

Main drivers in the structure and dynamics of the zooplankton community in a Pampean seepage shallow lake throughout an annual cycle during turbid and clear water regimes

Diego M. Ardohain · Néstor A. Gabellone · María C. Claps 

Received: 02 November 2020 / Accepted: 15 March 2021 / Published online: 28 March 2021

© The Author(s) 2021

Abstract We investigated the composition and dynamics of the zooplankton community in a Pampean seepage lake (Buenos Aires, Argentina) under different environmental (rainfall, hydrometric level, conductivity, transparency) and biotic (phytoplankton biomass and presence of submerged macrophytes) conditions. In the annual cycle analyzed, the shallow lake evidenced alternating turbid- and clear-water periods associated with changes in phytoplankton biomass and the extent of colonization by submerged macrophytes. Thirty-five species were identified (21 rotifers, nine cladocerans and five copepods). Only six species were perennial: the rotifers *Brachionus caudatus*, *Keratella tropica*; the cladoceran *Ceriodaphnia dubia*; and the copepods *Notodiaptomus incompositus*, *Metacyclops mendocinus*, and *Microcyclops dubitabilis*. The zooplankton manifested a similar annual-abundance pattern in the three sampling stations established. Density and biomass peaks occurred in autumn during the clear phase without submerged macrophytes, whereas minimum values were obtained during the turbid phase. The presence of submerged macrophytes favored the zooplankton community, as evidenced by an increased abundance (twice that recorded during the turbid period) and species richness (from 20 to 30 species), with both parameters being associated with increased possibilities for zooplankton refuge plus an incorporation of periphytic and benthic species. Rotifers always predominated numerically. The copepod contribution prevailed throughout the annual cycle with respect to biomass except in spring when the cladocerans were more prevalent. These findings demonstrated that the zooplankton community responded positively to the changes that occurred in the environmental conditions of the lake between the turbid- and the clear-water states.

Keywords Zooplankton · Biotic and abiotic factors · Shallow lake · Alternating turbid- and clear-water periods

Introduction

The shallow lakes experience two alternative states of equilibrium determined by the presence (clear state) or absence of submerged macrophytes (turbid state), which contrasting conditions contributed to structural modifications in the plankton community and in the nutrient dynamics, with a consequent change in the trophic status. The occurrence of biomanipulation (van de Haterd and Ter Heerdt 2007) or certain

Diego M. Ardohain
Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata (UNLP), La Plata, Argentina

Néstor A. Gabellone · María C. Claps (✉)
Instituto de Limnología Dr. Raúl A. Ringuelet. CCT-CONICET-La Plata, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata (UNLP), La Plata Argentina
e-mail: mc.claps@gmail.com



environmental conditions such as heavy rainfall and the subsequent water-level increase (van Nes et al. 2007) can promote a shift between these two alternative stable states.

A significant increase in the zooplankton specific richness and density occurs when submerged macrophytes are recorded in shallow lakes (Scheffer 2004). The macrophyte beds amplify the availability of niches for members of zooplankton and act as a refuge against the predation otherwise occurring open water. Nevertheless, many authors have postulated the limited effectiveness of macrophyte protection in subtropical shallow lakes because of the presence of predators such littoral fish and invertebrates (Iglesias et al. 2007; Merhoff et al. 2007; Bolduc et al. 2016). Another clear difference between these environments and those of temperate regions is the absence or limited occurrence of *Daphnia* species (Rennella and Quiros 2006; Sosnovsky et al. 2010), although the role of those filter feeders in the maintenance of the clear state is controversial. In order to explain correctly the alternative stable states in shallow lakes of the Neotropical region, during recent decades, a large number of limnological investigations has been performed, including comparative studies among tropical and subtropical lakes (Kosten et al. 2009, 2011, 2012).

The Pampean shallow lakes of Argentina are naturally eutrophic, and cyclic periods of floods and droughts cause a rapid succession of changes, especially in the depressed area of the Salado-River basin in particular (Gabellone et al. 2000). Furthermore, such environments can evidence phases of alternative states (Scheffer and Jeppessen 2007), and during our investigation in Lacombe Lake within that basin, both those states can occur during the same year. Because of Lacombe's relatively marginal degree of environmental degradation, that lake was chosen for a limnological study coinciding with a period of such alternative phases. The low-density cattle breeding and sport fishing comprising the only human activities recorded during the study period had no recognizable ecologic impact on this lake. Moreover, the lake is not connected with other aquatic environments, thus preventing species migration. In the Pampean shallow lakes of the Salado-River basin, in general, the structure and dynamics of the zooplankton community are affected by biotic (predation, food availability, the presence of macrophytes) and abiotic (rainfall, temperature, salinity, turbidity) conditions (Claps et al. 2004, 2011; González Sagrario and Balseiro 2010, among others). In this study we investigated the influence of the presence of both alternative states on the abundance and biomass of zooplankton during an entire annual cycle. We then evaluated the change in the composition of the zooplankton community taking into account the ecologic role played by aquatic macrophytes in this ecosystem along with the consequences of an exceptional rainfall recorded during the study period that promoted a notable increase in the water level and transparency and a long-lasting diminution in the salinity.

We expected that the presence of submerged macrophytes would promote a positive effect on the zooplankton community related to the greater refuge and niche availability that would, in turn, contribute to an increase in zooplankton complexity and crustacean biomass. Moreover, we predicted that an increase in transparency and an elevation in the hydrometric water level coupled with the absence of submerged macrophytes after a heavy rainfall would stimulate a heterogeneous spatial distribution of the zooplankton in order to avoid potential predators.

Materials and methods

Study area and sampling sites

Lacombe Lake—located in the Pampean region (35° 50' S, 57° 53' W) of Argentina—is a seepage shallow lake having an area of 130 ha, a maximum length of 1,750 m, and a maximum width of 1,500 m. The shoreline length is approximately of 5.6 km. During the sampling period the maximum depth was 2.5 m whereas the minimum was 1.6 m. The emergent and submerged macrophytes *Schoenoplectus californicus* (Meyer) Soják, *Stukenia pectinata* (L.), and *Myriophyllum quitense* Kunth had grown to colonize most of the lake surface. The samples were taken at three- or four-week intervals from July 2001 to June 2002. Three sampling stations were established (Figure 1): two located at deep sites among stands of *S. californicus* (St. 1: at the periphery of the stand, exposed to wind action and at a mean depth of 2.3 m; St. 2: at the center of



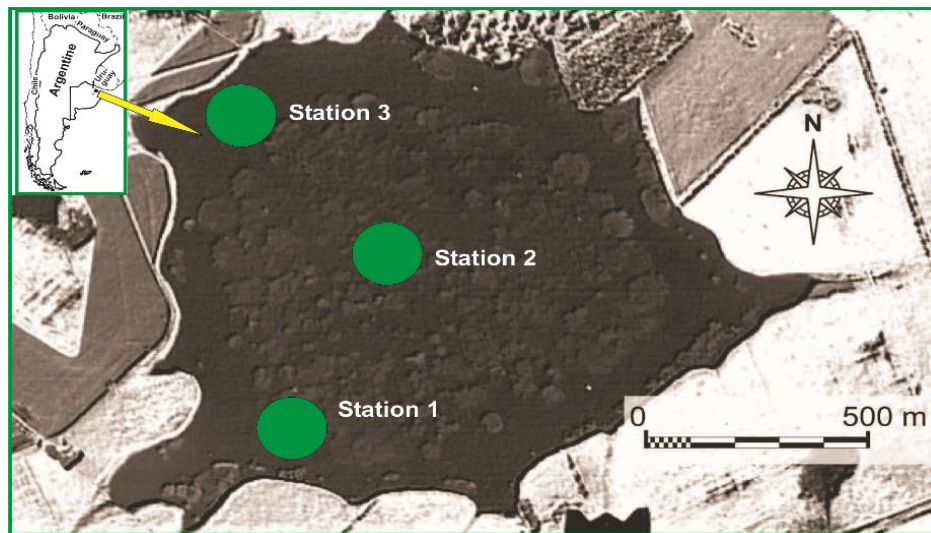


Fig. 1 Map of Lacombe Lake indicating the three sampling stations

the stand, not exposed to wind action) and one without emergent plants (St. 3: a deeper area near the littoral zone, but at a mean depth of 2.3 m).

Field sampling

The water temperature, pH, turbidity, conductivity, and dissolved-oxygen concentration were recorded with a Horiba U 10 multimeter in a vertical profile (five levels). At levels within the vertical profile, water samples for chlorophyll *a* and chemical analyses were collected in 1-L acid-cleaned polyethylene bottles for transportation back to the laboratory in an ice-cooled isolation box and subsequent storage in the dark at 5–8 °C before the analysis. Precipitation measurements were recorded daily at the Lacombe meteorological station. The water transparency in the lake was estimated by means of a Secchi disk. Zooplankton samples were taken with a suction pump at equal intervals over the vertical profile (five levels of 30 L) from the surface to the bottom and passed through a 25-mm-diameter hose into a 35- μ m-mesh net. The material retained was fixed in a 4% (v/v) aqueous formaldehyde solution.

Laboratory analysis

The total phosphorus was assayed by the ascorbic-acid method after digestion with acidic persulfate according to the American Public Health Association (APHA) (Method 4500-P B; APHA 1995) and dissolved polyphenols determined according to Method 5550 B; APHA (1995). For phytoplankton chlorophyll-*a* measurement, a volume of 500 ml was filtered through a Whatman GF/C filter and frozen (method 10200 H, APHA 1995).

