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Zooplankton and their driving factors in a large subtropical river during low water periods

Susana Beatriz José de Paggi[1, 2], **Melina Devercelli**[1] and **Florencia Rojas Molina**[1]

With 6 figures, 2 tables and 1 appendix

Abstract: The composition, abundance and functional diversity of zooplankton from the main channel of the Middle Paraná River were studied. Monthly samples were collected in both ordinary drought periods (1977, 1978, 1981, 2007) and extraordinary drought ones (La Niña events 1971–1972, 1999–2000). A constant pattern of zooplankton structure was recorded from 1971 to 1981 characterised by a strong rotifer dominance. Changes were observed in the last two periods, with the planktonic larvae of *Limnoperna fortunei* as a new component of zooplankton. The abundance of zooplankton showed a significant interannual variability and a decreasing trend over time with the maximum values almost 100 times lower from 1999 onwards, mainly resulting from a decline in rotifer density. Cladocerans and copepods occurred with very low abundance and were similar across years. *Bosmina* and *Bosminopsis* showed a decreasing trend through time. Evidence was found of intrazooplanktonic competition between rotifers and cladocerans. Zooplankton and phytoplankton abundance presented similar trends, but the edible algal fraction (< 20 µm) showed a negative relation with Bosminidae, suggesting cladoceran control. In the last period, zooplankton changes were not associated with physical parameters (except flow velocity), nutrients or phytoplankton. The absence of a constant pattern and the causes of the declining trend of zooplankton abundance over time could be related to biotic interactions and multiple-stressors throughout the study.

Key words: zooplankton abundance, phytoplankton, microphagous rotifers, selective filter feeding cladocerans, long-term study.

Introduction

The zooplankton of rivers, particularly those where human impact is low, is characterised by low density and by the dominance of rotifers, cladocerans of small size, and copepod nauplii (Pace et al. 1992, Lair 2006). Although it is considered that river zooplankton assemblages are driven by a mixture of abiotic and biotic factors (Rossetti et al. 2009), in large rivers physical conditions such as discharge, suspended sediments, current velocity and water residence time are the major determinants in structuring zooplankton assemblages (Saunders & Lewis 1989, Viroux 1997, Lair 2006). High waters or floods are challenging for river zooplankton, in these conditions the impact of turbulence on the plankton is important (Sluss et al. 2002), the short water residence time does not allow the development of large-sized zooplankton, and grazing pressure on the phytoplankton assemblage is light (Pace et al. 1992, Thorp et al. 1994, Gruberts et al. 2012). On the other hand, in several lowland rivers, it was found that at low flows and high temperatures, biotic factors were important in controlling phytoplankton and zooplankton communities (Gosselain et al. 1998, Ietswaart et al. 1999, Guelda et al. 2005, Bertani et al. 2012). Even trait-mediated predator–prey inter-

Authors' addresses:
[1] Instituto Nacional de Limnología (CONICET-UNL), Santa Fe, Argentina
[2] Facultad de Bioquímica y Ciencias Biológicas (UNL), Santa Fe, Argentina
[*] Corresponding author; sjdepaggi@gmail.com; sjose@inali.edu.ar

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actions can occur despite the turbulence and disruptive effect of the downstream transport (Bertain et al. 2013*)*. One might think then that the importance of biotic factors in shaping river zooplankton increases inversely to flow or discharge. The period of low flow, the "growing season", constitutes a hydrological scenario of less harsh environmental conditions for organisms, minor advection downstream, minor dilution, etc. During drought, at lower connectivity, all floodplain aquatic bodies recover their individuality, including habitat features and biota (Ward & Tockner 2001). The effects on zooplankton can be complex in at least two ways: there is a decrease in the recruitment of organisms from the plain and the physical constraints are reduced.

Knowledge of river zooplankton ecology comes mainly from studies in lowland rivers of the northern hemisphere, located in temperate climates and with a considerably lower discharge. Much of this knowledge has been generated from studies on rivers that have a mean annual discharge lower than 10,000 m^3 s^{-1}, such as the rivers Ohio, Danube, Rhine, and Po (Thorp et al. 1994, Baranyi et al. 2002, Friedrich & Pohlmann 2009, Rossetti et al. 2009), or even less, lower than 1,000 m^3 s^{-1} as rivers Hudson, Meuse, Moselle, or Loire (Pace et al. 1998, Viroux 1998, Lair 2005), among others. In contrast, South America is characterised by tropical or subtropical rivers with a higher discharge. In the Paraná River, its hydrosedimentological pulse is the main force that regulates plankton communities (José de Paggi & Paggi 2007, Zalocar de Domitrovic et al. 2007, Lansac-Tôha et al. 2009), and if biotic interactions affect their dynamics, these interactions may take place during droughts. The aim of this study is to analyse the zooplankton response to drought and extreme drought periods from 1977–2007 in the main channel of Paraná River and to address the following questions: i) is there a general pattern of zooplankton composition, structure, functional diversity and abundance?; ii) which factors govern zooplankton features during low waters?; iii) do zooplankton assemblages change over time?

Material and methods

Study site

The Amazonas, Paraná and Orinoco rivers are the three major fluvial systems of South America. Of these Paraná River is the second longest (4,400 km). Its water sources are located in Brazil (~15° S; 451° W) and its large fluvial net collects, modifies and transports water, nutrients and inorganic and organic matter from tropical environments to the middle latitudes of the South Atlantic Ocean (Iriondo et al. 2007).

The study site is located in its middle reach, at 603 km upstream from the mouth (Fig. 1), where the river is 700 m wide and 22 m of maximum depth. The mean annual discharge is approximately 16,400 m^3 s^{-1} but during exceptional flooding it can reach up to 60,000 m^3 s^{-1}. It annually transports an average of 130–135 million tons of sediments, about 80 % of which is wash load or suspended sediment load (Iriondo et al. 2007) causing low transparency.

The hydrological regime of the Paraná River is typically monomodal, historically including a low water phase in winter and spring and a high water phase in summer and early autumn (Paoli et al. 2000). The flood phase begins when river water enters the floodplain (~13.00 m.a.s.l., at Paraná Harbour Gauge station).

Analysis of historical data indicates the beginning of a wet phase in the early 1970s, with a statistically significant increase in mean annual discharge mainly during the seasonal low water period, and a greater interannual variability of the hydrological regime (García & Mechoso 2005, among others). Hydrological manipulations (dam building in the Upper Paraná) and climate variability may be the cause of these changes (Paoli et al. 2000, Marengo et al. 2009).

The Middle Paraná waters are bicarbonated sodium type, with low electrolyte contents, generally circumneutral pH, and with high phosphate and nitrate concentration during low waters. Many different fish species can be found but the detritivorous Prochilodontidae and Curimatidae comprise the bulk of fish biomass as in other South American rivers (Bonetto 1994, Fleckner 1996).

Sampling and laboratory analyses

The samples were collected monthly in 6 periods between the years 1971 and 2007; four of them corresponded to ordinary drought periods (1977, 1978, 1981, 2007; $n = 8, 9, 7, 7$, respectively), and the others corresponded to extreme drought periods influenced by La Niña events (1971–1972, 1999–2000; $n = 6$ each one). In the last four decades, long periods of high water (1979, 1980) and extreme floods of long duration (El Niño) were recorded (1982–1983, 1997–1998).

