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Wetlands

Official Scholarly Journal of the Society of Wetland Scientists

ISSN 0277-5212 Volume 36 Number 1

Wetlands (2016) 36:85-100 DOI 10.1007/s13157-015-0718-3





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ORIGINAL RESEARCH



Colonization and Succession of Zooplankton After a Drought: Influence of Hydrology and Free-Floating Plant Dynamics in a Floodplain Lake

Griselda Chaparro^{1,2} · María Soledad Fontanarrosa¹ · Inés O'Farrell¹

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Received: 27 May 2015 / Accepted: 29 October 2015 / Published online: 9 November 2015 © Society of Wetland Scientists 2015

Abstract We analyzed zooplankton colonization and succession following a temporary drought in a vegetated lake from a floodplain wetland of the Lower Paraná River (Argentina). We took samples of zooplankton and phytoplankton at four habitats of the lake characterized by the presence-absence of emergent or free-floating macrophytes along a 18-month period after the drought. Microzooplankton dominated along the study and macrozooplankton showed seasonal increments in cold seasons. Temporal patterns of broad taxonomic zooplankton groups were associated to hydrology-driven factors, like changes in water depth, conductivity and edible phytoplankton and seasonal changes and not related with freefloating plants. Nevertheless, spatial and temporal patterns of species composition were closely linked to the dynamics of free-floating plants. A clear shift from pelagic to littoral zooplankton taxa was registered when free-floating plants colonized. This study expands the knowledge on the composition and dynamics of zooplankton from floodplain lakes after the disturbance caused by a severe drought. Our results highlight the influence of water level fluctuations as drivers of zooplankton abundance and the joint effect of seasonal changes and free-floating plant dynamics on zooplankton species composition and richness.

Griselda Chaparro grichaparro@gmail.com Keywords Community composition · Disturbance · Habitat heterogeneity · Littoral and pelagic species

Introduction

In riverine floodplain wetlands, the pulsing of river discharge determines flushing and "flood homogenization" that reset environmental conditions and maintain the ecosystem in immature successional stages (Junk and Wantzen 2004; Thomaz et al. 2007). Some large South American rivers like the Lower Paraná are little predictable, with both low isochronism and pulse recurrence, and phases with highly variable magnitude (Neiff 1990). Extraordinary hydrological cycles may cause extreme drought or flood events that lead to the earliest successional stage in aquatic environments, namely the recolonization of an empty habitat after a drought. In these systems, the absence of floods constitutes a disturbance (Sparks 1995). Then, according to the ecological concept of disturbance sensu Pickett et al. (1989) and similar to Simões et al. (2013), drought is defined as a disturbance as it disrupts the natural development of communities or populations and changes the availability of resources and physical conditions. In contrast with the information on flood effects, there have been relatively few studies of faunal dynamics after droughts (Lake 2003). Most knowledge comes from studies performed in wetlands with seasonal predictable droughts, as those occurring in Mediterranean or tropical systems, where biota evolved adaptations that provide high resistance and/or resilience (Junk and Piedade 1993; Boulton 2003; Lake 2003; Serrano and Fahd 2005; Seminara et al. 2008). Much less is known about biotic responses to supra-seasonal droughts, which are those caused by lingering decline in rainfall and water availability (Lake 2003). In riverine systems the fluvial dynamics determines a higher level of randomness compared

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with closed lake systems, where sequences of predictable changes in time occur with high recurrency (PEG model, Sommer et al. 1986). However, it is possible to detect microsuccessions regarding plankton in some riverine segments like floodplain wetlands; changes in hydrometric level would exert a major impact in plankton abundance, while the hydroperiod (length of the high waters phase) would mainly influence on species richness (Neiff 1990).

The colonization after drought depends on the presence of propagules capable to colonize the environment (Brock et al. 2003). Abiotic environmental factors are main drivers of early successional stages, because these determine the species ability to establish in the environment (Jenkins and Boulton 2003). Later, the relevance of competitive interactions among species increases, as resources are consumed and become scarce (Margalef 1963). In this sense, Baranyi et al. (2002) reported the replacement of abundant small filter feeders (rotifers) by larger and more efficient herbivores (microcrustaceans) in floodplain wetlands from the Danube River.

The hydrological regime regulates zooplankton abundance through washing-out and dilution/concentration processes (José de Paggi 1981, 1993; Baranyi et al. 2002; Lansac-Tôha et al. 2009; Chaparro et al. 2011). Rotifers have short development times and show fast population recovery after floods/from dilution caused by water level increase, whereas microcrustaceans with longer growth rates, are more negatively affected (Baranyi et al. 2002; Costa Bonecker et al. 2005; Paidere 2009). Similarly, the rapid growth rate of small edible phytoplankton allows them to compensate dilution and washout effects in a more effective way than the larger inedible fraction (García de Emiliani 1997; Mihaljević et al. 2010; Stević et al. 2013). In this way, hydrology affects food availability and quality for zooplankton by affecting the abundance and composition of phytoplankton.

