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Zooplankton succession during extraordinary drought–flood cycles: A case study in a South American floodplain lake

Griselda Chaparro [a,b,*], María Cristina Marinone [c], Ruben J. Lombardo [a,d], María Romina Schiaffino [a,d], Alice de Souza Guimarães [e], Inés O'Farrell [a,d]

[a] *Laboratorio de Limnología, Departamento de Ecología Genética y Evolución, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, C1428EHA, Buenos Aires, Argentina*
[b] *ANCyPT (Agencia Nacional de Promoción Científica y Tecnológica), Argentina*
[c] *Laboratorio de Artrópodos, Departamento de Biodiversidad y Biología Experimental, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, C1428EHA, Buenos Aires, Argentina*
[d] *CONICET (Consejo Nacional de Investigaciones Científicas y Técnicas), Argentina*
[e] *Laboratório de Ecologia do Zooplâncton, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais, CEP 31270-901, Minas Gerais, Brazil*

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ABSTRACT

We examined the zooplankton abundance and composition of Laguna Grande, a floodplain wetland of the Lower Paraná Basin (Argentina), during an extraordinary drought–flood cycle that affected both the environment and the biological conditions of the lake. Low waters were characterised by remarkably high conductivities and pH values, and high phytoplankton and bacterioplankton abundances with cyanobacterial blooms, while high waters showed opposite features. In relation to zooplankton, the mean abundances of all the taxonomic groups (rotifers, cladocerans, copepods, ciliates, and heterotrophic nanoflagellates) were slightly higher at low waters. Major changes were observed in the specific composition of metazooplankton: the euryhaline species assemblage that dominated in the dry warm period was replaced by several oligohaline littoral and planktonic species characteristic of the Paraná River Basin, when the water level rose. Mean species richness values at high waters doubled those of low waters and were directly correlated to water depth. Most of the rotifers of the genus *Brachionus* and the cladoceran *Moina micrura* switched from parthenogenetic to sexual reproduction during low waters, as a response to a harsh environment and crowding. We suggest that the main changes in the environmental conditions in this eutrophic floodplain lake are driven by the hydrology, which regulates the zooplankton succession. The herein described shifts in the zooplankton structure and dynamics of Laguna Grande over an extraordinary drought–flood cycle contribute to the understanding of the processes that might occur under the scenarios predicted by climate change models.

Introduction

A large number and variety of shallow lakes develop where rivers meander across wide floodplains. These are known as *billabongs* in Australia, *baors* in India or Bangladesh, *varzea lakes* in Brazil and *lagunas* in Argentina (Kalff 2003). Periodic water level fluctuations constitute a primary factor influencing limnological changes in floodplain lakes (Junk et al. 1989; Neiff 1990). Such hydrological seasonality is accompanied by fluctuations in physical, chemical and biological conditions (Castillo 2000; Bouvy et al. 2003; Rennella and Quirós 2006; Havens et al. 2007). During low water periods, conductivity and inorganic turbidity increase (Hamilton and Lewis 1990; Kalff 2003), macrophyte vegetation is scarce (Hamilton and Lewis 1990; Kalff 2003), and high phytoplankton (Huszar 2000) and bacterioplankton biomass and productivity prevail (Castillo 2000; Kobayashi et al. 2009), while high water phases show opposite scenarios.

The zooplankton response to the hydrological regime is complex due to the interplay of environmental processes and the biology of zooplankters. Although some works have reported that low waters may lead to higher abundance of zooplankton (José de Paggi 1993; Crome and Carpenter 1988), other studies have suggested an adverse effect due to high concentrations of suspended solids (José de Paggi and Paggi 2007). The influence of hydrology and water residence time on reproductive rates differs among zooplankton groups. As an example, the abundance of microcrus-

* Corresponding author at: Laboratorio de Limnología, Departamento de Ecología Genética y Evolución, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, C1428EHA, Buenos Aires, Argentina. Tel.: +54 1145763300; fax: +54 1145763354.
E-mail addresses: griselda@ege.fcen.uba.ar, grichaparro@gmail.com (G. Chaparro).

taceans is strongly affected, whereas that of rotifers shows a minor response (Rennella and Quirós 2006; Bonecker et al. 2005; Paidere 2009). Since zooplankton species have different tolerance levels to conductivity and pH (Claps et al. 2009), hydrology-driven changes of these variables affect species composition. Likewise, the fluctuation in the submerged vegetation, which constitutes a refuge for predators, causes great changes in the zooplankton community composition (Havens et al. 2007). Higher diversity and species richness values have been found during low waters both in South American (Frutos et al. 2006) and in Australian floodplain lakes (Crome and Carpenter 1988).

In shallow lakes, exceptional changes in the water level can also induce shifts at the ecosystem level, which are evidenced as alternative stable states (Loverde-Oliveira et al. 2009). O'Farrell et al. (2011) suggested that extraordinary floods and droughts might drive the ecosystem regime from a state dominated by floating plants during high waters to a state dominated by phytoplankton with cyanobacterial blooms during low waters. Marked water level fluctuations are becoming increasingly important, as climate change models predict increased drought cycles for many regions of the world (Jentsch et al. 2007; IPCC 2010) as well as enhanced frequency of extreme hydrometeorological events such as El Niño Southern Oscillation (ENSO) (Timmermann et al. 1999).

A recent extraordinary drought in the Paraná River Basin region affected the adjacent floodplain systems and provided the opportunity to examine the zooplankton dynamics and structure of Laguna Grande (Otamendi Natural Reserve, Argentina) in response to the consequent changes both in its abiotic and in biological conditions. The aim of this study was to describe and analyse the zooplankton dynamics of an enriched shallow floodplain lake undergoing extraordinary water level fluctuations.

We hypothesised that the water level fluctuations regulate the zooplankton succession during extraordinary hydrological cycles in shallow eutrophic floodplain lakes and predicted that during the low water phase, few species tolerant to harsh conditions will develop dense populations, and that during the high water phase a richer community will develop.

Methods

Study area

The Otamendi Natural Reserve is a RAMSAR floodplain wetland that comprises several water bodies. It is delimited by the Paraná de las Palmas and Luján Rivers, Buenos Aires Province, Argentina (34°10′–34°17′S; 58°48′–58°53′W) (Fig. 1). The area was influenced by a high and fluctuating water table, being permanently or periodically flooded due to rainfall (Chichizola 1993) and not by river overflow. The main lake, Laguna Grande (~156 ha, $Z < 1$ m), is eutrophic and surrounded by marshy vegetation. The region has a temperate climate, with hot summers and without a dry season, according to the updated Köppen–Geiger classification (Peel et al. 2007). The mean annual temperature ranges between 16.7 and 18 °C and precipitations occur during the whole year with a mean annual value of 950 mm. Nevertheless, one of the worst droughts in southern South America in decades were recorded from mid-November 2008 through mid-February 2009.

Sampling and physico-chemical analyses

Samples were taken monthly in Laguna Grande during an exceptional cycle of drought and refilling (September 2008 to August 2009, except November 2008). The sampling site was located at a fixed point at 300 m from the shoreline, in an open water area lacking aquatic vegetation (Fig. 1). Temperature, pH, conductivity and dissolved oxygen were measured in situ using HI 991301 Hanna® and HI 9143 Hanna® (oxygen) portable instruments (Hanna Instruments, Woonsocket, RI, USA) and water depth was determined with a portable meter. Nutrients and suspended solids were analysed following the methods described by O'Farrell et al. (2009). Daily rainfall data were provided by the Servicio Meteorológico Nacional (Argentina) and the monthly water level and discharge of the Paraná River were measured by the Subsecretaría de Puertos y Vías Navegables at the nearest station (Zárate, Paraná de las Palmas River).

