainy period in that region. The conductivity values recorded in this study can be included in the group representing the highest levels recorded in the basin among the four categories defined by Claps et al. (2009). A comparison with previous data obtained at these two sampling points from 1995 on (Gabellone et al. 2001, Solari et al. 2002, Neschuk et al. 2002, Claps et al. 2009) revealed that the ciliate peaks recorded in the present study, represented mainly by *T. fluviatile*, exceeded by up to two orders in magnitude those of the preceding investigations (Table 6). The previous ciliate maximum at conductivity of 7,900 µS cm^{-1} had been reached at G, also in the summer, and that was lower than the value recorded during this sampling period (12,200 µS cm^{-1}). Conductivity values of the same order of magnitude had been measured at G on November 1995 (10,100 µS cm^{-1}) and February 1996 (15,100 µS cm^{-1}) but nevertheless coincided with, respectively, very scarce numbers of *T. fluviatile* (e. g., 4 individuals) and the complete absence of the species. A high abundance of tintinnid ciliates (*Tintinnopsis fimbriata* = *Codonaria fimbriata*) had only been obtained in a backwater pond with a direct connection to the river closest to G in November 1996 (9,960 individuals L^{-1}, Gabellone et al. 2001). The marked prevalence of ciliates in the present study caused the total zooplankton density to become the highest since 1995 (Table 6). The harpacticoid *C. deitersi* attained an abundance one order of magnitude higher than had been recorded for that copepod in previous studies. The abundance of the two most prominent *Brachionus* species was significantly higher than had been recorded in previous investigations – namely, the prevalence of *B. plicatilis* was three times higher than on previous occasions, and the same pattern was detected for *B. angularis*. *Keratella tropica* reached similar abundance to those registered in earlier investigations (Table 6). In the previous investigations, the samplings ($n = 75$) were made under different hydrologic and meteorologic conditions, some of which were similar to those of the present study. Nevertheless, the differences in abundance of the zoo-

Table 6. Comparison of the abundance (ind. L^{-1}) of the most representative taxa recorded in this study with the values obtained in previous investigations (cf. text)

	This study		Previous investigations	
	ED	G	ED	G
Codonella cratera	93 (2/4/04)	6168 (13/4/04)	5 (5/02)	14 (5/02)
Tintinnidium fluviatile	17587 (19/4/04)	4158 (19/4/04)	95 (5/99)	114 (3/99)
Tintinnopsis fimbriata	13 (26/3/04)	302 (4/04)	95 (5/99)	12 (5/95)
Brachionus angularis	497 (12/4/04)	158 (13/4/04)	76 (3/97)	23 (3/97)
B. plicatilis	1637 (2/6/04)	1842 (2/6/04)	608 (3/96)	174 (5/96)
Keratella tropica	483 (2/6/04)	642 (3/6/04)	707 (6/96)	710 (6/96)
Polyarthra vulgaris	117 (27/4/04)	12 (26/4/04)	23 (5/96)	130 (5/95)
Bosmina huaronensis	52 (5/7/04)	18 (28/6/04)	12 (5/96)	51 (5/95)
Nauplii of calanoids plus cyclopoids	11 (29/6/04)	5(22/6/04)	12 (6/96)	207 (5/95)
Cletocamptus deitersi	62 (7/6/04)	30 (28/6/04)	2 (5/96)	2 (6/95)
Total abundance	18160 (19/4/04)	10194 (12/4/04)	983 (5/96)	948(5/96)

plankters were notable within these comparable occasions. We believe that such a survey over a short time scale enabled an accurate documentation of the peaks in zooplankton abundance that occurred during those short time periods.

