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Seasonal Changes in the Vertical Distribution of Rotifers in a Eutrophic Shallow Lake with Contrasting States of Clear and Turbid Water

Maria C. Claps*, Nestor A. Gabellone, and Hernán H. Benítez

Institute of Limnology "Dr. R. Ringuelet" (CCT La Plata CONICET - UNLP), Av. Calchaquí Km 23.5 Florencio Varela 1888, Argentina

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Maria C. Claps, Nestor A. Gabellone, and Hernán H. Benítez (2011) Seasonal changes in the vertical distribution of rotifers in a eutrophic shallow lake with contrasting states of clear and turbid water. *Zoological Studies* **50**(4): 454-465. Monthly zooplankton samples were taken from a shallow Argentinean lake in 1997-1998, and spatiotemporal changes in rotifers in the water column were examined. The most abundant and frequent species were *Brachionus calyciflorus*, *B. caudatus*, *B. havanaensis*, *Keratella tropica*, *Filinia longiseta*, and *Polyarthra vulgaris*. These perennial species are considered to be common in eutrophic waters, are eurytopic, and are widely distributed. The phytoplankton composition, competition for food with other grazers, and predation pressure, plus the occurrence of different periods including a turbid phase, a phase with coverage of submerged macrophytes (*Potamogeton pectinatus*), and a flooding phase, defined the annual planktonic rotifer succession in the lake. Small-scale vertical distributions of rotifers in this homothermal lake were related to both biotic and abiotic forces. The presence of macrophytes favored an increase in planktonic-rotifer densities along with a specific richness associated with the possibility of refuge, the incorporation of littoral species, and food diversification. http://zoolstud.sinica.edu.tw/Journals/50.4/454.pdf

Key words: Rotifers, Vertical profile, Eutrophic shallow lake, Argentina, Clear and turbid water.

Identification of causal factors that explain spatial distributions of zooplankton in shallow lakes has acquired great importance in the last few decades (Burks et al. 2002). The majority of such studies focused on the horizontal (Balayla and Moss 2003, Romare et al. 2003) rather than the vertical (Cerbin et al. 2003, Cassiano Keppeler and Rodrígues Hardy 2004) distribution of zooplankton organisms.

Within the Neotropical region, the vertical distribution of planktonic rotifers was only analyzed in floodplain lakes of the Paraná River (José de Paggi 1995, Bini et al. 2001). In homothermal floodplain lakes of the middle Paraná River, rotifer distributions are related to biotic processes, whereas in stratified floodplain lakes of the upper Paraná, distributions are related to abiotic factors.

Malone and McQueen (1983) defined 4 basic types of zooplankton patches in lakes and identified 16 forces that affect these distributions. Later, in a review, Folt and Burns (1999) discussed the importance of the spatial heterogeneity of zooplankton in lakes and mentioned the most consequential factors that produce zooplankton patchiness (vertical migration, predator avoidance, the search for food, and mating). Cryer and Townsend (1989) and Wickham et al. (1993) demonstrated the effects of food availability, predation, and cladoceran-interference competition on the annual distribution of planktonic rotifers in lakes.

Two alternative equilibrium states (i.e., turbid and clear phases) which occur in some shallow lakes are associated with quite different physical and chemical conditions that in turn, are related to the presence or absence of submerged

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*To whom correspondence and reprint requests should be addressed. Fax: 54-11-42757799. E-mail:claps@ilpla.edu.ar macrophytes (Phillips et al. 1978, Scheffer et al. 1993). During these phases, plankton undergo remarkable changes in their structure and dynamics (Lauridsen et al. 1998, Jeppesen et al. 1999). During the clear phase in European lakes, planktonic rotifers are outcompeted by cladocerans, in spite of the simultaneous presence of zooplanktivorous juvenile fish, because of the presence of dense macrophyte beds, which the zooplankton use as refuges (Conde-Porcuna et al. 1994, Lauridsen and Buenk 1996, Moss et al. 1998). In summer, rotifers may be responsible for the collapse of phytoplankton populations in shallow lakes without submerged macrophytes, and could promote the appearance of brief clear-water periods (Jeppesen et al. 1990). In some shallow lakes, the grazing pressure by microzooplankton affects the size distribution of phytoplankton, favoring the dominance of larger algae over smaller ones (Hansson et al. 1998). None of those studies, however, explained whether or not the alternative phases influenced the vertical distribution of zooplankton organisms.

Shallow lakes of the Salado River basin are characterized by fluctuations in water level, conductivity, and nutrient concentrations; these parameters vary according to the degree of connectedness of the lakes with the river and with the hydrologic cycle (Gabellone et al. 2001, Solari et al. 2002). San Miguel del Monte Lake is one of a system of connected lakes within the middle basin of the Salado River. Microzooplankton (e.g., rotifers and the nauplii of cyclopoid and calanoid copepods) numerically predominate in this lake, with abundance peaks occurring in Nov. and Mar. Euplanktonic cladocerans; however, show their highest biomass in Dec., while calanoids peak in abundance during the winter (Claps et al. 2004). The phytoplankton is dominated by filamentous cyanophytes during the turbid period, but by colonial cyanophytes and coccal chlorophytes during the clear-water summer period (Solari et al. 2003).

In this investigation, we examined the significance of small-scale spatial and temporal changes in rotifer diversity and abundance within the vertical profile of a representative shallow lake during periods with and without submerged macrophytes in addition to hydrologic events. We took into account concepts such as spatial scales, heterogeneity, aggregation, and the sampling strategy of the zooplankton community. This study constitutes the 1st attempt to improve the ability to predict the function and changes of the zooplankton community with the aim of possible future biomanipulation projects in this polymictic lake.

