Plankton rotifers from a tropical lake: differences in distribution and migration patterns in two mixing events, with similar abiotic conditions.

Rotíferos planctónicos de un lago tropical: diferencias en la distribución y migración entre dos eventos de mezcla con condiciones abióticas similares.

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ABSTRACT

Vertical distribution of plankton rotifers is not random. Although the causes of this behavior are still under debate, it has been suggested, mainly from the study of stratified environments, that abiotic parameters play an important role in determining the presence and position of a species in the water column. We compared the composition and vertical distribution of planktonic rotifers in a tropical monomictic lake in Mexico during the mixing period of two years in which abiotic conditions were similar. We recorded 28 rotifer species. Total average densities ranged from 238 ± 39 ind l^{-1} to 517 ± 97 ind l^{-1}. The similarity of rotifer assemblages between the two compared dates was 46.4%. Our results showed that temperature and dissolved oxygen in the upper 13 meters and pH upper 8 meters, respectively, were homogeneous in the two dates. Nevertheless, the rotifer assemblages showed important differences in: a) the absolute population densities, b) the dominance ranking of species in the community, c) the preferential position of a specific species in the water column, d) the relationship between such preference and the studied abiotic factors and, e) the types and amplitudes of species' migrations. Given the resemblance of the abiotic factors in the analyzed years, we suggest that changes in rotifers distribution and abundance would involve biological factors, such as food availability, competition and predation. .

Key words: abiotic factors, diel vertical migration, distribution and abundance, freshwater zooplankton, Mexico.

RESUMEN

La distribución vertical de los rotíferos planctónicos no es aleatoria. Aunque las causas de este comportamiento todavía se debaten, se ha sugerido, principalmente a partir de estudios efectuados en ambientes estratificados, que los factores abióticos tienen un papel preponderante en la determinación de la presencia y la ubicación de una especie particular en la columna de agua. Se comparó la composición y distribución vertical de los rotíferos planctónicos de un lago monomíctico tropical de México durante el período de mezcla de dos años distintos en los que las condiciones abióticas fueron similares. Se registraron 28 especies de rotíferos. Su densidad promedio conjunta fluctuó entre 238 ± 39 ind l^{-1} y 517 ± 97 ind l^{-1}. La similitud de la comunidad de rotíferos en las fechas comparadas fue de 46.4%. Los resultados mostraron que la temperatura y el oxígeno disuelto en los 13 m superiores y el pH en los 8 m superiores de la columna de agua no difirieron significativamente en las fechas comparadas. No obstante, la comunidad de rotíferos mostró importantes diferencias en: a) las densidades absolutas de las poblaciones, b) el orden de dominancia de las especies

en la comunidad, c) la ubicación preferencial de las especies en la columna de agua, d) la relación entre tal preferencia y los factores abióticos analizados y e) los tipos y amplitudes de migración de las especies. Dada la semejanza de los factores abióticos en las fechas analizadas, se sugiere que los cambios observados en la distribución y abundancia de los rotíferos podría, más bien, involucrar factores biológicos, como la disponibilidad de alimento, la competencia y la depredación.

Palabras clave: Factores abióticos, migración vertical diaria, distribución y abundancia, zooplankton dulceacuícola, México.

INTRODUCTION

Most vertical distribution patterns of zooplankton species result from a daily active migration process. Nowadays, it is known that although migration can be produced by a multiplicity of factors, this behavior would be optimized by natural selection. This would be reflected in each population's fitness and in the entire dynamics of lake ecosystems (Lampert & Sommer, 1997).

Given the ecological importance of plankton rotifers and the scarcity of information on their communities in Mexican freshwaters, this study aims to describe some community parameters (composition, density, frequency and dominance), as well as the vertical distribution patterns and migration dynamics of the most important rotifer species in a Mexican lake.

Since rotifer communities comprise dynamic interacting populations, species assemblages may differ both temporally and spatially. Although it is recognized that species distribution of the planktonic rotifers is not random (Ruttner-Kolisko, 1974; Armengol *et al.*, 1998), the causes of these patterns are still under debate (Huntley, 1985). In several studies that have explored the relationship of plankton rotifers with abiotic, environmental parameters (e.g., temperature, pH, Secchi disk transparency and dissolved oxygen) it has been suggested that these parameters act as key factors in determining the composition (May, 1983; Matveeva, 1986; Berzins & Pejler, 1987, 1989a, 1989b; Mikschi, 1989) and vertical distribution (Ruttner-Kolisko, 1980; Armengol *et al.*, 1993; Armengol & Miracle, 1999; Esparcia *et al.*, 2001) of rotifer assemblages.

