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RESEARCH ARTICLE

Seasonal-dependence in the responses of biological communities to flood pulses in warm temperate floodplain lakes: implications for the "alternative stable states" model

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Abstract In floodplains located in temperate regions, seasonal variations in temperature affect biological communities and these effects may overlap with those of the flood regime. In this study we explored if and how timing (with regard to temperature seasonality) influences the responses of planktonic and free-floating plants communities to floods in a warm temperate floodplain lake and assessed its relevance for determining state shifts. We took samples of zooplankton, phytoplankton, picoplankton, heterotrophic nanoflagellates and free-floating macrophytes at four sites of the lake characterized by the presence-absence of emergent or free-floating macrophytes along a 2-year period with marked hydrological fluctuations associated to river flood dynamics. We performed ANOVA tests to compare the responses of these communities to floods in cold and warm seasons and among sites. Planktonic communities developed high abundances in response to floods that occurred in the cold season, while the growth of free-floating macrophytes was impaired by low winter temperatures. Spring and summer floods favored profuse colonization by free-floating plants and limited the development of planktonic communities. The prolonged absence of floods during warm periods caused environmental conditions that favored Cyanobacteria growth, leading to a "low turbid waters" regime. The occurrence of floods early in the warm season caused phytoplankton dilution and promoted free-floating plant colonization and a shift towards a "high clear waters" state. Zooplankton:phytoplankton biomass ratio was very low during floods in warm seasons, thus zooplankton grazing on phytoplankton seemed to play a minor role in the maintenance of the clear regime.

Keywords Flood pulses · Temperature seasonality · Zooplankton · Macrophytes · Alternative stable states

Introduction

Knowledge on riverine floodplain ecosystems has increasingly improved since the formulation of the Flood Pulse Concept (Junk et al. 1989), which states that the pulsing of river discharge is the major driving force responsible for the existence, productivity and interactions of biota in river floodplain systems. The Flood Pulse Concept is derived mainly from research carried out in tropical river floodplains with a predictable flood pulse (Junk 1997; Junk et al. 1989). At those latitudes, characterized by minor seasonal temperature variations, the regular occurrence of flood pulses is the main factor that determines the development of biological rhythms (Tockner et al. 2000). However, in temperate regions, seasonal variations in temperature and photoperiod are major factors affecting biological communities and their effects may overlap with those of the flood regime (Junk et al. 1989; Junk and Wantzen 2004). At these latitudes, organisms developed adaptations to seasonal variations, which determine the existence of "physiological and phenological windows of susceptibility" to the benefits and disturbances of flooding, thus timing (with regard to temperature seasonality) conditions whether an organism can profit from flood–borne resources or apply survival strategies (Junk et al. 1989; Junk and Wantzen 2004; Wantzen et al. 2008). Decomposition rates of organic matter and nutrient uptake

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also depend on the timing of inundation, usually being reduced during winter and accelerated in summer (Tockner et al. 2000). In this way, the amount of nutrients and organic carbon released to the aquatic environment, as well as their consumption rates and growth of biological communities, depend on the time of year when the flood occurs. In cold temperate regions, early spring floods stimulate phytoplankton development, but those occurring in late spring or summer have negative effects (Mihaljević et al. 2010). In floodplains located in warm temperate regions, periphyton and macrophyte growth rates are higher during spring floods than during summer ones (Robertson et al. 2001). Zooplankton abundance was similar irrespective of the season of flooding in experimental billabongs (Nielsen et al. 2002). However, another study suggested that suitable temperatures above 12 °C need to coincide with floods to boost zooplankton production (Górski et al. 2013). Although the Flood Pulse Concept has originally drawn attention to the importance of the time of year when flood pulses occur and the stage of the life cycle of organisms, comparative studies and data for detailed predictions are still insufficient (Junk and Wantzen 2004; Wantzen et al. 2008).

In floodplain environments, zooplankton abundance is regulated by the hydrological regime through dilution, washing-out or concentration processes (José de Paggi 1981, 1993; Baranyi et al. 2002; Lansac-Tôha et al. 2009; Chaparro et al. 2011). Zooplankton response to flushing effects differs among main groups, depending on their growth rates. Rotifers have short development times and show fast population recovery from flushing effects, whereas microcrustaceans with longer growth rates, are more negatively affected by floods (Baranyi et al. 2002; Costa Bonecker et al. 2005; Paidere 2009). Moreover, hydrology regulates their food availability and quality by affecting the abundance and composition of planktonic organisms that constitute their food resource. For example, high abundance of phytoplankton and bacteria are usually encountered at low waters (Castillo 2000; Casatti et al. 2003; Izaguirre et al. 2010); however, the dominance of large cyanobacteria during these periods (Bouvy et al. 2003; Paerl and Huisman 2009; Unrein et al. 2010; O'Farrell et al. 2011) may determine a low quality food resource (Deng et al. 2010; Laurén-Määttä et al. 1997). Flooding regime also affects macrophyte assemblages (Boschilia et al. 2008), which may change environmental conditions and affect the abundance and structure of zooplankton communities (Scheffer et al. 1993, 2003; Burks et al. 2006).

Besides the main effects of flood seasonality on planktonic communities (mainly related to processes of dilution/concentration or washing-out of organisms), hydrological fluctuations caused by the flood regime may have strong implications at the ecosystem level as drivers of shifts between "alternative stable states" originally described by Scheffer et al. (1993, 2003). Lakes can flip into another stable regime by occasional disturbances such as extremes in water level (Scheffer 2009). Large water level increases can provoke a shift from a turbid state with phytoplankton dominance towards a clear state dominated by submerged plants in tropical floodplain lakes (Loverde-Oliveira et al. 2009; Mihaljević et al. 2010). The supply of plant propagules by river flooding waters and the subsequent desiccation and decomposition of macrophytes during falling waters were some mechanisms suggested to explain the observed shift (Loverde-Oliveira et al. 2009). Flood dynamics controlled the migration of benthic fish, driving state shifts in a tropical floodplain pond (Mormul et al. 2012). Increased turbidity during low waters was caused by sediment resuspension by fish and water clarity was enhanced at high waters, when fish migrated and submerged macrophytes expanded (Mormul et al. 2012). Besides, extreme water level variations can trigger the change from free-floating plant (FFP) dominance at high waters to a turbid regime with cyanobacteria dominance at low waters (O'Farrell et al. 2011). The alternative stable regimes show self-stabilizing mechanisms, which are determined by the interactions of prevailing primary producers (phytoplankton, submerged or free-floating macrophytes) with other communities and by their effects on water quality (Jeppesen et al. 1997; Scheffer et al. 1993, 2003; Meerhoff et al. 2003). In cold temperate regions, submerged macrophytes exert negative effects on phytoplankton by shading, consumption of nutrients and release of allelopathic substances, as well as by providing refuge to grazers such as zooplankton (Jeppesen et al. 1997). In warm temperate or subtropical regions, dense mats of free-floating plants control phytoplankton and picoplankton biomass because of shading (de Tezanos et al. 2007; O'Farrell et al. 2011; Izaguirre et al. 2012). However, as free-floating plants constitute a poor refuge for large zooplankton (Meerhoff et al. 2003, 2006, 2007a), these would be scarce and would exert a weak effect on the self-stabilization of the FFP regime in warm regions (Iglesias et al. 2007; Meerhoff et al. 2007b). Knowledge on the role of zooplankton for maintaining the FFP regime comes from studies performed in shallow lakes not regulated by the flood regime and investigations on floodplain lakes remain scarce.