Study area

The investigation was carried out in the shallow San Miguel del Monte Lake. The study began during a turbid-water period, which was later superceded by a clear-water period. This changeover resulted from the overriding colonization of the basin by the submerged macrophyte, *Potamogeton pectinatus* L. This phenomenon was related to a drastic decrease in the water level of the lake that occurred during the summer of 1997, 6 months before our sampling began. During the following May; however, water exchanges occurred with a connected lake (Las Perdices) and the Salado River related to a flooding pulse in that river. San Miguel del Monte Lake, located in the Pampas depression in northeastern Buenos Aires Province, Argentina (35°27'S,58°48'W), is a small, shallow, eutrophic water body with an area of approximately 655 ha. The maximum depth during the sampling period was 2.4 m. One stream (El Totoral) flows into the lake from an extensive agricultural and cattle-breeding area. A town of 10,000 inhabitants is located on 1 shore. Floodgates bypass the natural connection with Las Perdices Lake and control the hydrometric level (Fig. 1). When the Salado River floods, this system of interconnected lakes acts as a backwater; such floods moreover decrease the salinity of the lakes and incorporate nutrients from the river into these lentic bodies of water.

MATERIALS AND METHODS

Field sampling

Duplicate samples were taken at 3- or 4-wk intervals during the period of Sept. 1997 to Aug. 1998 (except in May because of flooding) at a single sampling station located in the deepest part of the lake. Zooplankton samples (100 L) were obtained by means of a suction pump at intervals of 0.30 m, from the bottom to the surface during midmorning. Samples were concentrated (to 250 mL) during pumping by filtration through a plankton net with a 35-µm mesh and preserved in 5% (v/v) aqueous formaldehyde. At each depth of the vertical profile, physical and chemical parameters (temperature, pH, conductivity, and dissolved oxygen (DO)) were measured with a Horiba multimeter (Horiba Ltd., Japan), while transparency was estimated with a Secchi disc. In addition, samples of water were obtained to determine suspended solids (SS), total phosphorus (TP), and chlorophyll *a* (Chl-*a*) in the laboratory.

Laboratory analysis

The TP concentration was determined with ascorbic acid after digestion with acidic persulfate (method 4500-P B, APHA, 1995); Chl-*a* was determined by spectrophotometry at 665 nm on Whatman GF/C filters (Whatman Ltd. USA) (method 10200 H, APHA 1995); particulate organic matter was determined by the weight loss upon ignition at 550°C (method 2540 E, APHA 1995); total SS were determined by method 2540 D (APHA 1995); and dissolved polyphenols were determined by method 5550 B (APHA 1995). The concentration of inorganic particulate matter (clay) was estimated by the weight difference upon ignition of filter residues at 550°C. The dissolved organic matter was measured by spectrophotometry at 440 nm in water after passage through Whatman GF/C filters (Kirk 1983).

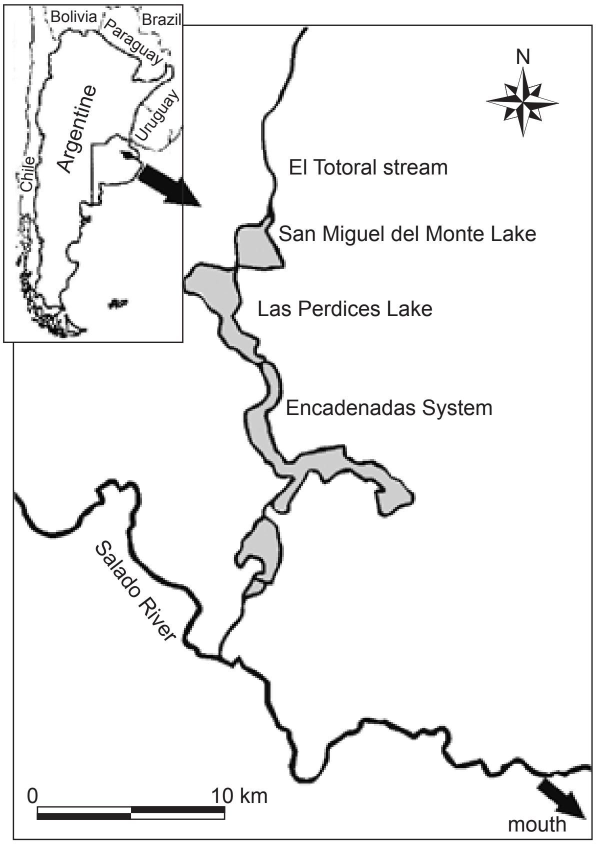


Fig. 1. Location of San Miguel del Monte Lake within the lake system interconnected with the Salado River, Argentina.

Rotifers were identified and counted in a Sedgwick-Rafter chamber (1 ml) under a compound light microscope. Samples were first mixed with a magnetic stirrer, and repeated subsamples were then enumerated. The coefficient of variation (maximum 20%) was used for abundance comparisons between dominant species in paired samples. Rotifer identification was based on Koste (1978), Segers (1995), and De Smet (1996).

Data analysis

In order to analyze the representation of the principal zooplankton families recorded in each vertical profile among species along with their spatial and temporal distribution, we performed 2 types of calculations: (a) the mean percentage was the average number of species from each family in the profile for a given month as a percent of the average total number of species recorded for that month; and (b) the maximum percentage was the maximum number of species from each family in the profile for a given month as a percent of the total of the maxima observed over all of the different species sampled. We then calculated correlation coefficients between specific physicochemical parameters and densities of both the most prevalent species and total rotifers ($*p < 0.05$, $**p < 0.01$). Multivariate analyses (principal-component analyses (PCAs)) were performed to compare rotifer assemblages and detect variables associated with underlying trends in the annual cycle. A PCA over the annual cycle was conducted on a log(x+1)-transformed mean monthly-density matrix to down-weight the dominant species.

A one-way analysis of variance (ANOVA) test was carried out to verify if there were significant differences in abiotic and biotic variables among the periods recorded in the shallow lake. The analysis was performed with all estimated values ($n = 77$). Before performing the ANOVA, a Kolmogorov-Smirnov test for normality, to assess the conditions for the ANOVA, was carried out, and only data for TP and Chl-*a* were log-transformed to meet the assumptions of the ANOVA. In contrast, to test for significant differences in the vertical distribution of species in each period, a one-way ANOVA and Kruskal-Wallis analyses were used.

