



## Horizontal distribution of rotifers in a subtropical shallow lake (Paraná floodplain, Argentina)

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With 6 figures and 2 tables

**Abstract:** In water bodies where cladocerans are typically small or present in low biomass, such as in the tropics and subtropics of South America, rotifers may play a larger role in ecosystem functioning than in temperate lakes. The aim of this study was to analyze the horizontal distribution of richness and abundance of rotifers, their diel distribution patterns, and the relative importance of physical and biotic characteristics as their shaping factors, in a subtropical shallow vegetated lake of the Paraná River floodplain (Argentina). Three sampling stations were located along the major axis of the lake, one in open waters and two in littoral area dominated by the emergent *Panicum elephantipes*, *Cyperus alternifolius* and floating mats of the filamentous algae *Cladophora* spp. Two further stations were located on the transverse axis. Rotifer samples were taken on four occasions (at noon and midnight) during a five week period in the summer to avoid possible changes in the pattern of distribution of macrophytes and hydrological variability of the lake. Rotifer richness was higher in the littoral zone whereas rotifer abundance was higher in the limnetic zone. Some rotifers, such as *Brachionus havanaensis* and *Keratella tropica* exhibited changes in their diel horizontal distribution with higher concentrations of organisms at vegetated zones during the day time. In contrast, *Polyarthra* sp. were more abundant at night-time in both limnetic and littoral areas. The heterogeneous horizontal distribution of rotifers cannot be explained by the rather homogeneous distribution of both physical environmental factors and phytoplankton abundance. Rotifer distribution may be related to a complex of factors including the presence or absence of vegetation, the relatively uniform distribution of visual predators (fishes) and the heterogeneous distribution of non-visual predators (insects and shrimps).

**Key words:** vertebrate and invertebrate predators, cladocerans, ostracods, emergent macrophytes, diel horizontal distribution.

### Introduction

Rotifers are the most numerous zooplankters in many aquatic systems (Ruttner-Kolisko 1974). They have high population growth rates and short development times, and may account for 50 % or more of zooplankton production (Wallace et al. 2006). Moreover, the functional diversity of rotifers is higher than that of

other zooplankton groups, with a broad range of feeding types (Arndt 1993). They typically consume microalgae and may have a significant impact on the size structure and species composition of phytoplankton. They can additionally feed upon detritus, large bacteria, heterotrophic nanoflagellates and small ciliates (Wallace et al. 2006). Despite this microcrustaceans such as cladocerans are often considered the main

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components of freshwater zooplankton in lakes. Cladocerans typically constitute a high proportion of zooplankton biomass, are more easily characterized functionally and play a crucial role in linking phytoplankton and fish communities via trophic interactions (Wetzel 2001). In water bodies where cladocerans are typically small or present in low biomass, such as in the tropics and subtropics of South America (e.g. Meerhoff et al. 2007, Kruk et al. 2009), the ecological role of rotifers may be more important than previously thought. For instance, the filtering rate of the rotifer *Keratella cochlearis* may be about 5–13 times higher than that of the small-bodied cladoceran *Bosmina longirostris* (Gilbert & Bogdan 1984).

The horizontal distribution of rotifers in shallow lakes could be controlled by a variety of abiotic and biotic factors, such as light, temperature, wind, transparency of water, dissolved oxygen, presence of macrophytes, food resources, intrazooplanktonic competition, invertebrate and fish predation, acting alone and in combination (Saunders-Davies 1989, Lair et al. 1996, Zurek & Bucka 2004, Kuczyńska-Kippen 2005, Kuczyńska-Kippen & Milecka 2009). However, the issue has not been sufficiently explored to allow for broad generalizations, because most studies have been conducted in temperate lakes located in the northern hemisphere (beforementioned references) and a few lakes in Africa, New Zealand (Wallace et al. 2006) and Argentina (Bastidas-Navarro & Modenutti 2007).

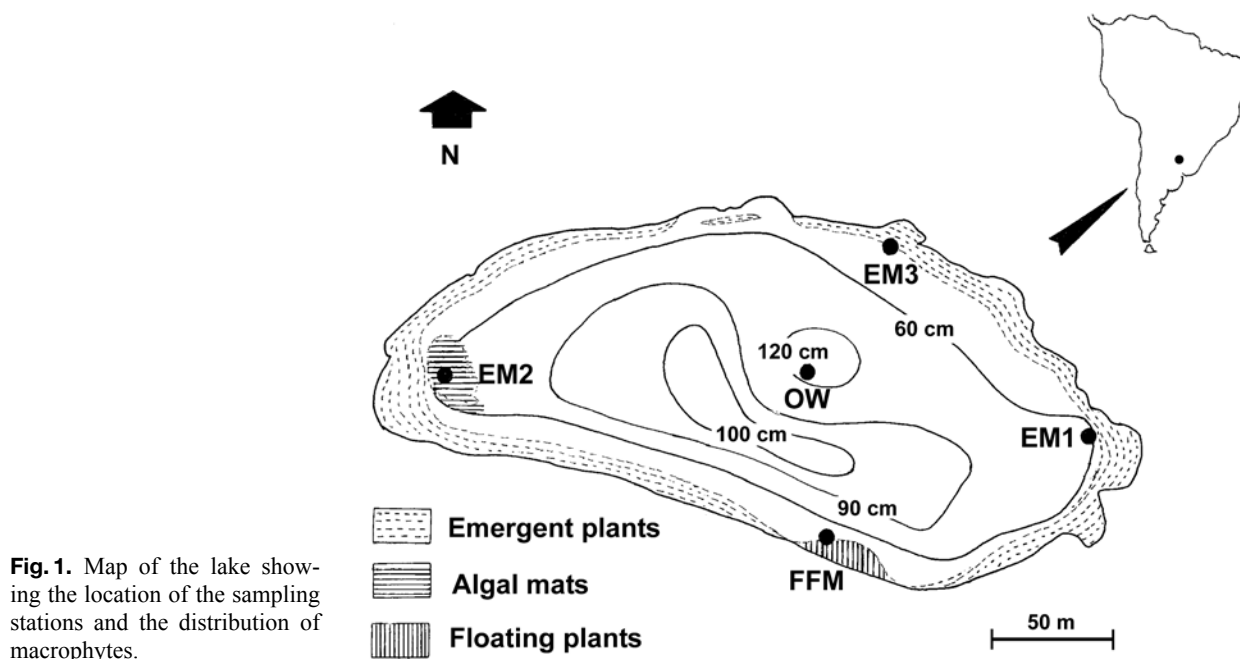
The diel horizontal distribution of rotifers has received comparatively less attention than that of cladocerans or copepods, probably due to the perception of weaker impact on trophic interactions, and their smaller body-size and slower travel speed. Most of the zooplankton studies on diel horizontal distribution did not include rotifers (e.g. Meerhoff et al. 2007, Cazanelli et al. 2008). Moreover, Iglesias et al. (2007), González-Sagrario & Balseiro (2010), who included rotifers in their studies, did not find evidence of rotifer horizontal migration in shallow subtropical lakes. These last-mentioned studies, however, do not match the observations of Kuczyńska-Kippen & Milecka (2009) who observed the movements of rotifers, between open waters and the vegetated littoral zone, in a European temperate shallow lake. In contrast, changes in diel vertical distribution attributed to vertical migration have been clearly demonstrated for several species of rotifers, such as *Asplanchna priodonta* (Dumont 1972), *Kellicottia longispina*, *Polyarthra* sp. (González 1998), *P. remata* (Gilbert & Hampton 2001), *Brachionus falcatus* and *B. caudatus* (Bezerra-Neto & Pinto-Coelho 2002).