The objectives of this study were: (1) to explore if and how timing influences the responses of biological communities to floods in a warm temperate floodplain lake, including zooplankton, planktonic communities that constitute their food resource (phytoplankton, picoplankton and heterotrophic nanoflagellates) and free-floating macrophytes; (2) to compare the abundance of planktonic communities among habitats characterized by the presence or absence of macrophytes of different life forms; (3) to compare the structure and function of zooplankton between two contrasting warm periods: "low turbid waters" and "high clear waters". The hypotheses addressed were: (1) the responses of planktonic communities and macrophytes to flood pulses are different depending on the time of year when the flood occurs; (2) planktonic communities will be more abundant in open waters habitats than in vegetated ones, (3) large herbivore biomass is higher at "low turbid waters" than at "high clear waters".

Materials and methods

Study area

The Lower Paraná River basin comprises a complex wetland system of 17,500 km^2 along the 300-km terminal portion of the river to its mouth in the Río de La Plata Estuary. The hydrological regime of the area is mainly determined by the dynamics of the Upper and Middle Paraná and influenced by the estuary tidal regime (Baigún et al. 2008). River regulation in the upper stretches provokes less intense water cycles among and within years and decreased amplitude of the flood pulse in the Lower basin when compared to historical unregulated periods (Quirós 2003). However, the Lower and Middle Paraná still offer mostly undisturbed floodplains with no regulations by dams and provide unique opportunities for examining how natural functional processes drive large river functioning (Nestler et al. 2007). The study was conducted in the Otamendi Natural Reserve, a RAMSAR floodplain wetland of 3,000 hectares 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 hydrometric levels of the water bodies within the wetland, since they are connected underground with adjacent rivers (Auge 2004; Silva Busso and Santa Cruz 2005); no over-bank connection exists between rivers and wetland environments. The main lake, Laguna Grande (~156 ha, mean depth <1 m), is eutrophic and exhibits profuse aquatic vegetation; rooted emergent and free-floating macrophytes are frequently found but submerged plants are generally absent. The bathymetric profile of Laguna Grande is rather flat, but a slightly deeper section exists towards its connection with "El Pescado" lake (Fig. 1). The region has a 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. During the study period, a marked drought affected the region from 2008 until March 2009.

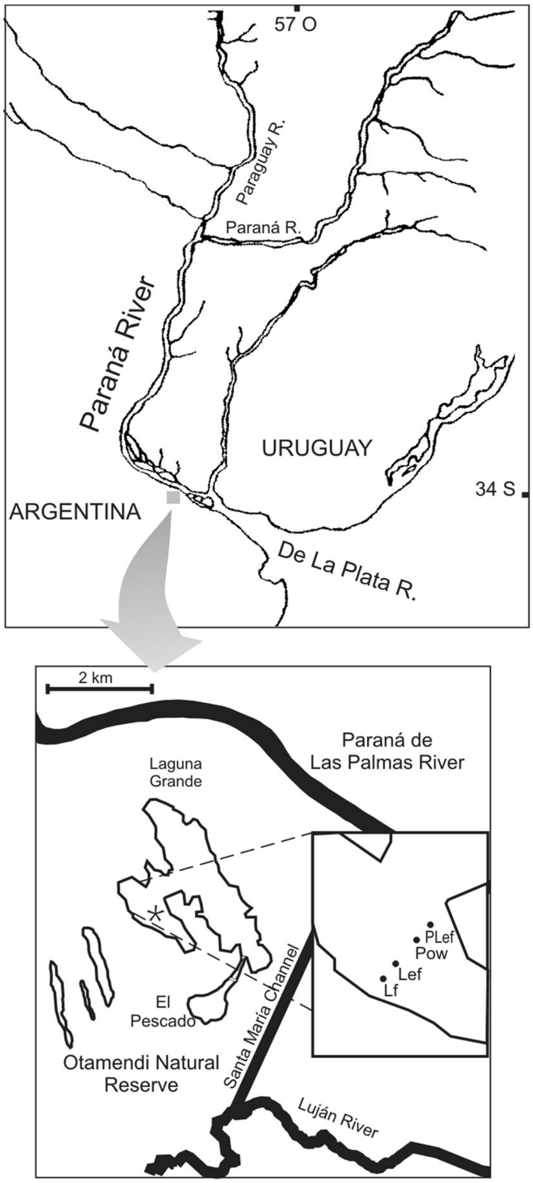


Fig. 1 Geographic location of the study area. *Black dots* indicate the sampling points. *PLef* Pelagic-littoral edge with emergent macrophytes and temporary cover by free-floating plants, *Pow* pelagic open waters, *Lef* littoral with emergent macrophytes and temporary cover by free-floating plants, *Lf* littoral temporarily covered with free-floating macrophytes

Sampling and physico-chemical analyses

Samples were taken monthly in Laguna Grande from September 2008 to February 2010 (except November 2008 and 2009) and then bimonthly until August 2010, comprising a total of 19 campaigns during a period with marked hydrological fluctuations. Four fixed sampling sites were established along a transect of 300 m perpendicular to the shoreline: pelagic open waters (*Pow*), pelagic-littoral edge 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 macrophytes (*Lf*) (Fig. 1). Temperature, pH, conductivity and dissolved oxygen were measured in situ using HI 991301 Hanna® and HI 9143 Hanna® (oxygen) portable instruments and water depth with a portable meter. Dissolved nutrients were analysed after sample filtration through fiberglass filters (0.7 μm pore): 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). Samples for chlorophyll-*a* were filtered through fibreglass filters (0.7 μm pore) and stored at −20 °C. After 24 h, pigments were extracted with ethanol (60–70 °C), measured with a spectrophotometer and calculated following Marker et al. (1980). Suspended solids were determined drying the non-filterable residue at 103–105 °C until constant weight (American Public Health Association) 2005. Daily rainfall and minimum and maximum temperature data were provided by the Servicio Meteorológico Nacional (Argentina) and water levels of the Paraná de las Palmas River in relation to the Reduction of Soundings to Chart Datum by the Subsecretaría de Puertos y Vías Navegables, measured at the nearest station (Zárate, Paraná de las Palmas River).

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 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. 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 %. Rotifer biovolume was estimated from geometric formule (Ruttner-Kolisko 1977) based on body measurements (length and width) and transformed into wet weight as follows: 10^6 μm^3 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). We measured 20–40 individuals from each species on every sampling date and site. For comparisons between the two contrasting warm periods, zooplankton species were classified into functional groups: rotifers and nauplii as *small herbivores*, copepodites, adult calanoid copepods and cladocerans as *large herbivores* and adult cyclopoid copepods as *predators*.

Phytoplankton (>2 μm), picoplankton (<2 μm) and heterotrophic nanoflagellates

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 μm, edible algae; >30 μm, inedible algae) following Sinistro et al. (2007). Phytoplankton biovolumes were calculated according to Hillebrand et al. (1999) and Jun and Dongyan (2003). Samples for picoplankton and heterotrophic nanoflagellates were taken at *PLef*, *Pow* and *Lef* at each date and preserved with ice-cold glutaraldehyde 2 %. A volume of 0.5–2 mL was filtered for picoplankton enumeration and of 5–10 mL for heterotrophic nanoflagellates; 0.2 and 0.6 μm pore-size black polycarbonate filters were used for picoplankton and heterotrophic nanoflagellates, respectively. The material was stained with DAPI (Porter and Feig 1980) and filters were mounted on a microscope slide with a drop of immersion oil for fluorescence. Using epifluorescence microscopy, autotrophic picoplankton were counted under blue and green light excitation (Callieri and Pinolini 1995) and hetetrotrophic picoplankton (bacteria) and heterotrophic nanoflagellates were counted under UV excitation.

Free-floating plants

Free-floating plants 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/m^2).