Zooplankton

Samples for zooplankton were taken in duplicate with a transparent acrylic bottle (15 cm diameter, 6 L volume). Twelve litres integrating the water column from surface to bottom were collected, filtered through a 40-μm mesh sieve and preserved with 4% formaldehyde. Microzooplankton (nauplii and rotifers) was counted in a 1-mL Sedgwick-Rafter counting cell using an optical microscope; subsamples were taken with a Hensen–Stempel pipette. Mesozooplankton (copepodites, adult copepods and cladocerans) was examined and enumerated in a 5-mL Bogorov chamber under a stereomicroscope and subsampled with a Russell device. The counting error was below 10%. Rotifers, cladocerans and copepods were identified to species or genus level. Fecundity of the most abundant rotifers was estimated as the egg ratio (number of eggs per female, following Edmondson 1965) in order to assess food availability and quality. The ratio was calculated considering the eggs attached to females and the total number of females. The biomass (dry weight) of the most abundant zooplankton species was calculated from wet weight (WW) and biovolume. Rotifer biovolume was estimated from geometric formulas (Ruttner-Kolisko 1977) from body measurements (length and width) and transformed into WW as follows: 10^6 μm^3 equals 1 μg of WW (Bottrell et al. 1976). Dry weight (DW) was determined as 10% of WW, except in the case of Asplanchna, in which it was determined as 3.9% (Bottrell et al. 1976). The dry weight of copepods and cladocerans was estimated from body length-dry weight relationships according to Bottrell et al. (1976) and Dumont et al. (1975). We measured 20–40 individuals from each species on every sampling date. Zooplankton species were classified into four groups, according to their occurrence in low waters (LW, hereinafter) and high waters (HW, hereinafter): exclusive of LW, prevailing in LW, exclusive of HW and prevailing in HW. Species that were present exclusively during one period were classified as exclusive, while those recorded in a higher frequency in one period than in another were classified as prevailing.

On the other hand, zooplankton species were classified in functional groups in order to analyse trophic interactions. Rotifers, copepodites and nauplii were classified as small herbivores, cladocerans as large herbivores, and adult cyclopoids as predators (Hulot et al. 2000).

Phytoplankton >2 μm and ciliates

Unfiltered water samples for quantitative analysis of phytoplankton and ciliates were preserved with 1% Lugol's iodine solution and counted under an inverted microscope according to Utermöhl (1958). Phytoplankton was classified in two size categories according to its palatability to zooplankton herbivores (<30 μm, edible algae; >30 μm, inedible algae), and biovolumes were calculated according to Hillebrand et al. (1999) and Jun and Dongyan (2003). Ciliate biovolumes were calculated on the basis of average cell dimensions using appropriate geometric formulae.
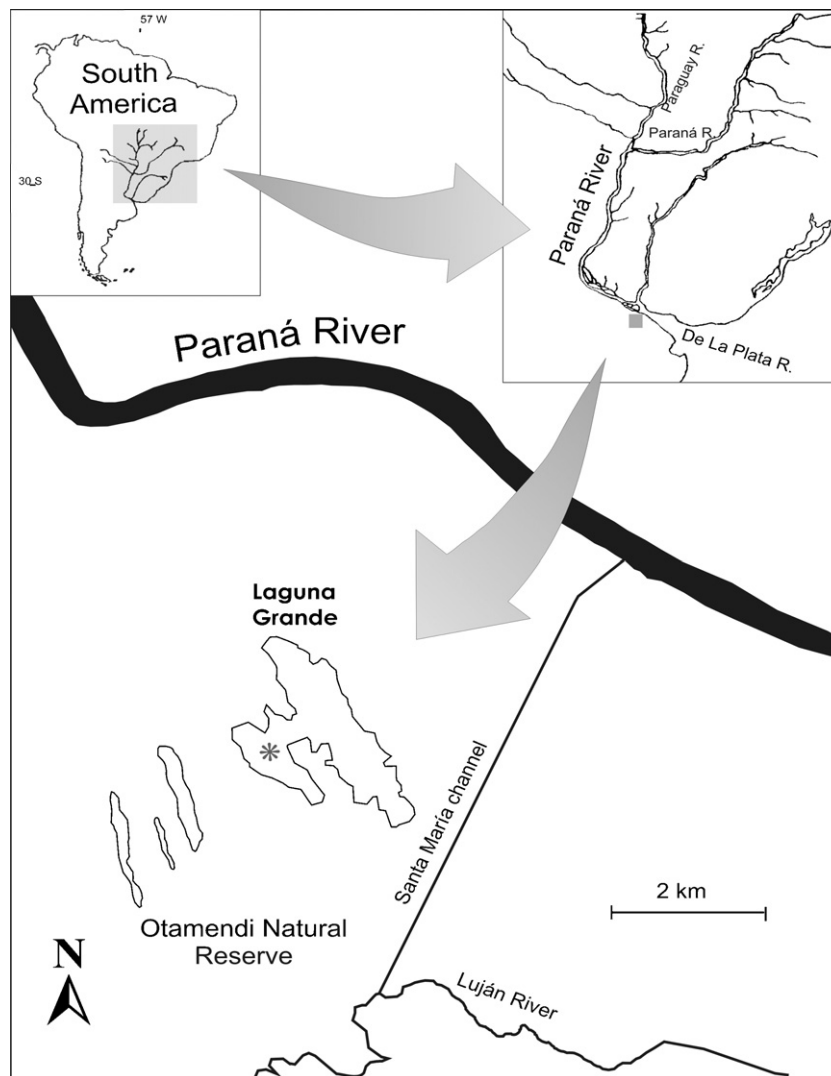
Fig. 1. Map of the study area. The sampling site is indicated with an asterisk.

Picoplankton (<2 μm) and heterotrophic nanoflagellates

Total abundances of bacterioplankton, picocyanobacteria, picoeukaryotes, and heterotrophic nanoflagellates were determined by epifluorescence following the methodology described by Sinistro et al. (2006). Biovolumes were calculated from body measurements and appropriate geometric formulae.

Pearson's correlation coefficient (r) was used to estimate correlations between environmental variables, assessing normality by the Shapiro–Wilk test. Principal component analysis (PCA) was performed to obtain ordination and identification of relatively homogeneous groups of samples based on physical and chemical data, which were standardised to reduce the variables to a common scale. A multivariate analysis of variance (MANOVA) was performed to test for differences in the physico-chemical composition between LW and HW. The Box test of equality of covariance matrices, which is sensitive to departures from multivariate normality, was used. One-way analysis of variance (ANOVA) was performed to test for differences between LW and HW in Shannon Diversity Index, species richness, evenness, and the total abundance and biomass (or biovolume) of the plankton groups. The Levene test was performed to check the homogeneity of variance. Abundance data of all plankton groups were log-transformed (natural logarithms), while biomass data were transformed as square root in

order to satisfy the homocedasticity. For the multivariate analyses, rare species occurring in less than 3% in all samples were removed. Agglomerative classification of the remaining species was performed on abundance data using the correlation coefficient as a similarity measure that lays emphasis on the relative proportions of the species in the samples. The UPGMA linkage procedure was used. Canonical correspondence ordination based on species abundance data was used to elucidate the relationships between species assemblages and environmental variables. Significance of the canonical axes was tested using Monte Carlo permutation of samples (ter Braak and Verdonschot 1995). Spearman's rank correlation coefficient (r) was used to estimate the correlation between zooplankton taxonomic and functional groups and their potential food resources: bacterioplankton, Pcy, Peuk, ciliates, HNF, and edible and inedible algae, in terms of biomass.