The rotifers were counted in (1-mL) Sedgwick-Rafter and the crustaceans in (10-mL) Bogorov chambers. The samples were first mixed with a magnetic stirrer and subsamples then enumerated after taking into account that the coefficient of variation was lower than 20%. The biomass values for rotifers were estimated from the volume measurements by means of geometric approximations (Ruttner Kolisko 1977) on each sampling date and at each station (with $n = 10$ –30 for each taxon sampled). The volume measured was converted to dry weight (DW) by assuming a specific gravity of 1.0 and a ratio of dry weight to wet weight of 10% (McCauley 1984). The DWs of the cladocerans and the larval, juvenile, and adult stages of the copepods were estimated on each sampling date and at each station from the available length-weight regressions (Dumont et al. 1975). The proportions of the biomasses of the different zooplankton functional groups within the total biomass were calculated and a functional-feeding-group classification made based on the feeding strategy employed by each genus or family. According to Obertegger et al. (2011), the rotifers were separated into the microphages and



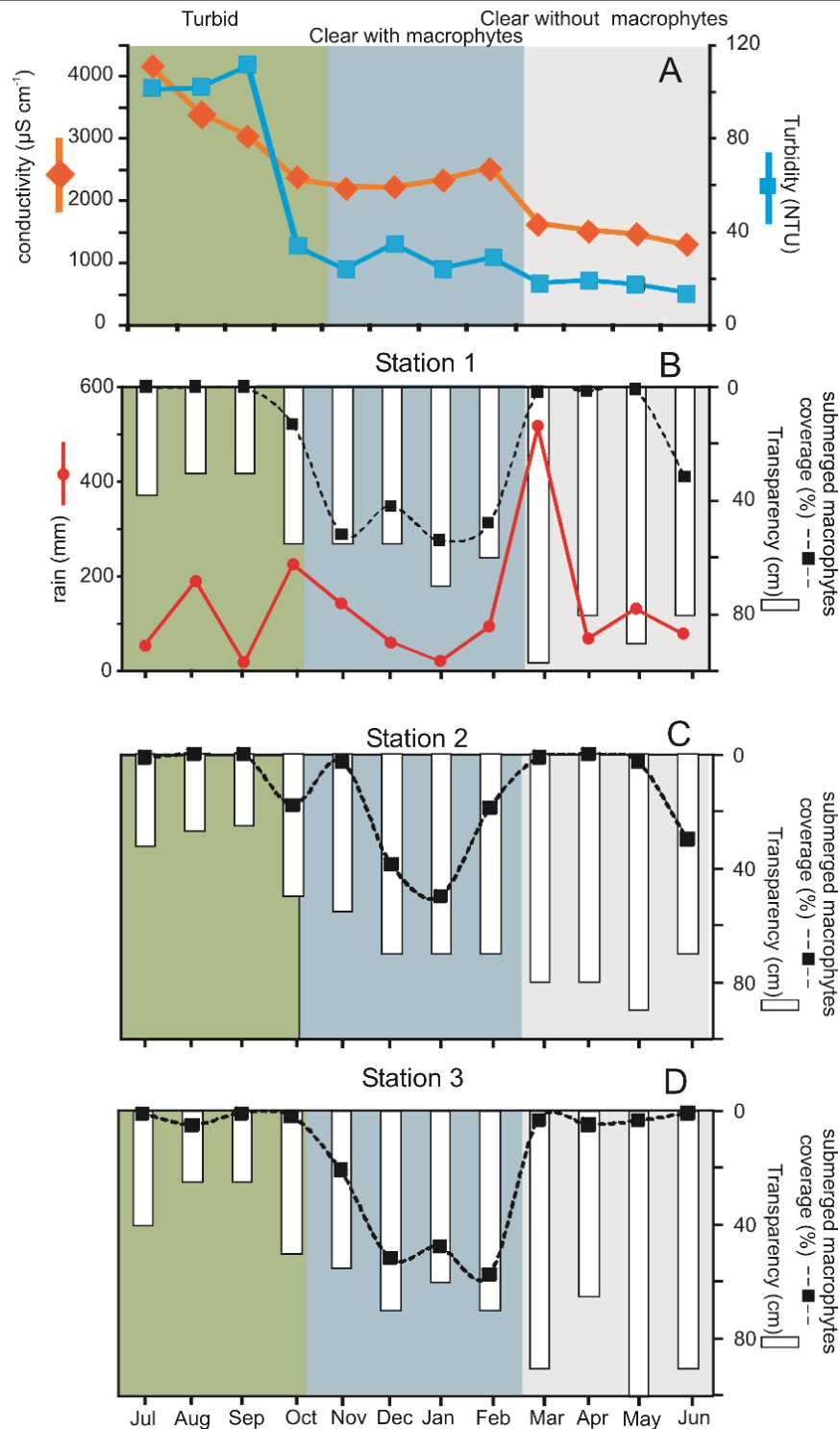


Fig. 2 Monthly variations of the conductivity and turbidity mean values recorded among the three sampling stations (Panel A), local rainfall (Panel B), water transparency, and submerged-macrophyte coverage recorded in each sampling station (Panels B–D) during different degrees of transparency and the presence or absence of submerged macrophytes. In all four panels, the dark background indicates turbid water without macrophytes, the medium background clear water with macrophytes, and the light background clear water without macrophytes.

the raptorial; while, after Barnett et al. (2007), the cladocerans and copepods were classified into the filtering Ctenopoda (*Diaphanosoma birgei*), the filtering Anomopoda (*Ceriodaphnia dubia* and *Moina micrura*), the selective filter feeders (*Bosmina huaronensis*), the filtering scrapers (Chydoridae), the microphagous herbivores (nauplii of Calanoida and Cyclopoida, adults and copepodites of *Notodiaptomus incompositus*), and the macrophagous carnivores (adults and copepodites of cyclopoids).



Table 1 Characteristics of the sampling stations located in Lacombe Lake during different conditions of water transparency and the presence of submerged macrophytes. Mean values and standard deviations (in parentheses) of selected physicochemical variables, phytoplanktic chlorophyll-*a* concentrations and density and biomass of zooplankton

TURBID CONDITION JULY-OCTOBER			
(maximum Secchi disc depth 0.55 m)			
	Station 1	Station 2	Station 3
Conductivity ($\mu\text{S cm}^{-1}$)	3219 (459)	3272 (633)	3205 (717)
pH	9.8 (0.1)	9.8 (0.2)	9.8 (0.3)
Temperature ($^{\circ}\text{C}$)	14.2 (1.3)	14.4 (0.9)	14.2 (4.4)
Dissolved oxygen (DO) (mg L^{-1})	8.8 (1)	8.7 (5.4)	8.4 (2.2)
Percent DO saturation	87 (16)	97 (33)	91 (12)
Turbidity (nephelometric turbidity units)	92 (23)	81 (34)	86 (29)
Total Phosphorus ($\mu\text{g L}^{-1}$)	348 (146)	397 (156)	353 (156)
Dissolved polyphenols (mg L^{-1})	2.0 (0.78)	1.9 (1.4)	2.2 (1.9)
Chlorophyll <i>a</i> (mg m^{-3})	37 (34)	39 (36)	31 (31)
Zooplankton species richness	11 (1)	10 (2)	10 (2)
Zooplankton abundance (individuals L^{-1})	510 (152)	505 (144)	487 (197)
Zooplankton biomass ($\mu\text{g DW L}^{-1}$)	489 (242)	491 (301)	399 (172)
CLEAR WITH SUBMERGED MACROPHYTES NOVEMBER-FEBRUARY			
(maximum Secchi disc depth 0.70 m)			
	Station 1	Station 2	Station 3
Conductivity ($\mu\text{S cm}^{-1}$)	2344 (103)	2346 (108)	2269 (165)
pH	9.9 (0.3)	10.0 (0.2)	10.2 (0.2)
Temperature ($^{\circ}\text{C}$)	19.5 (8.8)	17.4 (10)	17.4 (9.5)
Dissolved oxygen (DO) (mg L^{-1})	7.2 (3.9)	6.0 (3)	6.2 (2.5)
Percent DO saturation	100 (29)	90 (25)	81 (24)
Turbidity (nephelometric turbidity units)	26 (6)	28 (7)	30 (12)
Total Phosphorus ($\mu\text{g L}^{-1}$)	317 (146)	268 (98)	297 (126)
Dissolved polyphenols (mg L^{-1})	3.0 (1.1)	2.0 (0.6)	2.5 (0.7)
Chlorophyll <i>a</i> (mg m^{-3})	24 (17)	27 (12)	31 (20)
Zooplankton species richness	14 (5)	13 (4)	12 (3)
Zooplankton abundance (individuals L^{-1})	1249 (157)	1051 (529)	1149 (553)
Zooplankton biomass ($\mu\text{g DW L}^{-1}$)	544 (73)	505 (125)	583 (239)
CLEAR WITHOUT SUBMERGED MACROPHYTES MARCH-JUNE			
(maximum Secchi disc depth 1.00 m)			
	Station 1	Station 2	Station 3
Conductivity ($\mu\text{S cm}^{-1}$)	1502 (153)	1524 (137)	1407 (132)
pH	9.5 (0.6)	9.5 (0.6)	9.4 (0.6)
Temperature ($^{\circ}\text{C}$)	15.2 (2.9)	15.7 (3.1)	15.4 (3)
Dissolved oxygen (DO) (mg L^{-1})	9.3 (1.1)	9.4 (4)	8.7 (1.1)
Percent DO saturation	93 (14)	102 (21)	93 (13)
Turbidity (nephelometric turbidity units)	12 (8)	18 (4)	18 (5)
Total Phosphorus ($\mu\text{g L}^{-1}$)	169 (50)	164 (43)	172 (46)
Dissolved polyphenols (mg L^{-1})	2.0 (0.6)	1.9 (1)	2.1 (0.6)
Chlorophyll <i>a</i> (mg m^{-3})	21 (12)	29 (9)	23 (6)
Zooplankton species richness	20 (2)	21 (4)	19 (3)
Zooplankton abundance (individuals L^{-1})	1378 (1107)	1196 (844)	1548 (960)
Zooplankton biomass ($\mu\text{g DW L}^{-1}$)	576 (169)	615 (214)	655 (190)

Statistical analysis

To investigate the relationship between species composition and environmental variables throughout the study period, multivariate-ordination techniques from the CANOCO program (version 4.5) were used (ter Braak 1986). The method of redundancy analysis was selected because the lengths of the gradients of explanatory variables were short (ter Braak and Smilauer 2002). The analyses included only those environmental variables with a variance inflation smaller than 10, to mitigate the effect of multicollinearity (ter Braak and Verdonschot 1995). After standardization of the environmental data, the



statistical significance of the variability for each parameter and the general meaning of ordination were assessed by a Monte-Carlo test (499 permutations, $P < 0.01$).

