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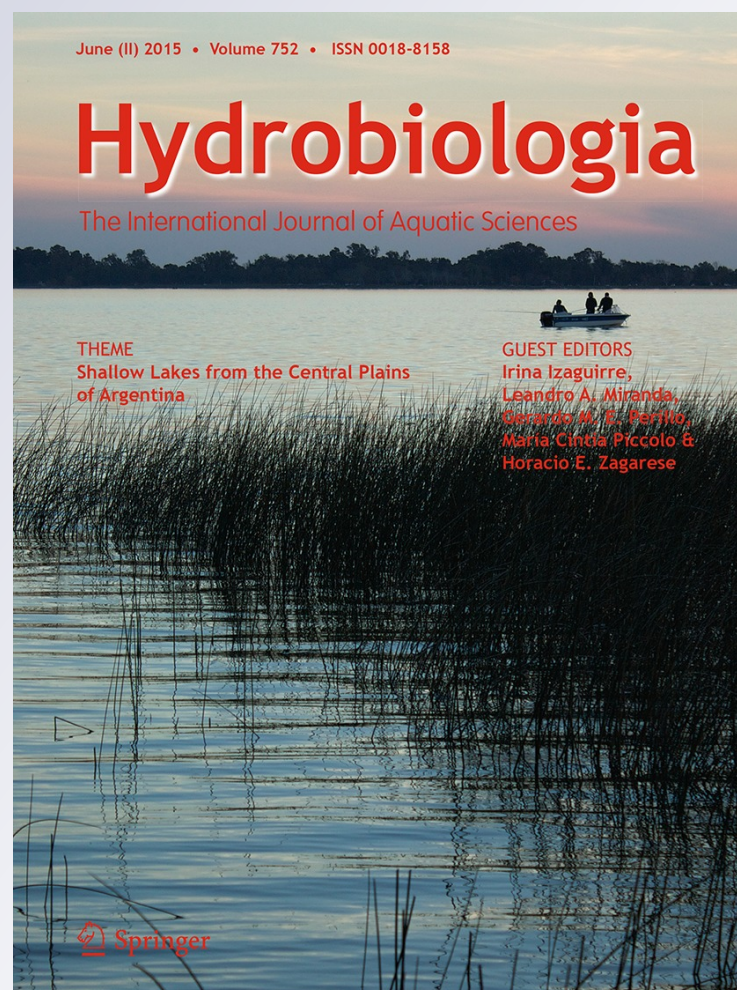
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# Hydrology driven factors might weaken fish predation effects on zooplankton structure in a vegetated warm temperate floodplain lake

Griselda Chaparro · María Soledad Fontanarrosa · Daniel Cataldo · Inés O'Farrell

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**Abstract** Fish predation on microcrustaceans is of key importance for dominance of small zooplankters in warm shallow lakes, yet its role in floodplain environments remains poorly explored. We studied seasonal and spatial variations of the abundance, diet composition and feeding selectivity of small omnivorous–planktivorous fish in relation to zooplankton at different habitats in a floodplain lake of the Lower Paraná River. Fish catches were very high in spring and summer and scarce in autumn and winter, and their distribution varied among habitats in response to changes in refuge provision and oxygen concentration. Fish diet comprised zooplankton, phytoplankton and detritus, except in summer when Cyanobacteria prevailed; in general, cyclopoid copepods and cladocerans were positively selected. Macrozooplankton biomass was the highest in spring when calanoid copepods dominated, probably because their fast swimming velocity enabled their escape from predators. Lower macrozooplankton biomass in summer

with low waters, was likely caused by harmful effects of Cyanobacteria or elevated salinity, while washing-out or dilution processes may explain macrozooplankton scarcity during cold seasons under low fish predation pressure. Our results indicate that in floodplain lakes, factors affected by or related to hydrology (salinity, Cyanobacteria development, dilution and washing-out processes) may have stronger influence than predation on zooplankton structure.

**Keywords** Trophic interactions · Microzooplankton · Macrozooplankton · Seasonality · Macrophytes · Water level

## Introduction

In shallow lakes from warm temperate or subtropical regions, small organisms such as rotifers and nauplii (microzooplankton) usually dominate zooplankton assemblages (Meerhoff et al., 2003; José de Paggi & Paggi, 2007; Gelós et al., 2010; Chaparro et al., 2011). Larger organisms, such as copepods and/or cladocerans (macrozooplankton), are usually scarce although seasonal increases can occur during autumn–winter (Iglesias et al., 2008; Chaparro, 2013). This pattern has frequently been explained because of the high predation pressure by omnivorous–planktivorous fish, which are particularly abundant in these latitudes (Mazzeo et al., 2003; Iglesias et al., 2008, 2011;

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Havens & Beaver, 2013). The reproductive season of these small fish may extend from early spring to autumn (Lorier & Berois, 1995; García et al., 2004), and they usually become very abundant in summer (Mazzeo et al., 2003; Iglesias et al., 2007, 2008). Omnivorous–planktivorous fish are visual predators and thus, large zooplankton organisms are more vulnerable to predation affecting the size structure of zooplankton communities.

Aquatic plants play a relevant role in affecting the spatial distribution of organisms and shaping predator–prey interactions in shallow lakes (Manatunge et al., 2000; Burks et al., 2006; Meerhoff et al., 2007; Padial et al., 2009). In warm regions planktivorous fish aggregate among aquatic plants that offer shelter against piscivorous fish and birds (Meerhoff et al., 2003; Iglesias et al., 2007; González Sagrario & Balseiro, 2010) and constitute feeding areas (Casatti et al., 2003; Pelicice & Agostinho, 2006). In particular, in shallow lakes from Uruguay this group occurred with higher abundances among submerged than among free-floating plants and were scarce in open waters (Meerhoff et al., 2003; Iglesias et al., 2008; Teixeira de Mello et al., 2009). In turbid conditions, fish (Snickars et al., 2004; Gelós et al., 2010) and zooplankton (Estlander et al., 2008) are more homogeneously distributed among vegetated and open water areas, suggesting that the relevance of aquatic plants as shelter for these organisms may depend on water clarity. Notwithstanding, the presence of macrophytes may reduce the efficiency of fish predation because their mobility is hampered and their invertebrate preys may hide among plant structures (Manatunge et al., 2000; Padial et al., 2009). Padial et al. (op. cit.) asserted that trophic interactions in vegetated Neotropical environments are complex and comparative studies including different plant architectures and analyses of the feeding strategies of predators (selective or opportunist) are required in order to improve their understanding.