Satellite imagery

Two Landsat-5 TM images of the study area (Path 225, Row 84) representing the contrasting warm periods comprised in the study, "low turbid waters" and "high clear waters", were analyzed (19 Jan 2009 and 22 Jan 2010,

Table 1 Description of the classes of environments present in Laguna Grande obtained by classification of Landsat 5 TM images from the warm periods compared in this study (modified from Chaparro et al. 2013)

Class of environment	Description
Pelagic clear waters	Open waters with low phytoplankton chlorophyll *a* concentration (mean $< 14\ \mu g\ L^{-1}$)
Pelagic turbid waters	Open waters with high phytoplankton chlorophyll *a* concentration (mean $> 300\ \mu g\ L^{-1}$)
Littoral with emergent macrophytes	Areas with emergent macrophytes (plant cover ~100 %)
Littoral with free-floating macrophytes	Areas with free-floating macrophytes in homogeneous stands or accompanied by emergent plants (total plant cover ~100 %)
Pelafic-littoral edge	Areas in the transition from littoral to pelagic with partial cover of emergent or free-floating plants (plant cover <50 %)
Dry sediments + terrestrial vegetation	Areas of the lake with exposed sediments and some terrestrial vegetation

respectively; images dates close to field sampling dates). After pre-processing, a hybrid classification method (supervised–unsupervised) was performed on the satellite data in order to characterize and quantify the area covered by open waters and/or vegetation at the entire lake scale. The classification method allowed us to distinguish six classes of environments present in the lake in the warm periods compared: (1) *pelagic clear waters*; (2) *pelagic turbid waters*; (3) *littoral with emergent macrophytes*; (4) *littoral with free-floating macrophytes*; (5) *pelagic-littoral edge;* (6) *dry sediments + terrestrial vegetation*; their characteristics are described in Table 1 (modified from Chaparro et al. 2013). Image pre-processing and analyses were performed with ERDAS Imagine 9.1 software. A detailed description of the methodology used is described by Chaparro et al. (2013).

Data analyses

The study was divided into hydrological periods delimited by the joint occurrence of Paraná de las Palmas river pulses (sharp increases of river water levels) and high amounts of local precipitation. It was required that each delimited consecutive period verified significant differences (increase) of water depth to effectively constitute a different hydrological period. In this way, three hydrological periods were defined: after the inicial *low waters*, a first pulse in late summer-early spring 2009 led to the *filling* period and the second pulse in early spring 2009 to the *permanence* of high waters period; constant water depths after the third pulse in summer 2010 determined the continuity of the *permanence* period but not a new one. The data collected at each site and sampling date was considered as independent observations and used for comparisons. Two-way ANOVA (hydrological period × site) were conducted to compare the abundance of each planktonic community (zooplankton, phytoplankton, total picoplankton and heterotrophic nanoflagellates) and environmental variable (water depth, conductivity, pH, dissolved oxygen and chlorophyll *a* concentrations). The littoral sampling sites (*Lef* and *Lf*) did not have surface water during the *low waters* period and, therefore, no data was available for these sites during this period; the sampling sites *PLef* and *Pow* had surface water in all hydrological periods and a complete data set was available for these sites. For this reason, we ran two independent ANOVA tests with the aim to compare data among all periods and sites: Two-way ANOVA *a* to compare data among the three hydrological periods (defined as *low waters, filling* and *permanence*) and the sampling sites with water in all of them (*Pow and PLef*), and Two-way ANOVA *b* to compare data among two hydrologic periods (*filling* and *permanence*) and all four sampling sites (*Pow*, *PLef, Lef* and *Lf*). Tukey–Kramer post hoc comparisons were performed, which are adequate for non-balanced designs (Zar 1999). One-way ANOVA was conducted between the contrasting warm periods comprised in this survey, "low turbid waters" and "high clear waters", to compare the biomass of phytoplankton, zooplankton and the ratios between them. Data on the abundance of planktonic communities, phytoplankton and zooplankton biomass and chlorophyll *a* concentrations were transformed with a natural logarithm function to satisfy the assumptions. Normality was checked by the Shapiro–Wilk test and homocedasticity by the Levene test.

Results

Environmental variables

During spring-summer 2008–2009, a period of *low waters* was registered at Laguna Grande, associated to the low hydrometric levels of the Paraná de las Palmas River and scarce precipitations (Fig. 2a) caused by the extreme hydro-meteorological event ENSO ("El Niño Southern Oscillation") (http://www.cpc.ncep.noaa.gov). During this period, lake water depth was very low (<0.3 m) and the littoral areas comprised in the sampled transect were dry; only the sites *Pow* and *PLef* had water, except in February 2009 when most of the lake surface dried. Abundant rainfall during February–March 2009 followed by a strong

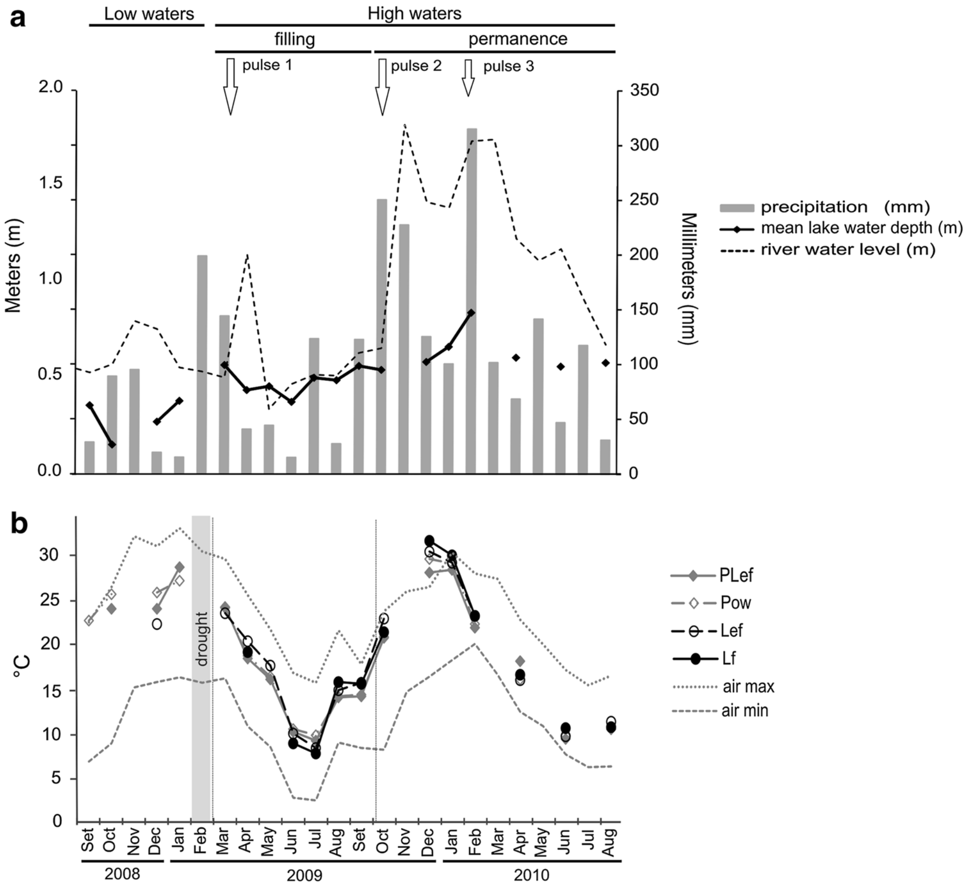


Fig. 2 **a** Water level variations of Laguna Grande (zero corresponds to the sediments level at a fixed point) and Paraná de las Palmas River and monthly accumulated precipitation in the study area. River water levels correspond to values in relation to the reduction of soundings to chart datum (=18 m at Zárate). *White arrows* indicate the occurrence of river pulses; *larger arrows* indicate higher pulse intensity. **b** Water temperature variations at each sampling site (*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 temporarily covered with free-floating macrophytes), and maximum and minimum air temperatures (monthly average)