In agreement with Keckeis et al. (2003) and Ferrari et al. (2006), a top-down effect by the zooplankton on the total phytoplankton biomass was not detected, though a diminution in the biomass of certain palatable algae was observed. The zooplankton consumption rates were similar to those obtained in the Danube River during the low-water period there, with rotifers likewise dominating the grazing activity (Keckeis et al. 2003). The replacement of the rotifers by small cladocerans as the dominant grazers was also detected at the end of the present sampling period in agreement with the results of Gosselain et al. (1998) and Keckeis et al. (2003). In disagreement with these latter authors, however, on one occasion the rotifers reached high algal-removal rates and managed to deplete the supply of nanoplankton (Fig. 9). These high removal rates coincided with maxima in the biomass of the rotifers during the second period (Fig. 10), with a notable maximum in ED at values of 700 % between the zooplankton and the two palatable nanoplankton fractions. These rates also corresponded to the highest grazing values estimated according to the models of Knoechel & Holtby (1986), Lampert (1988), and Keckeis et al. (2003). These results were confirmed by simple regression analyses between the biomasses of the grazers and the different size classes of the nanoplankton species (Fig. 8). Zooplankton grazing did not seem to be effective in controlling the algal biomass (Rossetti et al. 2009). The predominance of filter-feeder rotifers generally prevents a total depletion of the phytoplankton. Moreover, the edible fraction of the latter also never exceeded 20 % (mean, 8 %) of the total phytoplankton biomass. This peculiarity was not a limiting condition, however, for zooplankton growth (Fig. 10). The occurrence of grazing was more evident in ED, taking place twice in autumn—the first time of 3 days' duration and the second daily 15 days thereafter.

Finally, taking into account the results obtained in this investigation and the previous studies detailed here, we consider that seasonal regional surveys provide essential (large-scale) information related to the multiscale characteristic of the river system. This involves a sizeable quantity of tributaries along with connectivity to lentic environments and functioning in relationship to the water-table levels as well as to the different forms of land use within the basin (in terms of nutrient and material input). This (large-scale) information should be complemented with local investigations over short time periods to generate (fine-scale) data for the establishment of strategies for appropriate monitoring and management. The tactics of these latter investigations could also be targeted to achieve multiple outcomes and to provide information, for example, to insure that certain specific areas be set aside for the preservation of biodiversity. Furthermore, the inclusion of a detailed analysis of plankton structure enables an appreciation of its complexity, an identification of its most critical trophic interactions, and an understanding of its response to internal and external variables. The latter includes anthropic effects and the impact of land use on the ecological condition of the lotic system.

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References

American Public Health Association, 1995: Standard Methods for the Examination of Water and Wastewater. 18th ed. – APHA, Washington, D.C.

Basu, B. K. & Pick, F. R., 1996: Factors regulating phytoplankton and zooplankton biomass in temperate rivers. – Limnol. Oceanogr. **41**: 1572–577.

Bazzuri, M. E., Gabellone, N. A. & Solari, L. C., 2010: Seasonal variation in the phytoplankton of a saline lowland river (Buenos Aires, Argentina) throughout an intensive sampling period. – River Res. Applic. **26**: 766–78.

Beers, J. R. & Stewart, L., 1969: The vertical distribution of microzooplankton and some ecological observations. – Int. J. Cons. Int. Explor. Mer. **33**: 30–44.

Bonecker, C. C., Lansac-Toha, F. A., Bini, L. M. & Velho, L. F. M., 2002: Daily fluctuation in rotifer population abundance in two environments of the upper Parana River floodplain, Brazil. – Amazoniana **17**: 139–51.

Burdis, R. M. & Hoxmeier, R. J. H., 2011: Seasonal zooplankton dynamics in main channel and backwater habitats of the Upper Mississippi River. – Hydrobiologia **667**: 69–87.

Claps, M. C., Gabellone, N. A. & Neschuk, N. C., 2009: Influence of regional factors on zooplankton structure in a saline lowland river: the Salado River (Buenos Aires Province, Argentina). – River Res. Appl. **25**: 453–471.

Dumont, H. J., Van de Velde, I. & Dumont, S., 1975: The dry weight estimates o biomass in a selection of Cladocera,Copepoda and Rotifera, from the plankton periphyton anda benthos of continental waters. – Oecologia **19**: 75–97.

Ferrari, I., Farabegoli, A. & Masón R., 1989: Abundance and diversity of planktonic rotifers in the Po River. – Hydrobiologia **186/187**: 201–208.