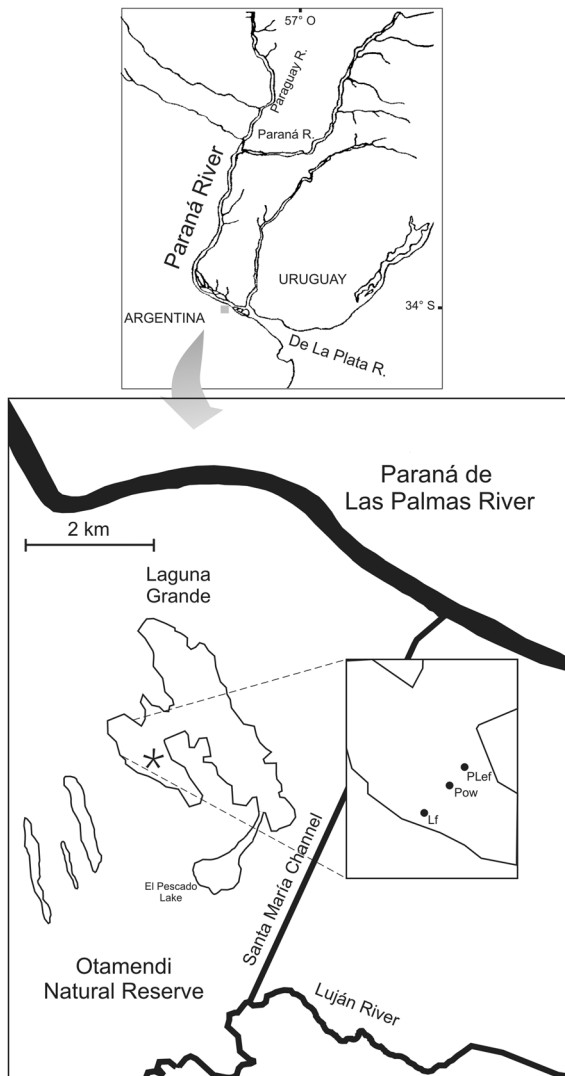
In floodplain environments, the hydrological regime exerts a strong influence on zooplankton structure (Baranyi et al., 2002; Lansac-Tôha et al., 2009; Chaparro et al., 2011). Rotifers have short development times and show fast population recovery from floods, whereas microcrustaceans have longer growth rates and are more negatively affected

(Baranyi et al., 2002; Paidere, 2009). Rennella & Quirós (2006) asserted that in shallow lakes from the Pampa Plain zooplankton development depends on water residence time, then hydrology might have stronger effects on macrozooplankton biomass than top–down control by planktivores. Likewise, Mormul et al. (2012) suggested that in a subtropical floodplain pond zooplankton is more likely affected by water level fluctuations than by fish predation. Hydrology also regulates food availability and quality by affecting the abundance and composition of phytoplankton, a main food resource for zooplankton. High abundance of phytoplankton usually occurs at low waters in the warm season (Izaguirre et al., 2010; Chaparro et al., 2011), however the dominance of large Cyanobacteria during these periods (Paerl & Huisman, 2009; Unrein et al., 2010; O'Farrell et al., 2011) may determine a low quality of this food resource (Laurén-Määttä et al., 1997; Deng et al., 2010).

Most studies focused on macrozooplankton from warm climates were performed in shallow lakes not regulated by flood regime, and thus knowledge in floodplain environments is still scarce. An experimental study accomplished in a Paraná River floodplain lake (Laguna Grande) corroborated the suppressive effect of the small omnivorous–planktivorous fish *Jenynsia multidentata* Jenyns on macrozooplankton (Sinistro, 2010), but annual studies including temperature and hydrological variability were not performed yet. Macrozooplankton comprise the most efficient filter feeders with the ability to reduce organic turbidity by the control of phytoplankton biomass (Jeppesen et al., 1997; Cyr & Curtis, 1999). Since many warm lakes are nutrient enriched, new insights are needed into trophic interactions in order to plan potential lake restoration methods, especially since eutrophication is expected to increase in the future owing to economic development and global warming (Jeppesen et al., 2007).

The objective of this study is to acquire further understanding of the influence of omnivorous–planktivorous fish predation on micro and macrozooplankton biomass in vegetated warm temperate floodplain lakes. We hypothesize that hydrology related factors might weaken the effects of fish predation on zooplankton structure in vegetated warm temperate floodplain lakes.





**Fig. 1** Geographic location of the study area. Asterisks indicate the sampling area at Laguna Grande. *PLef* pelagic–littoral edge with emergent macrophytes and temporary cover of free-floating plants, *Pow* pelagic open waters, *Lf* littoral with free-floating plants

## Materials and methods

### Study area

The study was performed in the Otamendi Natural Reserve, a RAMSAR floodplain wetland delimited by the Paraná de las Palmas and Luján Rivers in Buenos Aires Province, Argentina ( $34^{\circ}10'–34^{\circ}17'S$ ;  $58^{\circ}48'–58^{\circ}53'W$ ) (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; precipitations occur during the whole year with a mean annual value of 950 mm. 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 the adjacent rivers (Auge, 2004; Silva Busso & Santa Cruz, 2005). The water level of the main lake, Laguna Grande (~156 ha, mean depth <1 m), is largely influenced by hydrometric fluctuations of Paraná de las Palmas river and secondarily by local rainfall, as revealed in long and medium term studies performed in this lake (O'Farrell et al., 2011, Chaparro et al., 2013). Laguna Grande is eutrophic and exhibits profuse aquatic vegetation mainly composed by rooted emergent and free-floating macrophytes; submerged plants are generally absent.

### Sampling and physico-chemical analyses

One field sampling per season was performed in Laguna Grande from November 2011 to September 2012: spring (November 7), summer (March 7), autumn (June 12) and winter (September 5). Samples were taken from three distinct habitats located along a transect of 300 meters perpendicular to the shoreline, within an area of high heterogeneity where all environments of the lake (related to vegetation cover and life form) are represented (Chaparro et al., 2013): pelagic–littoral edge, with emergent macrophytes and temporarily covered by free-floating ones (*PLef*), pelagic open waters (*Pow*) and littoral with free-floating macrophytes (*Lf*) (Fig. 1). Temperature, pH, conductivity and dissolved oxygen were measured in situ at each habitat using HI 991301 Hanna® and HI 9143 Hanna® portable instruments, water depth with a portable meter and lake water level with a fixed scale located at the littoral close to the *Lf* sampling site. Free-floating plants (FFP) cover was estimated using a 0.25 m<sup>2</sup> quadrant placed at random three times within each habitat. Dissolved nutrients were analyzed 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 fiberglass filters (0.7  $\mu\text{m}$  pore) and stored at  $-20^{\circ}\text{C}$ . After 24 h, pigments were extracted with ethanol (60–70 $^{\circ}\text{C}$ ), measured with a spectrophotometer and its concentration was calculated following Marker et al. (1980). Suspended solids were determined drying the non-filterable residue at 70 $^{\circ}\text{C}$  until constant weight (American Public Health Association, 2005). Rainfall data were provided by the Servicio Meteorológico Nacional (Argentina) and hydrometric levels of the Paraná de las Palmas River by the Subsecretaría de Puertos y Vías Navegables, measured at the nearest station (Zárate).

### Zooplankton

Samples for zooplankton were taken with a transparent acrylic bottle adequate for both vegetated and open water areas (Paggi et al., 2001). Ten to twenty litres of integrated water (from surface to near bottom) were collected at each habitat, filtered through a 40- $\mu\text{m}$  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%. Rotifer biovolume was estimated from geometric formulas (Ruttner-Kolisko, 1977) based on body measurements (length and width) and transformed into wet weight as follows:  $10^6 \mu\text{m}^3$  equals 1  $\mu\text{g}$  (Bottrell et al., 1976). Dry weight was determined as 10% of wet weight. The dry weight of copepods and cladocerans was estimated from body length–dry weight relationships according to Dumont et al. (1975) and Bottrell et al. (1976). Twenty to forty individuals from each species were measured on every sampling date and habitat.