To explore the above-mentioned idea, we also analyzed the community structure and vertical distribution of the plankton rotifers of a lake in two different periods with very similar abiotic conditions. To make this inter-date comparison we chose two dates within turnover periods of the lake for two important reasons. First, because most abiotic parameters are more homogeneous throughout the water column during mixing (Wetzel, 2001; Kalff, 2002) and, second, because the majority of the studies that have found close relationships between abiotic factors and rotifer distribution patterns have been performed in stratified environments, which could lead us to understandable but questionable cause-effect assumptions.

In this study, we compared the patterns of abundance and vertical distribution of plankton rotifers of a tropical lake, derived from the analysis of two diel cycles carried out in different years. In addition, we explored the relationships among these patterns and some abiotic factors. Our study was performed under the hypothesis that if factors like temperature, dissolved oxygen and pH, are actually controlling rotifer populations behavior; when these factors do not differ significantly between two sampling times, the structure and behavior of the rotifer assemblages should not differ as well.

MATERIALS AND METHODS

Laguna Escondida is a warm tropical, monomictic lake located in South-eastern Mexico (18° 35′ N; 95° 06′ W, 130 m asl), in the middle of the Los Tuxtlas Region, at the Mexican State of Veracruz. The climate is warm and humid, with mean annual temperature of 27°C, and although it rains throughout the year, it is possible to distinguish a rainy season, from June to February, and a dry period from March to May (Torres-Orozco *et al.*, 1994). The lake is surrounded by the remnants of a tropical rain forest; it has an area of 18.23 ha and a maximum depth of 32.5 m, with annual narrow water-level variations. It circulates regularly between January and March and remains stratified the rest of the year. During mixing, the water column becomes homothermic at 20-21 °C or differs only by 1°C from surface to the bottom. In contrast, during the stratification period, a vertical temperature gradient of 6-7°C is established. Even under homothermic conditions, both the depth of the lake and constant input of allochthonous organic matter allow a clinograd profile of dissolved oxygen to persist; thus, hypolimnetic anoxia is common during the hottest and rainiest part of the year, from August to October (Torres-Orozco *et al.*, 1996).

We have been sampling with some regularity the plankton of this lake since 1993; so, to make the comparison that led us to test our working hypothesis, we chose the two available dates with the higher resemblance in vertical distribution of the water column abiotic factors during the mixing period of the lake. These dates were January 26-27, 1996 and February 2-3, 2003.

In both dates, a 24-hour sampling program was carried out at the center of the lake at a depth of 17.5 m, and samples were collected at three-hr intervals, between 15:00 hrs in the first day and 12:00 hrs the following day. The sampling depths were 0.25, 1.0, 1.5, 2.0, 3.0, 5.0, 8.0, 12.0 and 16.0 m in 1996, and 0.25, 1.5, 3.0, 5.0, 8.0, 12.0 and 17.0 m in 2003. Water samples were taken with a 3.0 l van Dorn bottle for the determination of temperature (digital thermometer Cole Parmer 90201-10, -40 to 120°C ±0.2 °C), pH (pH meter Corning M103) and dissolved oxygen (Winkler method). Secchi disk transparency was also measured. Plankton samples were collected with a Schindler-Patalas type trap with 30.85 l of capacity, provided with a 54-μm mesh net, and preserved in 4% buffered formaldehide.

Subsamples of previously concentrated plankton samples were placed in a 1.0 ml Sedgwick-Rafter plankton-counting cell (50 x 20 x 1 mm) and rotifers were counted with an optic microscope at ×100 magnification. The whole volume of three cells was counted in all cases.

A Mann-Whitney non-parametric test was used in order to evaluate the inter-annual differences in the mean values of temperature, dissolved oxygen and pH at different depths in the water column. Olmstead and Tukey association diagrams (Steel & Torrie, 1988) were used to identify the dominant species in the rotifer community, based on the frequency and abundance of each species. We analyzed individually each 24-hr cycle.

To assess the statistical differences in depth distribution of the dominant rotifer populations along the diel cycle (i.e. if the individuals of each species congregate in certain depths at different hours of the day), a log-likelihood ratio (G) test on contingency tables (Sokal & Rohlf, 1995) was performed.

The patterns of diel vertical migration were established from the shifts in the mean residence depth (MRD) of each dominant population. This was estimated by

$$MRD = \Sigma(n_i \times d_i) / \Sigma n_i$$

where n_i is the number of individuals at depth i, and d_i is the depth of the i-th sample (Armengol & Miracle, 2000).