Daily water stage heights were obtained from the Paraná Harbour Gauge. Current velocity (Siap current meter), temperature, water transparency (Secchi disc), pH, conductivity (Beckman and Hanna portable checkers) and dissolved oxygen (YSI and Hanna portable checker) were measured *in situ*. Subsurface water samples were analysed in the laboratory for nitrate and nitrite, ammonium, soluble reactive phosphorus and total suspended solids following APHA (1992).

Subsurface phytoplankton samples were collected and fixed with Lugol's acidified solution (1 %). Samples for taxonomic analysis were obtained with a 25 µm mesh net and fixed with formalin (2 %).

The zooplankton samples were taken with a Schindler-Patalas plankton trap from the centre of the river, at approximately 0.70 m below the surface. Each sample consisted of five pooled subsamples (20 litres each one). The samples were concentrated using a 50 µm mesh net, preserved with 4 % formalin and stained with erythrosine. In addition, to provide complementary information on taxon richness, qualitative samples of zooplankton were taken by horizontal dragging, with a net

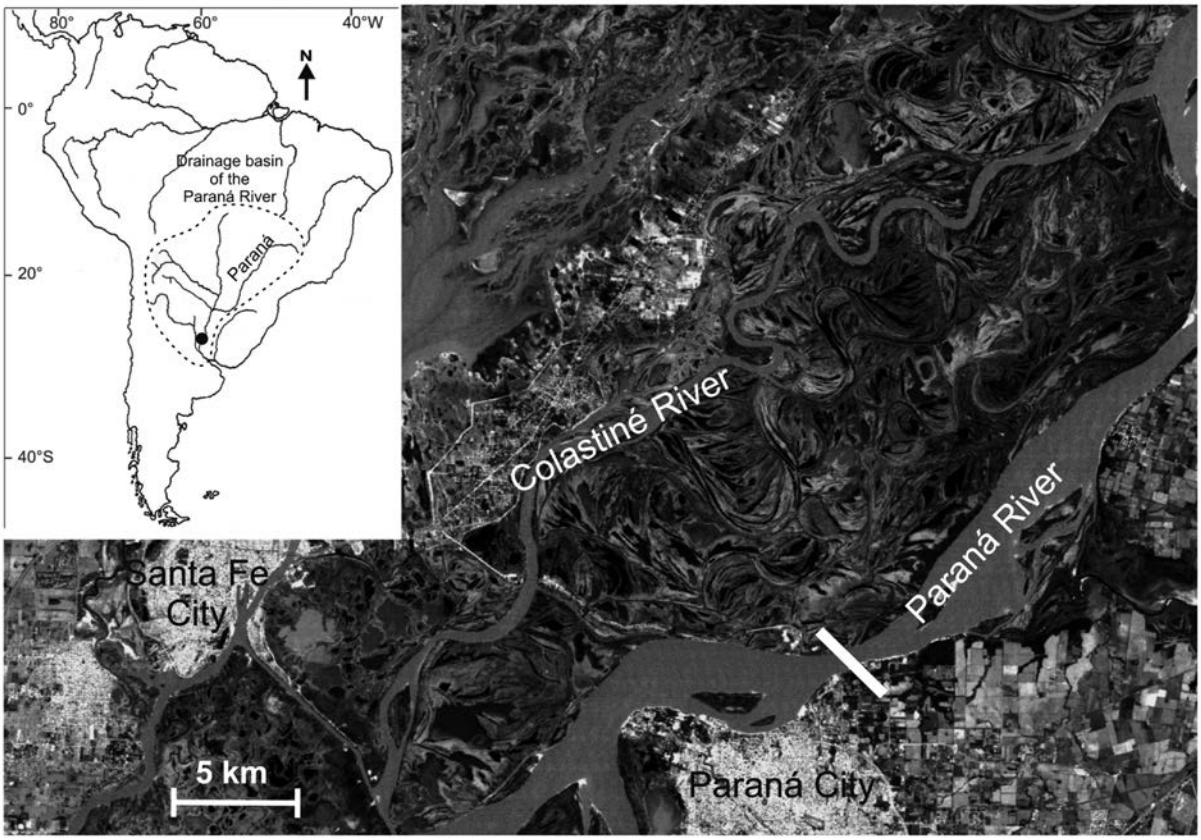

Fig. 1. Sampling site on the main channel of Paraná River (white bar).

(20 cm diameter at the mouth, 45 µm mesh). Other studies at the same site demonstrated that turbulence resulted in a highly mixed water column and thus zooplankton distribution did not differ horizontally or vertically (José de Paggi 1985).

Phytoplankton individuals (cells, colonies and filaments) were enumerated to determine density (ind. ml^{-1}) using the settling chamber and inverted microscope technique (Utermöhl 1958) with a magnification of 400×. The maximal linear dimension of individual algae was measured in order to classify phytoplankton as edible (< 20 µm without diatoms) or inedible (≥ 20 µm). This was based on previous findings that most of the filter-feeder or suspension-feeder rotifers can consume cells between 3–17 µm and most diatoms pass unharmed through their guts (Wallace et al. 2006). Diatoms were classified according to life forms as meroplanktonic, planktonic and tychoplanktonic (Sicko-Goad et al. 1989, Zalocar de Domitrovic & Maidana 1997, Shikata et al. 2008).

Zooplankton species were determined according to different authors (Koste 1978, Reid 1985, Paggi 1995, Segers 1995). Nauplius larvae and copepodite stages were differentiated into cyclopoids and calanoids.

Rotifers and microcrustaceans were counted under a binocular microscope, in 1 and 5 ml chambers, respectively. A minimum of 100 individuals were counted but on many occasions it was necessary to count the entire sample because of the low densities observed.

The similarities of the methods used for measuring environmental variables and the taxonomic criteria in each period were checked.

When fish larvae or ichthyoplankton (< 15 mm) were found in zooplankton samples (December 1999 and January 2000), their digestive tracts were analysed. For this purpose, 10 individuals were separated from each sample and the digestive tracts dissected and observed under an optic microscope.

Data analysis

The proportion of zooplankton functional groups was calculated. The classification was made based on the feeding strategy employed by each genus or family. According to Obertegger et al. (2011), the rotifers were separated in microphages and raptorials; the nauplii were included as microphages. Cladocerans and copepods were classified into filtering Ctenopoda (*Diaphanosoma* and *Pseudosida*), filtering Anomopoda (*Daphnia*, *Simocephalus*, *Ceriodaphnia* and *Moina*), selective filter feeders (*Bosmina* and *Bosminopsis*), filtering scrapers (Chydoridae and Macrotricidae), microphagous herbivores (*Diaptomus*, *Notodiaptomus*, Calanoidea copepodits), and macrophagous carnivores (*Mesocyclops*, *Acanthocyclops*, Cyclopoidea copepodits) (Barnett et al. 2007, Paggi, unpublished). Discrimination between planktonic and littoral-benthic species was made according to Shiel et al. (1982).

The Diversity Index of Shannon and Weaver and Beta diversity were calculated (Magurran 1988). ANOVA (F) with Tukey *post-hoc* test or the non-parametric alternative Kruskal-Wallis (KW) with Dunn *post-hoc* test were used to test significant differences between years. Spearman rank-order correlations (Rho) were performed among variables. Similarity

Cluster analyses based on Euclidean distance coefficients (zooplankton density) and Jaccards (zooplankton composition) with unweighted pair group average linkage were used to identify similarities between years. The analyses were carried out with PAST 2.4 Software (Hammer et al. 2001).