### Phytoplankton (>2 $\mu\text{m}$ )

Water samples for phytoplankton were taken at each habitat and season and preserved with 1% Lugol's iodine solution. Counts were performed according to Utermöhl (1958). Phytoplankton was classified in two size categories of greatest axial linear dimension

(GALD) according to its palatability to zooplankton (GALD < 30  $\mu\text{m}$ , edible algae; GALD > 30  $\mu\text{m}$ , inedible algae); this criterion was previously used by Sinistro et al. (2007) in studies performed in Laguna Grande in accordance to published food web studies (Lampman & Makarewicz, 1999; Bell, 2002; Buyukates & Roelke, 2005; Symons et al., 2012). Phytoplankton biovolumes were calculated according to Hillebrand et al. (1999) and Jun & Dongyan (2003).

### Small omnivorous–planktivorous fish

In the habitats PLef and Pow, fishes were sampled with a hand net (0.30  $\times$  0.25 m; 290  $\mu\text{m}$  mesh) by three 19-m long subsurface sweeps at each habitat, filtering 0.7–1.4  $\text{m}^3$  of water (on each occasion the sampling volume was estimated considering the area of the net, the length of the sweep and the depth of net immersion). In the littoral habitat (Lf), samples were taken with a hand net (0.7  $\times$  0.7 m; 290  $\mu\text{m}$  mesh) provided with a plastic net in the top for retaining free-floating plants. Three 11.7-m long sweeps were performed, filtering 1.2–2.8  $\text{m}^3$  of water. Individual sweeps were stored separated and preserved in formaldehyde (10%, final concentration). All samplings were performed during morning, between 10 and 12 am.

Fish species were determined following Ringuet et al. (1967) and counted under stereomicroscope. When fish abundance was very high, samples were fractionated with the Folsom technique (McEwen et al., 1954); fish abundance was expressed as individuals  $\text{m}^{-3}$ . For *Cnesterodon decemmaculatus* Jenyns (the most abundant fish species), 30–40 individuals of from each spring and summer sample and all individuals from autumn–winter samples (2–28 individuals) were measured; all the individuals of less abundant fish species were also measured. All the gut contents of these fish were analyzed (total of 271). The frequency of occurrence of each prey type encountered was calculated as the number of guts containing at least one individual of the prey type related to the total number of guts with some content (Hyslop, 1980). Zooplankton organisms present in the gut content were counted and classified to the maximum possible taxonomic level. The biovolume of each zooplankton group (rotifers, nauplii, cyclopoid copepods, calanoid copepods and cladocerans) was estimated on the basis of biovolume estimations

performed for the organisms collected in the environment at each respective habitat and date. The feeding selectivity of *C. decemmaculatus* to zooplankton groups was assessed using Pearre's index with a Yate's correction for continuity (Pearre, 1982):

$$C = \pm \left( \frac{(|a_d \cdot b_e - a_e \cdot b_d| - n/2)^2}{(a \cdot b \cdot e \cdot d)} \right)^{1/2},$$

where  $a = a_d + a_e$ ,  $b = b_e + b_d$ ,  $d = a_d + b_d$ ,  $e = a_e + b_e$ ,  $n = a + b$ ,  $a_d$  and  $a_e$  values represent the biomass of organisms of the type  $a$  in the diet and the environment, respectively;  $b_d$  and  $b_e$  represent the biomass of all other prey consumed in the diet and the environment, respectively, and  $n$  equals the total biomass of all prey types, considering the diet plus the environment. The index varies between  $-1$  and  $1$ ; values different from zero indicate that the prey type is positively (positive values) or negatively (negative values) selected, and values close to zero indicate neutral selection.

#### Data analyses

Spearman rank correlations were used to assess relationships among biological and environmental data (SPSS Statistics 17.0). Direct ordination analyses were used to assess for significant relationships between biological and environmental data. Previously, a detrended correspondence analysis (DCA) was performed and, as data showed a linear response, a redundancy analysis (RDA) was applied. All environmental parameters that were not highly correlated ( $r < 0.7$ ) and with an inflation factor  $< 15$  were included in the analysis as explanatory variables; the biomass of main zooplankton groups (rotifers, nauplii, cladocerans, cyclopoid and calanoid copepods), phytoplankton  $< 30 \mu\text{m}$  and  $> 30 \mu\text{m}$  and mean fish density were included as response variables. Significance of ordination axes was assessed by Monte Carlo permutation test (499 permutations). Multivariate analyses were performed using CANOCO program, version 4 (ter Braak & Smilauer, 2002). To explore the possible relationship between fish size and the size of organisms ingested, scatter plots were performed with the entire data set and separated by habitat and seasons. The statistical significance of Pearre's index was tested using the  $X^2$  statistic (Pearre, 1982):  $X^2 = n \times C^2$ , where  $n$  and  $C$  are calculated as

described above. In order to reduce type 1 error, a Bonferroni correction was applied to the  $X^2$  statistic.