The re-flooding is accompanied by changes in the spatial configuration of patches (Lake 2000), which in vegetated lakes is mainly related to changes in macrophyte assemblages (Thomaz et al. 2006; Bornette and Puijalon 2011). Aquatic macrophytes are a primary component of spatial heterogeneity affecting zooplankton and phytoplankton (de Tezanos Pinto et al. 2007; Avigliano et al. 2014; Chaparro et al. 2015). Freefloating plants are particularly relevant in tropical and warm temperate regions where these can develop large mats covering important water body areas (de Tezanos Pinto and O'Farrell 2014). These plants can rapidly recover from drought, which is usually associated with an increase in phosphorus concentration in the water after the water level recovery, derived from P release from re-flooded hydrosoils, and decomposition of terrestrial vegetation that had developed on the exposed sediments (Thomaz et al. 2006). Free-floating plants strongly affect the aquatic environment by reducing light penetration and oxygen availability in the water column (de Tezanos Pinto et al. 2007; O'Farrell et al. 2009), causing low phytoplankton diversity (O'Farrell et al. 2009) but high zooplankton (Gazulha et al. 2011; Villabona-González et al. 2011; Chaparro et al. 2015) and fish diversities (Agostinho et al. 2007; Teixeira de Mello et al. 2009). Free-floating plant dynamics, largely influenced by temperature and water level fluctuations (O'Farrell et al. 2011; Chaparro et al. 2014), affect environmental conditions in space and time, which may affect the course of plankton succession.

The objectives of this study are to analyze zooplankton colonization and succession following a severe drought period. We hypothesize that water level fluctuations and freefloating plant dynamics are main drivers of zooplankton succession in vegetated floodplain lakes, through their effects on zooplankton abundance and richness, respectively.

Methods

Study Area

The Otamendi Natural Reserve is a RAMSAR floodplain wetland of the Lower Paraná River, 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 is influenced by a high and fluctuating water table and periodically flooded by rainfall (Chichizola 1993). In periods of high waters, the river pulse contributes to the water levels of the aquatic systems within the wetland, since they are connected underground with adjacent rivers (Auge 2004; Silva Busso and Santa Cruz 2005). The main lake, Laguna Grande (~156 ha, mean depth < 1 m), is eutrophic and profusely vegetated with rooted emergent and free-floating macrophytes, whose spatial distribution and biomass experience marked seasonal fluctuations during the year and among years (O'Farrell et al. 2011; Fontanarrosa et al. 2013). The region has a warm temperate climate, with hot summers and without dry season, according to the updated Koppen-Geiger classification (Peel et al. 2007). The mean monthly temperature ranges between 10 and 24 °C in July and January, respectively; precipitation occurs during the whole year with a mean annual value of 950 mm. Drought affected the region from late spring 2007, causing a strong decrease of the lake water volume through 2008, until it dried out almost completely during one month in February 2009. Subsequent abundant rainfall in the area and increased river discharge triggered the lake re-filling in late-summer 2009.

Sampling and Physico-Chemical Analyses

Samples were taken monthly in Laguna Grande from March 2009, when it was re-filled, until February 2010 (except November) and then bimonthly until August 2010,

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plants (Lf)



comprising a total of 14 field campaigns. Four fixed sampling sites were established along a transect of 300 m perpendicular to the lake shoreline (Fig. 1): pelagic open waters (Pow), pelagic-littoral boundary area with emergent macrophytes and temporarily covered by free-floating plants (PLef), littoral with emergent macrophytes and temporarily covered by free-floating plants (Lef) and littoral temporarily covered by free-floating plants (Lf). No Lf samples were taken during March and May 2009. Temperature, pH, conductivity and dissolved oxygen were measured in situ in each sampling site using HI 991301 Hanna® and HI 9143 Hanna® (oxygen) portable instruments and water depth with a portable meter. Lake water level was measured with a fixed scale located at the shore. Dissolved nutrients were analyzed after sample filtration through Whatman GF/F filters: phosphate with the stannous chloride method, nitrate with the cadmium reduction method using Hach® reagents and ammonium with the phenate method (American Public Health Association 2005).