Redundancy Analysis (RDA, ter Braak & Smilauer 2002) was performed with CANOCO 4.5 software since species gradient length was < 3 standard deviations. Water level, current velocity, water temperature, Secchi disc, conductivity, pH, DO, nitrate, phytoplankton < 20 µm were considered as the explanatory variables (standardised), and densities of functional groups and *Limnoperna fortunei* larvae as the response variables (square root transformed). The forward selection option was used to identify the significant environmental variables (Monte Carlo test, 999 permutations).

Results

Physical and chemical parameters

The seasonality and duration of the low water period differed between the years under study but usually occurred from August to November (winter and spring) and lasted for three to four months (Fig. 2).

The highest mean values of temperature and suspended solids were found during the extraordinary drought of 1999–2000 (Table 1). Water transparency, electrical conductivity, nitrate and nitrite were different between the years ($F = 3.54$, $p = 0.009$; $F = 4.21$, $p = 0.007$; $KW = 9.85$, $p = 0.04$; $\mathrm{KW} = 13.32$, $p = 0.004$, respectively). Significantly higher values were observed during La Niña 1999–2000 for transparency in comparison to 1971–1972 and 2007, electric conductivity in comparison to 2007, nitrate in comparison to 1971–1972, and nitrite in comparison to 1977 ($p < 0.05$ for all comparisons).

Phytoplankton

The density ranged from 101 to 1784 ind. ml^{-1} with no significant differences between the years ($KW = 5.51$, $p = 0.23$) (Fig. 3). In contrast, the density of the algal fraction < 20 µm ($KW = 10.07$, $p = 0.0008$) was higher in 1999–2000 and 2007 than in 1977 and 1978 ($p < 0.05$) (Fig. 2). Bacillariophyceae, Chlorophyceae Chlorococcales and Cryptophyceae were the main

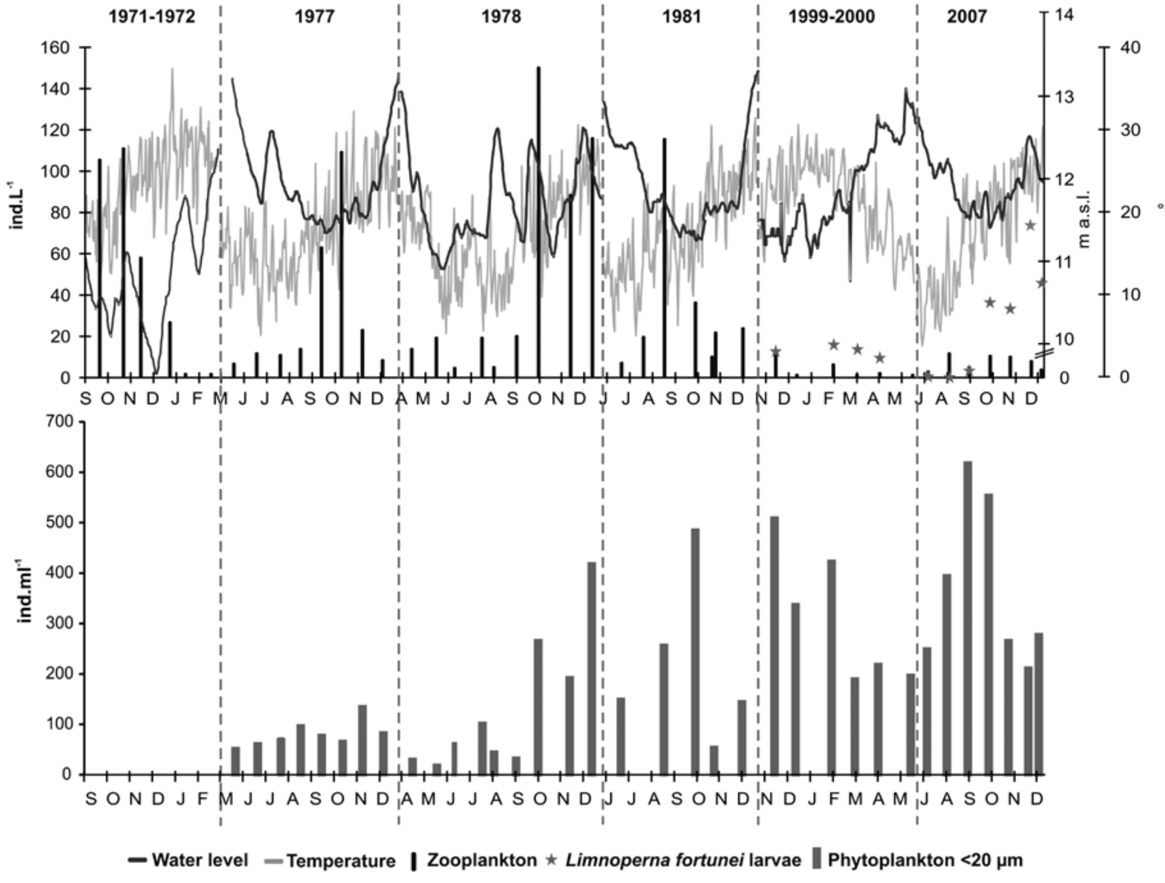

Fig. 2. Variation of zooplankton, *Limnoperna fortunei* larvae, water level, temperature and phytoplankton in the Paraná River, 1971–2007.

Table 1. Main environmental parameters, mean and coefficient of variation (in brackets). * Without data.

Period	Discharge $m^3 \cdot s^{-1}$	Flow velocity $m \cdot s^{-1}$	TSS $mg \cdot L^{-1}$	Secchi cm	pH	Temp. °C	Conductivity $\mu s \cdot cm^{-1}$	$N\text{-}NO_2^-$ $mg \cdot L^{-1}$	$N\text{-}NO_3^-$ $mg \cdot L^{-1}$	$N\text{-}NH_4^+$ $mg \cdot L^{-1}$	$P\text{-}PO_4^{-3}$ $mg \cdot L^{-1}$	DO $mg \cdot L^{-1}$
1971–1972	9851.80 (20)	1.03 (17)	*	15 (49)	7.81 (1)	26.21 (25)	88.60 (14)	0.01 (49)	0.68 (27)	0.06 (68)	0.13 (63)	*
1977	13213.45 (15)	1.09 (24)	85.01 (38)	32 (34)	7.78 (1)	20.10 (21)	84.43 (11)	0.01 (17)	0.85 (44)	0.16 (85)	0.09 (79)	8.46 (11)
1978	12145.98 (13)	1.18 (23)	187.30 (115)	28 (49)	7.55 (2)	20.31 (24)	92.00 (17)	0.01 (33)	1.01 (64)	0.06 (80)	0.07 (61)	8.52 (11)
1981	12766.13 (13)	0.92 (29)	*	31 (30)	7.45 (2)	21.01 (29)	94.50 (9)	*	*	*	*	8.13 (15)
1999–2000	11996.76 (11)	1.09 (55)	247.00 (153)	18 (74)	7.71 (5)	26.30 (6)	116.00 (17)	0.02 (57)	2.99 (77)	1.80 (124)	0.19 (83)	7.96 (11)
2007	12511.65 (7)	0.98 (33)	*	36 (17)	8.04 (3)	21.09 (24)	80.29 (14)	*	1.12 (106)	*	0.22 (76)	7.96 (19)