Here, data were standardized for each month to meet the assumptions of the ANOVA. The Kruskal-Wallis test was performed on data of those species without a normal distribution. Finally, to compare the vertical distribution of rotifers throughout the annual cycle, a two-way ANOVA with a standardized matrix was used with depth and period as independent parameters.

RESULTS

Physical and chemical parameters

The shallow San Miguel del Monte Lake is characterized by alkaline (pH 8.4-10.2) and oligohaline water, with high TP concentrations (with a minimum of 89 µg/L in June 1998 and a maximum of 652 µg/L in Nov. 1997). Values of conductivity and TP decreased throughout the sampling period, as indicated by the regression coefficients (Fig. 2). The pattern of SS differed according to the presence or absence of submerged macrophytes and to hydrometeorologic conditions. Concentrations of SS varied with respect to both depth and time during the turbid period. In the clear period, there were also considerable variations over time, with higher concentrations (0.266 mg/L) occurring near the sediments. After flooding episodes of the Salado River, maximal concentrations (0.210 mg/L) of SS were recorded in surface layers as a result of wind action. Transparency increased during the growth of *Potamogeton pectinatus*, but the maximum degree occurred in winter. In contrast, the minimum transparency was recorded within the turbid period (Fig. 3). In this shallow lake, the transparency is a result of phytoplankton density along with other factors, such as the level of SS (clay and organic matter) plus dissolved organic matter (mainly polyphenols). The lowest transparency was produced by a coincidence between phytoplankton density (a peak in Chl-*a* concentrations) and the amount of SS. In Mar., the high value of transparency was mainly a result of low concentrations of SS; in July this condition was coupled with an accompanying low phytoplankton density, although at that time, the shallow lake took on a yellowish-brown caste owing to a high concentration of dissolved polyphenols (Fig. 3).

The water column almost always had a uniform temperature. The mean DO concentration of the water column was 9.25 mg/L, with very low values recorded on some occasions near the bottom, when the saturation-percentage level was < 5%. The maximum pH was detected in Mar. near sediments (pH 10.3), with the minimum (pH 8.3) occurring in Dec. at a depth of 0.60 m.

Rotifer structure

In total, 65 rotifer species belonging to 19 families were identified during the study period, with the families Lecanidae and Brachionidae showing the highest numbers of species (14 and 12, respectively). The highest number of families (16 families) was recorded in the clear period and the lowest (8 families) in the turbid period. Species of the Brachionidae, Filinidae, and Notomatidae were present on all sampling occasions. The Brachionidae was always either dominant or else codominant, and then mainly with the Lecanidae. The percent contributions in terms of the numbers of species of both families within the vertical profile showed opposite behaviors. With respect to the mean number of species in the

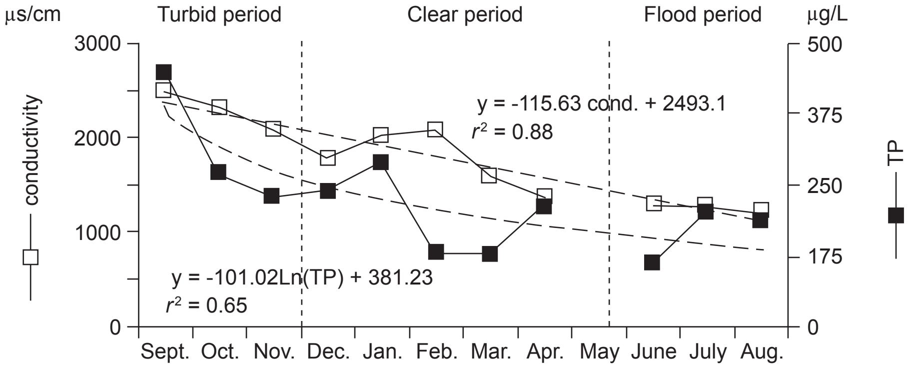


Fig. 2. Monthly mean variations in total phosphorus (TP) and conductivity in San Miguel del Monte Lake and the best-fit line (dotted line) determined by a regression analysis.

water column, the Brachionidae showed a clear prevalence in the period without macrophytes (Fig. 4A). This greater participation by the Brachionidae was related to an equal distribution of different species of this family in the water column. The contribution of the Lecanidae gradually increased once the submerged macrophytes had colonized, reaching the highest percentage in Jan., followed by an abrupt decrease in Feb. related to the cutting of the macrophytes (Fig. 4A). The Synchaetidae revealed a similar trend to that of the Brachionidae. In Dec., the Colurellidae reached its greatest representation coinciding with decreases in abundances of other families (Fig. 4B). The Notomatidae was present during the annual cycle, but at low densities, whereas the Trichocercidae achieved its highest level at the end of the turbid period (Fig. 4B). During the clear period, the latter's distribution in the vertical profile was homogeneous, with differences in its contribution being insufficient to affect either the mean or total number of species. The Testudinellidae, with 2 species, reached its maximum level in the flooding period; whereas the Filinidae was present during the entire annual cycle, with a relative increase occurring in periods without macrophytes.

Some *Lecane* species were recorded only once or twice (*L. arcula*, *L. hastata*, *L. hornemanni*, *L. nana*, *L. quadridentata*, and *L. signifera*); whereas *Brachionus caudatus*, *Filinia longiseta*, *Keratella tropica*, and 1 bdelloid species were found throughout the sampling period. Bdelloids were always present in low densities. Some species were recorded during all but 1 or 2 months (*B. calyciflorus*, *Cephalodella* sp., *Colurella colurus*, *L. closterocerca*, *Proales* sp., and *Polyarthra vulgaris*). *Notholca acuminata* and *Asphlanchna girodi* were found only in low-temperature periods. In Sept. and Dec. 1997, rotifers were scarce, whereas in Mar. and Apr. 1998, their abundance was maximal. The number of species showed significant differences with respect to depth only in Oct. and Dec. (Fig. 5A).