Studies on horizontal distribution and diel migration of zooplankton, in general, have been made mainly in submerged whorled plants-dominated lakes (e.g. Jeppesen et al. 1998, Kuczyńska-Kippen 2001), whereas studies in lakes dominated by emergent (Nurminen & Horppila 2002) or floating plants (Meerhoff et al. 2007) are scarce. Most of the floodplain shallow lakes of the Middle Paraná River (Argentina) are usually dominated by free-floating or emergent macrophytes and more rarely by submerged forms (Sabattini & Lallana 2007). The diverse and complex habitats created by macrophytes host a rich fauna of small fishes and macroinvertebrates which prey upon rotifers and microcrustaceans (Oliveros 1980, Collins et al. 2007, Neiff et al. 2009, Sinistro 2010).

The aim of this study was to analyze the horizontal distribution of richness and abundance of rotifers, as well as potential changes in the diel distribution, and the relative importance of abiotic and biotic variables as their shaping factors, in a vegetated small shallow lake of the Paraná River floodplain. We considered the potential competitors present in the lake: cladocerans and copepods, which are efficient filterers; and ostracods, which, like cladocerans, feed upon bacteria, algae, and detritus (Strayer 1985, Wetzel 2001, Smith & Delorme 2010). Although ostracods are mainly considered to be benthic or littoral organisms, they are rather common inhabitants of the open waters of shallow lakes and wetlands in Argentina, particularly in vegetated water bodies. Indeed, in deep tropical lakes, several species of ostracods, can be also found inhabiting the open waters (Hutchinson 1967, Strayer 1985, Smith & Delorme 2010). We also considered macrocrustaceans, insects and small fishes as predators. Our hypotheses were that: 1) rotifers present a heterogeneous horizontal distribution despite the small size of the lake; 2) rotifers show changes in their diel horizontal distribution, in response to potential competitors and predators.

### Study area

The lake (unnamed) is located in the Ecological Reserve of the University City (Reserva Ecológica de la Ciudad Universitaria), Santa Fe, Argentina (31° 37' S, 60° 41' W) and is part of the Middle Paraná River floodplain (Fig. 1). It is a subtropical shallow lake of fluvial origin, with a surface area of 12 ha and a maximum depth of 1.70 m, fed by groundwater, rainfall and, during high water periods, indirectly by the Paraná River through the overflow waters of a neighbouring swampy area. The perimeter of the lake is lined



**Fig. 1.** Map of the lake showing the location of the sampling stations and the distribution of macrophytes.

with a belt of emergent vegetation. Chlorophyll-*a* ranged from 4.1 to 239  $\mu\text{g l}^{-1}$  and phosphate from 59 to 535  $\mu\text{g l}^{-1}$  (2009–2010, Devercelli & Mayora, unpublished data), indicating a eutrophic lake. The zooplankton is numerically dominated by rotifers, and the fish community is represented largely by small characid species (<70 mm). Piscivorous fish are absent (Scarabotti, unpublished data).

## Material and methods

### Sampling and sample analysis

Three sampling stations were located along the major axis of the lake, one in open waters, OW, and two in littoral vegetated stations: EM1, with dominance of the emergent *Panicum elephantipes* Nees and EM2, also with dominance of emergent plants, *P. elephantipes* and *Cyperus alternifolius* Linn., together with dense floating mats of the green filamentous algae *Cladophora* spp. Two complementary stations were established, FFM, with small mats of the free-floating plant *Eichhornia crassipes* (Mart.) Solms and EM3, with *P. elephantipes* (Fig. 1). The sampling was carried out during a short summer period on four dates (February 11, 17, 24 and March 17, 2009) to avoid potential changes due to the pattern of distribution of macrophytes and to hydrological variability of the lake. We took the samples at noon and at midnight.

Depth, temperature, conductivity, pH, oxygen and water transparency were measured *in situ* in all the stations using a handheld echo-sounder, HANNA equipment and a Secchi disk. The location of stations was recorded using a Garmin Hand-GPS. Direction and speed of wind were obtained from daily readings of the meteorological stations at Sauce Viejo, Santa

Fe, (<http://espanol.wunderground.com/history/station>), not far from the study site, and representative of the environmental conditions of the Paraná River floodplain.

Water samples were collected for nutrient analysis at the OW station on two sampling dates (February 17th and March 17th, 2009). In order to collect an integrated zooplankton sample through the water column of the lake, three to five samples were taken at different depths, with a horizontal Van-Dorn bottle made of a transparent acrylic tube (three liters volume), and then combined in a composite sample per station. The deepest sample of each vertical series was taken about 15–20 cm above the bottom, sometimes constrained by the crowded shaft of emergent plants, and a thick layer of loose, re-suspended organic sediment also present in the OW station. For a better assessment of richness qualitative samples were taken by hauling a 50 micrometer mesh plankton net at the three sampling stations. In the laboratory, nitrate (cadmium-copper reduction) and orthophosphate (ascorbic acid-molibdate method) were determined using kits of reagents HACH 5000 with a spectrophotometer HACH 5000, after filtration of samples with Whatman GF/F filters.

Zooplankton samples were concentrated by filtering water through a 50- $\mu\text{m}$  mesh size net and fixed with formaldehyde (4%). The phytoplankton samples were collected and stored in 100-ml vials, and preserved in Lugol acidified solution (1%). Rotifers and nauplii were identified and counted using a compound microscope Nikon in a 1-mL Kolkwitz cell. Cladocerans and copepods were counted in a 5-mL Bogorov chamber using a stereoscopic microscope Motic. At least 100 individuals of the dominant species were counted in the analysis of rotifers and microcrustaceans. To further assess species richness in each sample more chambers were examined and species recorded until no additional species were seen in 3–4 chambers.