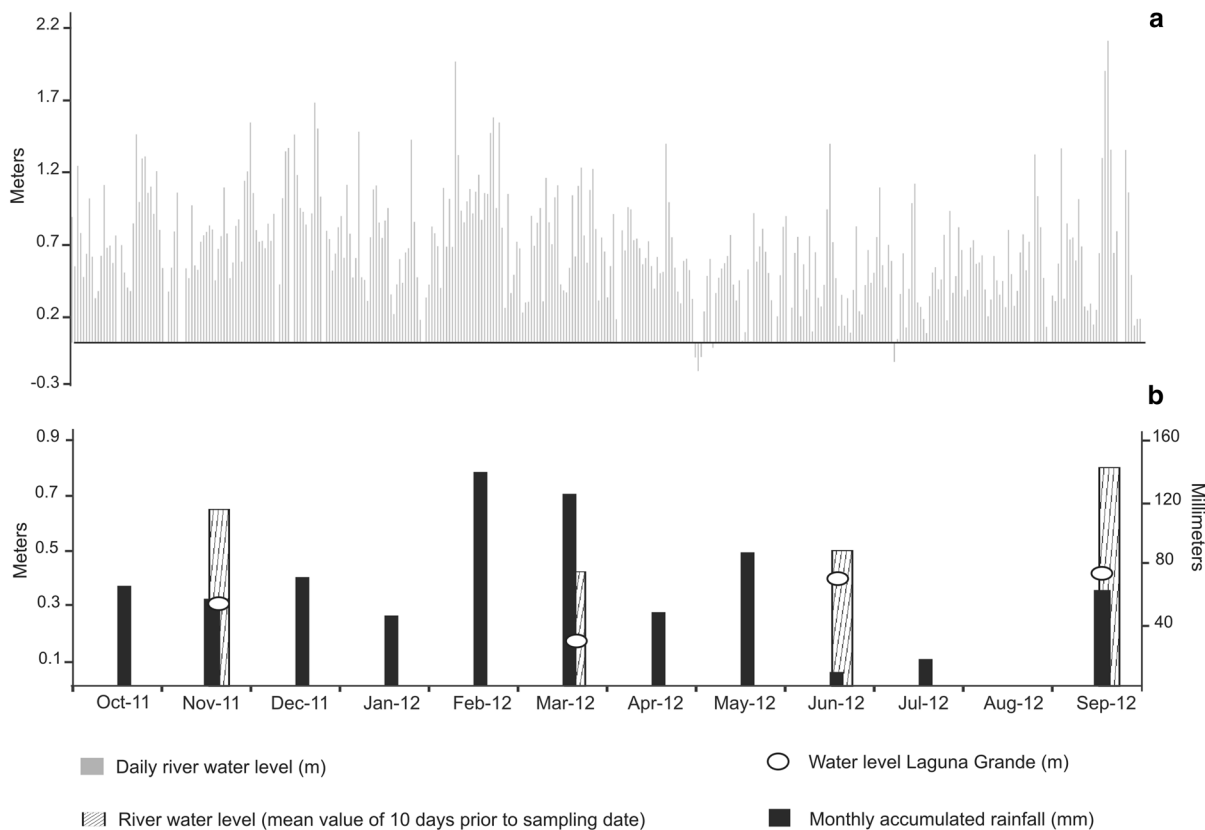
## Results

### Environmental variables

Daily variations of river water level are presented in Fig. 2a and mean values for 10-day prior to each sampling date in Fig. 2b. Water level of Laguna Grande fluctuated seasonally influenced mainly by the hydrometric level of the Paraná de las Palmas River and secondarily by local rainfall (Fig. 2b). In spring it was intermediate in coincidence with relatively high river water level, it decreased markedly in summer despite high river water level and rainfall, probably because of high evapotranspiration and then increased to higher values in autumn and winter, when river water level registered high values. Accordingly, water depth varied seasonally at the sampling sites, with lowest values in summer and highest in the cold seasons (Table 1). Water temperature varied according to the seasons and it was always lower at the littoral habitat (Lf), which also showed the lowest concentrations of dissolved oxygen ( $< 3.3 \text{ mg l}^{-1}$ ) and an extensive cover of free-floating plants (around 80–100%). Dissolved nitrogen (nitrate + ammonium) was scarce in the warm seasons, especially at PLef and Pow; phosphorous concentration was mostly high but it decreased markedly in summer at these habitats. Phytoplankton chlorophyll  $a$  concentration was lower at Lf, under floating plants, and was higher in summer at PLef and Pow (Table 1). Negative significant correlations were detected between water depth and conductivity ( $r = -0.78$ ,  $P < 0.01$ ), pH and chlorophyll  $a$  concentration ( $r = -0.75$ ,  $P < 0.01$ ) and dissolved oxygen and FFP cover ( $r = -0.77$ ,  $P < 0.01$ ).

### Phytoplankton and zooplankton

Total phytoplankton biomass was very high in summer ( $> 4 \times 10^8 \mu\text{m}^3 \text{ ml}^{-1}$ ), intermediate in spring and winter and minimum in autumn ( $< 4 \times 10^7 \mu\text{m}^3 \text{ ml}^{-1}$ ); higher biomass always occurred at pelagic open waters (Pow) (Fig. 3a). The edible fraction (algae  $< 30 \mu\text{m}$ ) dominated only in spring as in all other seasons the inedible fraction (algae  $> 30 \mu\text{m}$ )



**Fig. 2** a Daily variations of water levels of Paraná de las Palmas river; b monthly accumulated local rainfall, water level of Laguna Grande at each sampling date and mean values of river water levels corresponding to 10 days prior to each sampling date

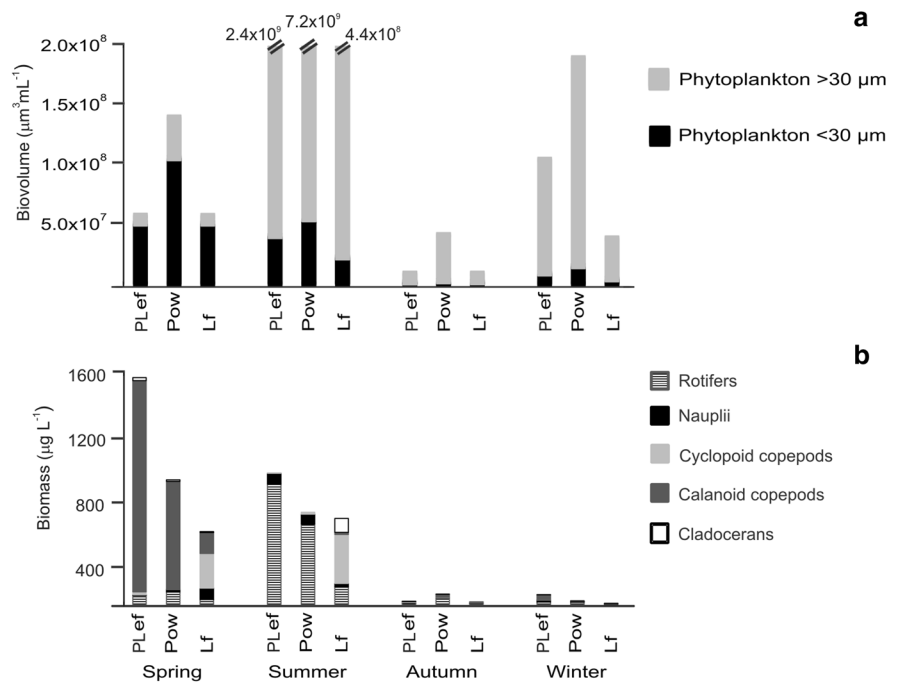
**Table 1** Limnological variables and percent of cover of free-floating plants measured at each habitat and season

Habitat	Spring			Summer			Autumn			Winter		
	PLef	Pow	Lf	PLef	Pow	Lf	PLef	Pow	Lf	PLef	Pow	Lf
Water depth (m)	0.40	0.50	0.35	0.39	0.50	0.27	0.40	0.58	0.47	0.60	0.70	0.53
Water temp. (°C)	25.8	25.3	20.5	28	29.5	22.6	7.8	8.2	5.3	13.3	13.5	13
Dissolv. O <sub>2</sub> (mg/l)	6.2	7.0	2.5	8.5	16.1	0.0	4.8	6.4	3.3	6.3	5.3	1.6
Susp. solids (mg/l)	64	13	74	274	190	115	53	11	16	3	52	9
pH	6.6	6.8	6.6	8.4	8.7	5.8	6.2	6.6	6.6	6.6	7	6.4
Conductivity (µS/cm)	2,050	1,900	2,150	1,790	1,720	2,630	890	1,030	1,040	627	460	550
N-NH <sub>4</sub> (mg/l)	ND	ND	0.06	0.06	0.04	2.21 <sup>1</sup>	0.23	1.12	0.19	0.03	0.45	0.04
N-NO <sub>3</sub> (mg/l)	ND	ND	ND	ND	0.01	ND	ND	ND	ND	ND	ND	ND
P-PO <sub>4</sub> (mg/l)	0.59	0.43	0.41	0.07	0.06	1.04	0.68	1.56	0.61	0.25	0.25	0.25
Chlorophyll <i>a</i> (µg/l)	8.7	10.9	1.5	448.4	124.1	41.4	8.7	13.1	9.8	19.6	47.9	10.9
Mean cover of free-floating plants (%)	0	0	80	2	0	95	50	0	100	2	0	100