river flood pulse (a 2.3 fold increase in water level of the river in March–April) determined the beginning of the *filling* phase, during which the whole lake area was reflooded and water depth increased significantly ($p < 0.05$) to near 0.4 and 0.6 meters at littoral and pelagic sites, respectively (Table 2). Following this pulse, a marked decrease in water temperature was registered at all sampling sites in accordance to autumn and winter seasons (Fig. 2b). Abundant local precipitation during October–November 2009 and a second strong pulse (a 2.8 fold increase in water level of the river) determined a new significant increase in water depth (0.4–0.7 m) and thus, the beginning of the period referred to as *permanence* of high waters, which coincided with the onset of the warm season, as depicted by increasing temperatures (Fig. 2a, b). Water depth was always higher at *Pow* and *PLef* than at *Lef* and *Lf* ($p < 0.05$) (Table 2). Mean values of conductivity, pH and dissolved oxygen, chlorophyll *a* and suspended solids concentrations were extremely high during *low waters* but decreased in the subsequent *filling* and *permanence* periods ($p < 0.05$); no significant differences were detected among sampling sites ($p > 0.05$) (Table 2). Dissolved nutrient concentrations were scarce during *low waters* and markedly increased after the onset of the *filling* (first flood pulse), especially phosphate and ammonium, but dropped after flood pulses 2 and 3 up to values similar to those of the beginning of the *low waters* (Fig. 3).

Biological communities

The abundance of edible phytoplankton (<30 μm) was extremely high and variable during *low waters*; at the beginning of the *filling* phase high densities were registered, which diminished markedly towards its end. Edible phytoplankton abundances were similar between *low waters* and *filling* periods ($p > 0.05$) (Table 3). This fraction remained scarce during the *permanence* of high waters, no increases were associated to the second or third flood pulses and the lowest values occurred during this period ($p < 0.05$). Inedible phytoplankton (>30 μm) was very abundant during *low waters* and it decreased markedly in each subsequent hydrological period ($p < 0.05$). Heterotrophic nanoflagellates abundance was maximal during *low waters* and values decreased significantly in high waters ($p < 0.05$). Although abundances were slightly higher in the *filling* phase, no significant differences were detected when compared with the *permanence* phase ($p > 0.05$). The abundance of total picoplankton (autotrophic picoplankton + bacteria) was highest in *low waters*, decreased markedly in the *filling* phase ($p < 0.05$)

Table 2 Mean values of physico-chemical parameters at each sampling site (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 temporarily covered with free-floating macrophytes) and hydrological period and results of Two way-ANOVA test and Tukey–Kramer post hoc comparisons

Hydrological period	Site	Depth (m)	Conduct. (μS cm^{-1})	Dissolved oxygen (mg L^{-1})	pH	Chlorophyll *a* (μg L^{-1})	Susp. sol. (mg L^{-1})
Low waters	PLef	0.1 (0.0; 3)	5,600 (1,680; 3)	9.8 (3.8; 3)	9.2 (0.5; 3)	283.6 (252.4; 3)	174 (75.2; 3)
	Pow	0.2 (0.1; 4)	5,565 (1,370; 4)	12.4 (3.6; 4)	9.4 (0.4; 4)	380.5 (175.7; 4)	160.2 (90.2; 4)
	Lef	ND	ND	ND	ND	ND	ND
	Lf	ND	ND	ND	ND	ND	ND
Filling	PLef	0.5 (0.0; 7)	2,187 (690; 7)	5.6 (3.4; 7)	7.5 (0.4; 7)	25.8 (43.6; 7)	28.0 (15.1; 7)
	Pow	0.6 (0.0; 7)	2,276 (717; 7)	5.6 (3.0; 7)	7.6 (0.4; 7)	44.0 (38.1; 7)	25.0 (21.6; 7)
	Lef	0.4 (0.0; 7)	2,474 (584; 7)	3.8 (2.0; 7)	7.3 (0.3; 7)	38.5 (29.7; 7)	23.3 (17.8; 7)
	Lf	0.3 (0.0; 7)	2,412 (694; 7)	4.5 (0.9; 7)	7.3 (0.2; 7)	44.4 (56.8; 7)	11.8 (7.8; 7)
Permanence	PLef	0.7 (0.1; 7)	1,047 (475; 7)	2.0 (1.4; 7)	6.5 (0.5; 7)	18.3 (9.0; 7)	26.0 (10.6; 7)
	Pow	0.7 (0.1; 7)	1,104 (641; 7)	3.7 (1.9; 7)	6.7 (0.4; 7)	15.8 (15.6; 7)	57.2 (29.4; 7)
	Lef	0.5 (0.0; 7)	1,424 (784; 7)	1.1 (1.6; 7)	6.4 (0.8; 7)	27.6 (18.0; 7)	62.0 (53.8; 7)
	Lf	0.4 (0.1; 7)	1,294 (511; 7)	2.2 (3.3; 7)	6.4 (1.2; 7)	18.7 (16.6; 7)	48.2 (29.3; 7)
Two-way Anova a	Site	$p > 0.05$	$p > 0.05$	$p > 0.05$	$p > 0.05$	$p > 0.05$	$p > 0.05$
	Period	$p < 0.05$	Low > Fill > Per	Low > Fill > Per	Low > Fill > Per	Low > Fill > Per	Low > Fill > Per
	Site × period	$p > 0.05$	$p > 0.05$	$p > 0.05$	$p > 0.05$	$p > 0.05$	$p > 0.05$
Two-way Anova *b*	Site	$p < 0.05$	$p > 0.05$	$p > 0.05$	$p > 0.05$	$p > 0.05$	$p > 0.05$
		PLef = Pow < Lef = Lf	–	–	–	–	–
	Period	$p < 0.05$	$p < 0.05$	$p < 0.05$	$p < 0.05$	$p < 0.05$	$p < 0.05$
		Low < Fill < Per	Fill > Per	Fill > Per	Fill > Per	Fill > Per	Fill > Per
	Site × period	$p > 0.05$	$p > 0.05$	$p > 0.05$	$p > 0.05$	$p > 0.05$	$p > 0.05$