Identifications were based on Koste (1978), Segers (1995), Alekseev (2002), Kořínek (2002), among others. Phytoplankton identifications were performed with a compound micro-

scope Nikon and an inverted Wild microscope was used for algal counts, following the Utermöhl's method. Although we counted the whole phytoplankton assemblage, here we only show data on the composition and abundance of algae <20 µm in size because most of filter-feeding or suspension-feeding rotifers consume cells between 3 to 17 µm (Wallace et al. 2006). Taxonomic identifications were performed following Komárek & Fott (1983) and Krammer & Lange-Bertalot (1991), among others.

Fish and macroinvertebrates were sampled on two dates (February 17th and March 17th, 2009), at noon and at midnight, at the three stations OW, EM1 and EM2 located along the major axis of the lake and selected for the rotifer migration analysis. Samples were obtained with a 10 × 1-m seine net, with 5-mm mesh in the bag and 1-cm mesh in the lateral wings. Seine hauls were performed from a paddle powered boat encircling an area of 10 m<sup>2</sup> with the net. Once the ends were close together, the net was quickly hauled to a point retrieving the lead line until it was lifted into the boat. Two seine hauls were performed per site, and per sampling date.

Fish and invertebrates were preserved in 70% ethanol and transported to the laboratory, where they were measured (total length to the nearest millimeter) and identified, following the available identification keys for the Paraná River basin (Ringuelet et al. 1967, Miquelarena et al. 2009). As we do not know the efficiency of the seine net used, we expressed the abundance as number of individuals collected per m<sup>2</sup> of hauled area.

### Data analysis

A one-way analysis of variance ANOVA, followed by *Dunn post hoc* tests, was applied to analyse differences in the environmental factors, densities of rotifers, phytoplankton, potential competitors and potential predators among the sampling stations in the lake. When basic assumptions of ANOVA were not satisfied (normality and homoscedasticity, by Kolmogorov-Smirnov and Levene's tests), the non parametric analogue Kruskal-Wallis test was applied. Diel changes in the abundance of rotifers, cladocerans and phytoplankton were analysed using a two-way ANOVA (factors: habitats and time) after transformation of data (ln (x+1)). The faunistic similarity among stations was compared using the Morisita index, only including species with an abundance greater than 10%. The statistical analyses were performed with PAST ver 2.14 (Hammer et al. 2001).

## Results

### Environmental conditions

During the first sampling the prevailing wind was from SW (46.3 km h<sup>-1</sup>) and during the second and third ones there was no wind but the previous nights winds were recorded from NW and S (22.0 and 18.5 km h<sup>-1</sup>), respectively. At the fourth sampling time, 3 hours before the start of sampling, a moderate wind (18.0 km h<sup>-1</sup>) blew from the S.

The main physical environmental parameters were rather homogeneous in distribution (Table 1). Conductivity was relatively high, about 1.000 µS cm<sup>-1</sup>. Water transparency was also high in all habitats, since Secchi disk depth in littoral sampling stations often coincided with the bottom. In the littoral zones, water temperature was slightly higher, while dissolved oxygen was slightly lower than in the OW. However, none of these differences were statistically significant.

### Potential food resources and competitors of rotifers

The most abundant genera of phytoplankton were *Monoraphidium*, *Plagioselmis* and *Trachelomonas*. The mean abundance and standard deviation (SD) of small-size algae (<20 µm) were 4034.7 ± 464.6, 3612.3 ± 16.7, 3568.9 ± 917.6, 4014.3 ± 162.4, 3277.6 ± 511.1 ind. ml<sup>-1</sup> in OW, FFM, EM1, EM2 and EM3, respectively. We did not observe significant differences in the horizontal distribution of these algae nor did we find any diel significant differences.

Cladocerans were comparatively less abundant than rotifers, the mean abundance and SD were 117.7 ± 134.7, 84.5 ± 48.3, 47.2 ± 16.1, 374.3 ± 113.2 and 110.9 ± 30.4 ind. l<sup>-1</sup> in OW, FFM, EM1, EM2 and EM3, respectively. Sampling stations differed significantly in cladocerans abundance (ANOVA,

**Table 1.** Mean and standard deviation (in brackets) of physical and chemical data of the lake at the different sampling stations. OW: open waters, FFM: free-floating plants, EM1 and EM3, emergent plants; EM2, emergent plants + green filamentous algae *Cladophora* spp.

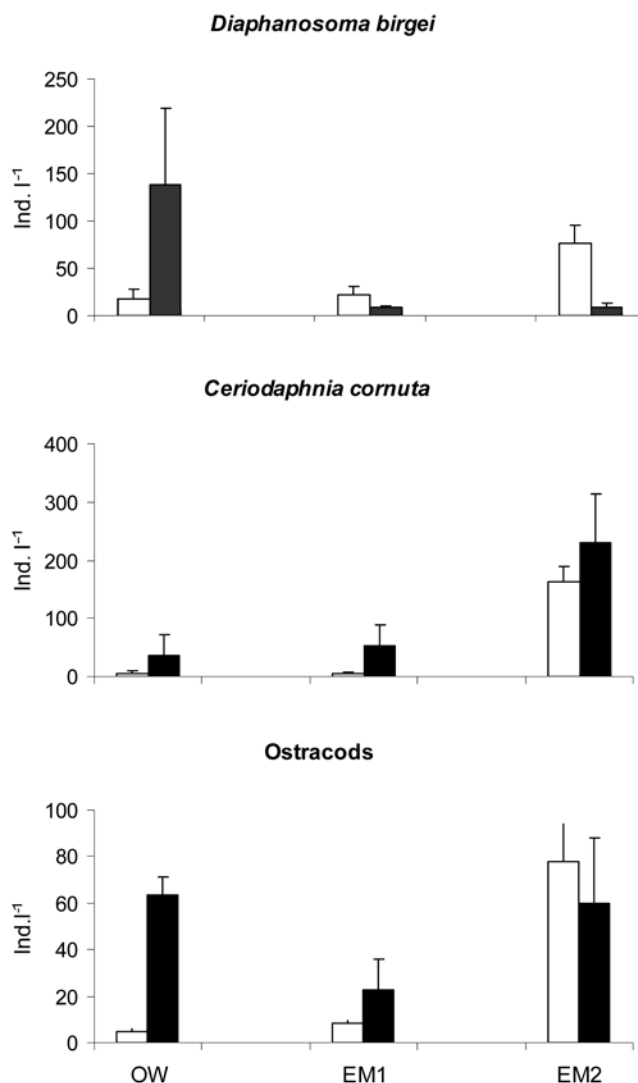
|                                      | OW             | FFM              | EM1              | EM2             | EM3              |
|--------------------------------------|----------------|------------------|------------------|-----------------|------------------|
| Depth (m)                            | 1.44 (0.21)    | 0.44 (0.08)      | 0.34 (0.12)      | 0.98 (0.06)     | 0.93 (0.12)      |
| Secchi Disk (m)                      | 1.34 (0.31)    | 0.44 (0.08)      | 0.34 (0.12)      | 0.98 (0.06)     | 0.93 (0.12)      |
| Temperature (°C)                     | 27.43 (2.09)   | 28.80 (2.45)     | 28.90 (2.22)     | 29.35 (0.07)    | 29.65 (2.24)     |
| pH                                   | 7.37 (0.51)    | 7.5 (0.53)       | 7.25 (0.46)      | 7.43 (0.49)     | 7.31 (0.45)      |
| Conductivity (µS cm <sup>-1</sup> )  | 116.50 (272.4) | 1272.25 (249.45) | 1164.00 (270.83) | 1040.00 (77.00) | 1160.75 (265.91) |
| Oxygen (% sat.)                      | 109.83 (24.61) | 90.83 (23.88)    | 91.97 (26.59)    | 82.23 (38.60)   | 118.15 (38.88)   |
| Orthophosphate (mg l <sup>-1</sup> ) | 0.10 (0.05)    |                  |                  |                 |                  |
| Nitrate (mg l <sup>-1</sup> )        | 0.23 (0.15)    |                  |                  |                 |                  |