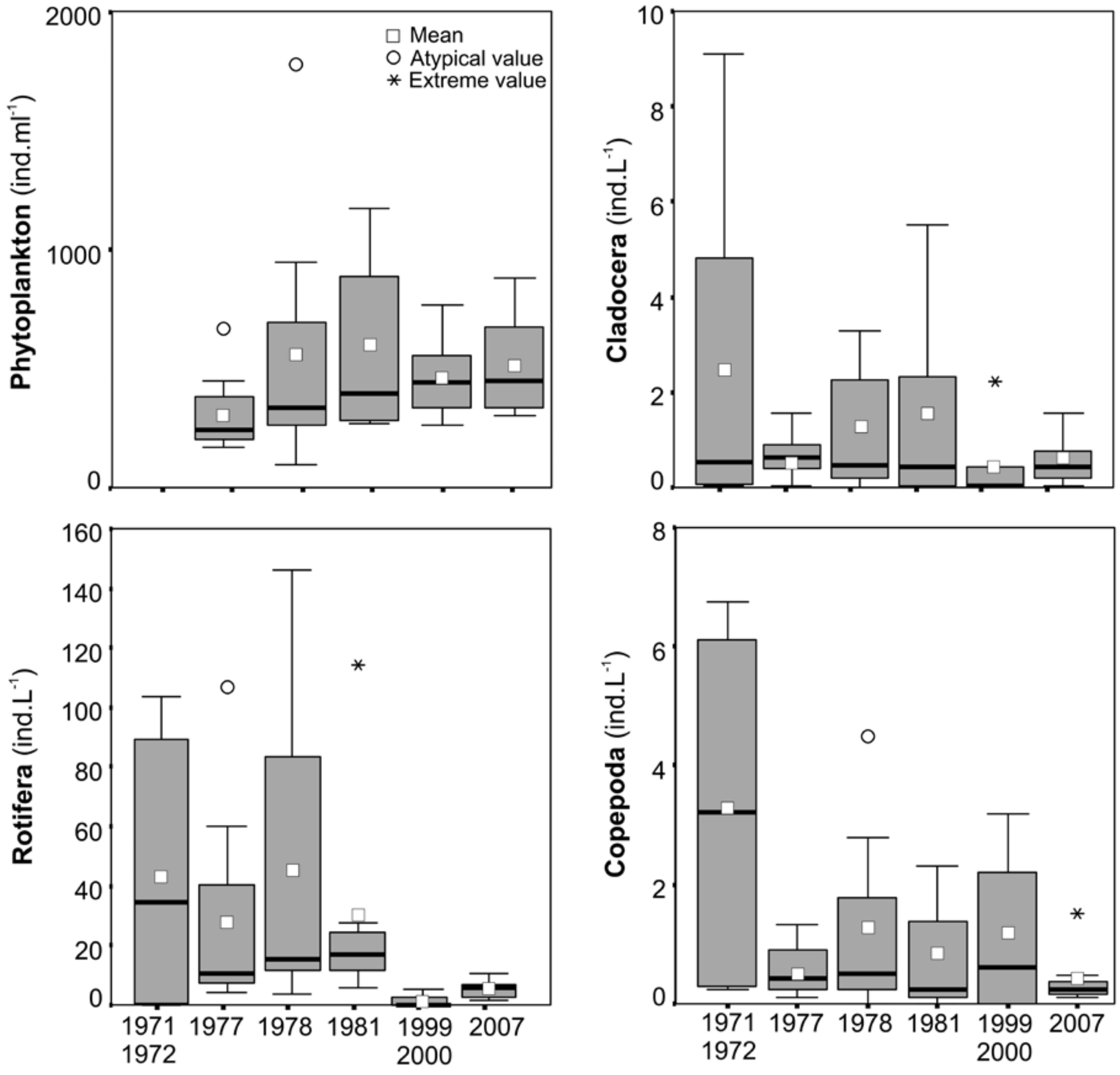

Fig. 3. Box-plot of abundance of phytoplankton and zooplankton groups in the Paraná River, 1971–2007.

Table 2. Mean relative abundance of the main algae groups.

	1977	1978	1981	1999–2000	2007
Bacillariophyceae					
Meroplanktonic	48.32	69.30	59.64	6.11	17.03
Planktonic	5.94	2.99	0.83	3.22	10.02
Tycoplanktonic	2.77	0.94	3.61	2.57	1.67
Chlorophyceae					
Chlorococcales	18.93	9.16	6.06	10.84	15.42
Volvocales	1.43	0.56	1.99	12.69	11.85
Cryptophyceae	10.30	6.65	17.53	45.85	32.11

taxonomic groups in the phytoplankton, followed by Chrysophyceae and Cyanobacteria. Diatoms were represented by meroplanktonic species (*Aulacoseira granulata*, *A. distans*, *Skeletonema* spp., *Fragilaria construens* and *Nitzschia acicularis*), planktonic species (*Cyclotella meneghiniana*, *Actinocyclus normanii* and small unidentified centrics of diameter < 7 µm) and a low percentage of tycoplanktonic species (e.g. *Eunotia pectinalis*, *Gyrosigma obtusatum*, *Navicula cryptocephala*, *Cymbella* sp., *Surirella* spp.). Meroplanktonic diatoms represented on average 48 to 69 % of the total phytoplankton density from 1977 to 1981 but they decreased substantially from 1999 onwards. In contrast Cryptophyceae (cryptomonadals and *Plagioselmis nannoplanctica*) and Volvocales (*Chlamydomonas* spp.) increased their contributions (Table 2). Significant differences for meroplanktonic diatoms ($KW = 17.36$, $p = 0.0016$) were only observed between 1999–2000 and 1978 ($p = 0.0316$), and for Cryptophyceae ($KW = 21.74$, $p = 0.00022$) and Volvocales ($KW = 26.51$, $p = 2.16e^{-5}$) during 1999–2000 and 2007 in comparison with the 1977 and 1978 periods ($p < 0.05$).

Zooplankton

Richness

A total of 104 taxa (rotifers, cladocerans and copepods) were recorded (Appendix 1). The richness of copepods was almost certainly underestimated because in most cases they were represented by nauplii and copepodites that could not be identified to species level.

The rotifer cumulative richness was 33, 50, 34, 21, 18 and 44, and the cladoceran cumulative richness was 13, 12, 7, 10, 8, and 13, for years 1971–72, 1977, 1978, 1981, 1999–2000, and 2007, respectively.

Taxon richness was significantly different between years ($F = 8.83$, $p < 0.0001$), and was lower during the two La Niña events than during 1978 and 2007 ($p < 0.05$ and $p < 0.001$, respectively). Taxon richness in 1977 was higher than in 1978, 1981 and 1999–2000 ($p < 0.005$).

The beta diversity was 2.58, 1.54, 2.45, 2.02, 3.22, and 1.60, for the six consecutive periods, showing a high species turnover during both La Niña events.

Abundance and composition

Zooplankton abundance differed between years (Figs 2 and 3) ($KW = 14.64$, $p = 0.01$) and during the extreme low waters of 1999–2000 was significantly lower than in 1978 and 1981 ($p < 0.05$).

Rotifers were numerically dominant (Fig. 4). Their abundance also showed differences between years ($KW = 18.14$, $p = 0.002$), with lower densities during 1999–2000 compared to 1971–1972, 1977, and 1981 ($p = 0.02$, < 0.01, 0.05, respectively) (Fig. 3).