Results

Parameters

The sampling period was the rainiest in the last 50 years (1,336 mm in 2001 and 1,375 mm in 2002), with 1,067 mm being the historical mean. During the sampling period three particularly heavy rainfalls occurred: in August (191 mm), in October (223 mm), and in March (515 mm), the most extensive one. Increments in the hydrometric level were markedly related to these rainfalls. As a result, a prolonged/continuous decrease in the conductivity was observed throughout the sampling period. In addition, the turbidity noticeably declined after the first three months of sampling (Figure 2, Table 1). The transparency fluctuated between 0.25 and 1.00 m. The submerged macrophytes reached a maximum cover in the summer months, and then decreased abruptly in March, though making a recovery by June. Three periods could be distinguished based on turbidity that coincided with different levels of macrophyte development (Figure 2): Phase 1 with high turbidity and without macrophytes (July through October), Phase 2 with low turbidity and with the highest macrophyte development (November through February), and Phase 3 with the lowest turbidity but without macrophyte development (March through June).

The temperature values displayed the typical seasonal pattern of this temperate climate with a maximum peak in December and a minimum, in July. At all the sampling stations and on all the dates the mean percent saturation of dissolved oxygen was high (always values higher than 80%; Table 1), except during January near the sediments (lower than 35%). An alkaline pH was recorded throughout the whole year of sampling. The total phosphorus concentrations increased markedly during the first two precipitations (August and October) but decreased with the rainfalls in March. After a substantial phosphorus input from runoff in October, the mean total phosphorus concentration diminished gradually throughout the growth period of the submerged macrophytes. The concentration of dissolved polyphenols was the highest during phases 2 and 3 in those sectors colonized by submerged macrophytes (*i. e.*, St. 1 and St. 3). The mean phytoplankton chlorophyll concentrations were maximal during the turbid period, whereas a notable reduction in those values occurred in both clear periods (Table 1).

Zooplankton composition

We identified 35 zooplankton species (21 rotifers, 9 cladocerans, and 5 copepods). The lowest species richness (24 species: 13 rotifers, 6 cladocerans, and all 5 copepod species) was recorded during the turbid phase; whereas in the second and third phases the zooplankton comprised 30 species (18 rotifers, 7 cladocerans, and all 5 copepod species) and 32 species (20 rotifers, 8 cladocerans and 4 copepods), respectively. Only six species were recorded throughout the entire annual cycle in at least one of the three sampling stations: the rotifers *Brachionus caudatus* and *Keratella tropica*; the cladoceran *C. dubia*; and the copepods *N. incompositus*, *Metacyclops mendocinus*, and *Microcyclops dubitabilis* (Tables 2a–2c).

Annual abundance dynamic of the entire community and predominant members

The rotifers were numerically dominant throughout the sampling period except in September, November, December, and March. Certain cladocerans predominated during the spring months, whereas the copepods (nauplii) prevailed in the summer months (Figure 3). In July, *K. tropica* achieved a peak (771 ind.L⁻¹) at St. 2. The abundance of adults of *M. mendocinus* (214 ind.L⁻¹) was significant in August at St. 1. In October, the population of *B. huaronensis* reached its maximum at St 2 (326 ind.L⁻¹), and in November *C. dubia* manifested a maximum abundance value (156 ind.L⁻¹) at St. 3. In January, *Brachionus havanaensis* (1,252 ind.L⁻¹ at St. 2) and the nauplii of copepods (1,385 ind.L⁻¹ at St. 3) prevailed throughout the entire lake. On the next sampling occasion, adults of *Acanthocyclops robustus* (51 ind.L⁻¹ at St. 1) and of *M. dubitabilis* (103 ind.L⁻¹ at St. 3) attained population peaks, whereas in March adults of *N. incompositus* exhibited the



Table 2a Density ranges (individuals L⁻¹) of zooplankton species recorded during the turbid period at the three stations established in Lacombe Lake, where *: <50, **: 50–100, ***: 100–500, ****: 500–1,000, *****: >1,000. The boldface number in parentheses marks the sampling station with the maximum density value.

	JULY	AUGUST	SEPTEMBER	OCTOBER
<i>Asplanchna girodi</i> de Guerne				*(123)
<i>Brachionus caudatus</i> Barrois & Daday	** (123)	*** (123)	*** (123)	*(13)
<i>B. plicatilis</i> Müller	*(1)		*(3)	*(12)
<i>Filinia longiseta</i> (Ehrenberg)				** (23)
<i>Keratella tropica</i> (Apstein)	*** (123)	*** (123)	*(123)	*** (123)
<i>Lecane closterocerca</i> (Schmarda)	*(2)		*(3)	
<i>L. pyriformis</i> (Daday)	*(23)			
<i>Lepadella ovalis</i> (Müller)	*(1)			
<i>Polyarthra vulgaris</i> Carlin				*(123)
<i>Proalides tentaculatus</i> de Beuchamp	*** (123)	*(123)	*(123)	
<i>Testudinella patina</i> (Hermann)	*(13)	*(13)	*(123)	
<i>Trichocerca stylata</i> (Gosse)	*(1)			
Bdelloids	*(1)	*(1)		
<i>Bosmina huaronensis</i> Delachaux		*(3)	*(23)	*** (123)
<i>Ceriodaphnia dubia</i> Richard	*(1)	*(123)	*(123)	** (123)
<i>Chydorus sphaericus</i> (Müller)		*(123)		
<i>Coronatella poppei</i> (Richard)	*(2)	*(123)	*(123)	
<i>Moina micrura</i> Kurz				*(123)
<i>Ovalona glabra</i> (Sars)	*(12)	*(123)	** (123)	*(2)
<i>Notodiaptomus incompressus</i> Brian	*(123)	*(123)	*(123)	*(123)
<i>Acanthocyclops robustus</i> Sars	*(13)	*(123)	*(12)	
<i>Metacyclops mendocinus</i> Wierzejski	*(123)	*(123)	*(123)	*(123)
<i>Microcyclops dubitabilis</i> Kiefer	*(13)	*(123)	*(123)	*(12)
<i>Cletocamptus tertius</i> Gómez & Gee	*(12)	*(123)	*(13)	*(12)

maximum abundance (52 ind.L⁻¹ at St. 3). In April, *Polyarthra vulgaris* achieved a population peak at 531 ind.L⁻¹ at St. 3. At the same sampling station in May, *B. caudatus* was dominant (767 ind.L⁻¹), and on the same sampling occasion, *Keratella lenzi* predominated (1,602 ind.L⁻¹) at St. 2. In addition, the same species (1,107 individuals.L⁻¹) along with *Pompholyx sulcata* (1,379 ind.L⁻¹) prevailed at St. 1.

The total zooplankton abundance evidenced a similar temporal pattern at all the sampling stations throughout the annual cycle (Figure 3). In general, certain rotifers and cladocerans were numerically dominant during the turbid phase, while other rotifer species and copepods prevailed in both clear phases. In the presence of submerged macrophytes and throughout the entire lake, the abundance of copepod nauplii tripled the values recorded in the other phases. Peaks in the total zooplankton were observed during the clear phase without submerged macrophytes in May at mean abundances within the vertical profile of 3,004 ind.L⁻¹ at St. 1, 2,437 ind.L⁻¹ at St. 2, and 2,900 ind.L⁻¹ at St. 3. The rotifers dominated (at more than 80% of the total abundance) in all the sampling stations (Figure 3). The minimum values of abundance were recorded during the turbid phase (Table 1), in September at mean values within the vertical profile of 311 ind.L⁻¹ at St. 1, 393 ind.L⁻¹ at St. 2, and 300 ind.L⁻¹ at St. 3. On this sampling occasion, no specific zooplankton group predominated at any sampling station (Figure 3).

Annual biomass dynamic of the entire community and predominant members

In general, the mean of total zooplankton biomass manifested a comparable pattern at the sampling stations throughout the annual cycle, with the observed at St. 1 and St.2 being especially similar (Figure 4).



Table 2b Density ranges (individuals L⁻¹) of zooplankton species recorded during the clear period with submerged macrophytes at the three stations established in Lacombe Lake, where *: <50, **: 50–100, ***: 100–500, ****: 500–1,000, *****: >1,000. The boldface number in parentheses marks the sampling station with the maximum density value.