$F=19, p=0.001$ ), in the post hoc tests,  $OW + FFM + EM1 > EM2$ . Among the cladocerans, *Diaphanosoma birgei* Kořinek and *Ceriodaphnia cornuta* Sars were the dominant species, whereas *Daphnia* and other large-bodied genera were absent. *D. birgei* showed significant differences in its temporal ( $p=0.05$ ), and spatial distribution ( $p=0.002$ ), while the interaction between both factors was also significant ( $p=0.0001$ ). This cladoceran was more abundant at day-time in the littoral zone and in open waters at night. The highest abundance of *C. cornuta* was recorded in the littoral zone, particularly in EM2. This species was more abundant at night-time, showing significant differences in time and space (ANOVA, time effect:  $p=0.01$  and habitat effect:  $p=0.003$ ), but we did not find significant interaction between both factors (Fig. 2).

Adult copepods were not abundant; the highest abundance of the calanoid *Notodiaptomus incom-*

*positus* (Brian) was recorded in open waters (mean  $\pm$  SD =  $13 \pm 14$  ind.  $l^{-1}$ ), whereas the cyclopoid omnivorous-herbivorous *Eucyclops neumani* (Pesta) appeared only in the littoral zone with its maximum abundance in EM2 (mean =  $9.8 \pm 15$  ind.  $l^{-1}$ ). The mean abundance of nauplii were  $230.2 \pm 154.1$ ,  $163.4 \pm 90.6$ ,  $137.4 \pm 107$ ,  $406.5 \pm 334.5$ ,  $131.7 \pm 70.7$  in OW, FFM, EM1, EM2 and EM3, respectively. They did not exhibit any significant differences regarding space or time.

Ostracods were abundant in the zooplankton of all sampling stations, with significant differences in both time and space (ANOVA, time effect:  $p=0.01$  and habitat effect:  $p=0.009$ , considering OW, EM1 and EM3). The interaction between both factors was also significant ( $p=0.02$ ). The maximum abundances occurred in open waters at night-time and in the littoral zone (EM2) at day-time (Fig. 2).

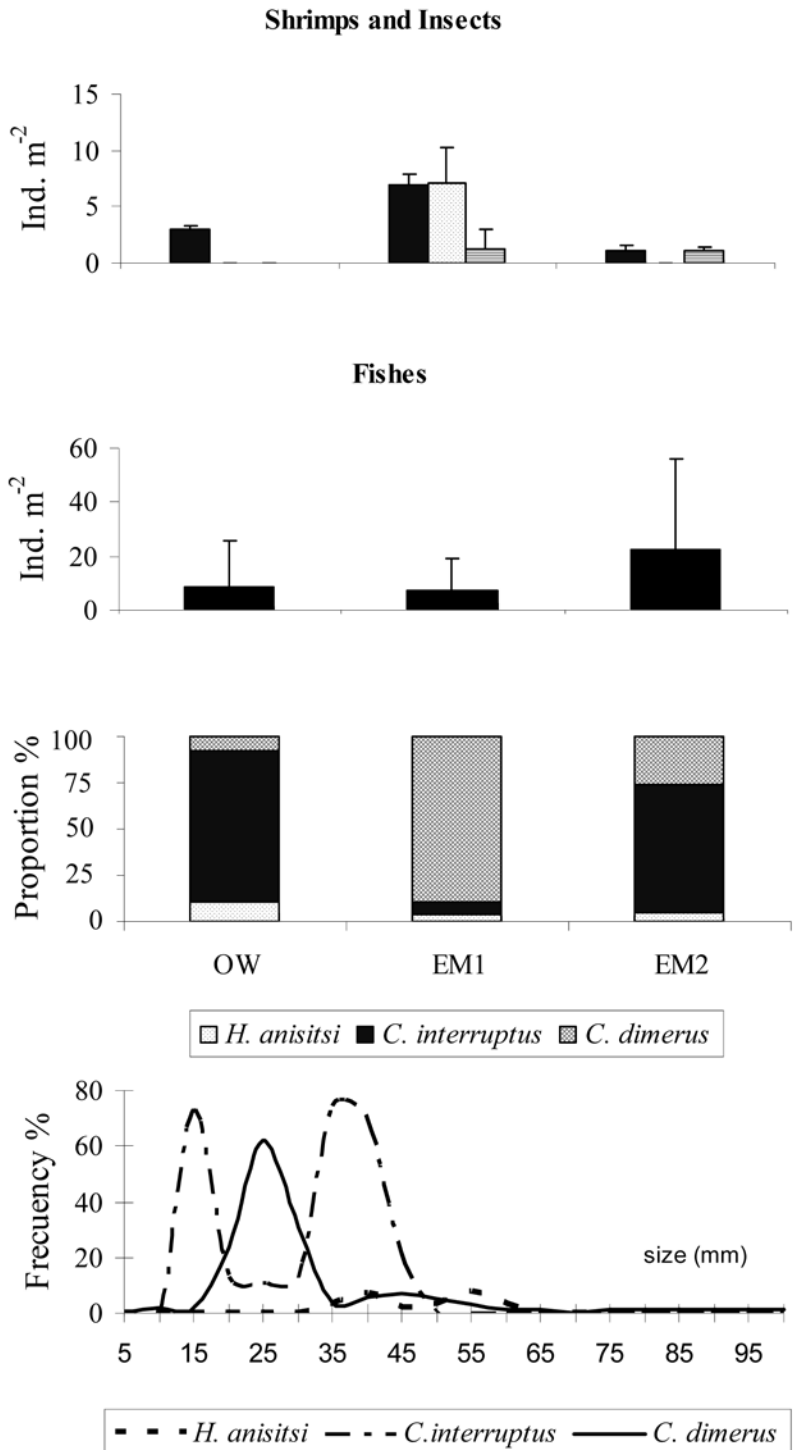


**Fig. 2.** Diel changes of the abundance of microcrustaceans at the open water (OW), emergent macrophytes (EM1) and emergent + algal mats (EM2). The data represent the mean of all sampling dates and SD. Day: empty bars, night: black bars.