The two migration patterns showed by each species were compared using Mann-Whitney non-parametric tests. Finally, the migration amplitude of species was settled as the extreme magnitude of its daily MRD variations.

RESULTS

The water temperature and DO in the upper 13 m during 1996 and 2003 did not differ significantly (*t*-test); this was true also for pH in the upper 8 m. Below these depths all these parameters differed significantly ($p < 0.004$, $p < 0.005$, and $p < 0.004$, respectively; Fig. 1). The main difference between both years was related to the location of oxygen drops, which varied from 8.4 to 6.0 mg O_2 l^{-1} (between 4.0 and 8.0 m) in 1996 and from 5.5 to 3.5 mg O_2 l^{-1} (between 12 and 13 m) in 2003. The depth of Secchi disk transparency was 1.2 m in both years

Rotifers constituted >70% of total zooplankton species during both years; 26 and 25 rotifer species were detected in 1996 and 2003, respectively. We recorded a total of 28 species (23 common to both dates) from 15 genera and 11 families. Brachionidae, with four genera and eight species, was the best represented family, and the most diverse genus was *Lecane* (Table 1).
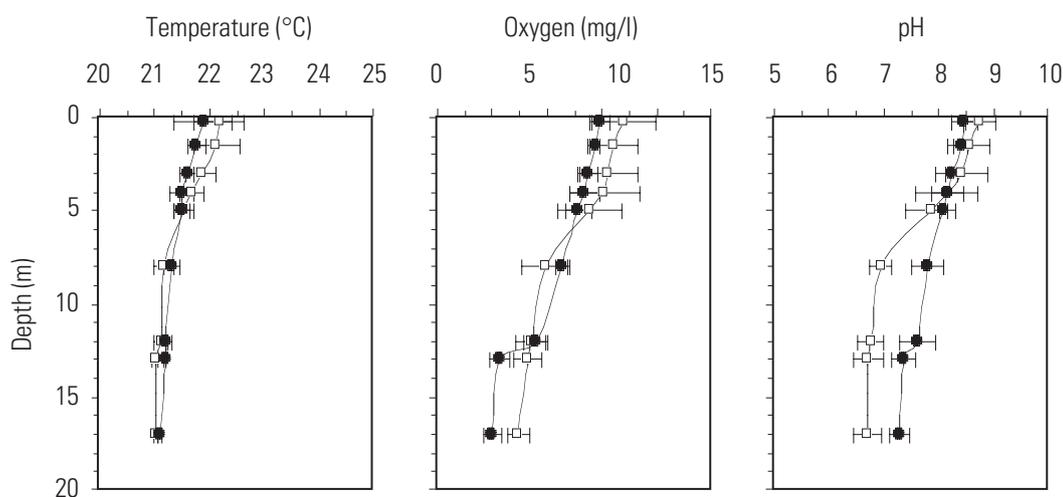

Fig. 1. Vertical profiles of temperature, oxygen and pH observed in the sampling dates in Laguna Escondida, Mexico. Squares correspond to 1996 and circles to 2003. Symbols indicate the average value for each parameter along the diel cycles; error bars refer to one standard deviation.

Table 1. Rotifer species recorded at Laguna Escondida, Mexico.* Present only in the 1996 sampling; ** present only in the 2003 sampling.

Brachionidae	**Trichocercidae**
Anuraeopsis fissa (Gosse, 1851).	*Trichocerca dixon-nuttalli* Jennings, 1903.
Brachionus calyciflorus Pallas, 1766.	*Trichocerca pusilla* (Lauterborn, 1898).
Brachionus havanaensis Rousselet, 1911.	*Trichocerca similis* (Wierzejski, 1893)
Brachionus quadridentatus (Hermann, 1783).	**Gastropodidae**
Keratella americana Carlin, 1943.	*Ascomorpha ecaudis* (Perty, 1850).
Keratella cochlearis (Gosse, 1851).	*Ascomorpha saltans* Bartsch,1870.
Keratella tropica (Apstein, 1907).	**Synchaetidae**
Platyias quadricornis (Ehrenberg, 1832)	*Synchaeta pectinata* Ehrenberg, 1832.
Euchlanidae	*Polyarthra vulgaris* Carlin, 1943.
Euchlanis sp. **	**Asplanchnidae**
Colurellidae	*Asplanchna brigthwelli* (Gosse,1850).
Lepadella dactyliseta (Stenroos, 1898).*	**Hexarthridae**
Lepadella patella (Müller, 1826).	*Hexarthra mira* (Hudson,1871).
Lecanidae	**Filiniidae**
Lecane bulla (Gosse, 1886).	*Filinia* sp. **
Lecane closterocerca (Schmarda, 1859).	**Collothecidae**
Lecane ludwigii (Eckstein, 1883).*	*Collotheca* sp.
Lecane monostyla (Daday, 1897).	
Lecane stenroosi (Meissner, 1908).*	
Lecane subtilis Harring and Myers,1926.	