Standard deviations and number of observations are shown in parentheses

ND no data available

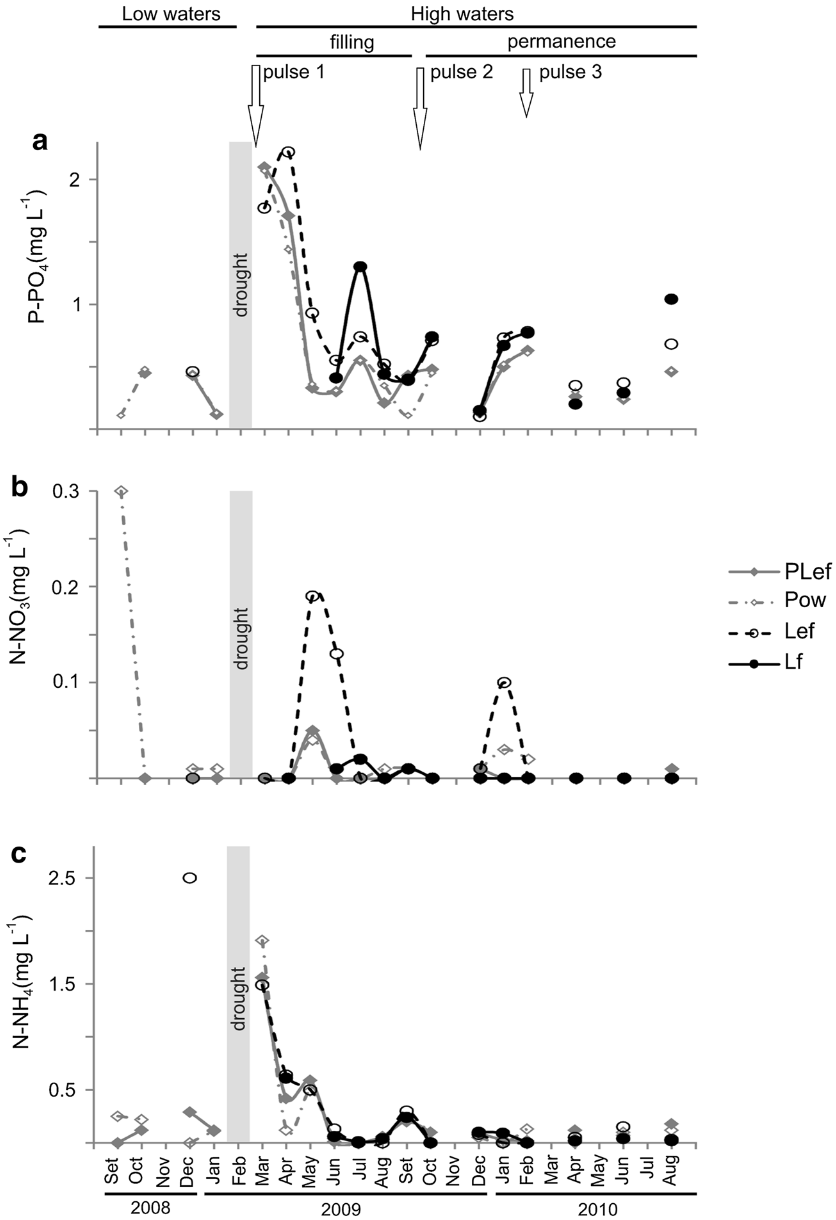


Fig. 3 Dissolved nutrient concentrations: **a** Phosphate ($P–PO_4$); **b** Nitrate ($N–NO_3$). **c** Ammonium ($N–NH_4$) at each sampling site. *PLef* Pelagic-littoral edge with emergent macrophytes and temporary cover by free-floating plants, *Pow* pelagic open waters, *Lef* littoral with emergent macrophytes and temporary cover by free-floating plants, *Lf* littoral temporarily covered with free-floating macrophytes

and increased in the *permanence* of high waters ($p < 0.05$). Bacteria comprised near 80 % of total picoplankton abundance. The abundances of phytoplankton, picoplankton and heterotrophic nanoflagellates were similar among sampling sites ($p > 0.05$) (Table 3).

Microzooplankton was largely dominated by rotifers and its abundance was extremely high during *low waters*, ranging from ~2,000 to 25,000 ind L^{-1} (Fig. 4a). During the *filling* phase, this group fluctuated markedly with high values at the beginning (~10,000 ind L^{-1}) and then decreased strongly (~1,000 ind L^{-1}); values were similar to those of *low waters* ($p > 0.05$). During the *permanence* period, microzooplankton abundance was low and a slight increase coincided with the occurrence of the third flood pulse; the values were lowest during this hydrological phase ($p < 0.05$). Macrozooplankton abundance was very high at *low waters* (Fig. 4b), with cyclopoid copepods and small cladocerans prevailing in the assemblage. The values decreased sharply in the *filling* phase ($p < 0.05$), when large cladocerans were registered, and were lowest in the *permanence* period ($p < 0.05$). Both micro and macrozooplankton abundances were similar among the sampling sites ($p > 0.05$).

Free-floating plants were absent during *low waters* (Fig. 5). During the *filling* phase, these colonised littoral sampling sites and were represented by the species *Pistia stratiotes* that reached a percent of cover ~80 % (Fig. 5a). The scarce plant biomass registered during this phase shows their very small size (Fig. 5b). By the end of the *filling* period, after the occurrence of minimum winter air

Table 3 Mean values of the abundance of planktonic organisms for each sampling site (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 temporarily covered with free-floating macrophytes) and hydrological period and results of Two-way ANOVA tests and Tukey–Kramer post hoc comparisons

Hydrological period	Site	Phytoplankton <30 μm (ind mL^{-1})	Phytoplankton >30 μm (ind mL^{-1})	HNF (cell mL^{-1})	Total picoplankton (cell mL^{-1})
Low waters	PLef	1.2×10^5 (1.8×10^5; 3)	2.8×10^5 (1.5×10^5; 3)	9.0×10^3 (4.7×10^3; 3)	4.4×10^7 (1.9×10^7; 3)
	Pow	1.0×10^5 (1.8×10^5; 4)	3.3×10^5 (2.6×10^5; 4)	5.2×10^3 (3.3×10^3; 4)	3.7×10^7 (2.8×10^7; 4)
	Lef	ND	ND	ND	ND
	Lf	ND	ND	ND	ND
Filling	PLef	7.1×10^4 (7.6×10^4; 7)	2.6×10^4 (2.8×10^4; 7)	1.9×10^3 (1.2×10^3; 7)	2.0×10^6 (1.4×10^6; 7)
	Pow	3.2×10^4 (3.1×10^4; 7)	1.4×10^4 (1.2×10^4; 7)	1.7×10^3 (1.4×10^3; 7)	2.2×10^6 (1.6×10^6; 7)
	Lef	4.3×10^4 (6.7×10^4; 7)	3.6×10^3 (4.6×10^3; 7)	1.4×10^3 (8.1×10^2; 7)	2.9×10^6 (2.5×10^6; 7)
	Lf	6.9×10^4 (9.5×10^4; 7)	2.8×10^3 (2.5×10^3; 7)	ND	ND
Permanence	PLef	5.4×10^3 (3.5×10^3; 7)	4.8×10^2 (2.6×10^2; 7)	1.0×10^3 (3.0×10^2; 7)	1.2×10^7 (5.3×10^6; 7)
	Pow	9.6×10^3 (8.3×10^3; 7)	1.8×10^3 (1.1×10^3; 7)	1.1×10^3 (9.5×10^2; 7)	5.8×10^6 (2.0×10^6; 7)
	Lef	7.2×10^3 (6.3×10^3; 7)	7.8×10^3 (4.3×10^3; 7)	1.0×10^3 (5.1×10^2; 7)	6.9×10^6 (3.0×10^6; 7)
	Lf	8.6×10^3 (7.7×10^3; 7)	1.5×10^4 (1.4×10^4; 7)	ND	ND
Two-way Anova *a*	Site	$p > 0.05$	$p > 0.05$	$p > 0.05$	$p > 0.05$
	Period	$p < 0.05$	$p < 0.05$	$p < 0.05$	$p < 0.05$
		Low = Fill > Per	Low > Fill > Per	Low > Fill = Per	Low > Fill > Per
	Site × period	$p > 0.05$	$p > 0.05$	$p > 0.05$	$p > 0.05$
Two-way Anova *b*	Site	$p > 0.05$	$p > 0.05$	$p > 0.05$	$p > 0.05$
	Period	$p < 0.05$	$p < 0.05$	$p > 0.05$	$p < 0.05$
		Fill > Per	Fill > Per		Fill > Per
	Site × period	$p > 0.05$	$p > 0.05$	$p > 0.05$	$p > 0.05$

Standard deviations and number of observations are presented in parentheses

ND no data available, *HNF* heterotrophic nanoflagellates

temperatures (Fig. 2a), no free-floating plants were registered. During spring-summer time in the *permanence* phase, *P. stratiotes* gradually re-colonised the lake. By late summer, all sampling sites were profusely covered (near 100 % of cover, Fig. 5a) with large plants, as reflected by their elevated biomass (Fig. 5b).