**Potential predators of rotifers**

Among the potential zooplanktonic predators, the rotifer *Asplanchna brightwellii* appeared in low densities, and only in EM1. Insects, shrimps and fishes were recorded with various patterns of frequency and

abundances. In the littoral stations EM1 and EM2, nymphs of Odonata Anisoptera appeared as the dominant group. They were represented by the first instars of an unidentified species of Libellulidae (along with perhaps few specimens of Corduliidae), which are rather small.



**Fig. 3.** Mean abundance (all sampling, day and night) of (a) predatory macroinvertebrates and (b) fishes. Shrimps (black), Heteroptera (dotted), and Odonata (streaked). Vertical bars indicate SD values. Proportion, as percentage, in (c) main habitats and (d) size distribution of the three main species of fish caught in the lake as percentage of frequency.

**Table 2.** List of taxa recorded in a subtropical shallow lake.

|   | OW | FFM | EM1 | EM2 | EM3 |
|---|----|-----|-----|-----|-----|
| <i>Acomorpha ecaudis</i> (Perty)                                |    |     | X   |     |     |
| <i>Asplanchna brightwelli</i> Gosse                             |    |     | X   | X   |     |
| <i>Brachionus angularis</i> Gosse                               | X  |     | X   |     | X   |
| <i>Brachionus calyciflorus</i> Pallas                           |    |     |     |     | X   |
| <i>Brachionus caudatus</i> Barrois & Daday                      | X  |     |     |     | X   |
| <i>Brachionus falcatus</i> Zacharias                            | X  | X   | X   | X   | X   |
| <i>Brachionus havanaensis</i> Rousselet                         | X  | X   | X   | X   | X   |
| <i>Brachionus quadridentatus</i> (Hermann)                      |    |     | X   |     |     |
| <i>Cephalodella catellina</i> (O. F. Müller)                    |    | X   | X   |     |     |
| <i>Colurella adriatica</i> Ehrenberg                            |    | X   | X   |     |     |
| <i>Colurella colurus</i> (Ehrenberg)                            |    | X   |     |     |     |
| <i>Dicranophorus</i> sp.  |    |     |     | X   | X   |
| <i>Euchlanis incisa</i> Carlin                                  |    | X   | X   | X   | X   |
| <i>Euchlanis meneta</i> Myers                                   |    |     |     | X   |     |
| <i>Filinia longiseta</i> (Ehrenberg)                            | X  | X   |     |     |     |
| <i>Filinia</i> sp.  | X  | X   | X   | X   | X   |
| <i>Hexarthra intermedia</i> Wiszniewski                         | X  | X   | X   | X   | X   |
| <i>Hexarthra fennica</i> (Levander)                             |    |     | X   |     | X   |
| <i>Keratella tropica</i> (Apstein)                              | X  | X   | X   | X   | X   |
| <i>Lecane arcula</i> Harring                                    |    | X   |     | X   |     |
| <i>Lecane bulla</i> (Gosse)                                     |    | X   |     |     | X   |
| <i>Lecane closterocerca</i> (Schmarda)                          |    | X   |     | X   |     |
| <i>Lecane copeis</i> (Harring & Myers)                          |    |     |     |     | X   |
| <i>Lecane curvicornis</i> (Murray)                              |    |     |     |     | X   |
| <i>Lecane furcata</i> (Murray)                                  | X  | X   |     |     |     |
| <i>Lecane hamata</i> (Stokes)                                   |    | X   | X   | X   | X   |
| <i>Lecane leontina</i> (Turner)                                 | X  |     | X   | X   | X   |
| <i>Lecane luna</i> O. F. Müller                                 |    | X   | X   | X   | X   |
| <i>Lecane lunaris</i> (Ehrenberg)                               |    |     |     | X   | X   |
| <i>Lecane pyriformis</i> (Daday)                                |    |     |     | X   |     |
| <i>Lecane quadridentata</i> (Ehrenberg)                         | X  | X   |     | X   |     |
| <i>Lecane rhopalura</i> (Harring & Myers)                       |    |     |     | X   |     |
| <i>Lecane stenroosi</i> (Meissner)                              |    |     |     | X   |     |
| <i>Lecane</i> sp.   | X  | X   |     | X   |     |
| <i>Lepadella patella</i> (O. F. Müller)                         |    |     |     | X   | X   |
| <i>Lepadella patella oblonga</i> (Ehrenberg)                    |    | X   | X   |     |     |
| <i>Lepadella latusinus</i> (Hilgendorf)                         |    |     |     | X   |     |
| <i>Lepadella rhomboides</i> (Gosse)                             |    | X   | X   | X   |     |
| <i>Lophocharis salpina</i> (Ehrenberg)                          |    |     | X   |     |     |
| <i>Mitylina mucronata</i> (O. F. Müller)                        |    | X   |     |     |     |
| <i>Mitylina ventralis</i> (Ehrenberg)                           |    | X   | X   | X   | X   |
| <i>Monommata longiseta</i> (O. F. Müller)                       | X  |     |     |     | X   |
| <i>Monommata</i> sp.  |    |     | X   | X   |     |
| <i>Plationus patulus</i> (O. F. Müller)                         | X  | X   |     |     |     |
| <i>Platylas quadricornis</i> (Ehrenberg)                        |    | X   | X   | X   | X   |
| <i>Polyarthra vulgaris</i> Carlin.                              |    | X   |     |     |     |
| <i>Polyarthra</i> sp.   | X  | X   | X   | X   | X   |
| <i>Pompholix complanata</i> Gosse                               | X  | X   | X   |     | X   |
| <i>Testudinella patina</i> (Hermann)                            | X  | X   | X   | X   | X   |
| <i>Trichocerca braziliensis</i> (Murray)                        |    |     |     |     | X   |
| <i>Trichocerca elongata</i> (Gosse)                             |    | X   |     |     | X   |
| <i>Trichocerca insignis</i> (Herrick)                           |    |     | X   | X   | X   |
| <i>Trichocerca pusilla</i> (Lauterborn)                         |    |     |     |     | X   |
| <i>Trichocerca rattus</i> (O. F. Müller)                        |    |     |     | X   |     |
| <i>Trichocerca similis</i> (Wierzejski)                         |    |     |     |     | X   |
| <i>Trichocerca similis</i> (Wierzejski) f. <i>grandis</i> Hauer |    |     | X   | X   |     |
| <i>Trichocerca</i> sp.  | X  | X   | X   | X   | X   |
| <i>Trichotria tetractis</i> (Ehrenberg)                         |    |     |     | X   | X   |
| <i>Tripleuchlanis plicata</i> Levander                          |    |     |     | X   |     |