In 1996, 11 species were the most frequent and abundant; in order of importance were *Keratella tropica, Trichocerca pusilla, Polyarthra vulgaris, Ascomorpha saltans, Keratella americana, Brachionus calyciflorus, Collotheca* sp., *Ascomorpha ecaudis, Hexarthra mira, Trichocerca similis* and *Synchaeta pectinata.* On the other hand, in 2003, only eight species were dominant: *B. calyciflorus, A. ecaudis, A. saltans, S. pectinata, K. tropica, P. vulgaris, K. americana* and *T. pusilla.* Thus, seven of the 11 dominant species in 1996 maintained their dominance also in 2003 (Fig. 2). The rest of the community included *Anuraeopsis fissa, Asplanchna brigthwelli, Brachionus quadridentatus, Lecane closterocerca, Trichocerca dixon-nuttalli,* and other 12 species with very low densities and frequencies (Fig. 2).

The average rotifer densities varied significantly (p < 0.001): from 238.09±39.21 ind l^{-1} in 1996 to 517.50±97.39 ind l^{-1} in 2003. Although species composition was similar in both years, important differences were observed in their dominance ranking (Fig. 2). In 1996, *Keratella tropica* was the most abundant and frequent species. With an average density of 104.50±165.09 ind l^{-1}, it contributed 42.9 % to the total density, whereas *B. calyciflorus* only contributed 3.6%. In 2003, *B. calyciflorus* became more

abundant (324.70±379.73 ind l^{-1}, on the average), comprising 63% of the total rotifer density, with *K. tropica* contributing only 4.6% to the total. The Morisita similarity index (Krebs, 1989) showed a resemblance value among the two years of 46.4%.

A *G* test showed that the vertical distributions of most of these species along the diel cycle were different (p<0.025) because of a real aggregation of species populations in certain depths as a function of the time of the day (Fig. 3). Exceptions to this were *K. americana, T. pusilla* and *P. vulgaris,* in 2003, whose vertical gradient in the water column showed to be independent of the time of the day (p> 0.1). The observed changes in the vertical distribution of the dominant species through the diel cycle suggest the existence of migratory behavior in most cases. This is more clearly depicted in the MRD plots (Fig. 4).

When MRD's were compared (Mann-Whitney test), important differences were noted for *Keratella tropica* (p< 0.001), *K. americana* (p<0.001), *Hexarthra mira* (p<0.001) and *Trichocerca pusilla* (p<0.016). In 1996, the preferred position of *K. tropica* in the water colum was from 5.0 to 7.5 m, while in 2003 this depth ranged between 2.07 and 3.86 m. *K. americana* was found mainly
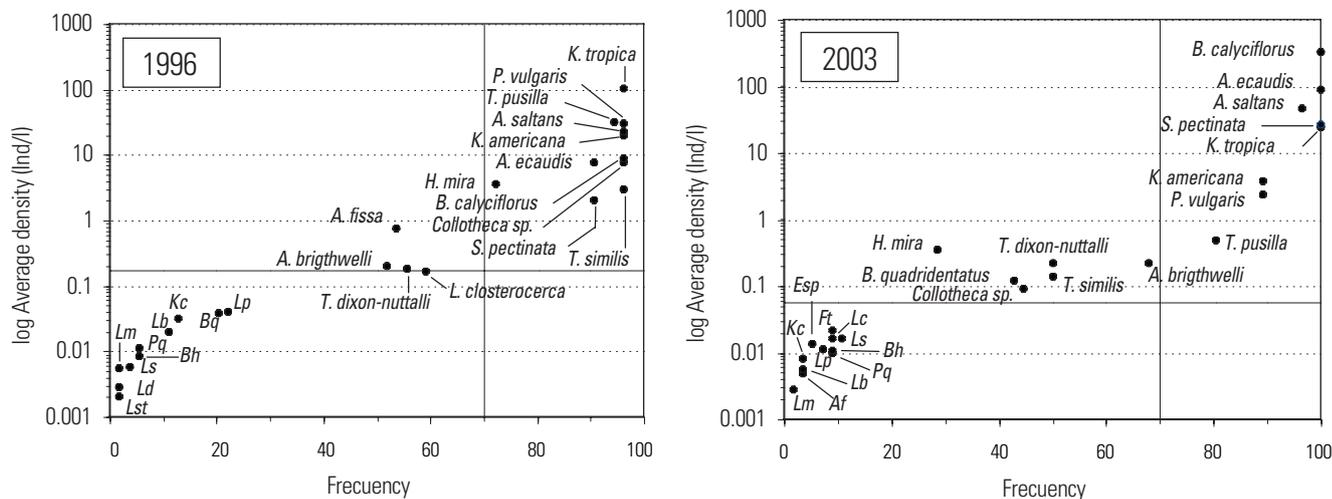
Fig. 2. Olmstead and Tukey association tests for the rotifer species of Laguna Escondida, Mexico in 1996 and 2003. Ld, *Lepadella dactyliseta*; Lst, *Lecane stenroosi*; Ll, *Lecane ludwigii*; Lm, *Lecane monostyla*; Esp, *Euchlanis* sp.; Fsp, *Filinia* sp.; Bh, *Brachionus havanaensis*; Ls, *Lecane subtilis*; Lb, *Lecane bulla*; Pq, *Platyias quadricornis*; Lp, *Lepadella patella*; Kc, *Keratella cochlearis*; Bq, *Brachionus quadridentatus*; Lc, *Lecane closterocerca*; Af, *Anuraeopsis fissa*.