Contrasting warm periods: “low turbid waters” and “high clear waters”

The described changes in environmental conditions and biological communities associated to the flood regime refer to a regime shift in Laguna Grande, from a *turbid* phytoplankton dominated regime in *low waters*, towards a *clear* regime in *high waters* with emergent and free-floating plants as dominant primary producers. These marked changes determined that the warm periods comprised in this study portrayed contrasting scenarios in the lake (Fig. 6a), according to the categories shown in Table 1. The warm period called “low turbid waters” extended from September 2008 to January 2009 and “high clear waters” lasted from October 2009 to February 2010 when considering air temperatures, hydrometric levels and phytoplankton chlorophyll *a* concentrations. In the “low turbid waters” period, the lake turbidity was a consequence of the extremely high concentrations of phytoplankton chlorophyll *a* (mean ~370 μg L^{-1}). A very small portion of the lake (<1 % of total area) close to its connection with “El Pescado” lake (Fig. 1) and with deeper waters presented *clear waters*. During this period, areas totally or partially covered with emergent macrophytes were registered (many of these comprised areas without water in the surface), free-floating plants were absent and some dry areas where sediments were exposed or presented terrestrial vegetation, were also detected (Fig. 6a). In the period of “high clear waters”, phytoplankton chlorophyll *a* concentration was much lower (mean ~22 μg L^{-1}) and both emergent and free-floating macrophytes with total or partial cover were registered in homogeneous or mixed stands (Fig. 6a).

The “low turbid waters” period was characterized by elevated algae biomass, mainly represented by inedible phytoplankton (>30 μm, most colony-forming and filamentous cyanobacteria) (Fig. 6b). In “high clear waters”, mean phytoplankton biomass was two orders of magnitude lower ($p < 0.05$) and, while still dominated by the inedible

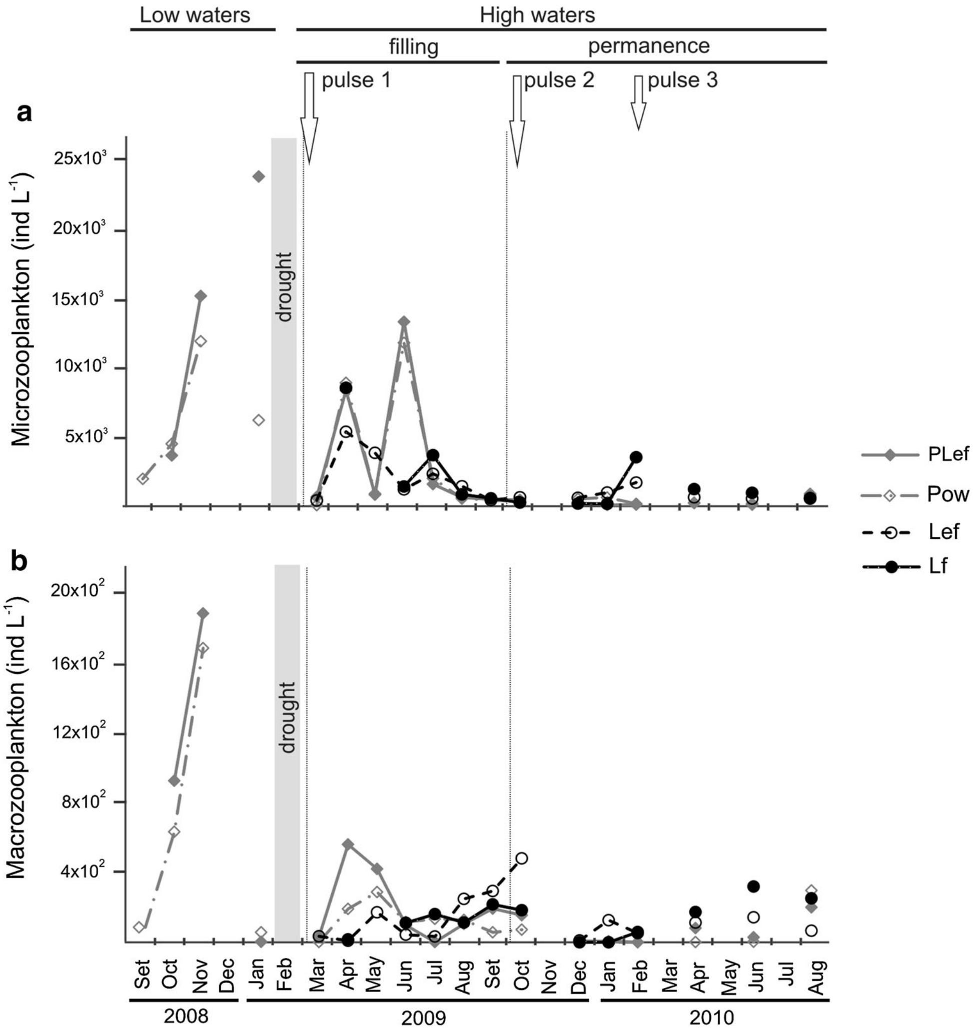


Fig. 4 Temporal variations in **a** Microzooplankton and **b** Macrozooplankton abundances at each sampling site. *PLef* Pelagic-littoral edge with emergent macrophytes and temporary cover by free-floating plants, *Pow* pelagic open waters, *Lef* littoral with emergent macrophytes and temporary cover by free-floating plants, *Lf* littoral temporarily covered with free-floating macrophytes

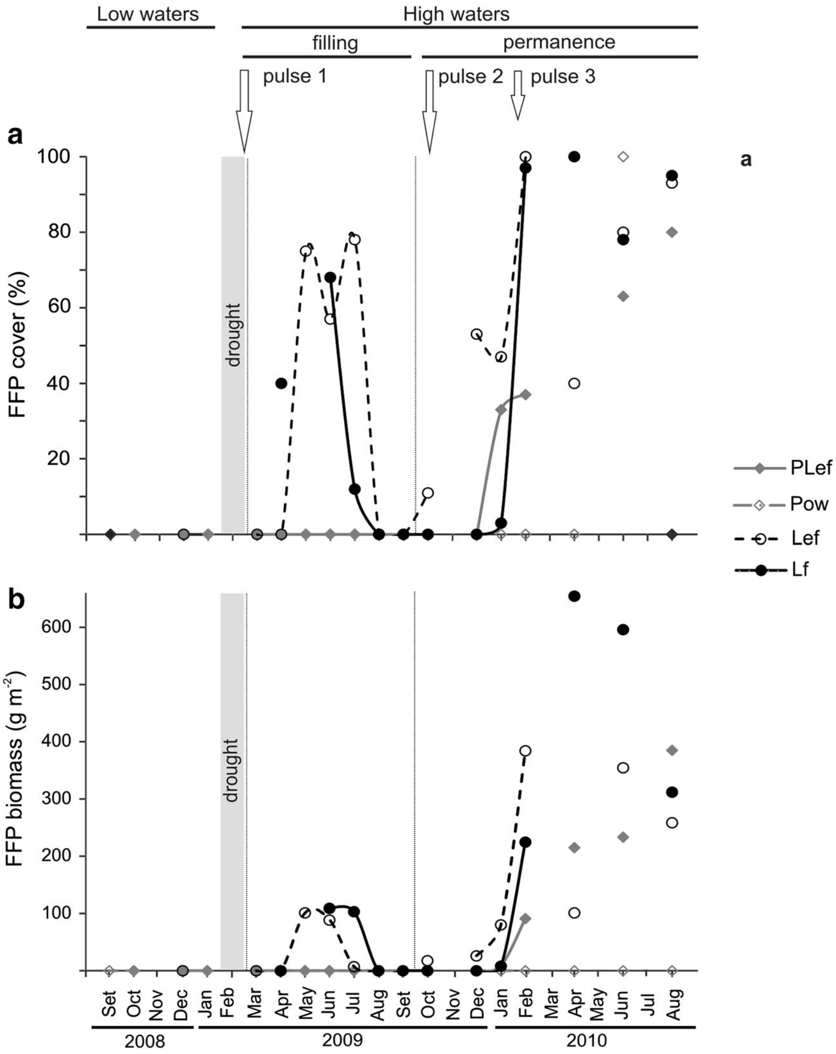
fraction, a slight increase in the proportion of edible algae was registered. Mean total zooplankton biomass was one order of magnitude higher in "low turbid waters" than in "high clear waters" ($p < 0.05$) (Fig. 6c). Microcrustacean biomass was higher in "low turbid waters" than in "high clear waters" and a shift from *predators* dominance (mainly composed of the cyclopoid copepod *Metacyclops mendocinus*) to *large herbivores* dominance (represented by the calanoid copepod *Notodiaptomus incompositus* and cladocerans of the genera *Acroperus* and *Ceriodaphnia*) was registered between these periods. The mean biomass of *large herbivores* in "low turbid waters" doubled that from "high clear waters", but no significant difference was detected ($p > 0.05$) (Fig. 6c). The ratio between herbivore zooplankton biomass and total phytoplankton biovolume was very low in both periods (Fig. 6d); the mean value was smaller in "low turbid waters" than in "high clear waters", but no significant difference was detected ($p > 0.05$). The same trend was observed when considering only the biovolume of edible phytoplankton for the calculation of this ratio.