Total zooplankton and rotifer abundance showed a decreasing trend over time ($Rho = –0.35$, $n = 43$, $p = 0.01$ and $Rho = –0.40$, $n = 43$, $p = 0.006$, respectively), in both maximum and average values (Fig. 3). Cladocerans were subdominant. The abundance of copepods and cladocerans was not significantly different between years (Fig. 3).

Including all sampling years, the percentage of cladocerans in the zooplankton was negatively correlated with the percentage of rotifers ($Rho = –0.65$, $n = 43$, $p < 0.0001$).

The major faunistc similarity (Jaccard index), was recorded between 1978 and 1981, and between 1971–1972 and 1977 (Fig. 5a). The cluster based on zooplankton density (Euclidian distance) allowed the distinction of a group of periods with the lowest density, 1999–2000 and 2007 (Fig. 5b).

Dominant rotifer genera were *Keratella*, *Brachionus* and *Lecane*. *Keratella* spp. was the most abundant and frequent rotifer, but its abundance decreased significantly over time ($Rho = – 0.36$, $n = 43$, $p = 0.01$). Between 1971 and 1981 its density represented about 40–99 % of rotifers, but at the end of the study (1999–2000, 2007) the proportions were under 40 %. The relative abundance of *Brachionus* was higher during both La Niña events. This genus was present in most samples but its density decreased in 2007. In contrast to *Keratella*, *Brachionus* and *Lecane* did not decrease significantly over time. Dominant cladocerans were Bosminidae (*Bosmina* and *Bosminopsis*) which showed a decreasing trend over time.

The Shannon diversity was low, with mean values of 1.50, 1.87, 1.79, 1.67, 1.27 and 2.40 from 1971 to 2007. The most frequent species assemblage was

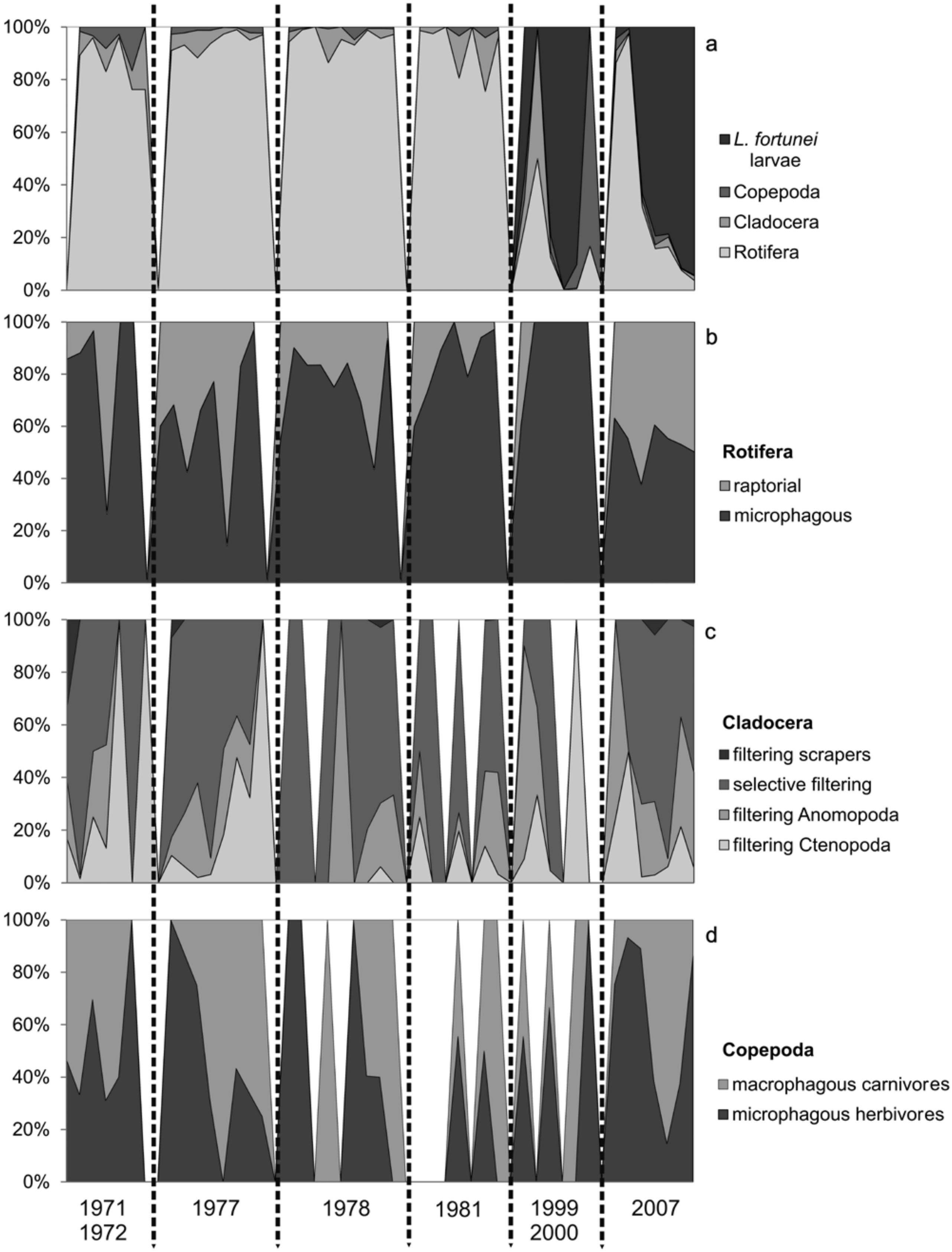

Fig. 4. Variations in the relative density of **(a)** zooplankton groups and *Limnoperna fortunei* larvae and **(b, c, d)** zooplankton functional groups in the Paraná River, 1971–2007.

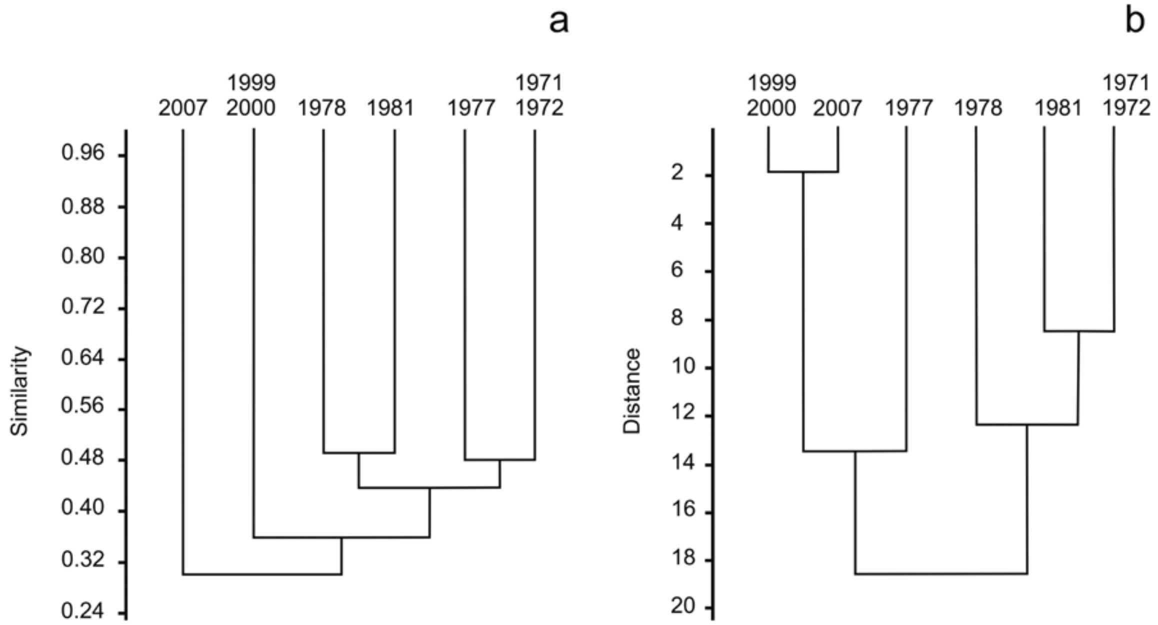

Fig. 5. Cluster analyses of the zooplankton community in the years 1971–2007 on the basis of **(a)** composition and **(b)** abundance.