Results

Environmental variables

Laguna Grande experienced great changes in its hydrometric level associated both with variations in the Paraná de las Palmas River discharge and with the rainfalls during the study period ($r = 0.76$, $p < 0.05$) (Fig. 2a). A LW phase (depth < 30 cm)
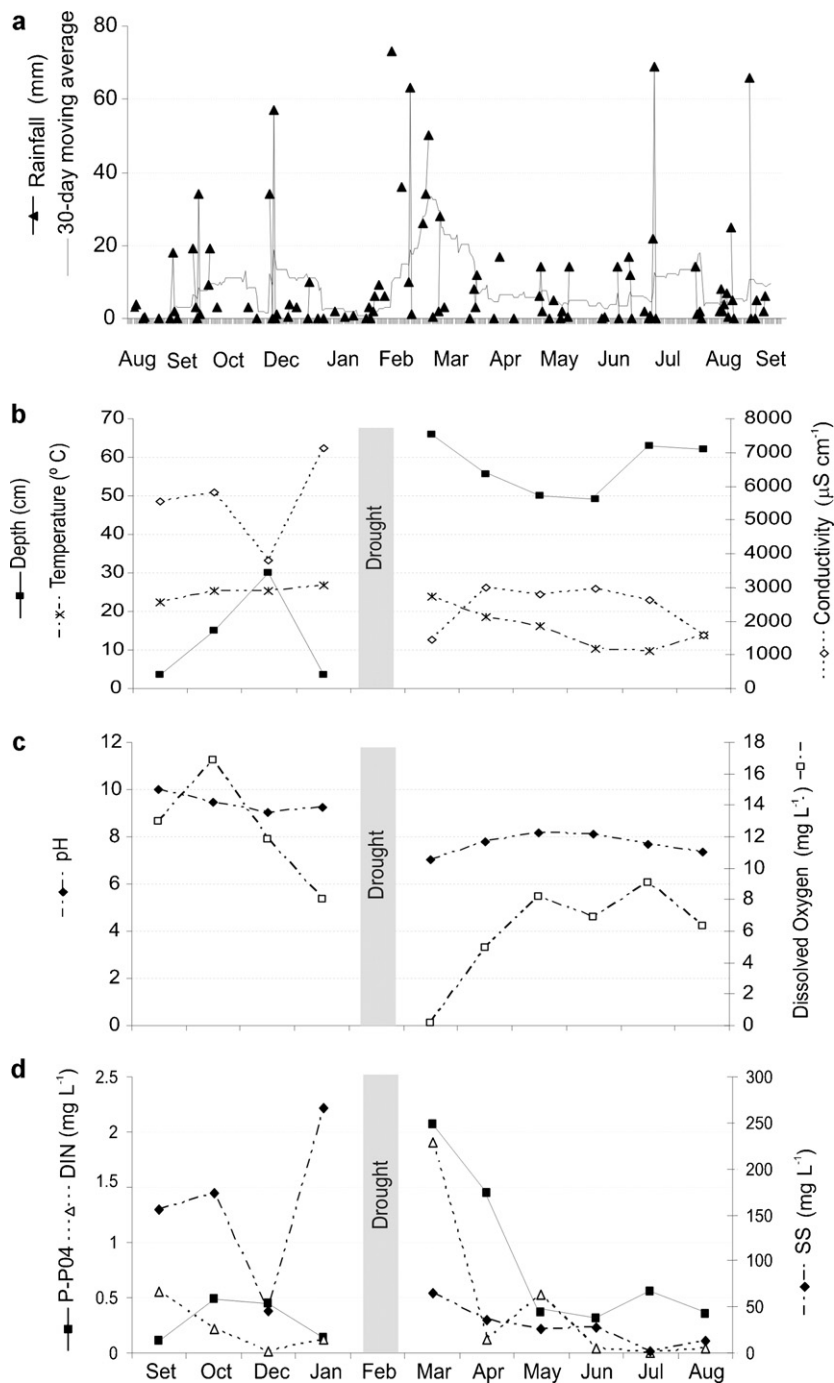
Fig. 2. Monthly dynamics of the physico-chemical parameters evaluated. (a) Rainfall recorded (mm) in the study area, 30-day rainfall moving average; (b) water depth (cm), temperature (°C) and conductivity ($\mu S\,cm^{-1}$); (c) pH and dissolved oxygen concentrations ($mg\,L^{-1}$) recorded in the water column; (d) PO$_4$, dissolved inorganic nitrogen (DIN) and suspended solid (SS) concentrations ($mg\,L^{-1}$).

Table 1
Mean values and standard deviation for the physico-chemical parameters recorded at low waters and high waters.

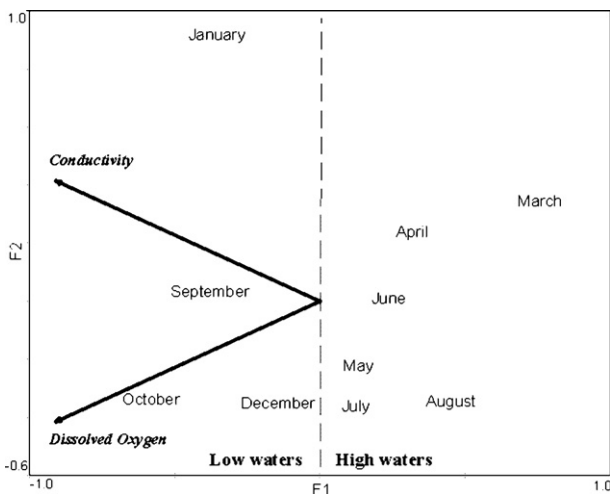|	Low waters		High waters	
	Mean	SD	Mean	SD
Water depth (cm)	13	12.6	57.6	7.1
Temperature (°C)	24.9	1.9	15.3	5.3
Dissolved oxygen ($mg\,L^{-1}$)	12.4	3.6	5.9	3.2
pH	9.4	0.4	7.7	0.4
Conductivity ($\mu S\,cm^{-1}$)	5565	1369.2	2399.8	699.3
P-P04 ($mg\,L^{-1}$)	0.3	0.2	0.8	0.7
DIN ($mg\,L^{-1}$)	0.2	0.2	0.4	0.7
Chlorophyll a ($\mu g\,L^{-1}$)	396.9	206.7	49.9	38.2
Suspended solids ($mg\,L^{-1}$)	160.3	0.2	28.1	22

Fig. 3. Principal component analysis performed on conductivity and dissolved oxygen concentrations. Sampling dates are plotted.

occurred during the austral spring-summer season (September 2008–January 2009). The lake was characterised by high temperature (22.3–26.7 °C), high conductivity (>3790 μS cm^{-1}), high dissolved oxygen (>8 mg L^{-1}), pH higher than 9, and intermediate concentrations of phosphate and dissolved inorganic nitrogen (0.29 and 0.22 mg L^{-1} mean values respectively) (Table 1 and Fig. 2). During this period, the river discharge dropped, the rainfall was scarce, the lake volume gradually diminished, and the area was partially colonised by herbs and shrubs. The lake dried out in February, in coincidence with the lowest river discharge and rainfalls (less than 15 mm in the previous month) and the highest evaporation (responding to summer temperatures). The HW phase started by late summer and remained until winter (March–August 2009); the water temperatures decreased in accordance with the season from 23.7 to 9.6 °C and water depth always exceeded 49 cm. Consequently, conductivity decreased to less than 3000 μS cm^{-1}, dissolved oxygen concentrations initially dropped to anoxia and then recovered to concentrations higher than 4.9 mg L^{-1} and pH decreased to less than 8.1. Regarding nutrients, both phosphate and DIN concentrations increased markedly in March, just after the water pulse, and then returned gradually to values similar to those recorded in LW (Table 1 and Fig. 2).

Water depth was correlated to pH ($r = -0.96$), conductivity ($r = -0.96$), temperature ($r = -0.63$), and suspended solids ($r = -0.87$) ($p < 0.001$), whereas conductivity was correlated to pH ($r = 0.89$) and suspended solids ($r = 0.91$) ($p < 0.001$) (Table 2).

The PCA performed on abiotic variables detected high colinearity between conductivity, water depth, pH, suspended solids, PO$_4$, and DIN concentrations. The first two principal components explained 83% of the total variance based on conductivity and dissolved oxygen. The ordination of the sampling dates along the first axis of the PCA is associated with water level: LW samples are on the left side of the plot, whereas HW samples appear on the right side (Fig. 3). The MANOVA based on conductivity and dissolved oxygen revealed significant differences between the LW and HW phases ($p = 0.004$).