Ferrari, I., Viglioli, S., Viaroli, P. & Rosetti, G., 2006: The impact of the summer 2003 drought event on the zooplankton of the Po River (Italy). – Verh. Internat. Verein. Limnol. **29**: 2143–2149.

Gabellone, N. A., Solari, L. C. & Claps, M. C., 2001: Planktonic and physical-chemical dynamics of a markedly fluctuating backwater pond associated with a lowland river (Salado River, Buenos Aires, Argentina). – Lakes & Reservoirs: Research and Management **6**: 133–142.

Gabellone, N. A., Claps, M. C., Solari, L. C. & Neschuk, N. C., 2005: Nutrients, conductivity and plankton in a landscape approach to a Pampean saline lowland river (Salado River, Argentina). – Biogeochemistry **75**: 455–477.

Gabellone, N. A., Solari, L. C., Claps, M. C. & Neschuk, N. C., 2008: Chemical classification of the water in a lowland river basin (Salado River, Buenos Aires, Argentina) affected by hydraulic modification. – Environ. Geol. **53**: 353–1363.

Gosselain, V., Viroux, L. & Descy, J. P., 1998: Can a community of small bodied grazers control phytoplankton in rivers? – Freshw. Biol. **39**: 9–24.

Gosselain, V., Descy, J. P., Viroux, L., Joaquim, J. C., Hammer, A., Métens, A. & Schweitzer, S., 1998: Grazing by large river zooplankton: a key to summer potamoplankton decline? The case of the Meuse and Moselle rivers in 1994 and 1995. – Hydrobiologia **369/370**: 199–216.

Graham, P., Harris, G. P. & Heathwaite, L., 2012: Why is achieving good ecological outcomes in rivers so difficult? – Freshw Biol. **57**: 91–107.

Hillebrand, H., Dürselen, C., Kirschtel, D., Pollingher, U. & Zohary, T., 1999: Biovolume calculation for pelagic and benthic microalgae. – J. Phycol. **35**: 403–424.

Jeppesen, E., Jensen, J. P., Søndergaard, M. & Lauridsen, T., 1999: Trophic dynamics in turbid and clearwater lakes with special emphasis on the role of zooplankton water clarity. – Hydrobiologia **408/409**: 217–231.

Karayanni, H., Christaki, U., Van Wambeke, F. & Dalby, A. P., 2004: Evaluations of double formalin-Lugol's fixation in assessing number and biomass of ciliates: an example of estimation at mesoscale in NE Atlantic. – J. Microbiol. Methods **56**: 349–358.

Keckeis, S., Baranyi, C., Hein, T., Holarek, C., Riedler, P. & Schiemer, F., 2003: The significance of zooplankton grazing in a floodplain system of the River Danube. – J. Plankton Res. **25**: 243–253.

Kirk, K.L., 1991: Inorganic particles alter competition in grazing plankton: the role of selective feeding. – Ecology **72**: 915–923.

Kirk, K. L. & Gilbert, J. J., 1990: Suspended clay and the population dynamics of planktonic rotifers and cladocerans. – Ecology **71**: 741–1755.

Kiss, A. K., Acs, E., Kiss, K. & Torok, J., 2009: Structure and seasonal dynamics of the protozoan community (heterotrophic flagellates, ciliates, amoeboid protozoa) in the plankton of a large river (River Danube, Hungary). – Eur. J. Protistol. **45**: 121–138.

Knoechel, R. & Holtby, L. B., 1986: Cladoceran filtering rate: body length relationship for bacterial and large algal particles. – Limnol. Oceanogr. **31**: 195–200.

Kobayashi, T., 1997: Associations between environmental variables and zooplankton body masses in a regulated Australian river. – Mar. Freshw. Res. **48**: 523–529.

Kobayashi, T., Shiel, R. J., Gibbs, P. & Dixon, P. I., 1998: Freshwater zooplankton in the Hawkesbury-Nepean River: comparison of community structure with other rivers. – Hydrobiologia **377**: 133–145.