Keratella americana, *K. cochlearis*, *K. tropica*, *Polyarthra* aff. *vulgaris* and *Bosminopsis deitersi*.

Functional diversity

Among rotifers, microphages and raptorials showed the same variation over time (*Rho* $=0.66$, $n=43$, $p=0.001$). However, the microphages dominated with 70 % mean relative density until 1981, proportions were lower during 1999–2000 (40 %) and 2007 (46 %). The microphagous rotifers contribution to total rotifer density varied significantly between years ($F=3.91$, $p=0.006$); in 2007, it was lower than in 1981 and 1999–2000 ($p<0.05$ and $p<0.01$, respectively) (Fig. 4b). This group was mainly composed of small-bodied (*Filinia*, *Keratella*) and medium sized (*Brachionus angularis*, *B. budapestinensis*) microphagous taxa. Raptorial rotifers were important only during 2007 (Fig. 4b).

Selective filter feeders prevailed among cladocerans. There were no significant differences between years ($KW=4.32$, $p=0.50$). Filtering scrapers were most scarce and filtering Ctenopoda showed their contribution during extreme low waters. Herbivorous microphages dominated in the Copepoda group (Fig. 4c–d).

Significant correlations were found between small microphages (rotifers) and the dominant filter feeder cladocerans, *Keratella* spp. and *Bosmina* spp. (*Rho* $=0.58$, $n=43$, $p<0.0001$) and *Brachionus* spp. and *Bosmina* spp. (*Rho* $=0.31$, $n=43$, $p=0.03$).

Zooplankton relationship with abiotic and biotic variables

The abundance of organisms was only significantly correlated with flow velocity (*Rho* $=-0.420$, $n=29$, $p=0.023$).

Phytoplankton temporal variation was similar to zooplankton (*Rho* $=0.344$, $n=35$, $p=0.04$), although the latter showed a more pronounced decrease during 2007 (Figs 2 and 3). The abundance of phytoplankton <20 µm increased over time (Fig. 2); a negative correlation between small algae and Bosminidae abundance was found (*Rho* $=-0.338$, $n=35$, $p=0.04$).

Planktonic veliger larvae of *Limnoperna fortunei* were recorded for the first time in 1999 and their abundance increased in 2007 (Fig. 2). These organisms represented more than 50 % of the zooplankton during warm months.

Fish larvae were only found in plankton samples during La Niña 1999–2000. The digestive tract analysis showed ingestion of rotifers and cladocerans, shown by the presence of numerous trophi, and remains of cladoceran valves.

The first two axes of the RDA (Fig. 6) accounted for 93 % of the cumulative variance, and the sum of both eigenvalues was 44.6 %. Secchi and phytoplankton <20 µm ($p=0.002$) were the significant explanatory variables. The periods 1999–2000 and 2007 were arranged on the right side of Fig. 6 related to small phytoplankton increment, and to *Limnoperna fortunei* larvae and microphagous copepods. On the opposite

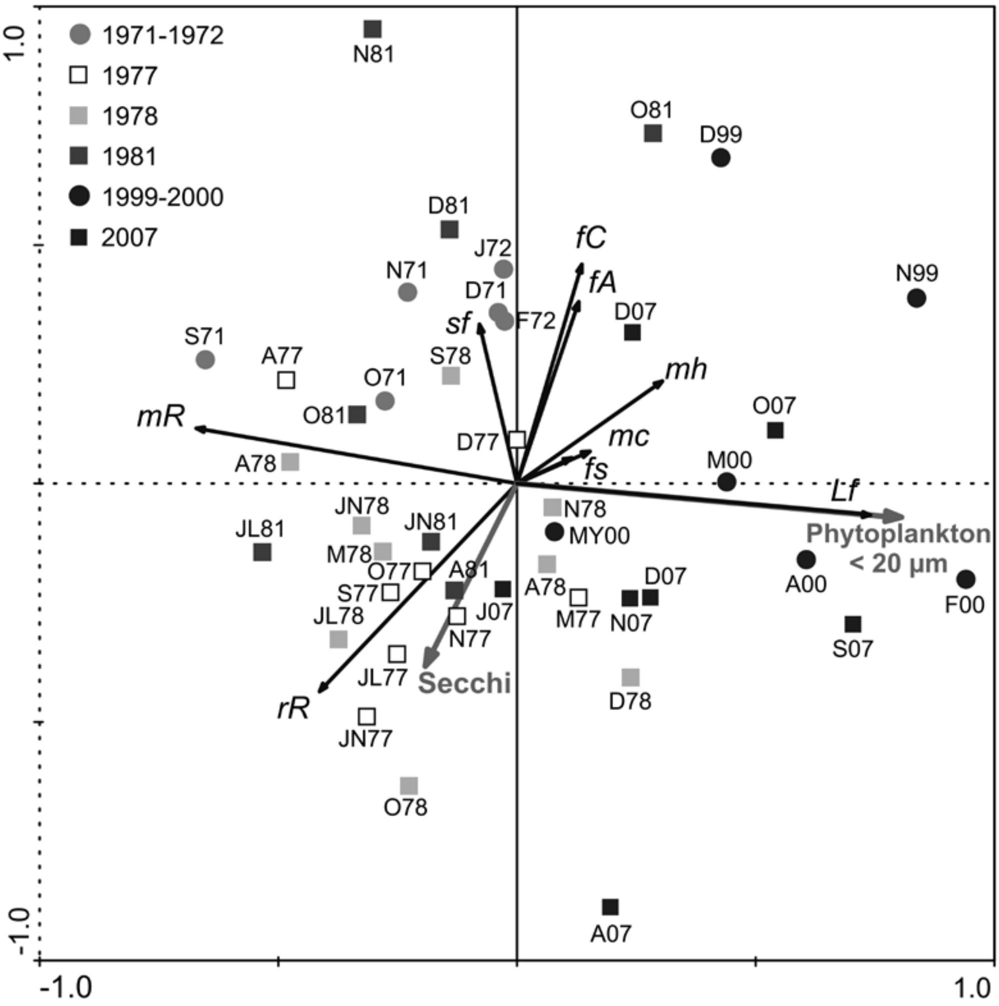

Fig. 6. Redundancy analysis (RDA) of zooplankton functional groups. Significant environmental variables are indicated by grey arrows and functional groups by black arrows. Samples are represented with a symbol and the corresponding month (abbreviated with the beginning letters) and year. mR: microphagous rotifers; rR: raptorial rotifers; fC: filtering Ctenopoda; fA: filtering Anomopoda; sf: selective filter feeders; fs: filtering scrapers; mh: herbivorous microphages; mc: carnivorous macrophages; Lf: *Limnoperna fortunei* larvae.

left side samples were related with the microphagous and raptorial rotifers. Secchi clustered the periods 1977–1978 on the left bottom of the graph. Selective filter feeders Cladocera, Ctenopoda and Anomopoda were loaded to the positive side of the second axis together with warmer month samples.