Annual vertical distribution

With respect to all vertical profiles, abundances of rotifers showed similar mean values in the turbid and flooding periods (Fig. 5B). Minimum and maximum mean values were recorded during the clear period. Marked vertical variations in density were observed in Nov. and Mar. (Fig. 5B). The highest values for species richness were coincident with density peaks and the greater variability in the water column during the clear period (Figs. 5A, B). Rotifer density showed 2 increases, with peaks in Nov. and Mar., followed by 2 decreases. The density distribution within the

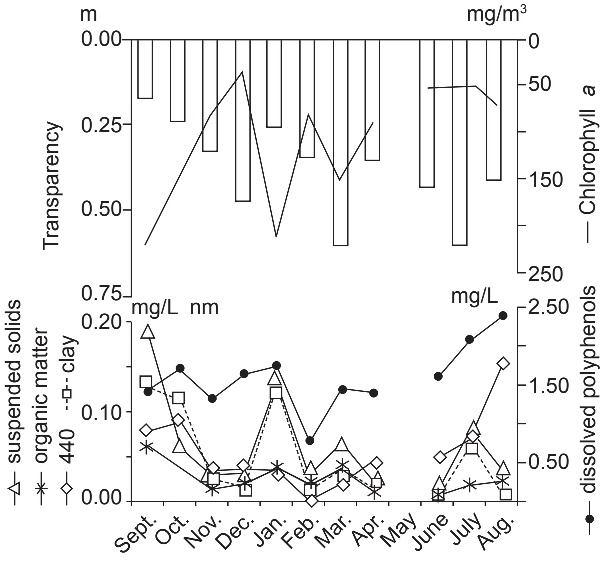


Fig. 3. Monthly mean variations in key variables (clay, suspended solids, and organic matter at 440 nm) related to transparency in San Miguel del Monte Lake.

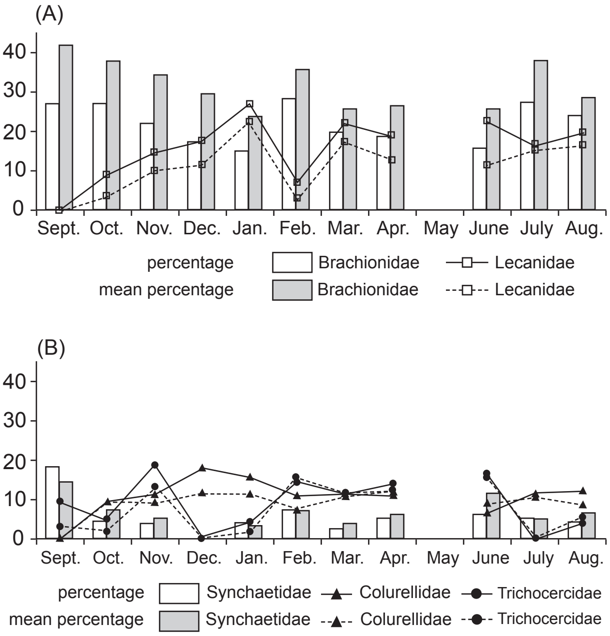


Fig. 4. (A, B) Percentage and mean percentage of species of the most abundant periphytic (lines) and planktonic (bars) families, during the annual cycle.

vertical profile exhibited a maximum at a depth of 0.60-0.90 m and a minimum near the sediments (Fig. 6). The density; however, was uniformly distributed in the water column during flooding conditions, with the exception of that of *Keratella tropica*. The total density fluctuated between 8 and 5160 individuals (ind.)/L. *B. caudatus* exhibited 2 peaks (in each of the turbid and clear periods). The density of this species began to decrease in autumn and evinced the lowest abundance in the flooding period (Fig. 6). *B. havanaensis* exhibited a similar temporal trend to that of *B. caudatus*, but was characterized by generally lower densities. The abundance of *B. plicatilis* was confined to the clear period, with peaks throughout the water column. *Filinia longiseta* was more abundant in the clear period, with the greatest density in the upper layers of the water column. *Brachionus calyciflorus* was the most abundant species during the turbid and flooding periods, with similar values throughout the water column (Fig. 6). *Polyarthra vulgaris* reached its maximum in the clear period with a sharp decrease occurring in deeper layers. *K. tropica* was at its maximum in the flooding period, whereas in other months, its density was significantly lower (Fig. 6). A typical winter species, *Notholca acuminata*, exhibited maximum abundance later during that season, coinciding with the lowest water temperatures. Although the predator, *Asphanchna girodi*, was recorded on 6 occasions, its maximum abundance was also found in winter. Among nonplanktonic rotifers, 2 species of *Lecane* (*L. bulla* and *L. closterocerca*) had density peaks in Mar. On that occasion, 3 species of *Trichocerca* (*T. pusilla*, *T. stylata*, and *Trichocerca* sp.) also reached their abundance peaks. One species of *Proalides* was registered on 5 occasions, 3 records of which were coincident with the maximum lake cover of *P. pectinatus*.

Statistical results

TP concentrations showed significant differences among the 3 periods ($F = 7.04$, $p = 0.002$, $n = 77$, ANOVA) along with the Chl-*a* concentrations ($F = 11.35$, $p = 0.000$, $n = 77$, ANOVA).

The ANOVA and Kruskal-Wallis tests indicated that some species showed an aggregate distribution in certain layers of the vertical profile in every period recorded during the annual cycle (Table 1). The proportion of planktonic rotifers in the total density ($F = 4.469$, $p < 0.001$, two-way ANOVA) and specific richness ($F = 3.29$, $p = 0.001$, two-way ANOVA) revealed significant differences in the vertical distribution among the periods.