Zooplankton

Samples for zooplankton were taken in duplicate at each sampling site with a transparent acrylic bottle adequate for both vegetated and open water areas (Paggi et al. 2001). Twelve to 24 l (a larger volume was collected when water depth increased) of integrated water (from surface to near bottom) were collected for each replicate, 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. Macrozooplankton (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 %. Individuals were determined to the lowest possible taxonomy level using specialized literature (Ahlstrom 1940, 1943; Ruttner-Kolisko 1974; Koste 1978; Battistoni 1995; José de Paggi 1995; José de Paggi and Paggi 1995; Paggi 1995; Segers 1995; Orlova-Bienkowskaja 1998; Nogrady and Segers 2002; Smirnov 1992; Benzie 2005). The species or genera were classified according to their habit into *pelagic* or littoral (associated to vegetation), following Costa Bonecker et al. (1998); Rossa and Costa Bonecker (2003); Viayeh (2010) and on the basis of the available information from Koste (1978) and Koste and Shiel (1990). Taxa with no available information or not belonging to a single habitat group, were grouped as non-classified. Rotifer biovolume was estimated from geometric formulae (Ruttner-Kolisko 1977) based on body measurements (length and width) and transformed into wet weight as follows: 106 µm3 equals 1 µg (Bottrell et al. 1976). Dry weight (DW) was determined as 10 % of wet weight. 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). Depending on species abundance, twenty to 40 individuals from each species were measured on every sampling date and site.

Phytoplankton

One water sample for phytoplankton was taken at each sampling site and date and preserved with 1 % Lugol's iodine solution. Counts were performed according to Utermöhl (1958). Phytoplankton was classified in two size categories according to its palatability to zooplankton herbivores (<30 μ m, edible algae; >30 μ m, inedible algae); this criterion was previously used by Sinistro et al. (2007) in trophic structure studies performed in Laguna Grande in accordance to published food web studies (Lampman and Makarewicz 1999; Bell 2002; Buyukates and Roelke 2005). The classification of species obtained was checked to verify that

organisms sorted as edible lacked large mucilaginous cover or siliceous exoskeleton with complicated architecture (Bergquist et al. 1985; Hamm et al. 2003). Phytoplankton biovolumes were calculated according to Hillebrand et al. (1999) and Jun and Dongyan (2003).

Free-Floating Plants

Free-floating plant cover was estimated using a 0.25 m^2 quadrant placed at random three times within each sampling point area. Plants enclosed in the quadrants were transported to the laboratory, identified taxonomically and dried at 70 °C until constant weight to estimate their biomass per area unit (dry weight, g/m²).

Data Analyses

Spearman Rank correlations were performed with the software SPSS 19 to assess the relationship among abiotic and biotic variables. To assess for significant relationships between broad taxonomic groups of zooplankton and environmental factors a Redundancy Analysis (RDA) was applied, as data showed a linear response in the Detrended Correspondence Analysis (DCA) previously performed. The abundance of main micro and macrozooplankton groups (rotifers, nauplii, cladocerans and copepods) were included as response variables and all environmental parameters (including free-floating plant, edible and inedible phytoplankton) that were not highly correlated (r < 0.7) and with an inflation factor < 15 were included as explanatory variables. To determine the relative importance of environmental factors on zooplankton species distribution, a Canonical Correspondence Analysis (CCA) was performed, as species showed a unimodal response in the DCA previously performed. All taxa that represented >3 % of total zooplankton abundance in a sampling site at least once, were included as response variables; juvenile stages of copepods (nauplii and copepodites) were discriminated because these have different ecological features than adults. The Monte Carlo test was used for the statistical validation of the association between the ordination values, with 499 iterations and a significance level of $p \le 0.05$ (ter Braak and Verdonschot 1995). These analyses were performed with the software CANOCO 4.5.

To assess the effect of free-floating plants presence on zooplankton assemblages, the ratio of littoral rotifer abundance/ total rotifer abundance, littoral rotifer richness/total rotifer richness, littoral cladoceran abundance/total cladoceran abundance and littoral cladoceran richness/total cladocerans richness were compared between scenarios of free-floating plants presence and absence. For this purpose, all the samples from the study were classified according to the presence/absence of free-floating plants and a Mann-Whitney test was performed between the two groups; *p* values were corrected by Bonferroni. This analysis was not performed for copepods because all taxa registered belong to the same habitat (pelagic).