Discussion

Composition, functional diversity and abundance patterns of zooplankton at low waters

The composition of zooplankton showed a pattern characterised by the dominance of small limnetic taxa, mainly *Keratella, Brachionus, Bosmina* and *Bosminopsis*, similar to those observed in other rivers (Pace et al. 1992, Kobayashi et al. 1998). These rotifers are frequent in the main channel of the rivers; they have a very short development time and can feed and reproduce parthenogenetically in a turbulent environment; the loricated *Keratella* and *Brachionus* appear to be better adapted to higher current velocity (Lair 2005). The selective feeding strategy of *Bosmina* and its ability to live with low food concentrations may give it a competitive advantage in riverine environments (Acharya et al. 2005). Large taxa such as *Daphnia* spp. and littoral and benthic species (tycoplankton) were occasionally found.

A constant pattern of zooplankton structure was recorded from 1971 to 1981; the taxa assemblage was very similar and there was a strong dominance of rotifers. Those periods were closely associated in the RDA and both microphagous and raptorial rotifers were the most important functional groups. Changes were observed in the last two periods (samples plotted on the opposite side of the RDA graph) with a strong influence of the planktonic larvae of *Limnoperna fortunei*. This mollusc was a new component of the zooplankton from 1999; comprising between 56 and 99 % of the total zooplankton density during warm months. This species is reproductively active for 6–10 months of the year from spring to autumn (Boltovskoy et al. 2009).

This bivalve was introduced at the beginning of the 1990s in the Río de la Plata Estuary (Pastorino et al. 1993). Its larvae were found for the first time in the main channel of the Middle Paraná River in the 1997–1998 summer during an extreme flood (José de Paggi, unpublished), and achieved higher densities during 2007 (up to 75 ind. L^{-1}).

The abundance of zooplankton was low. In the Paraná River, advection can be very important due to the high flows. This usually reduces zooplankton density (Kobayashi et al. 1998). Similar abundance values were found in other large rivers such as the Orinoco (Saunders & Lewis 1989). The abundance of zooplankton showed a significant interannual variability, mainly due to changes in rotifer numbers. A decreasing trend of zooplankton density was observed over time, and the maximum values of abundance were almost 100 times lower from 1999 onwards, largely driven by a decline in *Keratella*. However, the total zooplankton biomass was probably not much affected as the small size of rotifers means their contribution to total biomass is insignificant in comparison to crustaceans. The abundance of cladocerans and copepods, although very low was relatively similar over the years; only *Bosmina* and *Bosminopsis* showed a decreasing trend although this was not statistically significant.

Microphagous rotifers, selective filter feeding cladocerans and microphagous copepods achieved a higher contribution to abundance over time. Information on zooplankton functional groups in rivers is limited. Schöll et al. (2012) analysed the rotifer functional groups of the Danube River (guild ratio) but did not find a consistent pattern. Bertani et al. (2012) showed interactions between small and large microphagous rotifers in the Po River.

Which factors govern the zooplankton of a large river at low waters?

The hydrological pulse is recognised as a governing factor in riverine zooplankton communities; flow velocity is one of the related variables that influences zooplankton development and determines which organisms are able to proliferate in rivers (Lair 2006). At lower flow velocity the residence time of water is greater and increases the opportunities for species to stay and to reproduce in the mainstream (Basu & Pick 1996); a negative association between flow velocity and zooplankton density over time was found.

The low water conditions that shape the zooplankton community of each period are also affected by the annual hydrological behaviour of the river. As the floodplain acts as a source of biota for the mainstream (Schöll et al. 2006), when the annual hydrometric variation range is low, one can expect a lower recruitment of species and a low richness at the beginning of drought periods. The largest annual amplitude of water level was observed in 1971 and 2007 (4.15 and 3.6 m, respectively) and the greatest species numbers were recorded in the channel at these times.

The zooplankton assemblage is sensitive to decreases in river-floodplain connectivity during droughts. The low richness and abundance of *Lecane*, *Chydorus* and *Alona,* which are all littoral-benthic species, contrasts with the higher richness recorded in the main channel at high waters (José de Paggi & Paggi 2007).

Regarding biotic factors, evidence of intrazooplanktonic competition between rotifers and cladocerans was found. However, the importance of detritus in the Middle Paraná River (Iriondo et al. 2007) can decrease the competition for algal resources between dominant microphagous rotifers and small cladocerans, as evidenced by the coexistence of *Keratella-Brachionus-Bosmina.* Many species can be successful using non-living particulate organic matter as a food source (Wallace et al. 2006). Microphages and raptorials were able to coexist, probably because both consume particles of different size.

Phytoplankton is generally more abundant at low waters (Zalocar de Domitrovich et al. 2007, Devercelli 2010) which means greater resource availability for zooplankton. Despite the fact that zooplankton control on phytoplankton is expected during these periods, the pattern of density variability was similar for both. On the contrary, the edible algal fraction ($< 20\ \mu m$) showed a negative relation with Bosminidae, suggesting cladoceran control. As observed in the RDA, the bosminids decreased over time and the small-sized phytoplankton increased, indicating that the control effect decreases in more recent years. Data available from other rivers showed that *Bosmina* is one of the main grazers because of its high grazing rate (Keckeis et al.

2003). During extreme drought, La Niña 1999–2000, the proportion of the less edible algae, meroplanktonic diatoms decreased dramatically. Beaver et al. (2013) observed that the proportion of these algae decreases when the water residence time increases.

The intrazooplanktonic predation in the Paraná River was assumed to be negligible. Predators such as *Asplanchna* and *Ploesoma* were poorly represented in the main channel. In addition, cyclopoid copepod adults were scarce, probably because copepods require much more stable conditions to pass through their ontogenetic development (Keckeis et al. 2003).

We believe that the zooplankton community is not predominantly controlled by fish in the mainstream. The dominant fish species in the channel of the Middle Paraná River is the detritivorous migrator *Prochilodus linneatus*, followed by large predators such as *Salminus*, *Pimelodus* and *Pseudoplatystoma* (Quiros et al. 2007). However, fish larvae are planktivorous and they occur in the channel during summer high waters as a result of passive migration (Iriondo et al. 2007). We found evidence of fish larvae only from the extreme drought of 1999–2000, which lasted until late summer suggesting that fish control of the zooplankton community is very limited.

One of the most ecologically important events in the Paraná basin during the period under study was the biological invasion of the Asiatic bivalve *Limnoperna fortunei.* Rojas Molina et al. (2010) showed that their adults graze on phytoplankton and rotifer and microcrustacean zooplankters. In addition, in two secondary floodplain channels, Rojas Molina & José de Paggi (2008) found declines in zooplankton abundance (mainly *Keratella* spp.) and chlorophyll-*a* since the mollusc invasion. The invader filtering bivalves were frequently identified as a disturbance factor for planktonic communities (Strayer 2008). Pace et al. (1998) suggested that the decline of microzooplankton observed in the Hudson River after *Dreissena polymorpha* invasion, a mussel that shares ecological traits with *L. fortunei* (Karatayev et al. 2007), could be caused by direct predation by the freshwater invader. Delong (2010) pointed out that river turbulence appeared to enhance the ability of *D. polymorpha* to draw resources from the water column and Descy et al. (2003) reported that at lower discharge, water residence time increases allowing a greater volume of water to be filtered per unit time by *D. polymorpha*. We assumed that under low discharges the risk to zooplankton of *L. fortunei* predation will be increased. The cluster showed that the zooplankton community in the years following the invasion differed from that before the invasion, and the RDA showed contrasting trends between larvae and both microphagous and raptorial rotifers. In contrast the small algae did not seem to respond to the bivalve presence (Fig. 6), perhaps because their high reproductive rates can counteract the filtration effect.