Total-rotifer densities ($r = 0.61^{**}$, $r = -0.39^{**}$), and those of species such as *B. caudatus* ($r = 0.55^{**}$, $r = -0.32^{*}$), *B. havanaensis* ($r = 0.63^{**}$, $r = -0.44^{**}$), *F. longiseta* ($r = 0.48^{**}$, $r = -0.49^{**}$), and *P. vulgaris* ($r = 0.37^{**}$, $r = -0.30^{*}$), were positively correlated with pH and negatively correlated with dissolved-polyphenol concentrations, respectively. *Branchionus caudatus* ($r = 0.27^{*}$), *B. havanaensis* ($r = 0.33^{*}$), and *B. calyciflorus* ($r = -0.56^{**}$) were correlated with temperature as indicated; while *K. tropica* was negatively correlated with temperature ($r = -0.38^{**}$), pH ($r = -0.29^{*}$), DO ($r = -0.31^{*}$), and

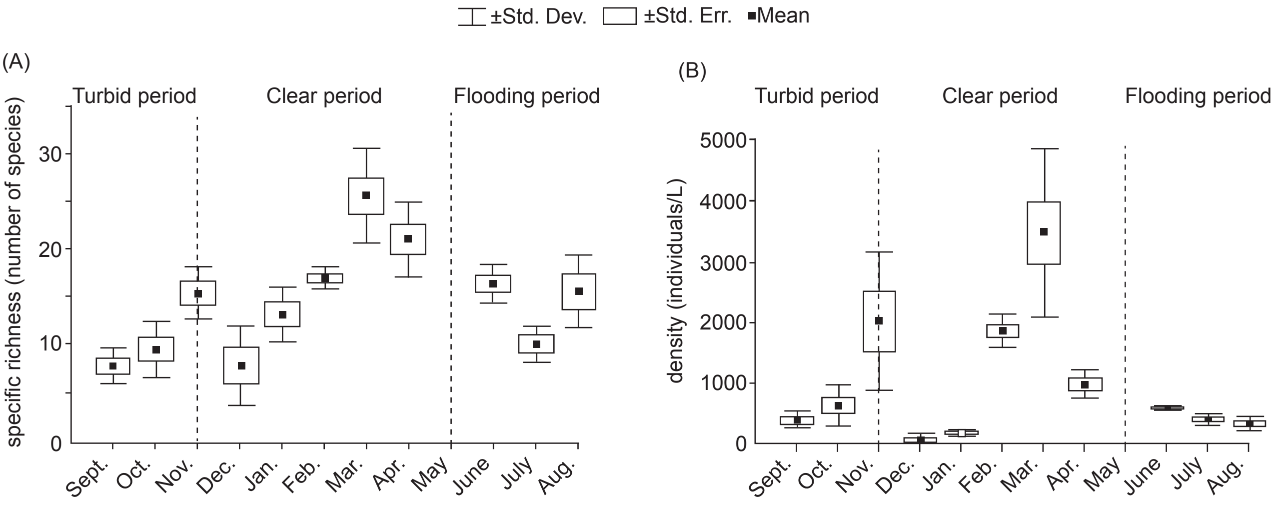


Fig. 5. Box plot of the mean, standard deviation, and standard error, ($n = 11$) of (A) rotifer-species richness (number of species) and (B) rotifer density (individuals/L), as estimated monthly in the vertical profile of San Miguel del Monte Lake.

conductivity (*r* = -0.31*).

In the PCA, the 1st 2 axes accounted for 71% of the total variation. Low rotifer densities, coinciding with low Chl-*a* concentrations, the presence of periphytic species, and exceptional rainfall, defined 1 sector of axis 1; whereas high rotifer densities and a predominance of planktonic species were associated with the other sector. The negative sector of the 2nd axis was related to the presence of submerged macrophytes and the predominance of grazer species; while the positive sector was strongly associated with the presence of a predator species (*A. girodi*) and the absence of *P. pectinatus* (Fig. 7).