Zooplankton

Fifty-seven zooplankton species, including one cyclopoid copepod, one calanoid copepod, seven cladocerans, and forty-eight rotifers, were identified (Table 3). Rotifers, which were the most abundant group throughout the study period, showed a clear species replacement pattern between the two hydrological phases:

species of the genera *Brachionus* Pallas, 1766, dominated in LW, while *Pompholyx* Gosse, 1951, *Synchaeta* Ehrenberg, 1832 and *Keratella* Bory de St. Vincent, 1822 dominated in HW. Cyclopoid copepods (nauplii, copepodites and adults), represented by *Metacyclops mendocinus*, were the second most abundant component. Calanoid copepods (represented by *Notodiaptomus incompositus*) and cladocerans were the least abundant group. The cluster analysis based on the relative proportions of the most abundant species (Fig. 4) showed two main groups, separating the LW species from those of HW. *Brachionus dimidiatus* was exclusive of the LW phase, whereas *M. mendocinus* (all stages), *Moina micrura*, *Brachionus angularis*, *Brachionus ibericus*, *Brachionus plicatilis*, and *Filinia novaezealandiae* prevailed in LW. Conversely, in the HW group, most of the species such as *Polyarthra remata*, *Pompholyx triloba* and *Brachionus havanaensis* were exclusive of this phase, while *Keratella morenoi* and *Brachionus calyciflorus* prevailed in HW.

Diversity (Shannon index) varied between 0.74 and 1.36 throughout the study period and mean values showed no significant differences between the two water phases; evenness fluctuated from 0.6 to 1.27 and was slightly higher in LW. No significant relationship was detected between these attributes and any environmental variable. Mean species richness (S) was significantly higher in HW, doubling values of LW (23 and 11 respectively, $p < 0.05$) (Fig. 5); S was correlated to water depth ($r = 0.81$, $p = 0.004$).

Mean total zooplankton abundance was 6866 ind L^{-1} at LW and 4160 ind L^{-1} at HW ($p > 0.05$). At the beginning of the study, during the LW phase, all zooplankton groups were very scarce (Fig. 6a). Cyclopoid copepods reached higher abundances during LW months, whereas rotifers increased in October and were still very abundant just before the drought, when they represented almost 100% of the zooplankton. Cladocerans were scarce during the LW phase, except in December when high densities of *M. micrura* were recorded in coincidence with a small water pulse. At the onset of the HW phase, zooplankton abundance was scarce again. During the following months, the abundance of nauplii and copepodites increased, whereas that of rotifers alternated between high and low values. Low densities of the cladocerans *M. micrura* or *Daphnia spinulata* were occasionally found. Interestingly, the dominant rotifer species presented high egg ratios, and their maximum values of fecundity coincided mostly with maximum densities (Table 3).

Mean total zooplankton biomass was 2588 μg L^{-1} at LW and 1656 μg L^{-1} at HW (Fig. 6b) ($p > 0.05$). During the LW phase, copepod biomass was higher due to the contribution of all cyclopoid stages, while rotifer biomass became dominant just before the drought. In the HW phase, copepod biomass was lower and all the stages decreased slightly towards winter time. However, they were dominant except in June and August, when rotifers and cladocerans prevailed respectively. Regarding the taxonomic groups, only copepod stages were correlated: nauplii to copepodites and adults ($r = 0.80$ and 0.88 respectively, $p < 0.05$) and copepodites to adults ($r = 0.88$, $p < 0.05$) (Table 2). Considering the functional groups, predators were correlated to small herbivores ($r = 0.93$, $p < 0.0001$) and to HNF ($r = 0.76$, $p < 0.05$), and small herbivores were correlated to HNF ($r = 0.76$, $p < 0.05$). No significant correlations were detected among zooplankton and other plankton groups, which may be considered as food resources.

Zooplankton–environment relationships

The canonical correspondence ordination (Fig. 7) performed on zooplankton species and selected environmental variables (conductivity and dissolved oxygen) detected high species–environment correlations ($r = 0.95$) and explained 65% of variance of this relationship ($p = 0.01$). Two main groups can be distinguished: the species prevailing in LW (on the left side of the

Table 2
Correlation coefficients between abiotic factors, zooplankton groups, richness and potential food resources ($p < 0.05$).

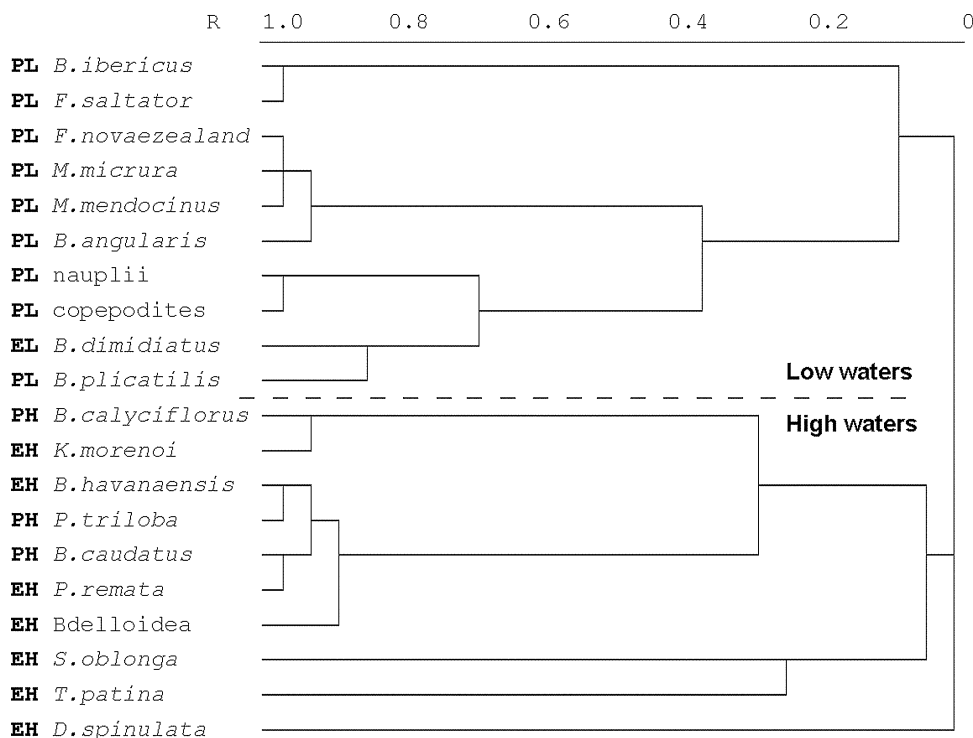|	Lake water depth	Conductivity	Species richness	Nauplii	Copepodites	Adult cyclopoids	Predators	Edible phytoplankton	Inedible phytoplankton	Picocyanobacteria
River discharge	0.76									
Conductivity	−0.96							0.72	0.97	
pH	−0.96	0.89								
Temperature	−0.63								0.72	
Suspended solids	−0.87	0.91								
Lake water depth			0.81						−0.93	
Species richness										
Copepodites				0.80						
Adult cyclopoids				0.88	0.88					
Small hervibores						0.93				
Heterotrophic nanoflagellates						0.70				
Edible phytoplankton										
Inedible phytoplankton								0.72		
Bacteria								0.75		0.83

Fig. 4. Cluster analysis performed on the zooplanktonic species on a correlation matrix basis.

plot, associated with both high conductivity and dissolved oxygen values), which comprised euryhaline species such as *B. plicatilis* and *B. ibericus*, among others, and the species that prevailed in HW (on the right side of the plot, in association with opposite environmental conditions) which comprised benthic-littoral species such as *Testudinella patina* and Bdelloidea (which were colonisers in March), and other planktonic species such as *P. remata*, *P. triloba*, and *Synchaeta oblonga*. The different stages of *M.*
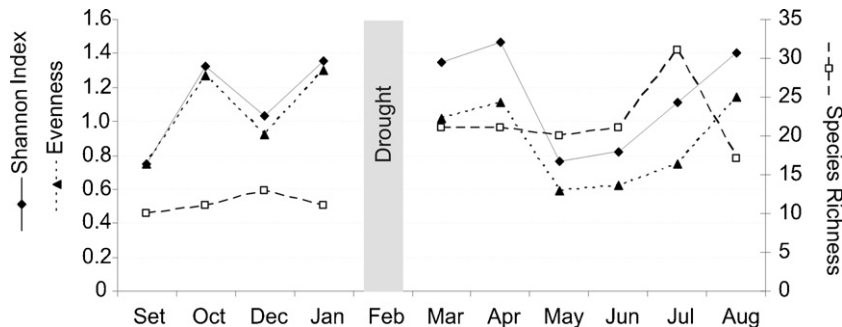

Fig. 5. Monthly dynamics of the structural parameters of the zooplankton assemblage: Shannon diversity index, evenness and species richness.