Results

Environmental Variables

A prolonged dry period led to a drought of a large surface of Laguna Grande at the onset of 2009; abundant rainfall and increasing waters of the Paraná River (a 2.3 fold increase in water level of the river in March-April) triggered the beginning of a high water phase in the lake by March 2009. Abundant local precipitation during spring and summer and high river water levels (a 2.8 fold increase in water level in November 2009) accounted for the prolonged length of this phase, which lasted the entire study period (Fig. 2). Water depth was always higher in pelagic than in littoral habitats (Fig. 3a) and water temperature varied markedly according to the season and was similar among habitats (Fig. 3b). Conductivity increased during the first months of the reflooding, with values around 3000 μ S cm⁻¹ in all habitats and then varied markedly, showing an inverse correlation with water depth (r = -0.6; p < 0.05) (Fig. 3c). pH values were rather stable around 8 and similar among habitats, a slight decrease was registered towards the end of the study (Fig. 3d). High concentrations of phosphate, nitrate and ammonia (close to 2 mg L^{-1} in each case) were registered after the re-flooding and then decreased along the study, with

Fig. 2 Water level variations of Laguna Grande (zero corresponds to the sediments level at a fixed point) and Paraná de las Palmas River and monthly accumulated precipitation in the study area. The black arrow indicates the moment of the drought period when most of the lake surface was dry similar values in all four habitats (Fig. 3e, f). Free-floating plants (*Pistia stratiotes*) colonized the littoral habitats shortly after the re-flooding and then decreased after the occurrence of minimum winter temperatures. In the following summer season, *P. stratiotes* re-colonized littoral habitats and developed very high biomass since February (Fig. 3g). Dissolved oxygen concentrations increased during the first months of the study; then it fluctuated markedly with higher values in sites and times with scarce or no plant development (Fig. 3h). Dissolved oxygen was negatively correlated to the biomass of free-floating plants (r = -0.6; p < 0.05) and positively with pH (r = 0.8; p < 0.05).

Zooplankton and Phytoplankton

Micro and macrozooplankton abundances were very scarce in March, a few days after the re-filling of the lake and then fluctuated markedly until late winter 2009, especially in Plef and Pow (between ~600 to 13,000 in. L⁻¹ and ~30 to 550 in. L⁻¹, respectively) (Fig. 4a, b). Then, microzooplankton showed a continuous decrease from July until October, while macrozooplankton tended to increase at the same time (except at the open waters site). Microzooplankton remained scarce until the end of the study and macrozooplankton decreased during summer and then recovered their abundance in autumn and winter 2010. Similarly, edible and inedible phytoplankton fractions fluctuated more markedly in Plef and Pow from March until July (between ~4000 and 205,000 in. L⁻¹ and 8000 to 74,000 in. L⁻¹, respectively) (Fig. 4c, d). Then, the edible fraction decreased and remained scarce until the end of



Fig. 3 Environmental variations in each habitat studied in Laguna Grande during the study period: PLef- pelagic-littoral edge with emergent macrophytes and temporary cover by free-floating plants; Pow- pelagic open waters; Lef-littoral with emergent macrophytes and temporary cover by free-floating plants; Lf- littoral with temporary cover of freefloating plants. a water depth; b water temperature; c conductivity; d pH; e phosphate; f nitrate and ammonia; g free-floating plant biomass; h dissolved oxygen



the study, while the inedible fraction also decreased and remained scarce in Plef and Pow but increased in Lef and Lf.

0.48; p < 0.05, respectively) and negatively with water depth (r = -0.45 and -0.3; p < 0.05, respectively) and water temperature (r = -0.33 and -0.39; p < 0.05, respectively). Microzooplankton abundance was positively correlated with

Microzooplankton and macrozooplankton abundances were positively correlated with conductivity (r = 0.64 and

Fig. 4 Temporal variations in a microzooplankton and b macrozooplankton abundance and c edible and d inedible phytoplankton abundance in each sampling site (PLef: pelagiclittoral edge with emergent macrophytes and temporary cover by free-floating ones; Pow: pelagic open waters; Lef: littoral with emergent macrophytes and temporary cover by free-floating plants; Lf: littoral temporary cover with free-floating macrophytes)



the abundances of edible and inedible phytoplankton (r = 0.46 and 0.47; p < 0.05, respectively). The abundance of edible and

inedible phytoplankton were positively correlated with conductivity (r = 0.48 and 0.34; p < 0.05, respectively). The ratio between zooplankton and edible phytoplankton biomass was very low along the study, varying monthly between 1.0×10^{-6} and 2.0×10^{-4} and with peaks up to 1.4×10^{-2} in winter 2009 in all sites.