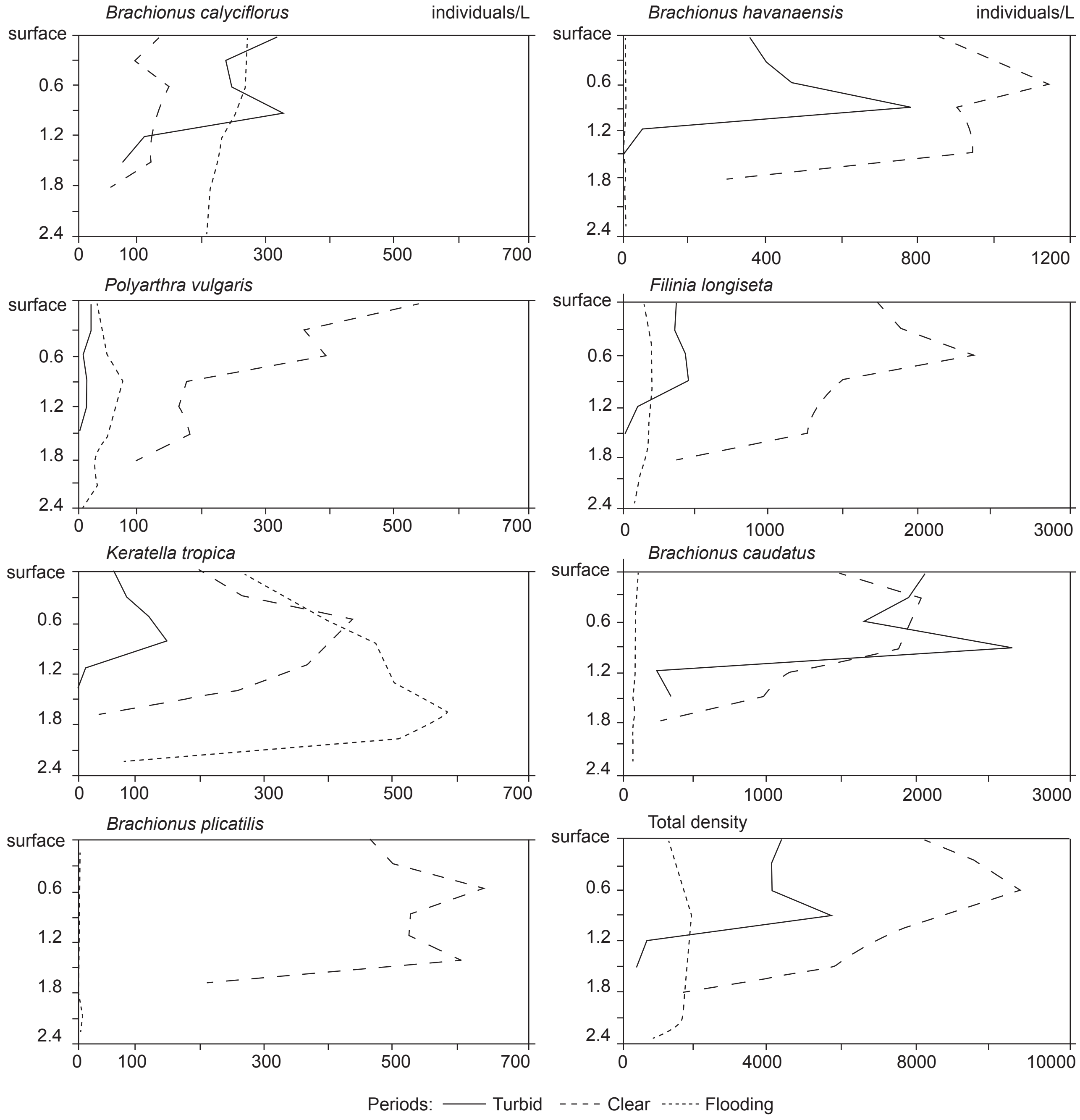
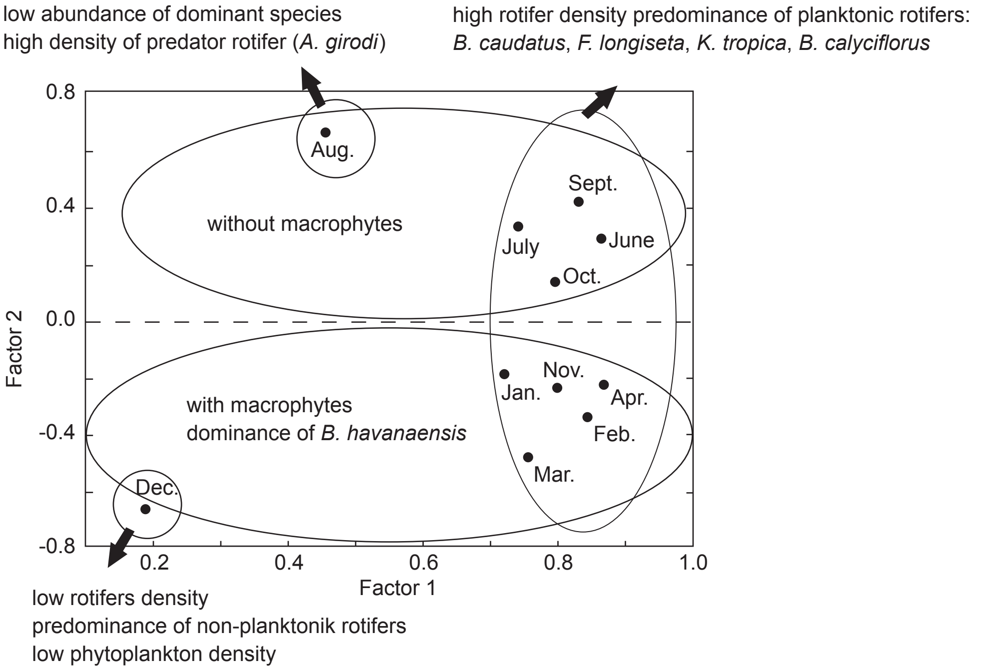


Fig. 6. Changes in the total rotifer density and in the most abundant rotifers within the vertical profile of San Miguel del Monte Lake during 3 periods (values correspond to the sum of the rotifer density for each period: turbid, 3 months; clear, 5 months; and flooding, 3 months).

DISCUSSION

In San Miguel del Monte Lake, high rotifer densities reflect its essentially eutrophic conditions (Ravera 1996, José de Paggi and Paggi 1998). The annual pattern of abundances of dominant rotifer species may be associated with a preference for or selection of the algae consumed (Xi et al. 2002). Furthermore, alternative foods, such as ciliates, detritus, and bacteria mentioned by Nogrady et al. (1993), are abundant in this shallow lake. Relationships of rotifer abundances with chlorophyll and particulate organic matter were not significant. Chlorophyll has clear limitations as an indicator of food quality because of the variability in algal biochemistry and grazer nutritional needs (Jeppesen et al. 2000). Nevertheless, the abundance of some rotifer species may be related to the presence of particular algae. Accordingly, the total rotifer peak recorded in Mar. was related to the availability of green coccal algae as a food source (Solari et al. 2003).

Some species showed a clear seasonal pattern with respect to temperature: *B. calyciflorus* and *A. girodi* were associated with lower temperatures, whereas *N. acuminata* was restricted to winter months (Pejler and Bērziņš 1989).



low abundance of dominant species
high density of predator rotifer (*A. girodi*)

high rotifer density predominance of planktonic rotifers:
B. caudatus, *F. longiseta*, *K. tropica*, *B. calyciflorus*

with macrophytes
dominance of *B. havanaensis*

low rotifers density
predominance of non-planktonik rotifers
low phytoplankton density

Fig. 7. Bi-dimensional principal component analysis representation of monthly mean rotifer densities. The scheme explains the annual rotifer distribution associated with certain identified control factors.