Discussion

Flood regime and temperature are the principal drivers of ecosystem processes and dynamics of biological communities in floodplain environments (Junk et al. 1989; Tockner et al. 2000). Our results highlight the major influence of the interaction between these main factors in determining both the responses of biological communities and the regime shifts in a warm temperate floodplain lake.

Laguna Grande experienced a marked drought provoked by scarce precipitation and low discharge of the Paraná de las Palmas River at the initial warm period in 2008–2009, which coincided with "El Niño" hydrometeorological event (Camilloni and Barros 2003). In the absence of flood pulses, elevated salinity, high temperatures and scarce nitrogen availability were favorable for the development of phytoplankton and especially for N-fixing cyanobacteria (O'Farrell et al. 2011). The concentration of organisms in the short water column determined extremely high zooplankton abundance, as found in similar environments and

Fig. 5 **a** Percent of cover and **b** biomass per unit area of free-floating plants at each sampling site. *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 temporarily covered with free-floating macrophytes



conditions (Alves et al. 2005; Frutos et al. 2006; Fantin-Cruz et al. 2011).

The first flood pulse in late summer initiated the *filling* of the wetland with flooding of littoral dry areas. Probably, the high amount of organic matter stored during the drought period contributed to the release of nutrients to the water column during the first water pulse. The subsequent increase in the abundance of most planktonic communities and the development of free-floating macrophytes showed the stimulant effect of the flood pulse. Low temperatures and reduced photoperiod are known to impair the growth of *Pistia stratiotes* (Cancian et al. 2009), thus explaining their limited cover and biomass during this period. The sub-freezing daily temperatures as those registered from June to August have harmful effects on these macrophytes (Dewald and Lounibos 1990) and surely determined their drop by late winter.

Phytoplankton developed high abundances with a greater proportion of the edible fraction composed of smaller algae. This pattern is consistent with previous investigations in similar systems and it is proposed that the rapid growth rate of small algae allows them to compensate dilution and wash-out effects in a more effective way than larger algae (García de Emiliani 1997; Mihaljević et al. 2010; Stević et al. 2013). As free-floating plants exert negative effects on phytoplankton by shading (de Tezanos et al. 2007; O'Farrell et al. 2009), their scarcity during this phase would determine a higher availability of resources for algae, thus benefiting their growth.

Picoplankton (dominated by bacteria) scarcity during the *filling* phase agrees with previous investigations regarding flooding periods in this and other lakes (de Huszar and Reynolds 1997; Izaguirre et al. 2010). Bacterial growth was found to be highly dependent on the availability of autochthonous organic material (Peduzzi et al. 2008). In this sense, it is likely that a higher contribution of allochthonous organic matter prevailed during the *filling* phase (as a result of decomposing terrestrial material accumulated during drought), explaining their low abundances. Moreover, as temperature limits the growth of

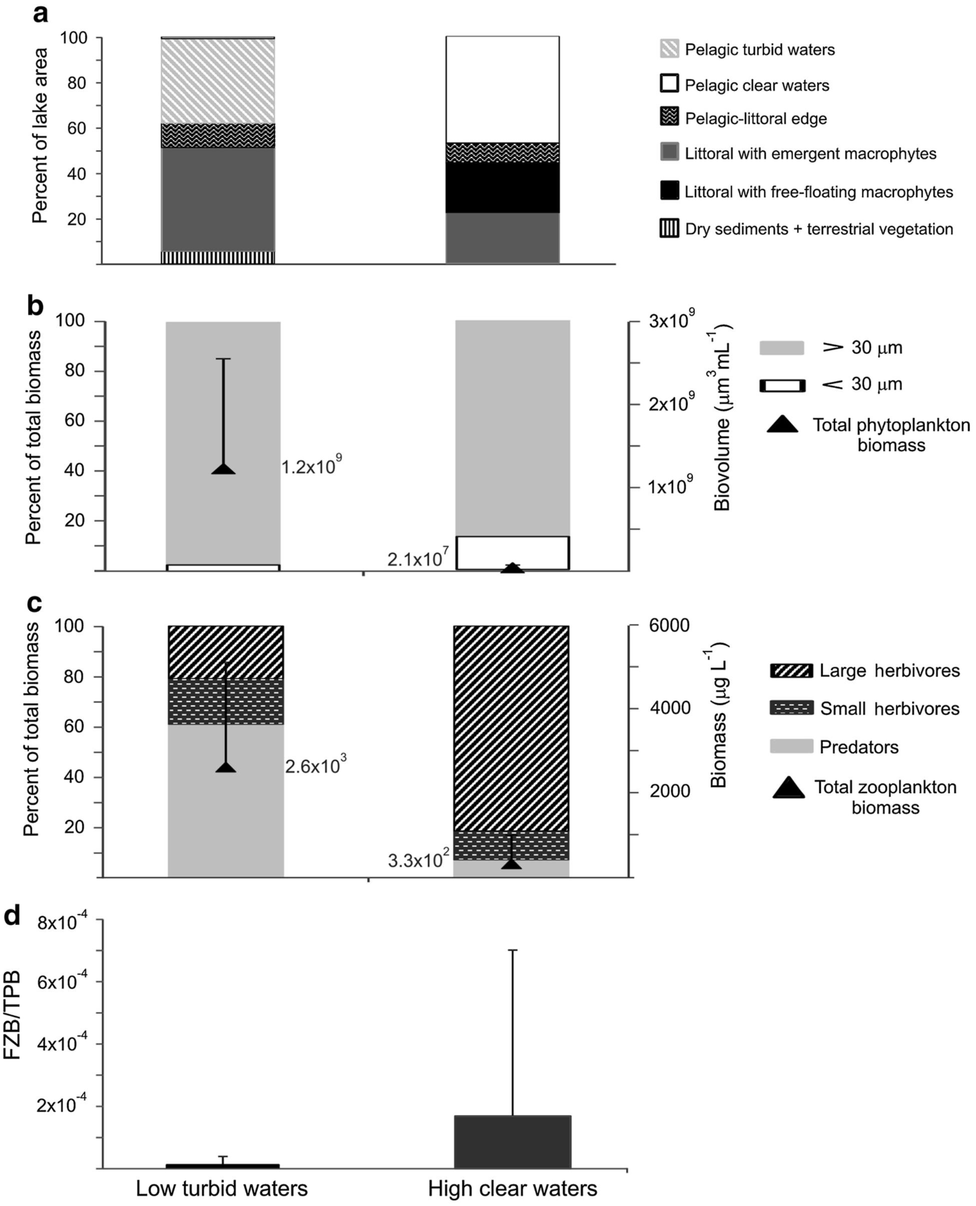


Fig. 6 Comparison between the contrasting warm periods “low turbid waters” and “high clear waters”. **a** Percent of lake area covered by each environmental type based on satellite imagery classifications. **b** Mean biomass of total phytoplankton and each size fraction (edible <30 µm; inedible >30 µm) in each warm period. **c** Mean biomass of total zooplankton and each functional feeding group (small herbivores, large herbivores and predators). **d** Mean ratios between zooplankton and phytoplankton biomass. *Bars* indicate standard deviations

bacteria (White et al. 1991), it is plausible that low autumn and winter temperatures limited their growth during this period.