PLef pelagic-littoral edge with emergent macrophytes and temporary cover of free-floating plants, Pow pelagic open waters, Lf littoral with free-floating plants. ND no detectable



**Fig. 3** Biovolume of edible (<30  $\mu\text{m}$ ) and inedible (>30  $\mu\text{m}$ ) phytoplankton (a) and biomass of each zooplankton group at each habitat and season (b). *PLef* pelagic–littoral edge with emergent macrophytes and temporary cover of free-floating plants, *Pow* pelagic open waters, *Lf* littoral with free-floating plants



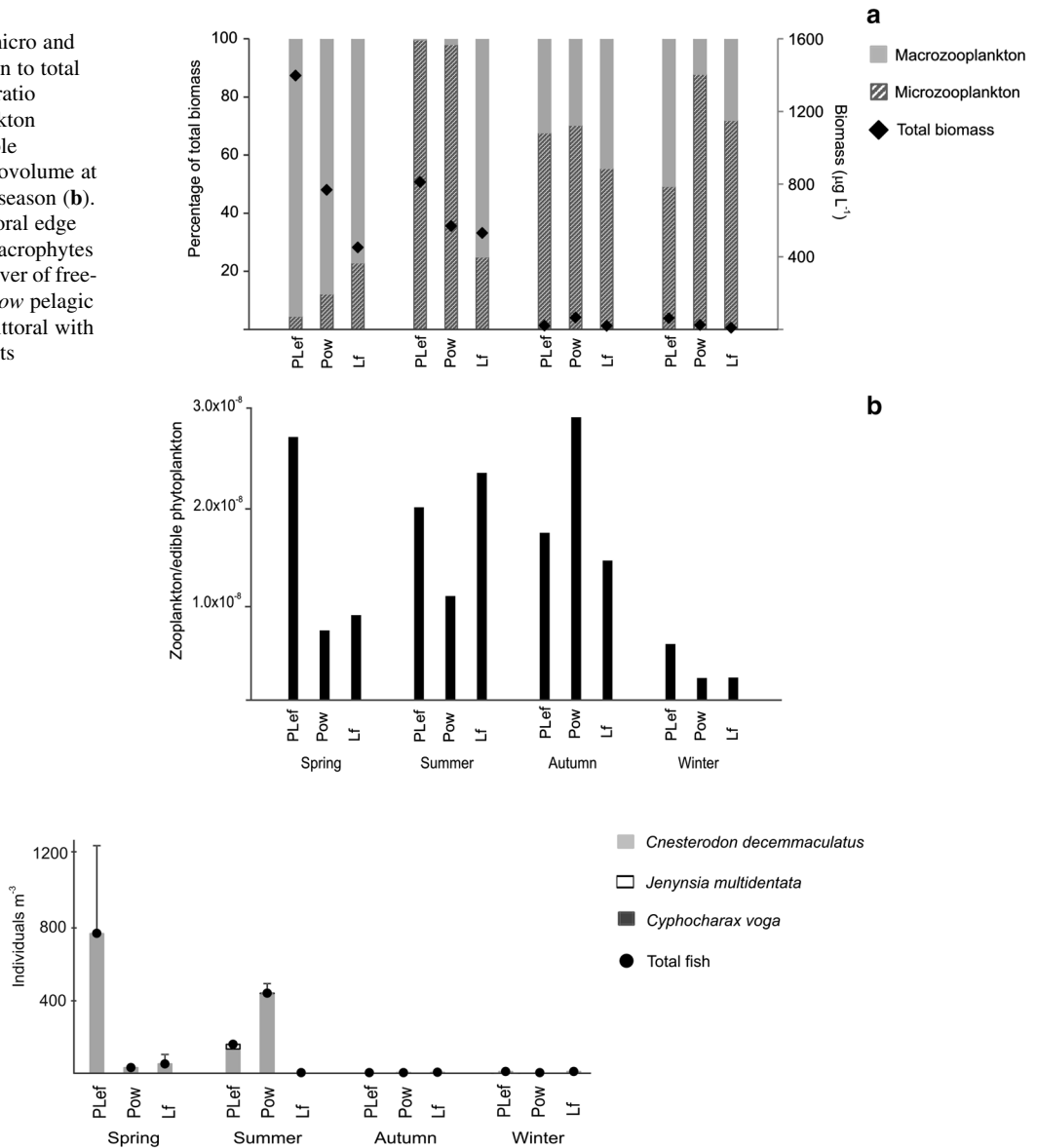
prevailed, and particularly in summer, it was represented by Cyanobacteria. Total zooplankton biomass was markedly higher in warm than in cold seasons (Fig. 3b). At *PLef* and *Pow*, biomass was higher in spring due to the dominance of calanoid copepods and then decreased in summer when euryhaline rotifers prevailed; in the littoral habitat (*Lf*) zooplankton was principally represented by cyclopoid copepods. These changes in zooplankton composition determined variations in the relative contribution of micro and macrozooplankton (Fig. 4a). At *PLef* and *Pow*, the macrozooplankton fraction was higher in spring (~90%), intermediate in autumn and winter, and minimum in summer (<10%). At the littoral habitat, it was higher in warm seasons (~80%) and decreased in cold ones (~40%). The ratio between zooplankton biomass and edible phytoplankton biovolume (ZB/EPB) was very low in all seasons at all habitats (Fig. 4b). The values varied around  $1 \times 10^{-8}$  from spring to autumn and then decreased in winter, when edible phytoplankton biomass increased relative to zooplankton (see Fig. 3a). Edible phytoplankton (<30  $\mu\text{m}$ ) was positively correlated with water temperature ( $r = 0.87$ ,  $P < 0.0001$ ) and conductivity ( $r = 0.62$ ,  $P < 0.05$ ). Microzooplankton biomass was positively correlated with edible phytoplankton

biomass ( $r = 0.73$ ,  $P < 0.01$ ), water temperature ( $r = 0.86$ ,  $P < 0.0001$ ) and conductivity ( $r = 0.71$ ,  $P < 0.01$ ); macrozooplankton biomass was positively correlated with conductivity ( $r = 0.71$ ,  $P < 0.01$ ). On behalf of the correlation results concerning conductivity, we consider this variable as a proxy of water level of the lake.