Table 1. Significant results of ANOVA test and Kruskal-Wallis test showing spatial differences of certain species in each period occurred in San Miguel del Monte Lake

Test		Turbid period	Clear period	Flooding period
ANOVA	*B. caudatus*	F = 3.158; *p* = 0.036	-	-
ANOVA	*K. tropica*	F = 3.485; *p* = 0.025	-	-
ANOVA	*F. longiseta*	F = 7.470; *p* < 0.001	F = 8.923; *p* < 0.001	-
K - W	*F. longiseta*	-	-	H = 15.295; *p* = 0.018
K - W	*Cephalodella* sp.	H = 20.000; *p* = 0.003	-	-
ANOVA	*B. havanaensis*	-	F = 4.153; *p* = 0.004	-
K - W	*P. vulgaris*	-	H = 16.141; *p* = 0.013	-
K - W	*Proales* sp.	-	H = 18.258; *p* = 0.006	-

Rotifers exhibited a clear decrease in density within the layers of the water column with low levels of DO, coinciding with results of Armengol Díaz et al. (1993) in a karstic lake. The other parameter influencing the abundance of the major rotifer species throughout the entire year was the pH (Duggan et al. 1998). In San Miguel del Monte Lake; however, species of the Lecanidae were more related to the presence of submerged macrophytes than to changes in pH, in contrast to the results of Duggan et al. (1998). Plant-associated rotifers had their highest densities when *P. pectinatus* reached its maximum cover in the lake. On other sampling occasions, nonplanktonic rotifers were recorded at lower densities than those of pelagic rotifers. This finding is in agreement with the results of Kuszyńska-Kippen (2000) in another polymictic lake. The decrease in pH in winter was related to flooding conditions; such episodes resulted in an input of dissolved polyphenols from associated shallow lakes along with emergent macrophytes. Some species (*B. caudatus*, *B. havanaensis*, *F. longiseta*, and *P. vulgaris*) could become negatively affected by this increase in dissolved polyphenol concentrations.

The dominant species of rotifers in shallow San Miguel del Monte Lake showed a clear partitioning of communities (Makarewicz and Likens 1979) to avoid adverse conditions present in this body of water during the sampling period. The prevalent species increased their abundances on 1 or 2 occasions, and at these times, they showed marked stratification within the water column.

Turbid period

A low rotifer tally was associated with the presence of cyanophytes along with high conductivity values. In Sept., 3 species (*B. calyciflorus*, *B. caudatus*, and *F. longiseta*) represented 75% of the total rotifer density within the vertical profile. There was a considerable scarcity of other species at that time, corresponding to the annual minimum with respect to species richness (Fig. 8). Maximum values of SS were recorded, along with a high contribution of mineral particles (i.e., clay), which may have affected the population dynamics of rotifers. This observation is in agreement with results of Lair et al. (1998), who suggested that high concentrations of particles negatively impact rotifer populations because such insoluble materials interfere with the ciliary ingestion process. In Sept., the presence of *B. calyciflorus* was found to be related to the abundance of *Chlamydomonas* sp. (Solari et al. 2003). Accordingly, Sterner (1989) reported that *B. calyciflorus* preferred this chlorophyte, among others, as food. The capacity of this rotifer species for growth and reproduction on a cyanobacterial diet (Liu et al. 2002) may explain the abundance of *B. calyciflorus* in Oct., when cyanophytes (*Oscillatoria limnetica* and *Raphidiopsis mediterranea*, among others) represented some 90% of the phytoplankton population (Solari et al. 2003). Later in spring, a progressive increase in species richness was detected, with a dominance of *B. caudatus* along with the presence of *B. calyciflorus* and *B. havanaensis* as sporadic codominants within the vertical profile.

Clear period

At the beginning of the period with macrophytes (Dec.), the rotifer abundance and species richness were both very low in response to abiotic and biotic factors. For example, the former included the highest local rainfall recorded (330 mm); while the latter involved submerged macrophyte beds, with stands occupying the entire basin, along with the highest crustacean densities detected (Claps et al. 2004). In Feb., the prevalence of the Brachionidae was probably related to the sudden decrease in dissolved polyphenol concentrations, compounds of which act negatively on most of this family; whereas species of the Lecanidae and Trichocercidae remained largely unaffected by these substances. Peak rotifer densities in Mar. may thus have been associated with a notable decline (an order of magnitude) in calanoid- and cyclopoid-copepod populations at that time (Claps et al. 2004), respectively suggesting decreases in competition for food and predation pressure. These results agree with findings of José de Paggi (1995) in Paraná River floodplain lakes. Lauridsen et al. (1998), in a calcareous lake in Denmark, observed a decline in rotifer populations during 2 consecutive summers and cited cyclopoid predation as a consequential regulator; while Cryer and Townsend (1989), in Alderfen Broad, a shallow eutrophic lake in England, pointed out the significance of the relative availability of rotifers and nauplii as food sources for cyclopoids (*Acanthocyclops robustus*). In addition, in San Miguel del Monte Lake, rotifer densities were negatively influenced during the Dec. sampling by the abundance of planktonic cladocerans

(*Diaphanosoma birgei* and *Ceriodaphnia* cf. *dubia*; Claps et al. 2004). Herbivorous rotifer populations were therefore reduced through competition with cladocerans for the same food, as a consequence of a higher cladoceran-filtering rate (José de Paggi 1995, Moss et al. 1998, Lauridsen et al. 1998, Tönno et al. 2003). Under these conditions within the vertical profile, only *B. havanaensis* and periphytic species (*Cephalodella* sp. and *Proales* sp.) managed to prevail, while strong rotifer stratification was observed (Fig. 8). In late summer, *B. caudatus* and *F. longiseta* dominated the vertical profile, coinciding with a significant increase in species richness. In Apr., *F. longiseta*, *Proalides* sp., and *P. vulgaris* showed an aggregated distribution in surface layers (see also Malone and McQueen 1983, Grzegorz et al. 2006) (Fig. 8). The Lecanidae and Trichocercidae alternated codominance with different instances of colonization of submerged macrophytes. The presence of macrophytes in the lake favored increases in both planktonic-rotifer densities and species richness, mainly through the possibilities of refuge plus the incorporation of plant-associated families and food diversification.