Table 3

Monthly presence of the zooplankton species. E indicates the dates when eggs were detected. Species classification considering both their occurrence and abundance at each water level period: EL (exclusive of low waters), PL (prevailing in low waters), EH (exclusive of high waters), PH (prevailing in high waters). Mean egg ratios (ER) of the dominant species (only E dates were considered for the calculation).

| Rotifera	S	O	D	J	M	A	M	J	J	A	Period	ER
Anuraeopsis fissa Gosse, 1851					X					X	EH	
Asplanchna silvestrii Daday, 1902	X		X						X		PL	
Brachionus angularis angularis Gosse, 1851		E	E	E	X	X	X	X			PL	0.62
Brachionus bidentatus bidentatus Anderson, 1889		E	E	E	X				X		PL	
Brachionus calyciflorus calyciflorus Pallas, 1766				X		E		E	E	E	PH	1.07
Brachionus caudatus Barrois & Daday, 1894	X					E	E	E	E	E	PH	0.60
Brachionus dimidiatus Bryce, 1931		E	E	E							EL	0.68
Brachionus havanaensis Rousselet, 1911						E	E				EH	0.12
Brachionus cf. *ibericus* Cirós-Pérez, Gómez & Serra 2001				X	X	X					PL	0.61
Brachionus cf. *plicatilis* Müller, 1786	E	E	E				X				PL	0.99
Brachionus quadridentatus quadridentatus Hermann, 1783	X										EL	
Brachionus urceolaris urceolaris Müller, 1773					X		X				EH	
Cephalodella spp. Bory de St. Vincent, 1826					X				X		EH	
Colurella cf. *obtusa obtusa* (Gosse, 1886)						X			X		EH	
Colurella cf. *uncinata uncinata* (Müller, 1773)									X		EH	
Colurella spp. Bory de St. Vincent, 1824					X						EH	
Epiphanes clavulata (Ehrenberg, 1832)						X					EH	
Euchlanis cf. *incisa* Carlin, 1939								X	X		EH	
Euchlanis sp. Ehrenberg, 1832									X		EH	
Filinia novaezealandiae Shiel & Sanoamuang, 1993	X	X	X	X	X	X					PL	
Filinia saltator (Gosse, 1886)				E	X			X			PL	0.04
Keratella morenoi Modenutti, Diéguez & Segers, 1998	X	X		E	E	E	E	E	E	E	PH	0.22
Lecane aculeata (Jakubski, 1912)									X		EH	
Lecane bulla bulla (Gosse, 1851)					X		X			X	EH	
Lecane closterocerca (Schmarda, 1859)				X	X	X	X	X			EH	
Lecane hamata (Stokes, 1896)				X		X	X	X			EH	
Lecane inermis (Bryce, 1892)						X		X			EH	
Lecane sp. Nitzsch, 1827				X	X						EH	
Lepadella acuminata (Ehrenberg, 1834)								X			EH	
Lepadella cf. *imbricata* Harring, 1914						X					EH	
Lepadella patella patella (Müller, 1786)				X							EH	
Mytilina ventralis ventralis (Ehrenberg, 1830)								X			EH	
Monommata sp. Bartsch, 1870										X	EH	
Notommata sp. Ehrenberg, 1830						X		X			EH	
Platyas quadricornis quadricornis (Ehrenberg, 1832)							X	X			EH	
Polyarthra remata Skorikov, 1896				E	E	E	E	E	E	E	EH	0.04
Pompholyx triloba Pejler, 1957						E	E	E	E	E	EH	0.27
Sinantherina semibullata (Thorpe, 1893)					X	X					EH	
Synchaeta oblonga Ehrenberg, 1832									X	X	EH	
Synchaeta pectinata Ehrenberg, 1832									X		EH	
Testudinella patina (Hermann, 1783)					X				X		EH	
Trichocerca bicristata (Gosse, 1887)									X		EH	
Trichocerca inermis (Linder, 1904) (*species inquirenda*)						X	X	X			EH	
Trichocerca rattus (Müller, 1776)									X		EH	
Trichocerca tenuior (Gosse, 1886)					X						EH	
Trichocerca sp. 1									X	X	EH	
Trichocerca sp. 2		X	X						X		PL	
Undetermined Bdelloidea					X	X					EH	
Copepoda												
Copepoda nauplii	X	X	X	X	X	X	X	X	X	X	PL	
Cyclopoida copepodites	X	X	X	X	X	X	X	X	X	X	PL	
Metacyclops mendocinus (Wierzejski 1892)	X	X	X	X	X	X	X	X	X	X	PL	
Calanoida copepodites									X	X	EH	
Notodiaptomus incompositus (Brian, 1925)				X				X	X	X	PH	
Cladocera												
Ceriodaphnia cf. *dubia* Richard, 1895										X	EH	
Daphnia spinulata Birabén, 1917										X	EH	
Diaphanosoma birgei Korinek, 1981			X			X	X	X			PL	
Ilyocryptus sp	X										EL	
Moina micrura Kurz, 1874		X	X		X	X	X				PL	
Macrothrix spinosa King, 1853			X								EL	
Simocephalus cf. *vetulus* (O.F. Müller, 1776)									X		EH	
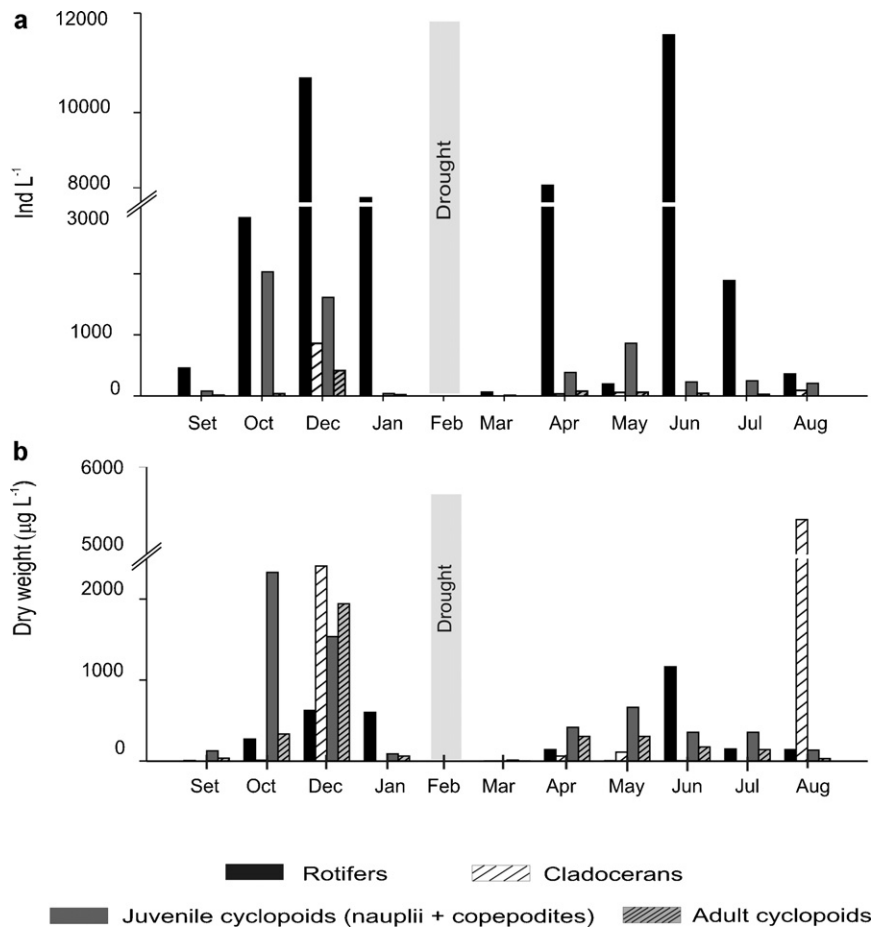
Fig. 6. Abundance (a) and biomass (b) of the main zooplankton taxonomic groups (rotifers, cladocerans, juvenile stages of cyclopoids, and adult cyclopoids) throughout the study period.

mendocinus, *M. micrura* and the rotifer *F. novaezealandiae*, which were found in both hydrological phases, appear in the centre of the graph.