#### Small omnivorous–planktivorous fish

*Cnesterodon decemmaculatus* Jenyns (Poeciliidae) was the dominant species accompanied by few individuals of *Jenynsia multidentata* Jenyns (Anabl-epidae) and *Cyphocharax voga* Hansel (Curimatidae). The abundance of these predators was markedly higher during spring–summer (total catch ~0–750 ind  $\text{m}^{-3}$ ) than in autumn–winter (~0–5 ind  $\text{m}^{-3}$ ) (Fig. 5). Fish abundance was maximum in spring at the pelagic–littoral edge (*PLef*), where the proportion of young of the year (YOY) was 0.15, and similar values were found in *Pow* and *Lf*, where YOY represented only a fraction of 0.03. In summer, fish were more abundant at *Pow*, where blooms of Cyanobacteria occurred, and were almost absent at the littoral site under a 95% cover of free-floating plants. YOY represented 0.05 of total summer

**Fig. 4** Relative contribution of micro and macrozooplankton to total biomass (a) and ratio between zooplankton biomass and edible phytoplankton biovolume at each habitat and season (b). *PLef* pelagic–littoral edge with emergent macrophytes and temporary cover of free-floating plants, *Pow* pelagic open waters, *Lf* littoral with free-floating plants



**Fig. 5** Abundance of omnivorous–planktivorous fish at each habitat and season (estimated by catch fish). Bars indicate standard deviation. *PLef* pelagic–littoral edge with emergent

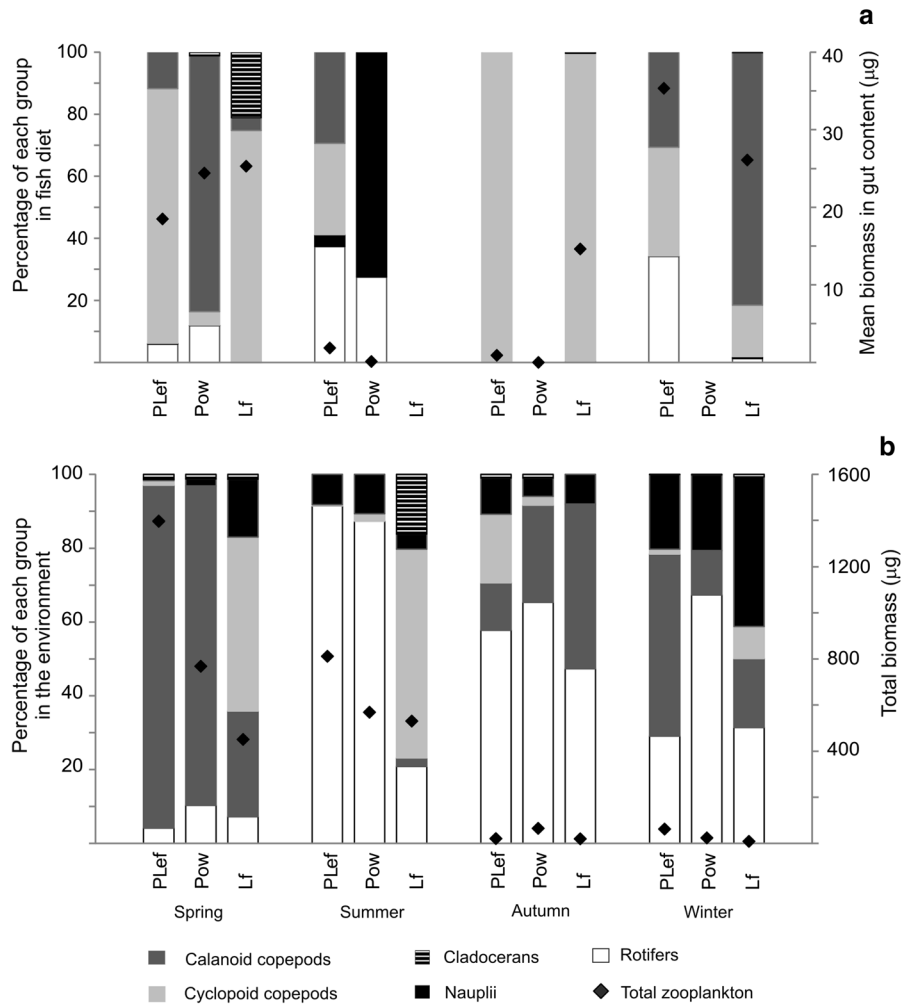
fish population and were almost absent during cold seasons. Fish size (total length) was similar among the species encountered and varied between 11 and 21 mm in autumn and winter, respectively and showed intermediate values in spring and summer. Scatter diagrams showed no relationship between fish size and the size of zooplankters ingested neither for the entire data set, nor separately by season or habitat. The density of *C. decemmaculatus* was positively

macrophytes and temporary cover of free-floating plants, *Pow* pelagic open waters, *Lf* littoral with free-floating plants

correlated with water temperature ( $r = 0.73$ ,  $P < 0.01$ ) and total zooplankton biomass ( $r = 0.66$ ,  $P < 0.05$ ).

The diet of *C. decemmaculatus* was mainly composed by zooplankton, algae and detritus; Cyanobacteria were largely represented in summer. From 271 dissected fishes, 95% presented some content in their gut. In spring rotifers were the most frequent prey encountered at *PLef* and *Pow* (frequency ~0.8), and

**Fig. 6** Percentage of each zooplankton group present in fish diet (a) and environment (b) at each respective habitat and season. *PLef* pelagic–littoral edge with emergent macrophytes and temporary cover of free-floating plants, *Pow* pelagic open waters, *Lf* littoral with free-floating plants



cyclopoid copepods and insects at the littoral (frequency  $\sim 0.5$ , each), whereas in summer the frequency of occurrence of all prey types was low, as Cyanobacteria prevailed in the fish diet (frequency  $\sim 1$ ; occupying  $\sim 100\%$  of gut volume). In autumn cyclopoid copepods and rotifers were present in all gut contents (frequency  $\sim 1$ ) and ostracods and insects had a frequency of 0.5 each. In winter calanoid copepods and cladocerans were best represented at the littoral (frequency  $\sim 0.8$ , each), accompanied by rotifers and nauplii (frequency  $\sim 0.5$ , each). The comparison between the composition of zooplankton from the environment and from the gut contents revealed that macrozooplankton were generally over-represented in the diet respective to their proportion in the environments, while microzooplankton (mainly rotifers) showed the opposite pattern (Fig. 6; Table 2).

In spring, in vegetated habitats (*PLef* and *Lf*) the proportion of cyclopoid copepods was higher in the diet than in the respective habitats, while in open waters (*Pow*) the composition of zooplankton was quite similar in the diets and the environment. Under rotifer dominance in summer, the proportion of cyclopoid and calanoid copepods was highest in the diets at *PLef*, and that of nauplii was highest at *Pow*. In autumn and winter, when zooplankton assemblages were mainly composed by rotifers and nauplii, the diets were mostly represented by cyclopoid and calanoid copepods.