Flooding period

This period showed a clear homogeneity in the vertical distribution of some species under conditions of maximum hydrometric levels after the entrance of water from other shallow lakes, in disagreement with observations by José de Paggi (1995) in a similar shallow lake associated

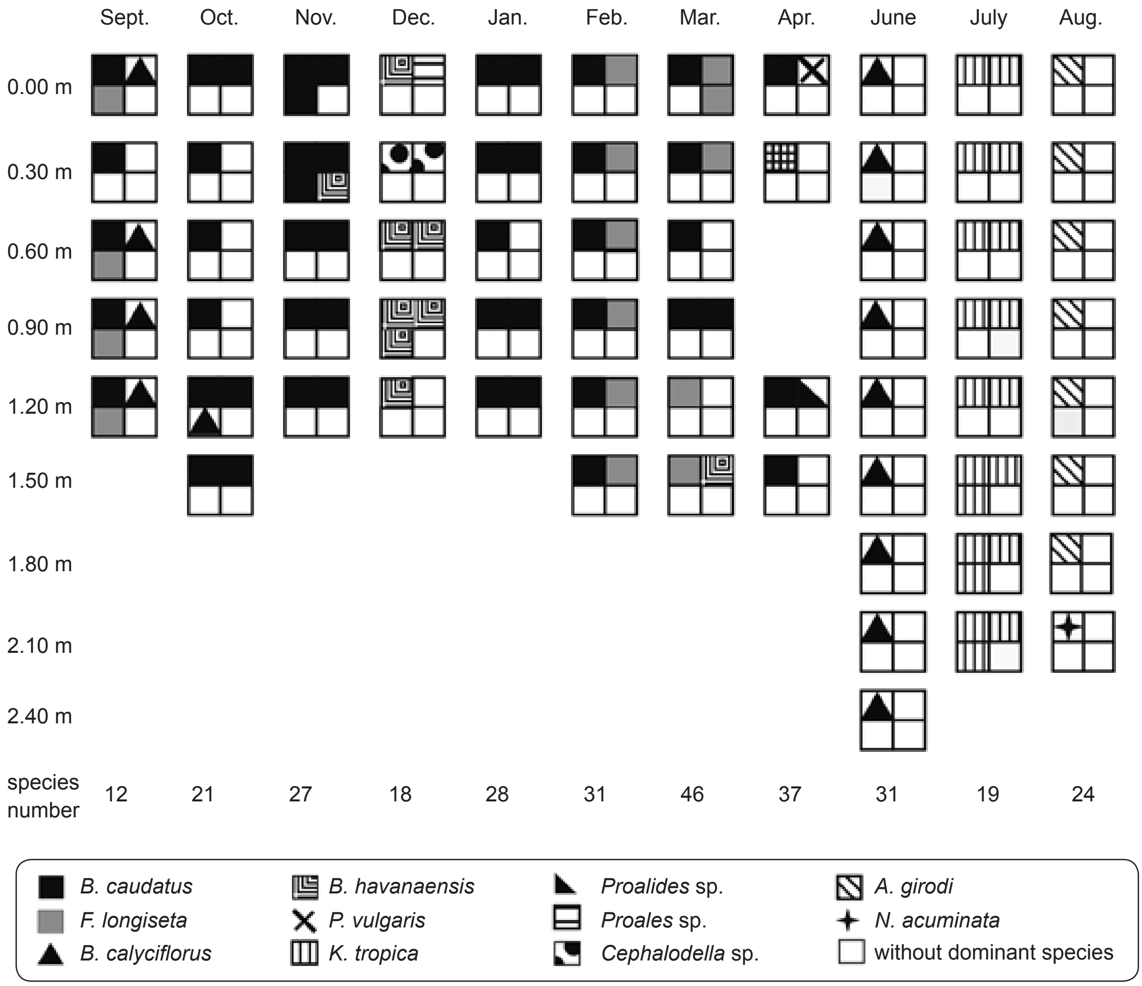


Fig. 8. Vertical and temporal distributions of the most representative rotifers in San Miguel del Monte Lake. The monthly number of species is indicated. Only species with almost 25% of the relative minimum density were included. Each quarter of the box indicates the relative abundance (25% of the total density) of the species, while the white quadrant indicates the absence of any species reaching a minimum relative abundance of 25% of the total rotifer density.

with the Paraná River. The present episode moreover coincided with winter months, which is characterized by the presence of stenothermal species. As a consequence of those floods and senescence of macrophytes, changes in the species composition were observed, consisting of a gradual diminution in richness along with both a decrease in their density and a homogenization of their distribution within the vertical profile (Fig. 8). The dominance of a particular species, or at least its relevant presence, characterized each month. The abundance of *B. calyciflorus* was notably related to the period immediately after flooding (June). *Keratella tropica* reached a maximum in this phase, coinciding with peaks of *Cryptomonas* spp. (Solari et al. 2003); those species, in turn, are the preferred food of rotifers (Gilbert and Bogdan 1981).

In conclusion, our results suggest that the small-scale vertical distribution of rotifers in this homothermal and open lake is at some level related to internal biotic factors (e.g., the presence or absence of submerged macrophytes), but is mainly a consequence of external and unpredictable abiotic forces. As to abiotic influences, external forces such as exceptional rainfall and flood conditions influence the vertical distribution, albeit in different ways. These climatic influences, coupled with the above biotic factors, promoted in certain layers of the vertical profile the dominance of some species that were either uncommon or else less abundant under other conditions.

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