The Redundancy Analysis performed with the abundance of zooplankton groups and environmental variables was significant (p = 0.01); the first and second axis explained 82.9 % of the variance (Fig. 5). The first axis was positively correlated with conductivity (r = 0.81), dissolved oxygen (r = 0.57), edible phytoplankton (r = 0.6) and inedible phytoplankton (r = 0.6) and negatively with water depth (r = -0.5). The second axis was negatively associated with water depth (r = -0.5). The samples from the beginning of the colonization (March 2009, month 1 in Fig. 5) are characterized by very scarce zooplankton. The following months (April to July 2009, months 2 to 5) are represented towards the right side of the figure, characterized by elevated abundance of rotifers, copepods (juvenile + adults) and nauplii; this period is characterized by very high conductivity, dissolved oxygen and abundance of phytoplankton. The samples from winter to early summer (August to December 2009, months 6 to 10) are plotted towards the center and upper side of the figure, characterized by the highest abundance of cladocerans and nauplii. This period is characterized by intermediate conductivity values and scarce phytoplankton. The samples corresponding

to the last part of the study period (January to August 2010) are located at the left side of the figure, characterized by low zooplankton abundance during a period of maximum water depth. Within this group, autumn-winter samples from vege-tated sites are located in the upper part of the figure, characterized by a higher contribution of cladocerans.

The zooplankton assemblage was very rich; among rotifers 120 taxa were differentiated including 81 species and 33 genera, cladocerans were represented by 16 taxa belonging to 11 genera and copepods were represented by five cyclopoid and one calanoid species (Table 1). The Canonical Correspondence Analysis performed with the most representative zooplankton species and environmental variables was significant (p = 0.01); the variance explained by the first and second axes was 47.1 %. The first axis was negatively correlated with dissolved oxygen (r = -0.76), inedible phytoplankton (r = -0.72) and conductivity (r = -0.51) and positively with free-floating plants (r = 0.62). The second axis was positively correlated with water temperature (r = 0.63) and ammonia (r = 0.6). Rotifer and microcrustacean species that colonized the lake and prevailed during the first period of the study, are located at the left side of the figure (March to July). These comprise pelagic taxa, like rotifers of the genera Brachionus and Keratella and the cyclopoid copepod Metacyclops mendocinus. The species composition changed

Fig. 5 RDA ordination triplot of samples, environmental variables and abundance of broad taxonomic groups of zooplankton and of edible and inedible phytotankton fractions. PLef: pelagic-littoral edge with emergent macrophytes and temporary cover by free-floating ones; Pow: pelagic open waters; Lef: littoral with emergent macrophytes and temporary cover by free-floating plants; Lf: littoral with temporary cover by freefloating macrophytes. Numbers 1 to 18 following name of sampling sites refers to the month number since re-filling (1 = March 2009)to 18 = August 2010). Black stars indicate the first sampling date



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Table 1List of zooplankton taxa recorded in Laguna Grande during
this study. L: littoral; P: pelagic; NC: non-classified

Table 1 (continued)

, , , , , , , , , , , , , , , , , , , ,		ROTIFERA	Habitat
ROTIFERA	Habitat	Keratella morenoi Modenutti Diéquez and Segers	р
Subclase Bdelloidea		K tronica Anstein	Р
Subclase Monogononta		K sp 1	Р
Anuraeopsis fissa Gosse	Р	K sn 2	р
Asplanchna brightwelli Gosse	Р	Lecane cf aculeata (Jakubski)	L
Beauchampiella sp.	L	L bulla (Gosse)	L
Brachionus angularis Gosse	Р	L. cornuta (Müller)	L
B. bidentata Anderson	Р	L. closterocerca (Scharma)	L
B. calyciflorus Pallas	Р	L. curvicornis (Murray)	L
B. caudatus Barrois and Daday	L	L. elsa Hauer	L
B. dimidiatus Bryce	Р	L. flexilis (Gosse)	L
B. havanaensis Rousselet	Р	L. hamata (Stokes)	L
B. ibericus Ciros-Pérez	Р	L. tenuiseta Harring	L
B. nilsoni Alhstrom	Р	L. furcata Murray	L
B. quadridentatus Hermann	Р	L. Januara Murray	L
<i>B. plicatilis</i> Müller	Р	L. hung (Müller)	L
B.urceolaris Müller	Р	L. hunaris (Ebrenberg)	I
B. zahniseri Alhstrom	Р	L. ludwigii (Eckstein)	L T
Cephalodella forficula (Ehrenberg)	NC	L. nuwigu (ECKStelli)	T
<i>C</i> .cf. <i>catellina</i> (Müller)	NC	L. monostyla Dodoy	L T
<i>C</i> . sp. 1	NC	L. monosiyiu Daday	L I
<i>C</i> . sp. 2	NC	L. myerst Segers	L T
C. sp. 3	NC		L
C. sp. 4	NC	L. municipating (Doday)	L
C sp 5	NC	L. pyrijormis (Daday)	L
C sp 6	NC	L. subulis Harring y Myers	L
C sp 7	NC	L. nalycusta Harring & Myers	L
$C \sin 8$	NC	L. ci. tenuiseta Haring	L
C sp 9	NC	L. sp. 1	L
$C \sin 10$	NC	L. sp. 2	L
C sp. 11	NC	L. sp. 3	L
Coluralla obtusa (Gosse)	I	Lepadella acuminata (Ehrenberg)	L
C uncingta Müller	I	L. imbricata Harring	L
C. ancinata Muller	L	L. ovalis (Müller)	L
C. sp.	L	L. patella (Müller)	L
Diployeblaria propatyla Gosso	D	L. cf. latusinus (Hilgendorf)	L
Dipreuchianis propaiula Gosse	r D	L. cf. benjamini braziliensis (Harring)	L
Dieranophorus sp. 1	I D	L. triptera (Ehrenberg)	L
Euchlanis of dilatata Ebrophora	Г т	L. sp. 1	L
Eucnanis ci. anana Enrenberg	L	Lindia sp.	L
E. CI. Inclsu Callill	L	Mytilina unguipes Lucks	L
<i>r unua novaezetanatae</i> Smel and Sanoamuang	۲ D	M. ventralis (Ehrenberg)	L
r. terminalis (Plate)	ľ	Monommata sp.	NC
r. sauaior (Gosse)	۲ ۲	Notholca acuminata Ehrenberg	L
<i>F. pejleri</i> Hutchinson	P	Notommata sp. 1	NC
<i>F. passa</i> (Muller)	Р	Notommata sp. 2	NC
Horaella sp.	Р	Platyas quadricornis (Ehrenberg)	Р
Gastropus sp.	L	Plationus patulus (Müller)	L
<i>Itura</i> sp. 1	NC	Polyarthra remata (Skorikov)	Р
<i>I.</i> sp.2	NC	P. cf. vulgaris Carlin	Р