In EM1 we recorded nymphs and adults of the genus *Sigara* (Heteroptera, Corixidae). In both the littoral and limnetic zones, the omnivorous shrimps *Macrobrachium borellii* (Nobili) and *Palaemonetes argentinus* (Nobili) were recorded, the former were dominant in the littoral and the latter were dominant in open waters. The highest abundance and diversity of insects and shrimps occurred in EM1 (Fig. 3).

Five species of fishes were recorded in the lake. Averaging across sites the general mean abundance of fishes was 9.2 ind. m<sup>-2</sup>. *Cheirodon interruptus* (Jenyns) was the most abundant species, followed by *Cichlasoma dimerus* (Heckel) and *Hyphessobrycon anisitsi* (Eigenmann). The mean abundances of these species were 27.4, 15.4, and 2.6 ind. m<sup>-2</sup>, respectively. *Synbranchus marmoratus* Bloch and *Cnesterodon decemmaculatus* (Jenyns) were also present but in very low abundance.

The spatial distribution of fish abundance was relatively uniform, with no significant differences among sampling stations, though the highest mean abundance was recorded in the littoral EM2 and the lowest mean abundance in OW (Fig. 3). Diel differences in total abundance were not significant. *Cichlasoma* was abundant only in the littoral zone and *Cheirodon interruptus* and *H. anisitsi* in OW (Fig. 3). The size (standard length) distribution of fishes was dominated by small individuals, since fish < 40 mm total length represented 87% of the total abundance. *C. interruptus* was the smallest species (range: 10–40 mm), followed by *H. anisitsi* (range: 33–59 mm) while *C. dimerus* was the largest species, but displaying a wide range of size variation (range: 10–99 mm).

#### Horizontal distribution of rotifers: diversity and abundance

A total of 59 species of rotifers were recorded belonging to 11 families, of which Brachionidae and Lecanidae were the richest (Table 2). Cumulative richness

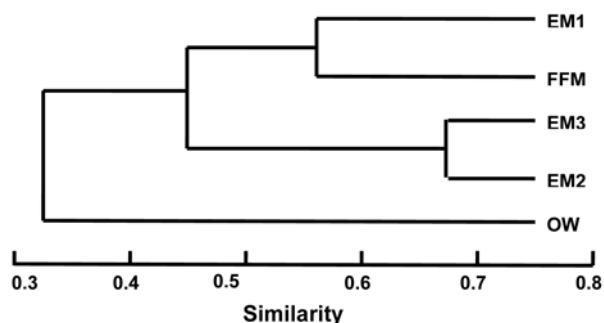


Fig. 4. Faunistic similarity dendrogram of sampling stations.

per station (total number of species recorded during the present study) varied among stations. The highest species richness occurred in littoral zones, with 35 species in EM3. The open water station OW showed the lowest richness, with 17 species. The faunistic similarity among littoral stations was high (Fig. 4). The limnetic and littoral zones had different rotifer assemblages regarding the relative abundances of their dominant taxa. *Keratella tropica* (Apstein), *Brachionus falcatus* Zacharias and *B. havanaensis* Rousset were more abundant in OW (ANOVA, habitat effect:  $p=0.006$ ,  $p=0.03$  and  $p=0.0006$ , respectively). On the other hand, the genus *Lecane* showed a more heterogeneous distribution among stations ( $p=0.0005$ ), being more abundant in FFM and EM2 than in OW ( $p=0.01$  and  $0.05$ , respectively), and more abundant in FFM than in EM1 ( $p=0.05$ ).

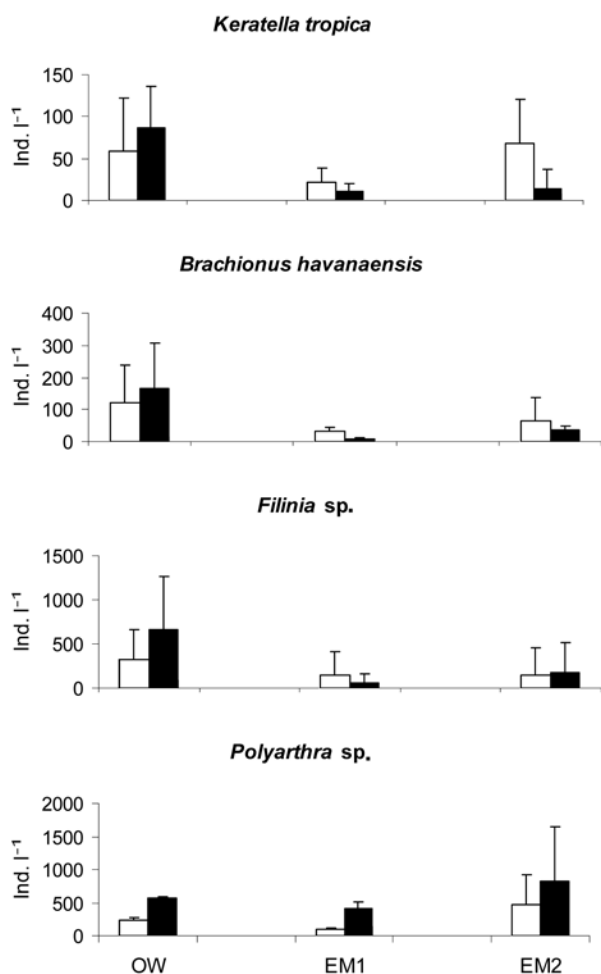
Mean abundance and SD (average of the day and night densities, for four weeks) was  $1556.5 \pm 712.5$ ,  $488.1 \pm 3.2$ ,  $500.1 \pm 144.8$ ,  $1045.4 \pm 55.3$  and  $1097.2 \pm 35.2$  ind. l<sup>-1</sup> in OW, FFM, EM1, EM2 and EM3 respectively. The rotifer abundance was significantly different between sampling stations (KW test = 12.98,  $p=0.011$ ). Dunn *post hoc* tests showed significant differences among several sampling stations: OW > FFM + EM1, EM1 < EM2 + EM3. The highest temporal variability in the abundance of rotifers occurred in open waters.