On the other hand, the harsh environmental conditions that prevailed during LW promoted the sexual reproduction of many

species of the community, as evidenced by the appearance of males, mictic females and resistant eggs of the above-mentioned species of *Brachionus* (from October to January 50–100% of these populations were either males or mictic females), as well as of males and ephippial females of *M. micrura* (in December).
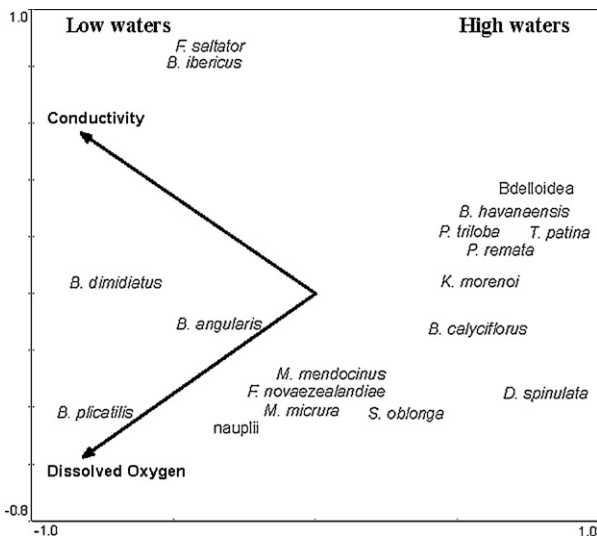
Heterotrophic nanoflagellates and ciliates

Mean abundances and biovolumes of heterotrophic nanoflagellates and ciliates were higher in LW (Table 4); significant differences were found in both groups in terms of biovolume ($p < 0.05$).

Phytoplankton >2 μm

Mean abundance and biomass of both edible and inedible phytoplankton were higher in LW ($p < 0.05$) (Table 4). Edible phytoplankton was dominated by *Merismopedia minima*, *Anabaenopsis elenkini* and an unidentified oscillatorean species, whereas inedible phytoplankton was represented mainly by *Microcystis aeruginosa*, *Sphaerospermum aphanizonemoides*, *Planktolyngbya limnetica*, and *Euglena communis*. The contribution of edible phytoplankton to total phytoplankton was higher in LW (63% of algal abundance and 35% of algal biovolume) than in HW (25% of algal density and 10% of algal biovolume). Moreover, edible and inedible phytoplankton biovolumes were correlated to each other ($r = 0.72$, $p < 0.03$) as well as to conductivity ($r = 0.72$ and 0.97, $p < 0.05$, respectively). Inedible phytoplankton was correlated to temperature and water depth ($r = 0.72$ and -0.93, $p < 0.05$, respectively).

Fig. 7. Canonical correspondence analysis based on the zooplankton species composition and their relationships with conductivity and dissolved oxygen. The species considered are plotted.

Table 4
Mean biovolumes and abundances of the plankton groups studied in low waters (LW) and high waters (HW). Different letters indicate significant differences between water level phases ($p < 0.05$).

	Biovolume ($\mu m^3\ mL^{-1}$)				Density (ind mL^{-1} or cells mL^{-1})			
	LW		HW		LW		HW	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Edible phytoplankton (<30 μm)	3.4×10^7	3.6×10^7	2.9×10^7	2.7×10^7	1.3×10^5	2.4×10^5	3.6×10^4	3.3×10^4
Unedible phytoplankton (>30 μm)	9.9×10^8	1.1×10^9	6.5×10^7	8.6×10^7	3.0×10^5	2.7×10^5	1.6×10^4	1.1×10^4
Picoeukaryotes	3.8×10^4	2.5×10^4	3.5×10^4	1.7×10^4	1.5×10^4	9.9×10^3	1.4×10^4	6.9×10^3
Picocyanobacteria	1.3×10^6	2.0×10^6	3.6×10^4	4.2×10^4	2.0×10^6	3.1×10^6	5.5×10^4	6.5×10^4
Bacteria	3.2×10^6	2.2×10^6	2.2×10^5	1.3×10^5	3.5×10^7	2.5×10^7	2.5×10^6	1.5×10^6
Heterotrophic nanoflagellates	8.6×10^5	5.5×10^5	3.6×10^5	2.5×10^5	5.3×10^3	3.4×10^3	2.2×10^3	1.5×10^3
Ciliates	1.1×10^6	7.5×10^5	5.8×10^5	6.2×10^5	2.2×10^2	1.4×10^2	1.1×10^2	1.2×10^2

Picophytoplankton (<2 μm)

Mean biovolumes and abundances of picophytoplankton in LW and HW are presented in Table 4. Regarding picoeukaryotes, similar maximum values were recorded in both hydrological phases ($p > 0.05$). Picocyanobacteria abundance was higher in LW ($p < 0.05$) and its biovolume showed the same pattern ($p > 0.05$). In relation to bacteria, both mean abundance and biovolume were higher in LW ($p < 0.05$). Bacteria were correlated to picocyanobacteria ($r = 0.83$, $p < 0.005$) and edible phytoplankton ($r = 0.75$, $p < 0.02$).

Discussion

Laguna Grande hosted a rich zooplankton community characterised by the dominance of rotifers and the scarcity of cladocerans, as previously reported in works conducted in this eutrophic floodplain lake (Sinistro 2007; Fontanarrosa et al. 2010) and in other studies conducted in South American shallow lakes (Meerhoff et al. 2007; Iglesias et al. 2007; Lansac-Tôha et al. 2009). Our results show that the hydrological regime strongly shaped the zooplankton composition, the community succession and the adaptation strategies of dominant species.

Water level fluctuations in Laguna Grande during the study period were associated with rainfall events and the Paraná de las Palmas River discharge. The extreme drought determined a gradual water volume loss in the lake, which led to a dry phase; later abundant rainfall caused a rapid refilling and the consequent HW phase. These exceptional fluctuations triggered major environmental changes that affected plankton communities. The extremely high conductivity values reached during the LW phase correspond to a mesohaline lake (Ringuelet 1957), with remarkably turbid waters because of both high algal abundance and high concentrations of suspended solids. Such conditions, together with high temperatures and pH values and scarcity of dissolved nitrogen, favoured the cyanobacterial blooms, as it is frequently reported for lakes undergoing severe droughts (Bouvy et al. 2003; Paerl and Huisman 2009; Unrein et al. 2010). In March, the water refilling triggered a pulse of nutrients and minimum values of conductivity, pH, suspended solids, and dissolved oxygen concentrations; later on, these parameters increased slightly.