Table 1 (continued)

ROTIFERA	Habitat
P. cf. dolichoptera Idelson	Р
Pompholyx cf. triloba Pejler	L
Scaridium sp. 1	L
Sinantherina semibullata (Thorpe)	L
S. spinosa (Thorpe)	L
Squatinella mutica (Ehrenberg)	Р
Synchaeta cf. oblonga Ehrenberg	Р
S. pectinata Ehrenberg	Р
S. sp. 1	Р
Testudinella patina (Hermann)	L
Trichocerca braziliensis (Murray)	L
T. bicristata (Gosse)	Р
T. cf. iernis (Gosse)	L
T. inermis (Linder)	Р
T. rattus (Müller)	L
T. similis (Wierzejski)	Р
T. tenuior (Gosse)	L
T. vernalis (Hauer)	L
T. cf. ruttneri Donner	Р
<i>T.</i> sp.1	NC
Unidentified Monogononta	NC
COPEPODA	
Metacyclops mendocinus (Wierzejski)	Р
Acanthocyclops robustus (Sars)	Р
Ciclopoidea 1	NC
Ciclopoidea 2	NC
Ciclopoidea 3	NC
Ciclopoidea 4	NC
Notodiaptomus incompositus (Brian)	Р
Harpacticoidea	L
CLADOCERA	
Bosmina sp.	Р
Acroperus sp. 1	L
Acroperus sp. 2	L
Alona sp.	L
Chydorus sphaericus (Müller)	L
Camptocercus sp.	L
Euryalona sp.	L
<i>Leydigia</i> sp.	L
Phryxura sp.	L
Pseudochydorus sp.	L
Ceriodaphnia cornuta Sars	Р
Daphnia spinulata Birabén	Р
Simocephalus vetulus (Müller)	Р
Scaphoeleberis sp.	L
Diaphanosoma birgei Korinek	Р
D. brevireme Sars	Р
Ilyocryptus sordidus (Liévin)	L
Macrothrix spinosa King	L

Table 1 (continued)

Table 1 (continued)		
ROTIFERA	Habitat	
Moina wierzejski Richard	Р	
M. micrura Kurz	Р	
Moinodaphnia sp.	Р	

towards winter months, when pelagic cladocerans (e.g., *Ceriodaphnia cornuta, Daphnia spinulata*) and calanoid copepods (*Notodiaptomus incompositus*) prevailed in the assemblage until the beginning of summer (August to December); these taxa are located at the center of the figure. A new shift in species composition was registered from early summer, when littoral taxa colonized in coincidence with the growing season of free-floating plants. These comprise littoral rotifers like those of the genera *Colurella, Lecane, Testudinella* and the littoral cladocerans of the genera *Alona* and *Acroperus*. Pelagic species, as rotifers of the genus *Synchaeta*, *Polyarthra* and *Horaella* prevailed in Pow during the last months of the study period.