#### Diel horizontal distribution patterns of rotifers

We focused this analysis on the more abundant rotifer species, i.e. *Keratella tropica*, *Brachionus havanaensis*, *Filinia* sp., and *Polyarthra* sp. (Fig. 5). *K. tropica* was more abundant at day-time in the littoral zones (mainly EM2) and in open waters at night-time, with a significant interaction between habitats and time (ANOVA,  $p=0.03$ ). *B. havanaensis*, exhibited also a similar pattern, with higher abundances at day-time in the littoral zones and a significant interaction between habitats and time (ANOVA,  $p=0.05$ ). Although higher densities of *Filinia* occurred in OW at night-time, during the day it was more abundant only in EM1 (EM2 showed similar densities to open waters). Differences were significant regarding time ( $p=0.01$ ) and space ( $p=0.03$ ), but no significant interaction time-habitat was detected.

Higher abundances of *Polyarthra* sp. were found at night-time in all sampling stations, both limnetic and littoral, though maximum densities occurred in EM2. Densities changed significantly with time (ANOVA,  $p=0.05$ ), but no time-habitat interaction was detected.





**Fig. 5.** Diel changes of the abundance of the main rotifer species, at the open water (OW), littoral with emergent macrophytes (EM1) and littoral with emergent macrophytes + algal mats (EM2). The data represent the mean of all sampling dates and SE. Day: empty bars, night: black bars.

## Discussion

### Spatial structure of the rotifer assemblage

The distribution of rotifer richness and abundance was heterogeneous, with a richer rotifer fauna in the littoral zone. The littoral assemblage was dominated by species with well developed foot and fingers, belonging to the genera *Lecane*, *Euchlanis*, *Lepadella*, *Mytilina*, *Trichocerca*, which are closely associated with vegetative substrates (Pejler 1995). On the other hand, species belonging to the genera *Filinia*, *Keratella* and *Pompholix* were mainly inhabitants of the limnetic zone. The species of *Brachionus*, having a ringed foot and quite short fingers, showed a wider and more diverse distribution, *B. falcatus* and *B. havanaensis* were more abundant in open waters, while *B. angularis*,

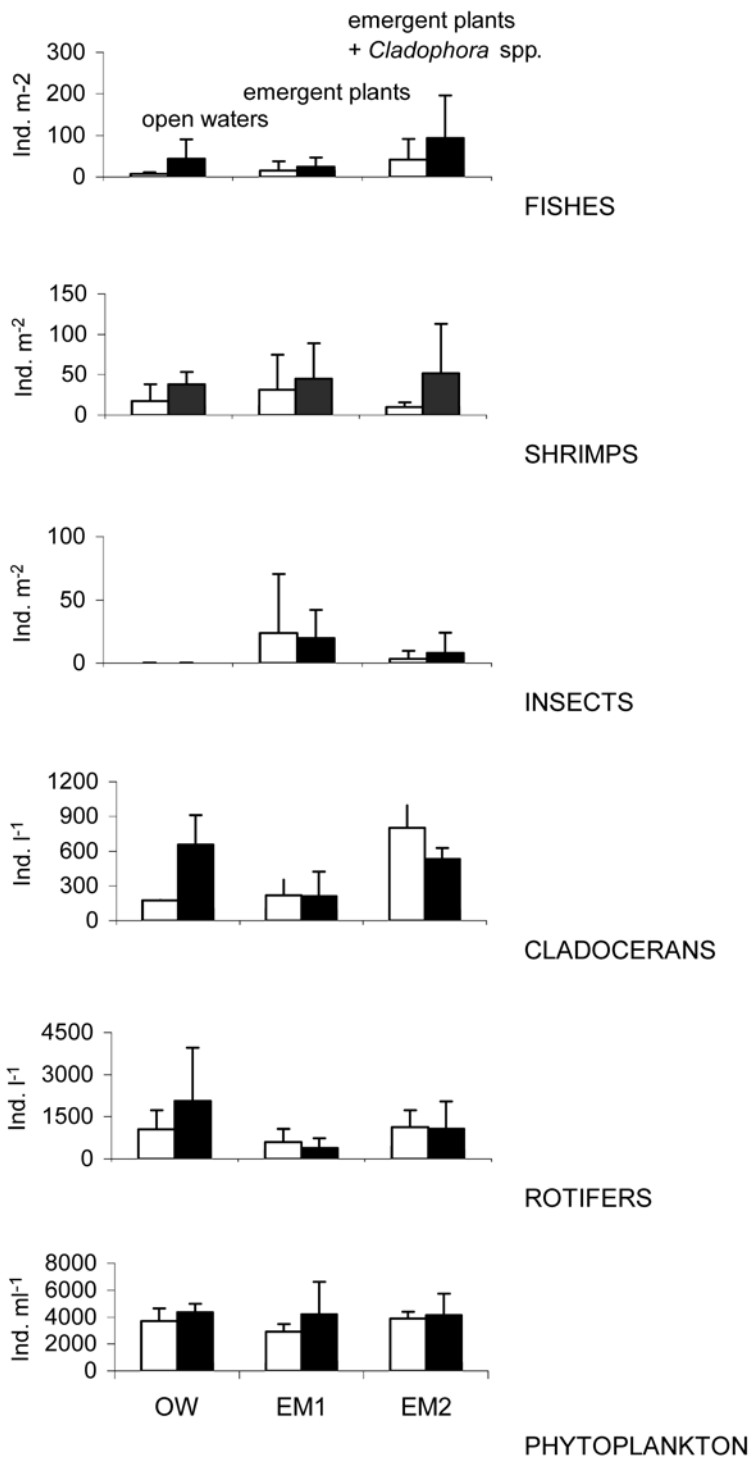
*B. caudatus* were common in both littoral and limnetic zones.

It is generally accepted that the highest richness of rotifers occurs in stands of submerged macrophytes, where the plant's architecture leads to the existence of many ecological niches (Pejler 1995, Duggan 2001, Kuczyńska-Kippen 2001). In our lake, the dominant plants were emergent and supported the highest diversity of rotifers within the lake. A similar situation was observed in another shallow subtropical lake belonging to the Paraná River floodplain, where *Typha* sp. and *Paspalum repens* Bergius were the dominant macrophytes (José de Paggi 1993), and in a temperate Polish lake where the richest species composition was found within emergent stands of *Typha* (Kuczyńska-Kippen 2005), despite it having a relatively simple architecture.