	NOVEMBER	DECEMBER	JANUARY	FEBRUARY
<i>Brachionus caudatus</i>	*(2)	*(123)	***(123)	*(123)
<i>B. havanaensis</i> Rousselet		*(1)	****(123)	***(123)
<i>B. plicatilis</i>			*(123)	*(12)
<i>Filinia longiseta</i>	*(23)		*(123)	*(1)
<i>Hexartra fennica</i> (Levander)			*(123)	***(23)
<i>Keratella lenzi</i> Hauer	** (12)	*** (123)		
<i>K. tropica</i>	*** (123)			*(123)
<i>Lecane bulla</i> (Gosse)			*(12)	*(12)
<i>L. closterocerca</i>		*(13)	*(123)	*(12)
<i>L. luna</i> (Müller)			*(123)	*(1)
<i>L. pyriformis</i>	*(3)	*(13)	*(12)	*(123)
<i>Lepadella ovalis</i>	*(1)		*(1)	*(1)
<i>Phompholyx sulcata</i> Hudson				*** (123)
<i>Polyartra vulgaris</i>	*(123)	** (123)	*(123)	*(123)
<i>Testudinella patina</i>		*(1)	*(13)	*(3)
<i>Trichocerca pusilla</i> (Jennings)		*(13)	*(123)	*(123)
<i>T. stylata</i>	** (123)			*(1)
Bdelloids				*(123)
<i>Bosmina huaronensis</i>	*		*(123)	*(123)
<i>Ceriodaphnia dubia</i>	*(123)	*(123)	*(123)	*(12)
<i>Coronatella poppei</i>			*(1)	*(1)
<i>Diaphanosoma birgei</i> Kořinek			*(123)	*(123)
<i>Moina micrura</i>	*(123)	*(123)	*(123)	*(123)
<i>Ovalona glabra</i>				
<i>Pseudochydorus globosus</i> (Baird)			*(3)	
<i>Notodiaptomus incompressus</i>	*(123)	*(123)	*(123)	*(123)
<i>Acanthocyclops robustus</i>	*(1)	*(123)	*(123)	*(123)
<i>Metacyclops mendocinus</i>	*(123)	*(123)	*(123)	*(123)
<i>Microcyclops dubitabilis</i>	*(123)	*(123)	*(123)	*(123)
<i>Cletocamptus tertius</i>		*(2)	*(12)	

The maximum values of total zooplankton biomass were recorded in October at stations 1 and 2 (1,459 and 1,401 $\mu\text{g DW.L}^{-1}$, respectively), with *B. huaronensis* being the principal species responsible for this biomass peak. At St. 3, a peak in biomass occurred in May (at 1,117 $\mu\text{g DW.L}^{-1}$), due to the biomass contribution of the cyclopoids, *D. birgei* and *B. huaronensis*. The minimum values were recorded in July at all stations (at St. 1: 10 $\mu\text{g DW.L}^{-1}$; at St. 2: 52 $\mu\text{g DW.L}^{-1}$; at St. 3: 97 $\mu\text{g DW.L}^{-1}$). In addition, the minimum mean value for the entire water column was detected in the same month (at St. 1, 204 $\mu\text{g DW.L}^{-1}$; at St. 2, 156 $\mu\text{g DW.L}^{-1}$, and at St. 3, 196 $\mu\text{g DW.L}^{-1}$).

The maximum mean values of the total zooplankton biomass for the vertical profile were observed in October and May at stations 1 and 2 (846 and 751 $\mu\text{g DW.L}^{-1}$ at St. 1, and 777 and 855 $\mu\text{g DW.L}^{-1}$ at St. 2, respectively), whereas at St. 3 those maxima occurred in November and May (at 928 and 937 $\mu\text{g DW.L}^{-1}$, respectively). In general, the contribution of the macrophagous copepods and microphagous herbivorous copepods to the biomass was significant and similar throughout the year at all the sampling stations. For example, in August the biomass of the cyclopoids represented more than 60% of the total



Table 2c Density ranges (individuals L⁻¹) of zooplankton species recorded during the clear period without submerged macrophytes at the three stations established in Lacombe Lake, where *: <50, **: 50–100, ***: 100–500, ****: 500–1,000, *****: >1,000. The boldface number in parentheses marks the sampling station with the maximum density value.

	MARCH	APRIL	MAY	JUNE
<i>Asplanchna girodi</i>		*(12)	*(123)	*(123)
<i>Brachionus calyciflorus</i> Pallas		** (123)	*(123)	*(123)
<i>B. caudatus</i>	*(123)	*(123)	*** (123)	*(123)
<i>B. havanaensis</i>	*(123)	*(123)		
<i>B. plicatilis</i>	*(3)	*(12)	*(23)	
<i>Filinia longiseta</i>	*(123)	*(23)	*(123)	*(123)
<i>Keratella lenzi</i>	*(123)	** (123)	***** (123)	** (123)
<i>K. tropica</i>	*(123)	*** (123)	*** (123)	*** (123)
<i>Lecane bulla</i>	*(2)	*(13)	*(123)	*(2)
<i>L. closterocerca</i>	*(3)	*(2)	*(123)	*(123)
<i>L. luna</i>	*(2)	*(23)	*(2)	*(23)
<i>L. pyriformis</i>	*(23)	*(123)	*(123)	*(3)
<i>Lepadella ovalis</i>	*(1)	*(1)	*(12)	*(1)
<i>Phompholyx sulcata</i>	*(123)	** (123)	**** (123)	** (123)
<i>Polyartra vulgaris</i>	*(123)	*** (123)	*** (123)	*** (123)
<i>Proalides tentaculatus</i>	*(123)	*(2)	*(1)	
<i>Testudinella patina</i>	*(23)	*(23)	*(123)	*(123)
<i>Trichocerca pusilla</i>	*(123)	*(12)	*(123)	*(2)
<i>T. stylata</i>	*(123)			
Bdelloids	*(23)		*(123)	*(123)
<i>Bosmina huaronensis</i>	*(123)	*(123)	*(123)	*(123)
<i>Ceriodaphnia dubia</i>	*(123)	*(123)	*(123)	*(123)
<i>Chydorus sphaericus</i>	*(1)	*(12)	*(123)	*(123)
<i>Coronatella poppei</i>	*(1)	*(1)	*(2)	*(2)
<i>Diaphanosoma birgei</i>	*(123)	*(123)	*(123)	*(123)
<i>Moina micrura</i>	*(123)	*(123)	*(123)	*(123)
<i>Ovalona glabra</i>			*(2)	
<i>Pseudochydorus globosus</i>	*(3)	*(13)	*(23)	*(123)
<i>Notodiaptomus incompositus</i>	*(123)	*(123)	*(123)	*(123)
<i>Acanthocyclops robustus</i>	*(1)	*(123)	*(123)	*(123)
<i>Metacyclops mendocinus</i>	*(123)	*(123)	*(123)	*(123)
<i>Microcyclops dubitabilis</i>	*(123)	*(123)	*(123)	*(123)

biomass in the layer immediately above the sediments at St. 1. In February and March, the three species (*M. mendocinus*, *M. dubitabilis* and *N. incompositus*) achieved more than 50% of the total biomass in different layers at St. 2, while in March and May a similar contribution was observed at St. 3. The larval stages of the copepods exhibited slight differences in their biomass values that were more evident at St. 1 and St. 3 when the submerged macrophytes were present and the populations of those larvae had reached the maxima. Conversely, the relevance of cladocerans manifested spatiotemporal variations. The biomass peaks of the filtering scrapers took place during the turbid period at all the sampling stations, whereas the contribution of the selective filter feeder *B. huaronensis* was restricted to the end of that period and occurred at only St. 1 and St. 2. This cladoceran achieved biomass peaks at those stations in October, whereas at St. 3, its biomass was more significant during the clear-water periods. The role of the filtering Anomopoda became conspicuous at the end of the turbid period and also in the subsequent