Addressing possible explanations of zooplankton changes over time in a large river

Most of our understanding about the ecology of the riverine zooplankton comes mainly from studies done during one or a few annual cycles. Long-term research projects are rare, but are valuable tools to assess general ecological trends. Lair (2005) did not find significant changes in rotifer assemblages of the Loire River, at low water over an 8-year study. On the other hand, Friedrich & Pohlmann (2009) in their 1979–2004 study on the lower Rhine which also took place during low waters, found that a decrease in phytoplankton densities, caused by decreases in nutrient levels, resulted in a decrease in zooplankton. Beaver et al. (2013) in a long term study in six reservoirs of Missouri River found important zooplankton seasonal changes according to the drought-flood conditions stressing the role of abiotic factors.

As regards the Paraná River Upper reach, Lansac-Tôha et al (2009), in an 8-year study of the zooplankton from both lotic and lenitic water bodies of the floodplain, were not able to determine the existence of any clearly defined trend. The interannual variation seems to depend on the duration of the hydrological phases. In our study, a decline of rotifers and a higher abundance of both *Limnoperna fortunei* larvae and small phytoplankton were shown. Controlled grazing experiments would better elucidate the potential biotic interactions.

Even though the number of periods analysed is limited, the absence of a constant pattern and the causes of the declining trend of zooplankton abundance (rotifers) over time could be related to multiple-stressor effects (changes in hydrology, dam building, alien species, and increase in the basin urbanization).

Low waters represent a '*window of ecological opportunity*'; however, a shift of this window could cause different effects on the communities (Tockner et al. 2010). In our case, a seasonal shift occurred in the changes in hydrological behaviour; for example, the duration and magnitude of droughts were different between years. The two extreme droughts lasted until February or March (summer). Extreme droughts for extended periods of time could be a stress condition for aquatic organisms (zooplankton), and like floods, they may reduce population densities, alter interspecific interactions, predation and competition (Lake 2003). Indirect effects of low levels for longer periods of time include important changes in the water quality (Lake 2003). In our study these changes were particularly important in 1999–2000, the suspended sediment load was very high, and the turbidity, conductivity, nitrate and ammonium increased. The mean Shannon diversity was also lower during both La Niña events.

In this context, it is not easy to elucidate the relative importance of each environmental stressor on zooplankton changes. It is possible that this is due to their combined action, the order in which they appeared in the scenario and their indirect effects through other communities such as phytoplankton and even fish. Undoubtedly, our major challenges will be to understand the nature of each stressor and their effect on river zooplankton assemblage. It is obvious that long-term data sets are necessary to allow a better understanding of process and assessment of changes, particularly considering that over the past few decades the large rivers have undergone rapid environmental changes (Kattel & Gell 2012).

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Appendix 1. List of zooplankton taxa found.

Rotifera
Anuraeopsis quadriantennata (Koste)
Ascomorpha ecaudis Perty
Asplanchna brightwelli Gosse
*Brachionus ahlstrom*i Lindeman
Brachionus angularis Gosse
Brachionus austrogenitus Ahlstrom
Brachionus bidentatus Anderson
Brachionus budapestinensis (Daday)
Brachionus calyciflorus Pallas
Brachionus caudatus Barrois & Daday
Brachionus falcatus Zacharias
Brachionus insuetus Ahlstrom
Brachionus dolabratus Harring
Brachionus havanaensis Rousselet
Brachionus mirus (Daday)
Brachionus quadridentatus (Hermann)
Brachionus urceolaris (O.F. Müller)
Brachionus zahniseri Ahlstrom
Cephalodella sp.
Colurella adriatica Ehrenberg
Colurella sp.
Collotheca sp.
Conochilus coenobasis Skorikov
Conochilus natans (Seligo)
Conochilus unicornis Rousselet
Dicranophorus hauerianus Wiszniewski
Dicranophorus sp.
Dipleuchlanis propatula (Gosse)
Epiphanes clavulata (Ehrenberg)
Epiphanes macrourus (Barrois and Daday)
Euchlanis cf. *dilatata* Ehrenberg
Filinia longiseta (Ehremberg)
Filinia opoliensis (Zacharias)
Filinia terminalis (Plate)
Hexarthra sp.
Kellicottia bostoniensis (Rousselet)
Keratella americana Carlin
Keratella cochlearis (Gosse)
Keratella tecta (Gosse)
Keratella tropica (Apstein)
Keratella lenzi (Hauer)
Lecane bulla (Gosse)
Lecane closterocerca (Schmarda)
Lecane cornuta (O.F. Müller)
Lecane curvicornis (Murray)
Lecane elsa Hauer
Lecane hamata (Stokes)
Lecane ludwigii (Eckstein)
Lecane luna O.F. Müller
Lecane lunaris (Ehrenberg)
Lecane proiecta Hauer
Lecane signifera (Jennings) f. *ploenensis* (Voigt)
Lecane stenroosi (Meissner)
Lecane sp.
Lepadella acuminata (Ehrenberg)
Lepadella ovalis (O.F. Müller)
Lepadella sp.
Lophocharis cf. *oxysternon* (Gosse)
Mytilina mucronata (O.F. Müller)
Paradicranophorus sp.
Plationus patulus (O.F. Müller)
Platyias quadricornis (Ehrenberg)
Ploesoma truncatum Levander
Polyarthra sp.
Pompholix complanata Gosse
Synchaeta sp.
Testudinella patina (Hermann)
Trichocerca braziliensis (Murray)
Trichocerca pusilla (Lauterborn)
Trichocerca similis (Wierzejski)
Trichocerca sp. 1
Trichocerca sp. 2
Trichocerca sp. 3
Trichotria tetractis (Ehrenberg)
Trochosphera aequatorialis Semper
Sinantherina sp.
Wolga spinfera (Western)
Bdelloid n.i.1.
Bdelloid n.i. 2

Cladocera
Bosmina hagmani Stingelin
Bosmina huaronensis Delachaux
Bosmina longirostris (O.F. Müller)
Bosmina tubicen Brehm
Bosminopsis deitersi Richard
Bosminopsis sp.
Ceriodaphnia cornuta Sars
Ceriodaphnia pulchella Sars
Chydorus sp.
Daphnia gessneri Herbst
Daphnia parvula Fordyce
Diaphanosoma birgei Korinek
Diaphanosoma brevirreme Sars
Diaphanosoma fluviatile Hansen
Diaphanosoma sp.
Ilyocryptus spinifer Herrick
Macrothrix squamosa Sars
Macrothrix sp.
Moina micrura Kurz
Moina minuta Hansen
Moinodaphnia macleayii (King)

Copepoda
Acanthocyclops robustus (Sars)
Notodiaptomus bidigitatus Brehm
Notodiaptomus conifer (Wright)
Notodiaptomus coniferoides (Wright)