In contrast, rotifer abundance showed the opposite pattern, being higher in the limnetic zone. Abiotic factors were not related to horizontal gradients in zooplankton density as has been observed in other shallow lakes (summarized by Burks et al. 2002). The heterogeneous distribution of rotifers could thus be related to biological factors, such as predation risk and competition.

The highest mean density of rotifers was recorded in the limnetic zone (OW), where the filter-feeder cladocerans were comparatively less abundant. The lower abundance of rotifers in the littoral zone (FFM, EM1, EM2, EM3) may, in contrast, be related to various factors. Although the littoral zone provides a high diversity of ecological niches (expressed as a higher taxonomic richness), these habitats often host vertebrate and macroinvertebrate predators that may control the abundance of zooplankton populations (González-Sagrario et al. 2009, González-Sagrario & Balseiro 2010).

The fish assemblage in our lake was dominated by small omnivorous-planktivorous fishes, such as the characid *Cheirodon interruptus*, and *Hyphessobrycon anisitsi*, and the cichlid *Cichlasoma dimerus* whose diets include insects, ostracods, cladocerans, copepods, and also rotifers in smaller amounts (Oliveros 1980, Escalante 1983, Lopez Cazorla et al. 2003, Soneira et al. 2006). In EM1, where the abundance of fishes was comparatively lower, but the densities of invertebrate predators such as Odonata and Heteroptera was higher, the abundance of both rotifers and cladocerans was low (Fig. 6), suggesting a negative effect of insects as found by previous authors (Hampton et al. 2000, Burks et al. 2001, Gilbert & Hampton 2001), preliminary observations of Odonata stomach contents show that they actively feed on rotifers.



**Fig. 6.** Mean day and night (all sampling dates) abundance of rotifers and their main food resources (phytoplankton,  $<20\ \mu\text{m}$ ), competitors (cladocerans) and predators (fishes, shrimps and insects)

In EM2, although fishes were more abundant, rotifers and cladocerans were also more abundant than in the other littoral sampling stations (i.e. FFM and EM1). The dense mats of *Cladophora* here might have provided habitat and food for rotifers, as well as refuge against predators (Dodds & Gudder 1992), thus helping to reduce competition and predation pressure.

Subtropical vegetated shallow lakes are characterised by all year round dense fish assemblages of small-sized and visual-feeder species (Lazzaro 1997, Neiff et al. 2009, Texeira de Mello et al. 2009). The horizontal distribution of the richness and abundance of the rotifers in the study lake seems to depend upon a delicate balanced trade-off, where macrophytes, com-

petition and predation set a variable trend and where the boundaries of the respective influences may not be easily distinguishable (Lair et al. 1996, Iglesias et al. 2008).

### Diel horizontal distribution patterns

We found that populations of some rotifers, such as *Brachionus havanaensis* and *Keratella tropica* exhibited changes in the diel horizontal distribution with higher concentrations of organisms at vegetated zones during day time. The highest diel differences occurred in the sampling station EM2, dominated by the filamentous algae *Cladophora*. Higher concentration of cladocerans in vegetated zones during day time has been interpreted as a consequence of an horizontal migration which allow them to use these areas as refuges (Burks et al. 2002). Regarding rotifers there is no evidence that they can move, swimming, at a horizontal distance as far as several meters. However, it is known that water currents and winds can cause aggregation of individuals or assist their active movements over short distances (Saunders-Davies 1989). Winds recorded during sampling had variable directions and their effect was also modified by the presence of a peripheral forest. The frequent wind mixing of the water column of the lake induced a polymictic environment with transient water currents suggesting that the movements of the water were able to alter the distribution patterns of organisms such as rotifers whose displacement is mainly passive. Several studies confirm the 'shore avoidance' hypothesis, i.e. that zooplankters, including rotifers (*Keratella* and *Polyarthra*), move horizontally away from the shore during day to avoid planktivorous, mainly large-bodied zooplankton (Saunders-Davies 1989, Gliwicz & Rykowska 1992). In our case, however, the distribution patterns of *B. havanaensis* and *K. tropica* are similar to those of some cladocerans (Burks et al. 2002) including *Diaphanosoma* which is present in the study lake. Moreover, the avoidance response to predators infochemicals also occurs in rotifers although their mobility is quite restricted compared to that of cladocerans. This requires further exploration perhaps through the use of traps or through a fine scale transect across open and littoral waters.

On the contrary, *Polyarthra* does not show the same pattern; at night time there were higher densities at all sampling sites (statistically, significant effect of 'time', two-way ANOVA). It may be interpreted as a consequence of a diel vertical migration of a species living close to or just above the sediments which are less efficiently captured by zooplankton sampling

devices (De Stasio 1993, Meerhoff et al 2007, Jensen et al 2010). Vertical and horizontal diel movements of *Polyarthra* spp have been observed by other authors (Saunders-Davies 1989, González 1998, Gilbert & Hampton 2001). However, the causal factors that determine different responses by different species within the same genus have not been clearly discerned yet. It is likely that these behavioural differences, often occurring even at the clone level (De Meester 1993), likely promote a greater survival at the population level in a changing environment.

The more abundant potential competitors, *Diaphanosoma*, *Ceriodaphnia* and ostracods showed different patterns of diel distribution. Other potential competitors *Notodiaptomus incompositus* and *Eucyclops neumani* were present in very low density. Though cyclopids copepods have generally been considered as exclusive carnivores, it has been shown that the members of the subfamily Eucyclopinæ, particularly *Eucyclops*, are predominantly herbivorous and competitors of cladocerans (Fryer 1957, Hutchinson 1967, Parker 1961). The larger, and thus more sensitive to predation, *Diaphanosoma*, and ostracods had lower density in open waters during the daytime, both show evidence of horizontal migration. On the other hand, *Ceriodaphnia* reached the highest abundance in the littoral zones, and increased its abundance in all habitats at night. This pattern is consistent with a vertical displacement as suggested for *Polyarthra*.

The relatively high importance of fish predators on the long-term ecological and evolutionary trends of the zooplankton community structure is evident through the small mean size of zooplankters and due to the fact that rotifers and their potential competitors (i.e. filter feeder cladocerans or ostracods) showed different but interrelated patterns of spatial distribution. Given the active dynamics and functional complexity of these alluvial plain environments, future studies should address how these horizontal distribution patterns, and likely enhanced survival, could change during the different environmental conditions controlled by the hydrological cycle. Our study highlights the need to consider the diel behaviour of all zooplankton groups, not only cladocerans, to understand the trophic ecology and ecological functioning of the shallow and vegetated lakes in tropical and subtropical regions.

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