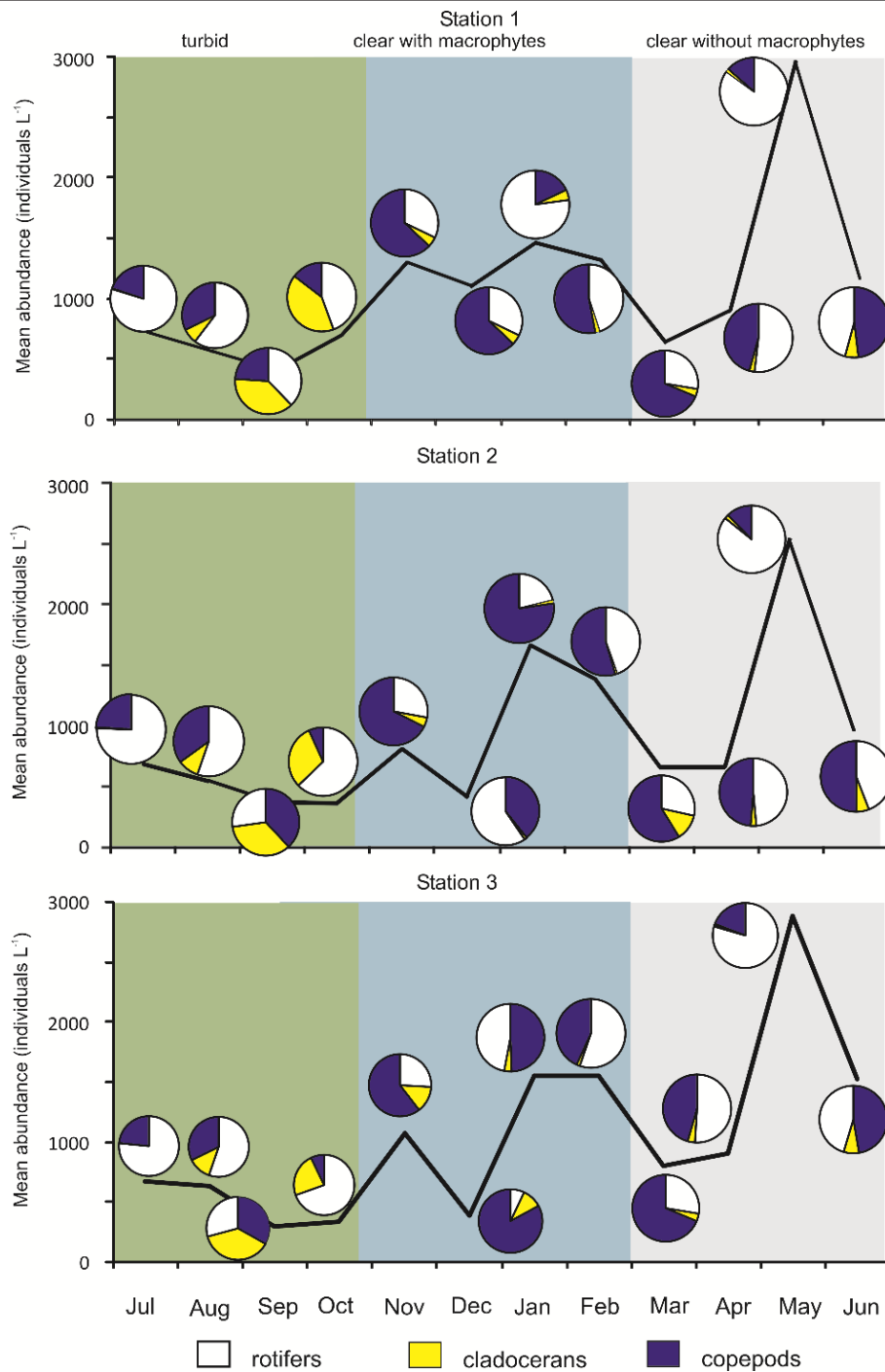


Fig. 3 Monthly variation in the mean total zooplankton abundance within the vertical profile (line) and the percent contribution of the main groups on each sampling occasion at the three sampling stations in Lacombe Lake during different degrees of transparency and the presence or absence of submerged macrophytes. In all three panels, the dark background indicates turbid water without macrophytes, the medium background clear water with macrophytes, and the light background clear water without macrophytes.

clear-water phase characterized by submerged-macrophyte colonization—then, though, mainly at St. 3. The biomass contribution of the filtering Ctenopoda *D. birgei* was limited to the end of that period with submerged macrophytes but also included the entire clear-water period without macrophytes. During that last period, half of the total biomass was contributed by various functional groups (Figure 4).

Redundancy analysis



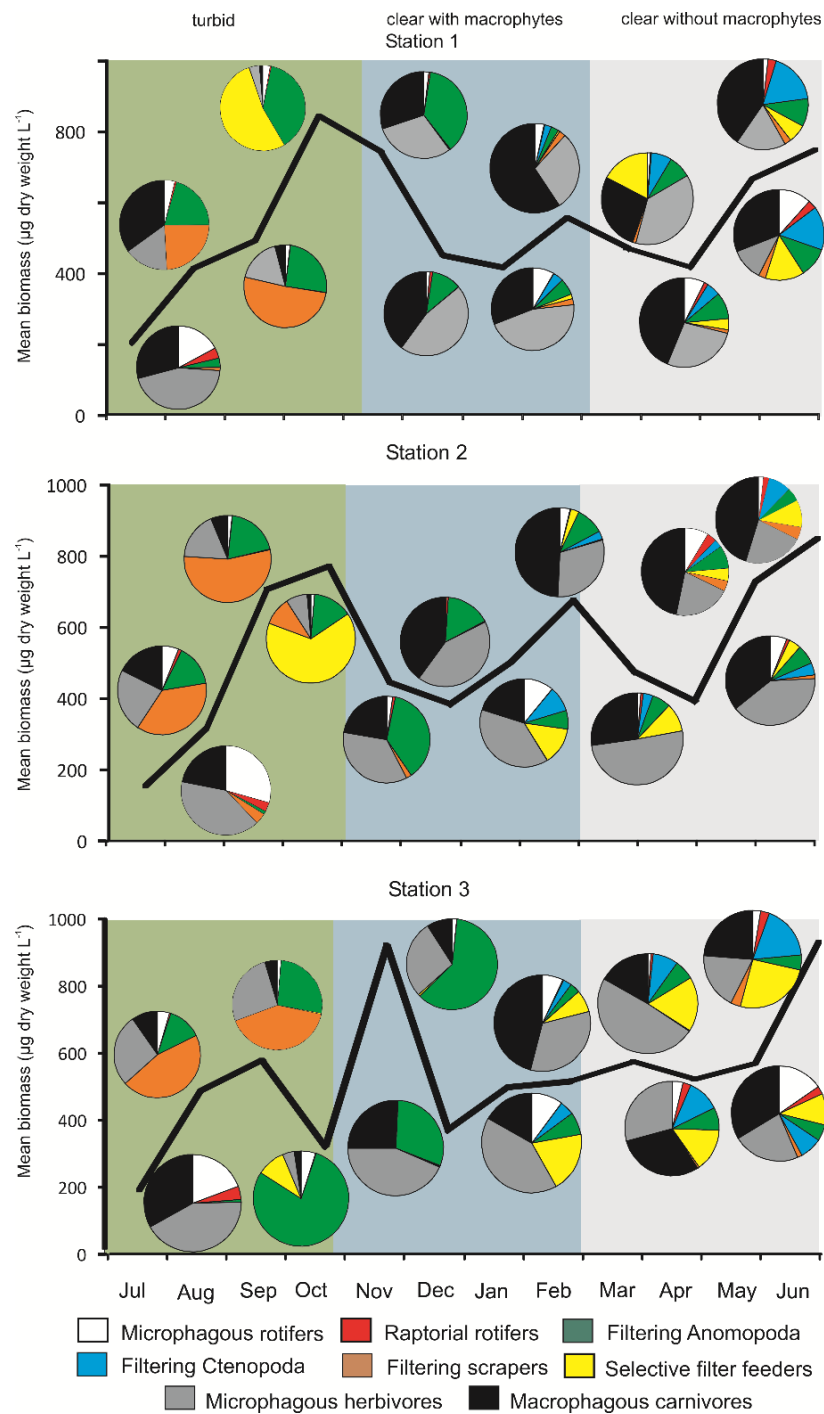


Fig. 4 Monthly variation in the mean total zooplankton biomass within the vertical profile (line) and the percent contribution of the functional feeding groups on each sampling occasion at the three sampling stations in Lacombe Lake during different degrees of transparency and the presence or absence of submerged macrophytes. In all three panels, the dark background indicates turbid water without macrophytes, the medium background clear water with macrophytes, and the light background clear water without macrophytes.

The first canonical axis and the sum of all canonical axes explained a significant portion of the variance in the zooplankton abundance ($p = 0.006$; $p = 0.002$, respectively). The first two canonical axes explained 92% of the cumulative variance. Turbidity was correlated negatively with the first axis ($R = -0.45$, $p < 0.05$) and dissolved oxygen with the second axis ($R = -0.48$, $p < 0.05$), whereas temperature was correlated positively with the latter axis (0.52 , $p < 0.05$). At the outermost of the positive sector of the first axis, the samples of only May were located in positions corresponding to the maximum oxygen concentration, high water transparency, and the lowest phytoplankton biomass. The rotifers and crustaceans with planktonic