As stated by José de Paggi and Paggi (2007), the variation in the hydrometric level in floodplain environments is a complex phenomenon, as it involves changes in the water volume in the basin and in the environmental conditions that affect the abundance of organisms. The multivariate analyses here performed support the existence of two distinct water phases and highlight the differences in the composition of both assemblages. During the LW phase, the zooplankton was represented by few species with extremely high abundances. Planktonic euryhaline species such as the rotifers *B. plicatilis*, *B. ibericus*, and *B. dimidiatus*, and the cyclopoid *Metacyclops mendocinus*, frequently found in saline lakes (Claps et al. 2009; Cirós-Pérez et al. 2001; Sterza and Loureiro Fernandes 2006) represented this assemblage. Evidently, the switch from parthenogenetic to sexual reproduction of some of the dominant species found in the lake during LW reflects their adaptation to highly fluctuating environmental conditions, as described by Gyllström and Hansson (2004). The crowding of *Moina* (700 ind L^{-1}) and the blooms of potentially toxic cyanobacteria (mean 9.9×10^8 ind mL^{-1}) recorded during this phase may be responsible for the high production of *Moina* ephippia. Crowding conditions, poor food quality and potential cyanobacteria toxicity have been previously reported to be cues for diapause initiation (Pagano et al. 2000; Daogui et al. 2010; Lauren-Määttä et al. 1997). Likewise, crowding seems to have promoted the high abundance of males and females of *Brachionus* recorded (ca. 3400 ind L^{-1}) in the LW phase; this factor is crucial to induce sexual reproduction in species of this genus (Schröder and Gilbert 2004; Gilbert 2004).

During HW, a richer community constituted by both planktonic and littoral oligohaline species, usually reported for the Paraná River Basin (José de Paggi 1993; Frutos 1998; Sinistro 2007; Fontanarrosa et al. 2010) replaced the zooplankters that prevailed in LW. More favourable environmental conditions, namely lower conductivity and lower suspended solids (Panarelli et al. 2008), can be related to the increase in species richness. In this sense, no evidence of sexual reproduction was observed throughout this phase. The exchange between the persistent rooted emergent macrophyte beds and open waters when the water level rises, which has been recognised as the principal factor for zooplankton colonization (Crome and Carpenter 1988; Bonecker and Lansac-Tôha 1996), may have played a significant role in our study case. On the other hand, the hatching of zooplankton eggs and resting stages from sediments could also be a source of organisms and responsible for the increase in zooplankton richness (Lindholm and Hessen 2007; Panarelli et al. 2008).

Trophic interactions appear to have played a minor role in the regulation of zooplankton during the study period. The relationship between food availability (bacteria, HNF, algae, and ciliates) and the dominant filter-feeding zooplankters suggests that there is no bottom-up regulation. In particular, during LW under extreme abiotic conditions, when zooplankton was abundant, there was high food availability as shown by both high fecundity and crowding (evidenced by sexual reproduction). As for top-down control, fish abundance can be considered negligible during both periods. During LW and the onset of HW, environmental conditions were highly unfavourable to fish, whereas HW mostly coincided with winter time and lower fish occurrence in this latitude (Mazzeo et al. 2003; Scasso et al. 2001).

Final remarks

Our results support the fact that water level fluctuation is the main driving force in shaping the zooplankton succession during

extraordinary hydrological cycles in Laguna Grande. Likewise, the environmental modulation of the reproduction of zooplankton species was evident. Drastic water level changes, mainly associated with global hydrometeorological events such as the ENSO phenomenon, triggered major changes in the floodplain lake studied, as depicted over a 10-year period O'Farrell et al. (2011). The described shifts in zooplankton structure and dynamics over a drought–flood transition period further contribute to the understanding of the processes that might occur under the scenarios predicted for this region by climate change models.

Acknowledgements

References

Bonecker, C.C., Da Costa, C., Velho, L., Lansac-Tôha, F., 2005. Diversity and abundance of the planktonic rotifers in different environments of the Upper Paraná River floodplain (Paraná State – Mato Grosso do Sul State, Brazil). Hydrobiologia 181, 405–414.

Bonecker, C.C., Lansac-Tôha, F.A., 1996. Community structure of rotifers in two environments of the high Paraná River floodplain (MS), Brazil. Hydrobiologia 325, 137–150.

Bottrell, H.H., Duncan, A., Gliwicz, Z.M., Grygierek, E., Herzig, A., Hillbricht-Ilkowska, A., Kurasawa, H., Larsson, P., Weglenska, T., 1976. A review of some problems in zooplankton production studies. Norw. J. Zool. 24, 419–456.

Bouvy, M., Nascimento, S.M., Molica, R.J.R., Ferreira, A., Huszar, V., Azevedo, S.M.F.O., 2003. Limnological features in Tapacurá reservoir (northeast Brazil) during a severe drought. Hydrobiologia 493, 115–130.

Castillo, M., 2000. Influence of hydrological seasonality on bacterioplankton in two Neotropical floodplain lakes. Hydrobiologia 437, 57–69.

Chichizola, S.E., 1993. Las comunidades vegetales de la Reserva Natural Estricta Otamendi y sus relaciones con el ambiente. Parodiana 8, 227–263.

Cirós-Pérez, J., Gómez, A., Serra, M., 2001. On the taxonomy of three sympatric sibling species of the *Brachionus plicatilis* (Rotifera) complex form Spain, with the description of *B. ibericus* n. sp. J. Plankton Res. 23, 1311–1328.

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.

Crome, F.H.J., Carpenter, S.M., 1988. Plankton community cycling and recovery after drought – dynamics in a basin on a flood plain. Hydrobiologia 164, 193–211.

Daogui, S., Sai, Z., Yuying, L., Xiaoli, M., Wei, Y., Yan, L., Xiulxiu, L., 2010. Effects of Microcystis aeruginosa on population dynamics and sexual reproduction in two *Daphnia* species. J. Plankton Res. 0, 1–8.

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

Edmondson, W.T., 1965. Reproductive rate of planktonic rotifers as related to food and temperature in nature. Ecol. Monogr. 35, 61–111.

Fontanarrosa, M.S., Chaparro, G., de Tezanos Pinto, P., Rodriguez, P., O'Farrell, I., 2010. Zooplankton response to shading effects of free-floating plants in shallow warm temperate lakes: a field mesocosm experiment. Hydrobiologia 646, 231–242.

Frutos, S.M., 1998. Densidad y diversidad del zooplancton en los ríos Salado y Negro – planicie del río Paraná–Argentina. Rev. Bras. Biol. 58, 431–444.

Frutos, S.M., Poi de Neiff, A.S.G., Neiff, J.J., 2006. Zooplankton of the Paraguay River: a comparison between sections and hydrological phases. Int. J. Limnol. 42, 277–288.

Gilbert, J.J., 2004. Population density, sexual reproduction and diapause in monogonont rotifers: new data for Brachionus and a review. J. Limnol. 63, 32–36.

Gyllström, M., Hansson, L.-A., 2004. Dormancy in freshwater zooplankton: Induction, termination and the importance of benthic-pelagic coupling. Aquat. Sci. 66, 274–295.

Hamilton, S.K., Lewis Jr., W.M., 1990. Physical characteristics of the fringing floodplain of the Orinoco River, Venezuela. Interciencia 15, 491–500.

Havens, K.E., East, T.L., Beaver, J.R., 2007. Zooplankton response to extreme drought in a large subtropical lake. Hydrobiologia 589, 187–198.

Hillebrand, H., Durselen, C.D., Kirshtel, D., Pollingher, U., Zohary, T., 1999. Biovolume calculation for pelagic and benthic microalgae. J. Phycol. 35, 403–424.

Hulot, F., Lacroix, G., Lescher-Moutoueâ, F., Loreau, M., 2000. Functional diversity governs ecosystem response to nutrient enrichment. Nature 405, 340–344.

Huszar, H.L.V., 2000. A comunidade fitoplanctônica e sua relação com o pulso hidrologico e o rejeito de bauxita. In: Bozelli, R., Esteves, F.A., Roland, F. (Eds.), Lago Batata: Impacto e reuperação de um ecossitema Amazônico. Instituto de Biologia-Universidade Federal de Río de Janeiro/Sociedade Brasileira de Limnologia, Rio de Janeiro, pp. 91–104.

Iglesias, C., Goyenola, G., Mazzeo, N., Meerhoff, M., Rodó, E., Jeppesen, E., 2007. Horizontal dynamics of zooplankton in subtropical Lake Blanca (Uruguay) hosting multiple zooplankton predators and aquatic plant refuges. Hydrobiologia 584, 179–189.