Lair, N., Jacquet, V. & Reyes-Marchant, P., 1999: Factors related to autotrophic potamoplankton, heterotrophic protists and micrometazoan abundance, at two sites in a lowland temperate river during low water flow. – Hydrobiologia **394**: 13–28.

Lair, N., 2005: Abiotic vs. biotic factors: lessons draw from rotifers in the Middle Loire, a meandering river monitored from 1995 to 2002, during low flow periods. – Hydrobiologia **564**: 457–472.

Lair, N., 2006: A review of regulation mechanisms of metazoan plankton in riverine ecosystems: aquatic habitat versus biota. – River Res. Appl. **22**: 567–593.

Lampert, W., 1988: The relationship between zooplankton biomass and grazing: a review. – Limnologica **19**: 11–20.

Marneffe, Y., Descy, J. P. & Thome, J. P., 1996: The zooplankton of the lower river Meuse, Belgium: seasonal changes and impact of industrial and municipal discharges. – Hydrobiologia **319**: 1–13.

McCauley, E., 1984: The estimation of the abundance and biomass of zooplankton in samples. – In: Downing, J. & Rigler, F. (eds): A manual on methods for the assessment of secondary productivity in fresh waters. – Blackwell Science Publishers, pp. 228–265.

Neschuk, N., Claps, M. & Gabellone, N., 2002: Planktonic rotifers of a saline-lowland river: the Salado River (Argentina). – Ann. Limnol. **38**: 191–198.

Neschuk, N., Gabellone, N. & Claps, M., 2002: Plankton characterization of a lowland river (Salado River, Argentina). – Verh. Internat. Verein. Limnol. **28**: 1336–1339.

Pace, M, L., Findlay, S. E. G. & Lints, D., 1992: Zooplankton in advective environments: The Hudson River community and a comparative analysis. – Can. J. Fish. Aquat. Sci. **49**: 1060–1069.

Park, G.S. & Marshall, H. G., 2000: Estuarine relationships between zooplankton community structure and trophic gradients. – J. Plankton Res. **22**: 121–135.

Picard, V. & Lair, N., 2005: Spatio temporal investigations on the planktonic organism of the Middle Loire (France), during the low water period: biodiversity and community dynamics. – Hydrobiologia **551**: 69–86.

Pielou, E. C., 1984: The Interpretation of Ecological Data. – Wiley, New York (NY).

Primer Ltd., 2001: Statistical Package PRIMER Versión 5. 2. 9. – Product AP 5200.

Ramsar Convention Bureau, 2004: The List of Wetlands of International Importance.

Rossetti, G., Viaroli, P. &, Ferrari, I., 2009: Role of abiotic and biotic factors in structuring the metazoan plankton community in a lowland river. – River Res. Appl. **25**: 814–835.

Ruttner Kolisko, A., 1977: Suggestions for biomass calculation of plankton rotifers. – Arch. Hydrobiol. **8**: 71–76.

Shiel, R. J., Costello, J. F., Reid, J. R.W., Hudson, P. & Powling, J. 2006: Zooplankton diversity and assemblages in arid zone rivers of the lake Eyre basin, Australia. – Mar. Freshw. Res. **57**: 49–60.

Solari, L., Claps, M. & Gabellone, N., 2002: River backwater-pond interactions in the lower basin of Salado River (Buenos Aires, Argentina). – Arch. Hydrobiol., Suppl. **141**: 99–119.

ter Braak, C. J. F., 1986: Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. – Ecology **67**: 1167–1179.

ter Braak, C. J. F. & Smilauer, P., 1998: CANOCO Reference Manual and Canoco Draw for Windows User's Guide: Software for Canonical Community Ordination (Version 4.5). – Microcomputer Power (Ithaca, NY, USA).

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ter Braak, C. J. F. & Verdonschot, P. F. M., 1995: Canonical correspondence analysis and related multivariate methods in aquatic ecology. – Aquat. Sci. **57**: 255–289.

Thorp, J. H. & Casper, A. F., 2003: Importance of biotic interactions in large rivers: an experiment with planktivorous fish, dreissenid mussels and zooplankton in the St Lawrence River. – River Res. Appl. **19**: 265–279.