During first months of the high water phase, rotifer richness varied and then tended to decrease towards October in all sampling sites, while cladoceran richness showed an opposite pattern, increasing at this same time. During this period when free-floating plants scarcely developed in some sampling sites (March to October 2009), littoral and pelagic species were evenly represented in the assemblages (Fig. 7). From spring onwards, rotifer and cladoceran richness tended to augment with increasing length of the high water phase, reaching maximum values towards the end of the study. During this period, when free-floating plants profusely developed, the number of littoral species was higher than the number of pelagic ones at all vegetated sites but not at the open waters site (Pow). The ratios of both abundance and richness of littoral rotifers and cladocerans to total rotifers and cladocerans abundance and richness were significantly higher in presence of free-floating plants than in their absence (Mann-Whitney, W = 160 and 180.5 and p = 0.04 and 0.08 for proportion of littoral rotifer and cladoceran abundance, respectively; W = 152.5 and 200 and p = 0.01 and 0.02 for proportion of littoral rotifer and cladoceran richness, respectively).

Discussion

The zooplankton recovery after a temporary severe drought was influenced by multiple factors affecting the assemblage at different taxonomic levels. The dynamics of broad taxonomic groups (i.e. rotifers, cladocerans, copepods) was associated to hydrology-driven variations, like changes in water depth, conductivity and phytoplankton abundance and to seasonal changes and was not related to free-floating plant dynamics. Nevertheless, a clear temporal and spatial dynamics associated to free-floating plants variations appeared for species (or genera) composition.

Zooplankton dynamics after the drought period in Laguna Grande consisted of two main phases. An initial phase, from March to September 2009, was characterized by extremely high variability in the abundance of the broad taxonomic zooplankton groups and phytoplankton fractions. The second phase, from October 2009 to August 2010, presented much lower and stable zooplankton and phytoplankton abundances. Previous studies suggested that severe droughts have deep effects disrupting zooplankton natural dynamics (Seminara et al. 2008; Simões et al. 2013), which might be reestablished 1 year after the re-filling and recovery of normal hydrological regime (Crome and Carpenter 1998). The long persistence of the high water phase together with a gradual increase of water depth probably explain the shift in community dynamics, from extremely fluctuating and abundant to scarce stable zooplankton abundance. It is also worth to mention that, as these factors (time since re-filling and water depth) were also correlated with temperature seasonality, it is difficult to establish a clear separation of seasonal patterns from successional ones (Boulton et al. 1992).

Rotifers and cyclopoid copepods were colonizers at the earliest stage of succession, in coincidence with previous findings (Frisch and Green 2007). These groups have higher dispersal abilities than cladocerans (Cohen and Shurin 2003) and rotifers reproductive rates are faster than any metazoan, so they can populate vacant niches rapidly (Serrano and Fahd 2005). Additionally, considering the isolated nature of the studied floodplain lake (with no definite/clear surface connections to adjacent rivers), it is very likely that zooplankton resting stages played a primary role in the initial phase of the succession, as previously reported in similar systems (Havel et al. 2000; Jenkins and Boulton 2003; Lindholm and Hessen 2007; Panarelli et al. 2008). The activation of resting stages of the cyclopoid copepod Metacyclops mendocinus (juvenile and adults) would explain their great abundance from the beginning of the colonization. The euryhaline M. mendocinus was registered after 48 h in hatching experiments performed in South American wetlands (Echaniz and Vignatti 2010; Torres and Zoppi de Roa 2010), thus making it a ready

Fig. 6 CCA ordination biplot of environmental variables and the abundance of dominant zooplankton taxa. FFP = freefloating plants biomass. Species names are abbreviated with the initial for the genus name and the first the letters for the specific name or with the first four letters of the genus name. Cope = cyclopoid copepodites, naup = nauplii



colonizer in saline environments (Medina-Júnior and Rietzler 2005). Interestingly, many other early colonizer species in Laguna Grande are euryhaline taxa, such as *Moina micrura*, *Brachionus calyciflorus*, *Keratella tropica* and *K. morenoi*. Their tolerance to high salinity levels, as those registered in the early re-filling phase, evidences the relevance of the role of abiotic factors at early successional stages, as these regulate which species can successfully colonize the environment

(Lampert and Sommer 1997; Jenkins and Boulton 2003). Later, seasonal changes of temperature and biotic interactions might have played critical roles for zooplankton dynamics. The observed shift from rotifers to cladocerans prevalence in winter, within a few months after re-filling (Fig. 5, RDA), agrees with a known pattern of succession in floodplain wetlands, where small filter-feeders are replaced by larger and more efficient ones by competitive exclusion (Baranyi et al.