Intergovernmental Panel of Climate Change, 2010. http://ipcc.ch.

Jentsch, A.J., Kreyling, J., Beierkuhnlein, C., 2007. A new generation of climate-change experiments: events, not trends. Front. Ecol. Environ. 5, 365–374.

José de Paggi, S., 1993. Composition and seasonality of planktonic rotifers in limnetic and littoral regions of a floodplain lake (Parana River system). Rev. Hydrobiol. Trop. 26, 53–63.

José de Paggi, S., Paggi, J.C., 2007. Zooplankton. In: Iriondo, M., Paggi, J.C., Parma, J. (Eds.), The Middle Paraná River: Limnology of a Subtropical Wetland. Springer-Verlag, Berlin, Heidelberg, pp. 229–245.

Jun, S., Dongyan, L., 2003. Geometric models for calculating cell biovolume and surface area for phytoplankton. J. Plankton Res. 25, 1331–1346.

Junk, W.J., Bayley, P.B., Sparks, R.E., 1989. The flood pulse concept in River-floodplain systems. In: Dodge, D.P. (Ed.), Proceeding of the International Large River Symposium, Canadian Special Publication of Fisheries and Aquatic Sciences, 106. Canada, pp. 110–127.

Kalff, J., 2003. Limnology. Prentice Hall, New Jersey.

Kobayashi, T., Ryder, D.S., Gordon, G., Shannon, I., Ingleton, T., Carpenter, M., Jacobs, S.J., 2009. Short-term response of nutrients, carbon and planktonic microbial communities to floodplain wetland inundation. Aquat. Ecol. 43, 843–858.

Lansac-Tôha, F.A., Bonecker, C.C., Velho, L.F.M., Simões, N.R., Dias, J.D., Alves, G.M., Takahashi, E.M., 2009. Biodiversity of zooplankton communities in the Upper Paraná River floodplain: interannual variation from long-term studies. Braz. J. Biol. 69 (Suppl.), 539–549.

Lauren-Määttä, C., Hietala, J., Walls, M., 1997. Responses of *Daphnia pulex* populations to toxic cyanobacteria. Freshw. Biol. 37, 635–647.

Lindholm, M., Hessen, D.O., 2007. Zooplankton succession on seasonal floodplains: surfing on a wave of food. Hydrobiologia 592, 95–104.

Loverde-Oliveira, S.M., Huszar, V.L.M., Mazzeo, N., Scheffer, M., 2009. Hydrology-driven regime shifts in a shallow tropical lake. Ecosystems 12, 807–819.

Mazzeo, N., Rodríguez-Gallego, L., Kruk, C., Meehroff, M., Gorga, J., Lacerot, G., Quintans, F., Loureiro, M., Larrea, D., García-Rodríguez, F., 2003. Effects of *Egeria densa* Planch. beds on a shallow lake without piscivorous fish. Hydrobiologia 506, 591–602.

Meerhoff, M., Iglesias, C., Teixeira De Mello, F., Clemente, J.M., Jensen, E., Lauridsen, T.L., Jeppesen, E., 2007. Effects of habitat complexity on community structure and predator avoidance behaviour of littoral zooplankton in temperate versus subtropical shallow lakes. Freshw. Biol. 52, 1009–1021.

Neiff, J.J., 1990. Aspects of primary productivity in the Lower Paraná and Paraguay riverine system. Acta Limnol. Bras. 3, 73–113.

O'Farrell, I., de Tezanos Pinto, P., Rodriguez, P., Chaparro, G., Pizarro, H., 2009. Experimental evidence of the dynamic effect of free-floating plants on phytoplankton ecology. Freshw. Biol. 54, 363–375.

O'Farrell, I., Izaguirre, I., Chaparro, G., Unrein, F., Sinistro, R., Pizarro, H., Rodriguez, P., de Tezanos Pinto, P., Lombardo, G., Tell, G., 2011. Water level as the main driver of the alternation between a free-floating plant and a phytoplankton dominated state: a long-term study in a floodplain lake. Aquat. Sci., doi:10.1007/s00027-010-0175-2.

Paerl, H.W., Huisman, J., 2009. Climate change: a catalyst for global expansion of harmful cyanobacterial blooms. Environ. Microbiol. Rep. 1, 27–37.

Pagano, M., Saint-Jean, L., Arfi, R., Bouvy, M., Shep, H., 2000. Population growth capacities and regulatory factors in monospecific cultures of the cladocerans *Moina micrura* and *Diaphanosoma excisum* and the copepod *Thermocyclops decipiens* from Côte d'Ivoire (West Africa). Aquat. Living Resour. 13, 163–172.

Paidere, J., 2009. Influence of flooding frequency on zooplankton in the floodplains of the Daugava River (Latvia). Acta Zool. Lituanica 19, 306–313.

Panarelli, E.A., Casanova, S.M.C., Henry, R., 2008. The role of resting eggs in the recovery of zooplankton community in a marginal lake of the Paranapanema River. Acta Limnol. Bras. 20, 73–88.

Peel, M.C., Finlayson, B.L., McMahon, T.A., 2007. Updated world map of the Köppen–Geiger climate classification. Hydrol. Earth Syst. Sci. 11, 1633–1644.

Rennella, A.M., Quirós, R., 2006. The effects of hydrology on plankton biomass in shallow lakes of the Pampa Plain. Hydrobiologia 556, 181–191.

Ringuelet, R.A., 1957. Ambientes acuáticos continentales, Ensayo bioecológico con particular aplicación a la República Argentina. Holmbergia 5, 155–207.

Ruttner-Kolisko, A., 1977. Suggestions for biomass calculations of plankton rotifers. Arch. Hydrobiol. Beih. Ergebn. Limnol. 8, 71–76.

Scasso, F., Mazzeo, N., Gorga, J., Kruk, C., Lacerot, G., Clemente, J., Fabian, D., Bonilla, S., 2001. Limnological changes in a sub-tropical shallow hypertrophic lake during its restoration: two years of a whole-lake experiment. Aquatic Conserv: Mar. Freshw. Ecosyst. 11, 31–44.

Schröder, T., Gilbert, J.J., 2004. Transgenerational plasticity for sexual reproduction and diapause in the life cycle of monogonont rotifers: intraclonal, intraspecific and interspecific variation in the response to crowding. Funct. Ecol. 18, 458–466.

Sinistro, R., 2007. Estructura de las comunidades planctónicas y análisis de sus interacciones tróficas en un humedal de la cuenca del Paraná inferior (Reserva de Otamendi, Buenos Aires, Argentina). PhD Thesis, Departamento de Ecología, Genética y Evolución, Universidad de Buenos Aires, Buenos Aires.

Sinistro, R., Izaguirre, I., Asikian, V., 2006. Experimental study on the microbial plankton community in a South American wetland (Lower Paraná River Basin) and the effect of the light deficiency due to the floating macrophytes. J. Plankton Res. 28, 53–768.

Sterza, J.M., Loureiro Fernandes, L., 2006. Distribution and abundance of Cladocera (Branchiopoda) in the Paraíba do Sul River Estuary, Rio de Janeiro, Brazil. Braz. J. Oceanogr. 54, 193–204.

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.

Timmermann, A., Oberhuber, J., Bacher, A., Esch, M., Latif, M., Roeckner, E., 1999. Increased El Niño frequency in a climate model forced by future greenhouse warming. Nature 398, 694–697.

Unrein, F., O'Farell, I., Izaguirre, I., Sinistro, R., dos Santos Afonso, M., Tell, G., 2010. Phytoplankton response to pH rise in a N-limited floodplain lake: relevance of N_2- fixing heterocystous cyanobacteria. Aquat. Sci. 72, 179–190.

Utermöhl, H., 1958. Zur Vervollkommnung der quantitativen Phytoplankton-Methodik. Mitteil. Int. Ver. Theor. Angew. Limnol. 9, 1–38.