The feeding selectivity index of *C. decemmaculatus* (Table 2) reflects the described differences between the proportions of zooplankton groups in the diets and their respective environments. In spring, cyclopoid copepods were positively and nauplii negatively

**Table 2** Pearre's index of selectivity for *C. decemmaculatus* towards zooplankton groups at each habitat and season

*PLef* pelagic–littoral edge with emergent macrophytes and temporary cover of free-floating plants, *Pow* pelagic open waters, *Lf* littoral with free-floating plants. Bold numbers indicate values significantly different from zero (after Bonferroni correction  $P < 0.01$ )

Habitat	Rotifers	Nauplii	Calanoid copepods	Cyclopoid copepods	Cladocerans
Spring					
PLef	0.02	<b>-0.20</b>	-0.09	<b>0.44</b>	-0.04
Pow	0.00	-0.13	-0.12	0.10	-0.03
Lf	-0.08	-0.12	-0.12	0.07	<b>0.23</b>
Summer					
PLef	<b>-0.13</b>	0.05	0.05	0.04	-
Pow	<b>-0.21</b>	0.14	-	<b>-0.49</b>	-
Lf	-	-	-	-	-
Autumn					
PLef	-0.46	-0.46	-0.42	0.12	-0.17
Pow	-	-	-	-	-
Lf	-0.59	-0.38	-0.51	<b>0.74</b>	<b>0.83</b>
Winter					
PLef	0.01	-0.36	0.14	<b>0.41</b>	<b>0.58</b>
Pow	-	-	-	-	-
Lf	<b>-0.75</b>	-0.44	<b>-0.57</b>	0.21	0.46

selected in PLef, while cladocerans were positively selected in Lf. In summer, all groups were negatively or neutrally selected, as fish diet was composed by Cyanobacteria despite the great abundance of zooplankton in the lake. In autumn and winter, cyclopoid copepods and cladocerans were positively selected and rotifers, nauplii and calanoid copepods were negatively selected in most cases.

The diet of *J. multidentata* was analyzed only at PLef in summer, when these were more abundant. It was composed by zooplankton, algae and detritus and no Cyanobacteria were encountered in their gut contents, despite its high abundance in the environment. The analysis of a few individuals of *C. voga* revealed a diet composed by zooplankton, mainly cyclopoid copepods and cladocerans.

#### Relationship among biological and environmental data

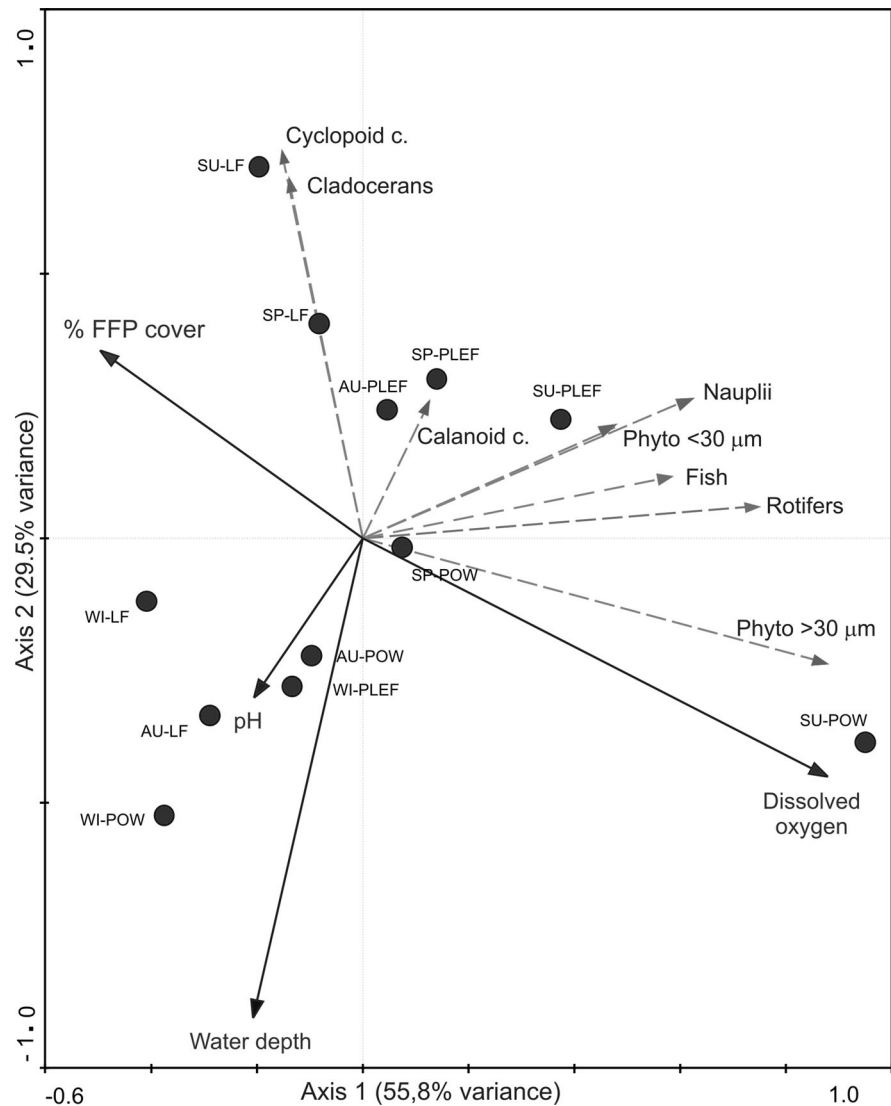
The RDA revealed a high correlation between biological communities and environmental parameters ( $r = 0.92$  and  $0.81$  for axis 1 and 2, respectively). The first and second axis explained 85.3% of variance in this relationship; the Monte Carlo permutation test for the first axis was significant ( $P = 0.03$ ). The first axis represented changes in FFP cover and associated variations of dissolved oxygen (intraset correlation

coefficients:  $-0.45$  and  $0.8$ , respectively); the second axis represented changes in water depth (intraset correlation coefficient:  $-0.73$ ) (Fig. 7). Samples with high FFP cover and low water depth are located at the upper-left part of the figure; these are samples from spring and summer and are characterized by high cladocerans and cyclopoid copepods biomass and scarce phytoplankton and fish. Samples from warm seasons and with scarce FFP cover and elevated dissolved oxygen are plotted towards the center and right side of the figure; these show elevated biomass of rotifers, nauplii, phytoplankton (both edible and inedible fractions) and high fish density. At the lower-left side of the figure appear most of autumn–winter samples, which show highest water depth and lower biomass of phyto and zooplankton and fish scarcity.

#### Discussion

Aquatic macrophytes and temperature seasonality are major factors affecting the spatial distribution and temporal dynamics of fish in warm temperate and subtropical shallow lakes (García et al., 2004; Iglesias et al., 2008; Teixeira de Mello et al., 2009; Goyenola et al., 2011). Our results in a floodplain lake show marked seasonal fluctuations in the catch of small

**Fig. 7** RDA triplot of environmental variables, biological communities (biomass of zooplankton groups and phytoplankton fractions and fish density) and sample sites. *PLEf* pelagic–littoral edge with emergent macrophytes and temporary cover of free-floating plants, *Pow* pelagic open waters, *Lf* littoral with free-floating plants. *SP* spring, *SU* summer, *AU* autumn, *WI* winter



omnivorous–planktivorous fish, which was high in spring and summer and very low in autumn and winter. Fish distribution varied among vegetated and open waters habitats, probably in response to changes in refuge provision and environmental conditions, namely oxygen concentration.

The seasonal fluctuations of fish catch in the studied floodplain lake agree with previous findings in shallow lakes from warm temperate (Mazzeo et al., 2003; Iglesias et al., 2008; Gelós et al., 2010) and subtropical regions (García et al., 2004). Studies on *J. multidentata* revealed low survival to winter temperatures and decreasing duration of their breeding season (during spring–summer) with increasing latitude (García et al.,

2004; Goyenola et al., 2011). Similarly, *C. decemmaculatus* presents a breeding season restricted to warm months (Lorier & Berois, 1995). Besides, the temperature drop during cold seasons may have caused a decrease of fish activity, resulting in low fish catch, as explained by Scasso et al. (2001), Mazzeo et al. (2003) and Iglesias et al. (2008).