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classified rotifers and cladoceran species in each sampling site. The letter

F above the bars represent the presence of free-floating plants. **a**, **b**) PLef:

pelagic-littoral edge with emergent macrophytes and temporary cover by

free-floating ones; c, d) Pow: pelagic open waters; e, f) Lef: littoral with emergent macrophytes and temporary cover by free-floating ones; g, h) Lf: littoral with temporary cover of free-floating macrophytes

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2002). Although the ratio of zooplankton to edible phytoplankton biomass remained very low, highest values coincided with winter months, thus reflecting lower food availability at this moment. On the other hand, macrozooplankton increase in winter season agrees with seasonal patterns in warm temperate regions, where a lower predation pressure by fish would allow for the development of larger organisms (Scasso et al. 2001; Mazzeo et al. 2003; Iglesias et al. 2008, 2011).

Abundant local rains and increasing river waters favored a prolonged duration of the high water phase in Laguna Grande. Decreased salinities, sufficient nutrient availability and warm temperatures are critical conditions for free-floating plants growth (Haller et al. 1974; Junk and Piedade 1993; den Hollander et al. 1999; Thomaz et al. 2006) and surely allowed their fast recovery during the high water phase. The spatial and temporal dynamics of free-floating plants strongly influenced the species composition of zooplankton. Pelagic species prevailed at the pelagic non-vegetated habitat (Pow) and at the littoral sites when free-floating plants were absent or scarce (Fig. 7; Mann-Whitney results). Colonization by littoral zooplankton species was related to the growth of free-floating plants and also modulated by seasonal changes that determined the dominance of littoral microzooplankton (rotifers) in the warm season and the increase of littoral macrozooplankton (cladocerans) in the cold vegetated period in 2010 (Fig. 6, CCA; Fig. 7, littoral and pelagic species richness).

The role of macrophytes as habitats for numerous species is well documented (Serafim et al. 2003; Maia-Barbosa et al. 2008) and is related to the structural complexity added by their stems, leaves and/or roots (Thomaz and Ribeiro Da Cunha 2010). In temperate shallow lakes from the Northern Hemisphere, submerged plant biomass was a good predictor of cladoceran abundance while plant stem volume referred to rotifers, which may reflect the complexity of the aquatic plant habitat, indirectly relating to the effectiveness of the macrophyte stand as anti-predator refuge (Jeppesen et al. 1997; Kuczyńska-Kippen et al. 2009). In wetlands from warm temperate or subtropical regions, free-floating plants are main components of habitat structure and complexity (Thomaz and Ribeiro da Cunha 2010) influencing phytoplankton and zooplankton assemblages (de Tezanos Pinto et al. 2007; Villabona-González et al. 2011; Gazulha et al. 2011; Avigliano et al. 2014). In an experiment performed in South Korea, the complete removal of free-floating plants resulted in a much lower number and density of zooplankton species than in treatments with intermediate free-floating plant cover, even though the complete removal promoted submerged plants development (Choi et al. 2014). Free-floating plants habitats host richer zooplankton communities than open water zones, though effects on zooplankton abundances are usually weak (Villabona-González et al. 2011; Gazulha et al. 2011; Chaparro et al. 2015). Field surveys and experimental studies suggest that these plants would not act as effective antipredator refuge for zooplankton, as these host numerous predators (Meerhoff et al. 2006; Iglesias et al. 2007; Gazulha et al. 2011; Fontanarrosa et al. 2013). The higher abundance and richness of littoral taxa (associated to vegetation) under freefloating plant mats suggest that their effect on species richness is primarily mediated by increased niche availability for organisms of this habit. In this sense, enhanced abundances of *Chydoridae* species was related to a higher availability of organic matter among these plants, which constitutes a food resource for detritivorous cladocerans (Villabona-González et al. 2011). Likewise, these plants host rich epiphytic communities (Rodríguez et al. 2011) that would serve as food resource for scraper species.

This study expands the knowledge on the composition and dynamics of zooplankton from floodplain lakes after the disturbance caused by a severe drought. Our results highlight the influence of water level fluctuations as drivers of zooplankton abundance and the joint effect of seasonal changes and freefloating plant dynamics on zooplankton species composition and richness.

Acknowledgments We are grateful to the staff of the Limnology Laboratory (UBA) and the Reserva Natural Otamendi for their field assistance and to the Servicio Meteorológico Nacional and the Subsecretaría de Puertos y Vías Navegables (Argentina) for the meteorological and hydrological data. We thank the valuable suggestions by 2 anonymous reviewers and Editor, which contributed to improvement of the manuscript.

Compliance with Ethical Standards

Funding This work was supported by Agencia Nacional de Promoción Científica y Tecnológica (PICT 536) and Consejo Nacional de Investigaciones Científicas y Técnicas (PIP 5355), Argentina.

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