Microzooplankton abundance was as high as in the previous *low waters* phase, which reflects their ability to recover from the disturbance caused by floods (Baranyi et al. 2002; Paidere 2009). Macrozooplankton developed high abundances during the first months of the *filling* period, but the marked decrease compared to the previous phase reflects their susceptibility to flood conditions (Baranyi et al. 2002; Rennella and Quirós 2006). The increase in planktonic abundances at early successional stages and its posterior decline was described in the PEG Model during colonization and succession in response to the initial resources availability and its subsequent depletion, as these are consumed and incorporated as biomass (Sommer et al. 1986; Lampert and Sommer 1997).

The second and third flood pulses in early spring and summer, respectively, led to the *permanence* of high waters. The onset of this period coincided with the growing season of free-floating macrophytes. Decreased salinity, relatively deep waters and sufficient nutrient availability are required for free-floating plant development (Haller et al. 1974; Junk and Piedade 1997; den Hollander et al. 1999; O’Farrell et al. 2011), which together with warm temperatures (near 25 °C) (Cancian et al. 2009), stimulated their profuse colonization. In contrast, phytoplankton was very scarce, in accordance with dilution and washing-out effects provoked by flood pulses (García de Emiliani 1997; Zalocar de Domitrovic 2003; Mihaljević and Stević 2011;

Stević et al. 2013) and shading by free-floating plants (de Tezanos et al. 2007). During this phase, several factors—driven by floods—accounted for the zooplankton decline: dilution effects (Baranyi et al. 2002; Rennella and Quirós 2006; José de Paggi and Paggi 2008), decreased food availability (mainly phytoplankton) (Costa Bonecker et al. 2005) and scarce oxygen concentrations under large free-floating mats (Fontanarrosa et al. 2010).

Our results show similar findings across sampling sites, regardless of the macrophyte life forms (without vegetation, with emergent and/or free-floating macrophytes). Nevertheless, dissolved oxygen concentrations were low beneath dense free-floating mats and zooplankton abundances were sometimes enhanced in pelagic non-vegetated sites. The strong temporal variations associated to the hydrological fluctuations registered during this study seemed to be more important in driving environmental and biological parameters.

Hydrometric variations may determine regime shifts in floodplain lakes; increased water levels drive shifts from turbid to clear water conditions (Van Geest et al. 2007; Loverde-Oliveira et al. 2009; Mihaljević et al. 2010; O'Farrell et al. 2011; Mormul et al. 2012). Results from a 10-year study performed in Laguna Grande suggested that extreme hydrological variations associated to ENSO phenomenon drove the ecosystem shift from a clear regime with FFP dominance at high waters, towards a turbid one dominated by phytoplankton at low waters (O'Farrell et al. 2011). Here we report the inverse trajectory determined by hydrology-driven changes on dominant primary producers. Warm periods of low waters characterized by enhanced salinity, depleted nutrients and poor underwater light caused by high turbidity favored cyanobacteria and impaired free-floating plants. In this scenario, the dominance of *small herbivores* (mainly rotifers) and *predators* (cyclopoid copepods) (Chaparro et al. 2011) gave a low grazing pressure on cyanobacteria, as reflected by the low zooplankton:phytoplankton biomass ratios. In this way, inefficient grazing by zooplankton and the competitive advantage of cyanobacteria over other algae and macrophytes favored the stability of the "low turbid waters" regime, provided that environmental conditions do not change (Scheffer 1998). A different scenario was encountered in the warm period of high waters, where prevailing environmental conditions determined that free-floating plants were at advantage over algae and led to the "high clear waters" regime. As expected, large herbivore zooplankton were scarce at high warm waters as a consequence of both dilution and enhanced predation pressure by planktivorous fishes usually reported for these seasons (Iglesias et al. 2008, 2011; Havens et al. 2009; Havens and Beaver 2012). Then, the low ratio zooplankton:phytoplankton biomass reflected a poor ability of zooplankton to control algae. Under this scenario, the dilution and washing-out effects determined by flooding, as well as shading by free-floating plants (de Tezanos et al. 2007) contributed to the maintenance of the "high clear waters" regime.

Understanding the effects of hydrological fluctuations on aquatic communities and ecosystem functioning of shallow lakes is a major and urgent issue (Wantzen et al. 2008; Scheffer and Van Ness 2007), especially under the current scenario of climate change where prolonged droughts and floods are predicted (Jentsch et al. 2007; Williamson et al. 2009). Changes in climate could increase the risk of abrupt and non-linear changes in many ecosystems, which would affect their function, biodiversity and productivity (Tockner and Standford 2002). This is the case of the community changes described for Laguna Grande, where a shift from a turbid to a clear regime was produced as a consequence of a marked water level increase after a severe drought.

It has been stated that hydrological fluctuations have major effects on small than in large lakes (Rennella and Quirós 2006; Wantzen et al. 2008); therefore, it would be expected that even minor fluctuations may produce remarkable effects on small lakes. However, it was found that small lakes are more frequently in the clear vegetated regime than in the turbid one (Scheffer and Van Ness 2007; Van Geest et al. 2003), probably due to time required for macrophyte colonization across a large lake. In this sense, it was not until summer 2010 (more than a year after the filling of the lake) that floating macrophytes achieved a high cover percentage in the analysed sites (Fig. 5) and chlorophyll a consequently diminished to values in correspondence to clear waters (Tables 2, 3). Our results are especially relevant for nutrient rich shallow lakes from warm to warm-temperate climates, where cyanobacteria or free-floating plants become very abundant (Rodríguez-Gallego et al. 2004; Bicudo et al. 2007; O'Farrell et al. 2011; Giblin et al. 2014). Notwithstanding, the dominance by either free-floating plants or cyanobacteria is predicted to expand even to cooler regions because of climate warming (Paerl and Huisman 2009; Kosten et al. 2011; Scheffer et al. 2003; Netten et al. 2011), which is an undesirable scenario due to their known harmful effects on water quality, ecosystem functioning and biodiversity, among others (Paerl et al. 2001; de Tezanos et al. 2007; Ibelings and Havens 2008; O'Farrell et al. 2009; Fontanarrosa et al. 2010). Knowledge on the factors that drive ecosystems from one regime to another in natural ecosystems, where these communities are native constitutes the basis for planning successful ecosystems management (Schooler et al. 2011).

This study highlights the relevance of timing in determining the responses of biological communities to the flood pulses in systems from warm temperate climates. Floods occurring during colder seasons may constitute an initial stimulus for both phytoplankton and free-floating macrophyte growth; however, the latter are impaired by low sub-freezing temperatures. Nutrient input allows the development of large phytoplankton populations, which in turn promote zooplankton growth. Spring and early summer floods determine optimal conditions for free-floating plant growth, which expand through the lake and outcompete phytoplankton. On an inter-annual scale, water level fluctuations associated to flood dynamics determine regime shifts at the ecosystem level. The prolonged absence of floods during warm periods causes environmental conditions favoring phytoplankton leading to the "low turbid waters" regime. The occurrence of floods early in the warm season promotes macrophyte growth and the shift towards a free-floating plant clear regime. Large herbivores are scarce during floods at warm seasons and thus, zooplankton grazing on phytoplankton seems to play a minor role for the maintenance of the "high clear waters" regime.

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