The trends on fish catch changes among open waters and vegetated habitats between spring and summer were probably driven by environmental conditions influenced by macrophytes and water level fluctuations. In spring, with intermediate water levels and clear waters (low chlorophyll *a* and suspended solids concentrations), fish were more captured among



emergent plants (PLef) and similar lower catches were obtained at open waters and free-floating habitats (Pow and Lf). As asserted by Iglesias et al. (2007), fish preference for emergent plants is related to the characteristics of this habitat that offers good shelter against piscivorous fish and birds, as well as sufficient food availability (zooplankton and phytoplankton). Despite free-floating plants may also constitute an adequate habitat for small fish (Meerhoff et al., 2007), the low oxygen concentrations such as those registered in this study beneath dense floating mats ( $<3 \text{ mg l}^{-1}$ ), were considered harmful for many fish species (Mossa & Scotta, 1961; Miranda & Hodges, 2000; McNeil & Closs, 2007) and may explain the low fish catches among dense FFP mats (RDA analysis, Fig. 7). Previous findings reported fish migration within water bodies, from hypoxic to more oxygenated areas (Miranda et al., 2000; Agostinho et al., 2007); this behavior supports the pattern found in our study, where small omnivorous–planktivorous fish aggregated in well-oxygenated habitats with emergent plants. Additionally, dense floating mats strongly limit light availability in the water column (de Tezanos Pinto et al., 2007), impairing the feeding efficiency of these small visual predators and further contributing to their scarcity in this vegetated environment. Low fish catches at open waters coincide with patterns reported for other lakes in similar latitudes (Meerhoff et al., 2003; Iglesias et al., 2007), possibly because of higher predation risk in this less protected habitat. In summer, when water level dropped, the enhanced turbidity caused by cyanobacteria blooms may have promoted a more even distribution among open waters and habitats with emergent plants. Experimental results suggested that high water turbidity impairs the predation efficiency of piscivorous (De Robertis et al., 2003; Snickars et al., 2004) and thus, small omnivorous–planktivorous fish would have less need for shelter in turbid conditions. This idea is supported by findings on decreased anti-predator behavior of fish (seek for refuge among macrophytes during daytime) in conditions of elevated turbidity (Gelós et al., 2010). Besides, Engström-Öst et al. (2006) showed that some small fish used cyanobacteria blooms as shelter against predators. Our results suggest that the spatial distribution of omnivorous–planktivorous fish in vegetated shallow lakes might be influenced by a suite of interacting factors, namely oxygen availability and shelter that are

in turn affected by the macrophyte cover and water turbidity.

The diet of *C. decemmaculatus* mostly comprised zooplankton, algae and detritus, in agreement with previous analyses (López Cazorla et al., 2003; Iglesias et al., 2008; Quintans et al., 2009). In general, fish selected positively cyclopoid copepods and cladocerans in the more complex vegetated environments (PLef and Lf), while at open waters neutral selection occurred. Similar findings were reported on other aquatic predators (*Perca flavescens* Mitchell, *Menippe mercenaria* Gmelin and *Busy concharica* Say) that showed a higher selectivity in structurally more complex habitats than in simpler ones (Hughes & Grabowski, 2006; Weber et al., 2010). Selectivity may occur because it promotes the coexistence of predators by decreasing competition, or simply because predators choose the more easily captured prey. The different swimming velocities of copepods and cladocerans determine unequal escape probabilities and may result in apparent prey selection by fish (Drenner et al., 1978). The positive selection towards cyclopoid copepods here described may reflect that these are more easily captured than fast swimming calanoid copepods, which likely use this ability as antipredatory strategy (Drenner et al., 1978; González Sagrario & Balseiro, 2010). In summer, the elevated turbidity caused by Cyanobacteria may have impaired fish vision and consequently, their feeding on zooplankton. Our results suggest different feeding behavior between the prevailing fish species: habitat structure and water turbidity influenced *C. decemmaculatus* selectivity towards macrozooplankton, whereas *J. multidentata* fed on the most abundant prey (rotifers) and clearly avoided Cyanobacteria.

The variations of the relative biomass of micro and macrozooplankton seemed not to be solely driven by fish predation, but probably by a combination of factors, as showed by the RDA analysis (Fig. 7). Calanoid copepods were very abundant in spring even in habitats with high fish abundance, probably on behalf of their ability to escape from fish predation by fast swimming (Drenner et al., 1978; Lenz & Hartline, 1999; Lenz et al., 2000). Cladocerans and cyclopoid copepods, with slower swimming velocities, dominated in habitats with dense FFP where fish were very scarce. These findings suggest that FFP may act as a refuge for macrozooplankton, especially when plant cover is high and planktivorous fish seem to avoid

them. These results do not agree with those from other warm lakes, where macrophytes constituted a poor refuge for zooplankton because of high predation risk (Meerhoff et al., 2003, 2007) and indicate that plant cover should be considered to evaluate their role as refuge. In summer, fish predation was potentially elevated in environments lacking FFP, because of high fish abundance. However, fish diet was mainly composed by Cyanobacteria and scarce zooplankton. Macrozooplankton scarcity in these environments would not be a response to top-down control by fish, but was most likely a cause of the harmful effects of Cyanobacteria and/or elevated salinity, as suggested by Havens et al. (2000) and Jeppesen et al. (1994, 2007). These environmental conditions favored the dominance of euryhaline rotifers, as previously reported in Laguna Grande (Chaparro et al., 2011) and other shallow lakes (Crome & Carpenter, 1988; Cirós-Pérez et al., 2001; Claps et al., 2009). In the cold seasons coinciding with enhanced water depth, fish abundance was lowest and no increase of macrozooplankton biomass was observed. The lake water level rise, related to higher rainfall and increased water levels of Paraná de las Palmas river (O'Farrell et al., 2011; Chaparro et al., 2013), may have provoked a change to more lotic conditions in the lake, which impaired macrozooplankton development through washing-out and dilution (Baranyi et al., 2002; Rennella & Quirós, 2006). The availability of phytoplankton as food resource remained sufficient during the study period (as depicted by the very low ratios of zooplankton to phytoplankton biomass) and would have minor impact on the variations of zooplankton structure.

Our results suggest that fish predation is not the only driver of macro and microzooplankton biomass in warm temperate floodplain lakes, implying that fish manipulation alone is not an efficient measure to control water turbidity through trophic cascades. Water level variations constitute a major factor affecting macrozooplankton populations in these environments, through washing-out or dilution processes (Baranyi et al., 2002; José de Paggi & Paggi, 2007; Paidere, 2009). Considering that hydrology also plays a major role for phytoplankton development from floodplain lakes, and particularly cyanobacteria blooms are favored at low waters during warm seasons (Paerl & Huisman, 2009; O'Farrell et al., 2011), measures to control water turbidity in these

environments should deal with the maintenance of water level fluctuations through the periodical occurrence of floods.

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