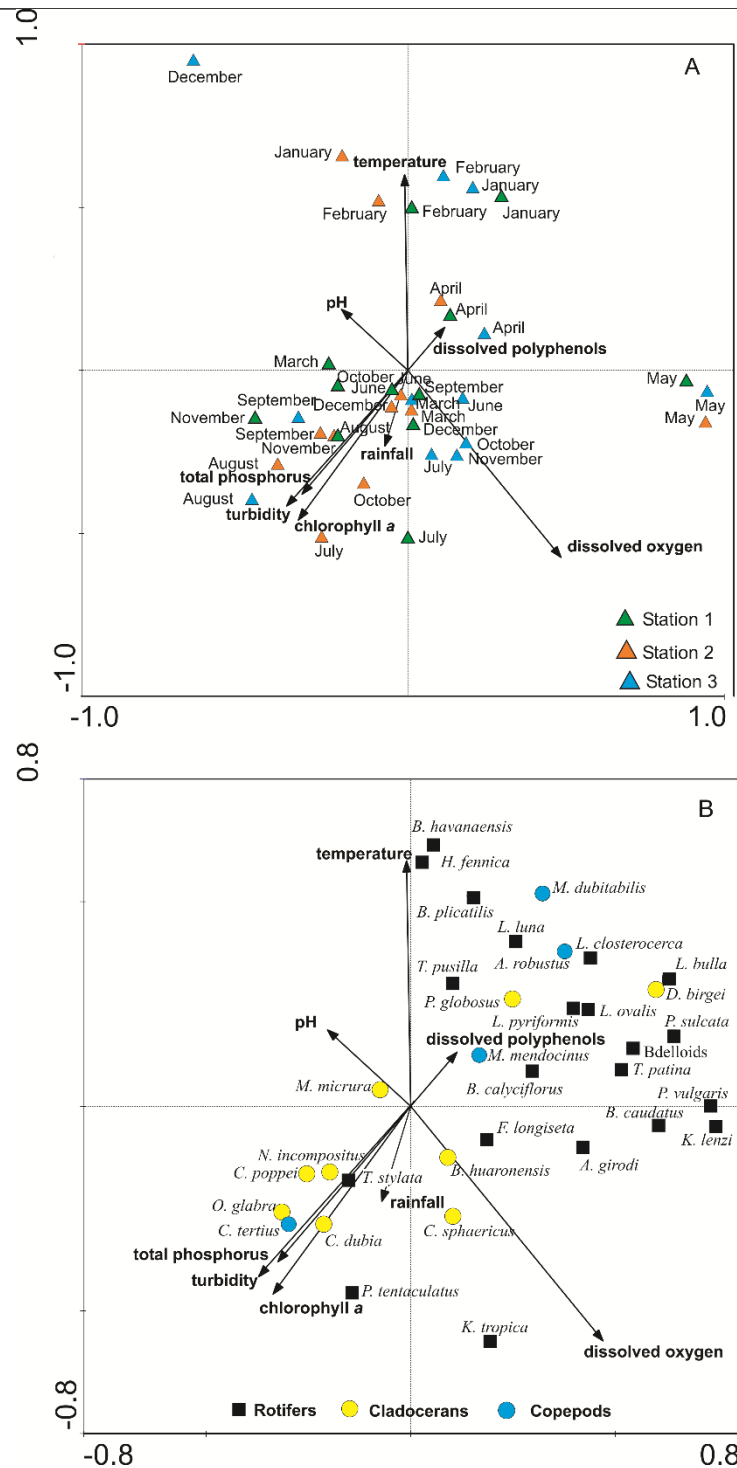


Fig. 5 Redundancy-analysis–ordination plots for the first two dimensions of the relationship between (Panel A) the samples and the environmental variables and (Panel B) the species and the environmental variables in Lacombe Lake.

or periphytic habitus were recorded in that sector. In the negative sector were located the samples of the turbid phase (the highest phytoplankton biomass), with those coinciding with heavy rainfalls and characterized by the highest total phosphorus concentrations. In this sector, the benthic cladocerans and the harpacticoid *Cletocamptus tertius* were accompanied by planktonic species such *K. tropica*, *N. incompositus*, and *C. dubia*. The majority of the samples collected in the lake during the summer months of December through February were located in the positive sector of the second axis in relation to the



highest temperature values, dissolved polyphenol concentrations related to the presence of submerged macrophytes, and water transparency recorded during this period along with an abundant presence of thermophilic rotifers and one cyclopoid. In contrast, species exhibiting a predominance during winter are located at the outermost portion of the negative sector of the second axis (Figure 5).

Discussion

Turbid period (July–October)

During winter and early spring, the vertical distribution of the zooplankton, especially the crustaceans, was similar over the vertical profile. This peculiarity could be related to the low water transparency. No significant differences of zooplankton density were found among the sites and at different depths, thus coinciding with the results of Castro et al. (2007) in a shallow Mediterranean lake under similar conditions. According to Liljendahl-Nurminen et al. (2008), turbidity may serve as a refuge from the invertebrate predators of zooplankton; and Gophen (2015) and Špoljar et al. (2018) have speculated that turbidity interferes visually with the attack of fish, thus promoting the survival of large zooplankters.

In coincidence with the observations of Havens et al. (2016) in Florida lakes, the cladocerans peaked in spring and then rapidly declined in summer. Ekvall and Hansson (2012) had observed that planktonic cladocerans increased the populations they studied during the spring in response to elevated temperatures. In the present work, the temperature had a positive effect during late spring and early summer that coincided with the transitional period and beginning of the clear period. The highest abundance and biomass of cladocerans achieved in Lacombe Lake could be related to the predominance of the coccal unicellular chlorophytes and *Cyclotella meneghiniana* in the water column (Cano et al. 2008). The chydorids were abundant in the early spring when only emergent vegetation was observed. Furthermore, in contrast to the ubiquitousness of *M. micrura* at all sampling times, the populations of *B. huaronensis* were much higher during this period since the macrophytes constituted an available refuge for certain planktonic cladocerans (Semenchenko 2008; Stefanidis and Papastergiadou 2010). Šorf and Devetter (2011) postulated that species of *Bosmina* tended to aggregate at food-rich places (Cerbin et al. 2003) and that their grazing was significant. The grazing activity of the littoral cladocerans was promoted in this period by a single-layered epiphyton structure on *S. californicus* (Cano et al. 2012).

Clear period with submerged macrophytes (November–February)

The decline in the cladoceran biomass in the summer recorded at Lacombe Lake when submerged macrophytes were dominant is not unusual and has been reported in several lakes with abundant submerged vegetation (Jeppesen et al. 2002). This occurrence could be related to predation pressure by littoral fish (Fermani et al. 2013) along with food quality (Agasild and Nöges 2005). During the summer, the phytoplankton biomass tends to be low in clear-water lakes owing to nutrient competition or allelopathic effects of submerged macrophytes and the predation of various zooplankton functional groups (Muylaert et al. 2006).

In Lacombe Lake, the nanoplanktonic chlorophytes that Casco et al. (2009) had recorded in the spring were found to be replaced by colonial cyanophytes in the summer, the latter being nonpalatable for the majority of zooplankton species (Agasild and Nöges 2005). Moreover, the low abundance or absence of chydorids during this season would be related to predation by chironomid and other insect larvae in contact with the macrophytes (Cano et al. 2013) and mentioned by Sakuma et al. (2004) as a controlling influence on their populations.

The rotifer populations were lower in the early summer in response to predation by copepods and fish larvae (José de Paggi et al. 2012). Nevertheless, the abundance of the rotifers *B. havanaensis*, *Hexarthra fennica*, and *Brachionus plicatilis* was restricted to the summer months. The first of those species is considered to be thermophilic and has achieved a high density in Pampean lakes during the warmer months (Fermani et al. 2013). *Brachionus plicatilis*, like *H. fennica*, is characterized as halophilous and is common in the Pampean shallow lakes with high salinity and at elevated temperatures (Ferrando et al. 2018). Species of the genera *Lecane*, *Trichocerca*, and *Lepadella* were found to be restricted to macrophyte-associated



habitats (Kuczynska-Kippen 2000; Green 2003).

In general, the cyclopoid copepods were more abundant in the presence of submerged macrophytes characterized by a complex morphology in contrast to the calanoid copepods that avoided those sectors (Merhoff et al. 2007). Plants with complex or dissected leaves provide a greater substrate area for foraging and more cover from predators than undissected ones (Ali et al. 2007), but certain authors (Meerhoff et al. 2007; Gutierrez and Paggi 2014) concluded that macrophytes, mainly those floating, are a dangerous location, rather than a refuge, for the organisms, especially in subtropical shallow lakes. Nevertheless, Iglesias et al. (2007) postulated that the protection of macrophytes is useful when the densities of fish and invertebrate predators are intermediate.

The nauplii stages of copepods were dominant in number and biomass during the summer months. This peculiarity could be related to the predation of littoral fish and macroinvertebrates on cladocerans and adult copepods (Claps et al. 2004; González Sagrario et al. 2007). Although adults of the calanoid copepods are less vulnerable to fish predation because of their skills in evasiveness (Drenner and McComas 1980), possibly their low density during the entire year-long period was associated with the preference of fish for copepodites that had been demonstrated in tanks by Frau et al. (2017).

In contrast, cladocerans are more threatened than cyclopoid copepods by fish predation because the former exhibit a very poor ability to escape in response to attack by planktivorous fish (Cazzanelli et al. 2008). In tank experiments, however, Chang et al. (2004) established that cyclopoids were more heavily preyed on than calanoids because the movements of the former are more conspicuous and thus attract the attention of the fish. That *O. bonariensis* also selectively preyed on copepods is possible (Colautti et al. 2010) because the large cladoceran *Daphnia spinulata*, which is that fish's favorite prey (Rennella et al. 2019), was absent in the lake during this entire sampling period. Nevertheless, the cyclopoids achieved their biomass peaks during summer and autumn, with values somewhat higher than those recorded during the spring. The difference could be linked to the high rains that occurred within our sampling period during August and October. With this same rainy condition in Canadian lakes, Lévesque et al. (2017) had also detected a low zooplankton abundance and a decline in calanoids. In addition, Choi et al. (2015) had demonstrated that the density of the pelagic rotifer species decreased with high rainfalls.

Clear period without submerged macrophytes (March–June)

Certain euplanktonic rotifers (*K. lenzi*, *P. vulgaris*, and *P. sulcata*) were predominant, in association with the lowest salinity recorded (Bielanska-Grajner and Cudak 2014) and the highest hydrometric level. The presence of *D. birgei* was mainly restricted to this period, confirming its sporadic recordings in other similar shallow lakes (Gerhard et al. 2016). The populations of *B. huaronensis* increased in abundance related to the absence of competition with *C. dubia* and *M. micrura* for food that has been detected by Chang et al. (2004) in tank experiments.

In Lacombe Lake, these cladocerans always reached their maxima in abundance and biomass on different occasions. During this phase, the spatial distribution of the members of the community was relatively homogeneous in the entire lake—in disagreement with our expectation that the populations would select or prefer a particular sector for predator avoidance. Furthermore, when the water temperature was unfavorable for food intake of the planktonic fishes (Colautti et al. 2010), a crustacean-biomass peak was observed at the end of the period (late autumn). The negative effect of *O. bonariensis* on crustacean populations would have been less intense because the increased rainfall in late summer promoted a significant decrease in salinity, which drop would be unfavorable for that zooplankton predator (Elisio et al. 2018). In addition, Sosnovsky et al. (2010) mentioned that turbid conditions in the Pampean lakes were more advantageous for the growth of that fish.

Comparison with other Pampean shallow lakes

The zooplankton richness in Lacombe Lake was similar to that recorded in other lakes with rotifers as the most diverse group (Claps et al. 2004; Fermani et al. 2013). In Lacombe, the presence of macrophytes during the summer enabled a large number of littoral and planktonic species to coexist in the water column,



Table 3 Comparison of zooplankton characteristics between Lacombe Lake and other Pampean shallow lakes distinguished by the presence of planktivorous fish

	Lacombe (this study)	Lacombe (2006)	San Miguel del Monte (1997–1998)	Chascomús (2008–2009)	Gómez (1999, 2000, 2001)	Carpincho (1999, 2000 and 2001)	Salada de Monasterio (2008–2009 ^a , 2009 ^b , 2010 ^c)
With submerged macrophytes	Yes	No	Yes	No	No	No	No
Analyzed groups	rotifers, cladocerans, copepods	cladocerans, copepods	rotifers, cladocerans, copepods	rotifers, cladocerans, copepods	rotifers, cladocerans, copepods	rotifers, cladocerans, copepods	rotifers, cladocerans, copepods
Mean abundance (ind. L ⁻¹)	1025	770	1076	1870			1341 ^b
Highest abundance group	rotifers	cladocerans	rotifers	rotifers	rotifers	rotifers	rotifers
Abundance peak	autumn	spring	summer	spring and summer	summer	summer	summer
Mean biomass (µg dw L ⁻¹)	406	3269	1123		2581	1425	566 ^a , 271 ^b , 258 ^c
Highest biomass group	cladocerans and copepods	cladocerans and cyclopoids	calanoids		cladocerans and cyclopoids	cladocerans and cyclopoids	cladocerans and cyclopoids ^{a,b} rotifers ^c
Biomass peak	spring and autumn	spring	winter		summer	summer	spring ^a , autumn–winter ^b , summer ^c
Presence of <i>Daphnia</i> spp.	No	No	Yes	No	Yes	Yes	No
Reference		Colautti et al. 2010	Claps et al. 2004	Fermani et al. 2013	Rennella and Quiros 2006	Rennella and Quiros 2006	^a Garcia de Souza et al. 2017 ^b Solimano et al. 2015 ^c Garcia de Souza et al. 2015

as had been similarly observed by Claps et al. (2011). The seasonal pattern of planktonic cladocerans involving a summer diminution had also been detected by Garcia de Souza et al. (2017). Furthermore, in our investigation, the abundance and biomass peaks occurred mainly in autumn, unlike the spring or summer maxima observed by many authors (*e. g.* Rennella and Quiros 2006; Fermani et al. 2013). The total zooplankton density and biomass were lower than the values estimated in the same lake during 2006 and for other lakes of the region (Table 3).

Conclusions

Our results emphasize that the presence of submerged macrophytes and the increase in the hydrometric level recorded in this seepage lake after heavy rainfalls had a direct positive effect on the zooplankton structure, abundance, and functional diversity. We need also to emphasize the role of abiotic conditions and influences such as temperature and turbidity, which parameters affect the composition and spatial distribution of the zooplankton assemblages. Furthermore, in the clear-water periods over the entire shallow lake, the risk of predation increased, but the majority of the crustacean populations evidenced a limited preference for specific lake sectors to try to evade such imminent predation. Unfortunately, the occurrence of those extreme clear-water periods has not been recorded again in this seepage lake, which water body in recent years has evidenced a progressive deterioration in its limnologic variables. We must emphasize highlight, however, that the composition of the zooplankton nevertheless remains quite comparable, thus reflecting the marked resilience of the members of this distinctive and typical community within the Pampean shallow lakes.

Acknowledgments The authors are grateful to Marcelo Martínez Leanes, who kindly allowed us access to the lake in his estancia (rural estate), and to Roberto Aranda for his help in the fieldwork. This work was funded by the National Council of Sciences and Technology (CONICET) (Grant PIP 2216) and by La Plata University (Grant N343). Dr. Donald F. Haggerty, a retired academic career



investigator and native English speaker, edited the final version of the manuscript. Scientific Contribution N° 1189 of the Institute of Limnology Dr. Raúl A. Ringuelet (ILPLA, CCT La Plata CONICET, UNLP).

Authors' contributions DMA, NAG and MCC performed the field work. DMA analyzed the zooplankton samples. All authors discussed the results and contributed to the final manuscript.

Competing interests The authors declare that they have no competing interests.

References

- Agasild H, Nøges T (2005) Cladoceran and rotifer grazing on bacteria and phytoplankton in two shallow eutrophic lakes: *in situ* measurement with fluorescent microspheres. *J Plankton Res* 27:1155–1174
- Ali MM, Mageed AA, Mahmoud H (2007) Importance of aquatic macrophyte for invertebrate diversity in large subtropical reservoir. *Limnologia* 37:155–169
- APHA (1995) Standard Methods for the Examination of Waters and Wastewaters, 19th edn. APHA/AWWA/WPCF, Washington DC
- Barnett AJ, Finlay K, Beisner BE (2007) Functional diversity of crustacean zooplankton communities: towards a trait-based classification. *Freshw Biol* 52:796–813
- Bielanska-Grajner I, Cudak A (2014) Effects of salinity on species diversity of rotifers in anthropogenic water bodies. *Pol J Environ Stud* 23:21–28
- Bolduc P, Bertolo A, Pinel-Alloul B (2016) Does submerged aquatic vegetation shape zooplankton community structure and functional diversity? A test with a shallow fluvial lake system. *Hydrobiologia* 778:151–165
- Cano MG, Casco MA, Solari LC, Mac Donagh ME, Gabellone NA, Claps MC (2008) Implications of rapid changes in chlorophyll-a of plankton, epipelon, and epiphyton in a Pampean shallow lake: an interpretation in terms of a conceptual model. *Hydrobiologia* 614:33–45
- Cano MG, Casco MA, Claps MC (2012) Effect of environmental variables on epiphyton in a pampean lake with sTable turbid- and clear-water states. *Aquat Biol* 15:47–59
- Cano MG, Casco M.A., Claps MC (2013) Vertical distribution of epiphyton biomass and diversity in a shallow lake during contrasting ecosystems regimes. *Aquat Bot* 110:38–47
- Casco MA, Mac Donagh ME, Cano MG, Solari LC, Claps MC, Gabellone NA (2009) Phytoplankton and epipelon responses to clear and turbid phases in a seepage lake (Buenos Aires, Argentina). *Int Rev Hydrobiol* 94:153–168
- Castro BB, Marques SM, Gonçalves F (2007) Habitat selection and diel distribution of the crustacean zooplankton from a shallow Mediterranean lake during the turbid and clear water phases. *Freshw Biol* 52:421–433
- Cazzanelli M, Warming TP, Christoffersen K (2008) Emergent and floating-leaved macrophytes as refuge for zooplankton in a eutrophic temperate lake without submerged vegetation. *Hydrobiologia* 605:113–122
- Cerbin S, Balayla DJ, Van de Bund WJ (2003) Small-scale distribution and diel vertical migration of zooplankton in a shallow lake (Lake Naardermeer, the Netherlands). *Hydrobiologia* 491:111–117
- Chang KH, Nagata T, Hanazato T (2004) Direct and indirect impacts of predation by fish on the zooplankton community: an experimental analysis using tanks. *Limnology* 5:121–124
- Choi J-Y, Jeong K-S, Joo G-J (2015) Rainfall as dominant driver of rotifer dynamics in shallow wetlands: Evidence from a long-term data record (Upo Wetlands, South Korea). *Int Rev Hydrobiol* 100: 21–33
- Claps M, Gabellone N, Benítez H (2004) Zooplankton biomass in an eutrophic shallow lake (Buenos Aires, Argentina): Spatio-temporal variations. *Ann Limnol-Int J Limnol* 40:201–210
- Claps MC, Gabellone NA, Benítez HH (2011) Seasonal changes in the vertical distribution of rotifers in a eutrophic shallow lake with contrasting states of clear and turbid water. *Zool Stud* 50:454–465
- Colautti DC, Garcia de Souza JR, Balboni L, Baigún CR (2010) Extensive cage culture of pejerrey (*Odontesthes bonariensis*) in a shallow pampean lake in Argentina. *Aquac Res* 41:376–384
- Dumont H, Van De Velde I, Dumont S. (1975) The dry weight estimate of biomass in a selection of Cladocera, Copepoda and Rotifera from the plankton, periphyton and benthos of continental waters. *Oecologia* 19:75–97
- Drenner R, McComas S (1980) The roles of zooplankton escape ability and fish size selectivity in the selective feeding and impact of planktivorous fish. In: Kerfoot WC (ed) *Evolution and Ecology of Zooplankton Communities*. University Press of New England, Hanover
- Ekvall MK, Hansson L-A (2012) Differences in recruitment and life-history strategy alter zooplankton spring dynamics under climate-change conditions. *PLoS ONE* 7:e44614
- Elisio M, Vera C, Miranda LA (2018) Influences of ENSO and PDO phenomena on the local climate variability can drive extreme temperature and depth conditions in a Pampean shallow lake affecting fish communities. *Environ Biol Fishes* 101:653–666
- Fermani P, Diovisalvi N, Torremorell A, Lagomarsino L, Zagarese HE, Unrein F (2013) The microbial food web structure of a hypertrophic warm-temperate shallow lake, as affected by contrasting zooplankton assemblages. *Hydrobiologia* 714:115–130
- Ferrando NS, Claps MC, Benítez HH, Gabellone NA (2018) Influence of temperature and conductivity on the life-history characteristics of a pampean strain of *Brachionus plicatilis*. *An Acad Bras Ciênc* 90:1431–1444
- Frau D, Battauz Y, Sinistro R (2017) Why predation is not a controlling factor of phytoplankton in a Neotropical shallow lake: a morpho-functional perspective. *Hydrobiologia* 788:115
- Gabellone NA, Solari LC, Claps MC, Mac Donagh ME, Ardohain DM, Benítez HH, Ruiz, G (2000) Estado trófico de la laguna San Miguel del Monte (Pdo de San Miguel del Monte, Buenos Aires). *Diversidad y Ambiente* 1:29–35.
- Garcia de Souza JR, Solimano PJ, Maiztegui T, Baigún CRM, Colautti DC (2015) Effects of stocking density and natural food availability on the extensive cage culture of pejerrey (*Odontesthes bonariensis*) in a shallow Pampean lake in Argentina. *Aquac Res* 46:1332–1344
- Garcia de Souza JR, Solimano PJ, Maiztegui T, Baigún CRM, Claps MC, Colautti DC (2017) Seasonality effects over the ecological aquaculture of the native zooplanktivorous fish from South America *Odontesthes bonariensis*. *Aquaculture* 471:19–27



- Gerhard M, Iglesias C, Clemente JM, Goyenola G, Meerhoff M, Pacheco JP, Teixeira-de Mello F, Mazzeo N (2017) What can resting egg banks tell about cladoceran diversity in a shallow subtropical lake? *Hydrobiologia* 798:75–86
- González Sagrario MD, Balseiro E, Ituarte R, Spivak E (2009) Macrophytes as refuge or risky area for zooplankton: a balance set by littoral predacious macroinvertebrates. *Freshw Biol* 54:1042–1053
- González Sagrario MD, Balseiro E (2010) The role of macroinvertebrates and fish in regulating the provision by macrophytes of refugia for zooplankton in a warm temperate shallow lake. *Freshw Biol* 55:2153–2166
- Gophen M (2015) The impact of turbidity on zooplankton densities in Lake Kinneret (Israel). *O J M H* 5:87–94. doi.org/10.4236/ojmh.2015.54008
- Green J (2003) Associations of planktonic and periphytic rotifers in a tropical swamp, the Okavango Delta, Southern Africa. *Hydrobiologia* 490:197–209
- Gutiérrez MF, Paggi JC (2014) Chemical repellency and adverse effects of free-floating macrophytes on the cladoceran *Ceriodaphnia dubia* under two temperature levels *Limnology* 15:37–45
- Havens KE, Fulton III RS, Beaver JR, Samples EE, Colee J (2016) Effects of climate variability on cladoceran zooplankton and cyanobacteria in a shallow subtropical lake. *J Plankton Res* 38:418–430
- Iglesias C, Goyenola G, Mazzeo N, Meerhoff M, Rodó E, Jeppesen E (2007) Horizontal dynamics of zooplankton in subtropical Lake Bianca (Uruguay) hosting multiple zooplankton predators and aquatic plant refuges. In: Gulati RD, Lammens E, De Pauw N, Van Donk E (eds) *Shallow lakes in a changing world*. Developments in Hydrobiology, vol 196. Springer, Dordrecht, pp 179–189
- Jeppesen E, Jensen JP, Søndergaard M (2002) Response of phytoplankton, zooplankton, and fish to re-oligotrophication: An 11 year study of 23 Danish lakes, *Aquat Ecosyst Health Manag* 5:31–43
- José de Paggi SB, Muñoz S, Frau D, Paggi JC, Scarabotti P, Devercelli M, Meerhoff M (2012) Horizontal distribution of rotifers in a subtropical shallow lake (Paraná floodplain, Argentina). *Fund Appl Limnol* 180:321–333
- Kosten S, Huszar VLM, Mazzeo N, Scheffer M, Sternberg LSL, Jeppesen E (2009) Lake and watershed characteristics rather than climate influence nutrient limitation in shallow lakes. *Ecol Appl* 19:1791–1804
- Kosten S, Jeppesen E, Huszar VL, Mazzeo N, Van Nes EH, Peeters ET, Scheffer M (2011) Ambiguous climate impacts on competition between submerged macrophytes and phytoplankton in shallow lakes. *Freshw Biol* 56:1540–1553
- Kosten S, Vermooij M, Van Nes EH, Sagrario MDLÁG, Clevers JGPW, Scheffer M (2012) Bimodal transparency as an indicator for alternative states in South American lakes. *Freshw Biol* 57:1191–1201
- Kuczyńska-Kippen N (2000) Seasonal changes of the rotifer community in the littoral of a polymictic lake. *Verh Internat Verein Limnol* 27:2964–2967
- Lévesque D, Pinel-Aloul B, Méthot G, Steedman R (2017) Effects of climate, limnological features and watershed clearcut logging on long-term variation in zooplankton communities of Boreal Shield lakes. *Water* 9:733
- Liljendahl-Nurminen A, Horppila J, Uusitalo L, Niemistö J (2008) Spatial variability in the abundance of pelagic invertebrate predators in relation to depth and turbidity. *Aquat Ecol* 42:25–33
- Mc Cauley E (1984) The estimation of the abundance and biomass of zooplankton in samples. In: Downing J, Rigler F (eds) *A manual on methods for the assessment of secondary productivity in fresh waters*. Blackwell Scientific Publications
- Meerhoff M, Iglesias C, De Mello FT, Clemente JM, Jensen E, Lauridsen TL, Jeppesen E (2007) Effects of habitat complexity on community structure and predator avoidance behaviour of littoral zooplankton in temperate versus subtropical shallow lakes. *Freshw Biol* 52:1009–1021
- Muylaert K, Declerck S, Van Wichelen J, De Meester L, Vyverman W (2006) An evaluation of the role of daphnids in controlling phytoplankton biomass in clear versus turbid shallow lakes. *Limnologica* 36:69–78
- Obertegger U, Smith HA, Flaim G, Wallace RL (2011) Using the guild ratio to characterize pelagic rotifer communities. *Hydrobiologia* 662:157–162
- Rennella A, Quirós R (2006) The effects of hydrology on plankton biomass in shallow lakes of the Pampa plain. *Hydrobiologia* 556:181–191
- Rennella AM, Geronazzo MD, Romero ME, Boveri M, Rosso JJ (2019) Hydrological variability, zooplankton availability and the shift between planktivore-benthivore feeding behaviour in the visual predator fish, *Odontesthes bonariensis*. *Environ Biol Fish* 102:713–725
- Ruttner-Kolisko A (1977) Suggestions for biomass calculations of plankton rotifers. *Arch Hydrobiol* 8:71–76
- Sakuma M, Hanazato T, Saji A, Nakazato R (2004) Migration from plant to plant: an important factor controlling densities of the epiphytic cladoceran *Alona* (Chydoridae, Anomopoda) on lake vegetation. *Limnology* 5:17–23
- Solimano PJ, Garcia de Souza JR, Maiztegui T, Baigún CRM, Colautti DC (2015) New approaches for growth improvement in pejerrey *Odontesthes bonariensis* (Valenciennes, 1835) culture (Atherinomorpha: Atherinopsidae). *Neotrop. Ichthyol.* 13:213–220
- Scheffer M (2004) *Ecology of Shallow Lakes*. Springer, Dordrecht
- Scheffer M, Jeppesen E (2007) Regime Shifts in Shallow Lakes. *Ecosystems* 10:1–3
- Semenchenko V (2008) Role of macrophytes in the variability of zooplankton community structure in the littoral zone of shallow lakes. *Contemp Probl Ecol* 1:257–262
- Šorf M, Devetter M (2011) Coupling of seasonal variations in the zooplankton community within the limnetic and littoral zones of a shallow pond. *Ann Limnol-Internat J Limnol* 47:259–268
- Sosnovsky A., Rosso J.J. & Quirós R (2010) Trophic interactions in shallow lakes of the Pampa plain (Argentina) and their effects on water transparency during two cold seasons of contrasting fish abundance. *Limnetica* 29:233–246
- Špoljar M, Dražina T, Lajtner J, Kovačević G, Pestić A, Matijašec D, Tomljanović T (2018) Impact of water level fluctuation in the shaping of zooplankton assemblage in a shallow lake. *Ribarstvo* 76:27–34
- Stefanidis K, Papastergiadou E (2010) Influence of hydrophyte abundance on the spatial distribution of zooplankton in selected lakes in Greece. *Hydrobiologia* 656:55–65
- ter Braak CJF (1986) Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67:1167–1179
- ter Braak CJF, Smilauer P (2002) *CANOCO Reference Manual and Canoco Draw for Windows User's Guide: Software for Canonical Community Ordination (Version 4.5)*. Microcomputer Power, Ithaca



- ter Braak CJF, Verdonschot PFM (1995) Canonical correspondence analysis and related multivariate methods in aquatic ecology. *Aquat Sci* 57:255–289
- van de Haterd R, Ter Heerdt G (2007) Potential for the development of submerged macrophytes in eutrophicated shallow peaty lakes after restoration measures. *Hydrobiologia* 584:277–290
- van Nes EH, Rip WJ, Scheffer M (2007) A theory for cyclic shifts between alternative states in shallow lakes. *Ecosystems* 10:17

Publisher's Note

IAU remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