between 5-8 m depth in 1996, and between 10-16 m in 2003. *H. mira* was located at ca. 8.0 m depth in the first year but below the 16.0 m depth in the second. For *T. pusilla* these depths ranged between 2.2 and 4.7 in 1996 and from 2.6 to 6.1 m in 2003. It is worth pointing out that densities of the last three species were notably lower in 2003.

Hexarthra mira had the highest migration amplitude, 6.42 m, in 1996 and *Polyarthra vulgaris* the lowest, 1.72 m, in 2003. Except for *K. americana* and *H. mira,* migration amplitudes were similar for all species in both cycles (Table 2).

DISCUSSION

Most of the studies that relate the distribution patterns of plankton rotifers with abiotic factors have been carried out in stratified environments (e. gr. Armengol *et al.*, 1998; Armengol & Miracle, 1999; Baião & Boavida, 2000; Esparcia *et al.*, 2001). Under these hydrological conditions, close correlations between such factors and rotifer populations have been recognized. In the above mentioned studies it is concluded that in correspondence to water stratification there are rotifer assemblages characteristic of each main strata. Under this scenario, it is clear that the position of a species within a stratum would show a strong correlation with the prevailing abiotic factors. Nevertheless, the existence of such correlations does not necessarily imply a cause-effect relationship because very different factors could actually be involved in the control of rotifer populations.

Temperature and oxygen are among the most important environmental factors acknowledged to explain the space-time fluctuations of rotifer populations (Bogaert & Dumont, 1989; Mikschi, 1989). However, in addition to direct effects of temperature and oxygen, the effects of these variables on rotifer fluctuations could be mediated via other biotic and abiotic factors.

Although seven years elapsed between the two sampling dates, when comparing the vertical distribution of temperature, oxygen and pH no significant differences were observed in the uppermost 10 meters of the water column. Secchi disk transparency was also the same in both periods. Given that our results show that most of the dominant rotifer populations had their abundance peaks and vertical movements within this part of the water column, the observed differences in rotifer vertical distributions could hardly be attributed to the influence of these factors.

In both years, the lake was practically homothermic and differences of only 1 to 1.3 °C were detected in the 18-m water column. Additionally, oxygen levels were always far from anoxia and compatible with the physiological requirements of the rotifer species. The oxygen content in 2003, generally lower and with a more pronounced drop than that in 1996, could be attributed to increased input of allochthonous organic matter due to a heavy rain that occurred the day before the sampling date. Under such conditions, the organic matter can deplete oxygen concentrations quickly, but at the same time, it constitutes an important food source for certain rotifer populations. Therefore, probably, rotifer species in such situations did not respond to changes in oxygen levels but to food availability.

In both years, species composition of rotifers was similar, just as in other lakes (Miracle & Armengol, 1995; Armengol *et al.*, 1998), but the order of dominance and overall densities of species
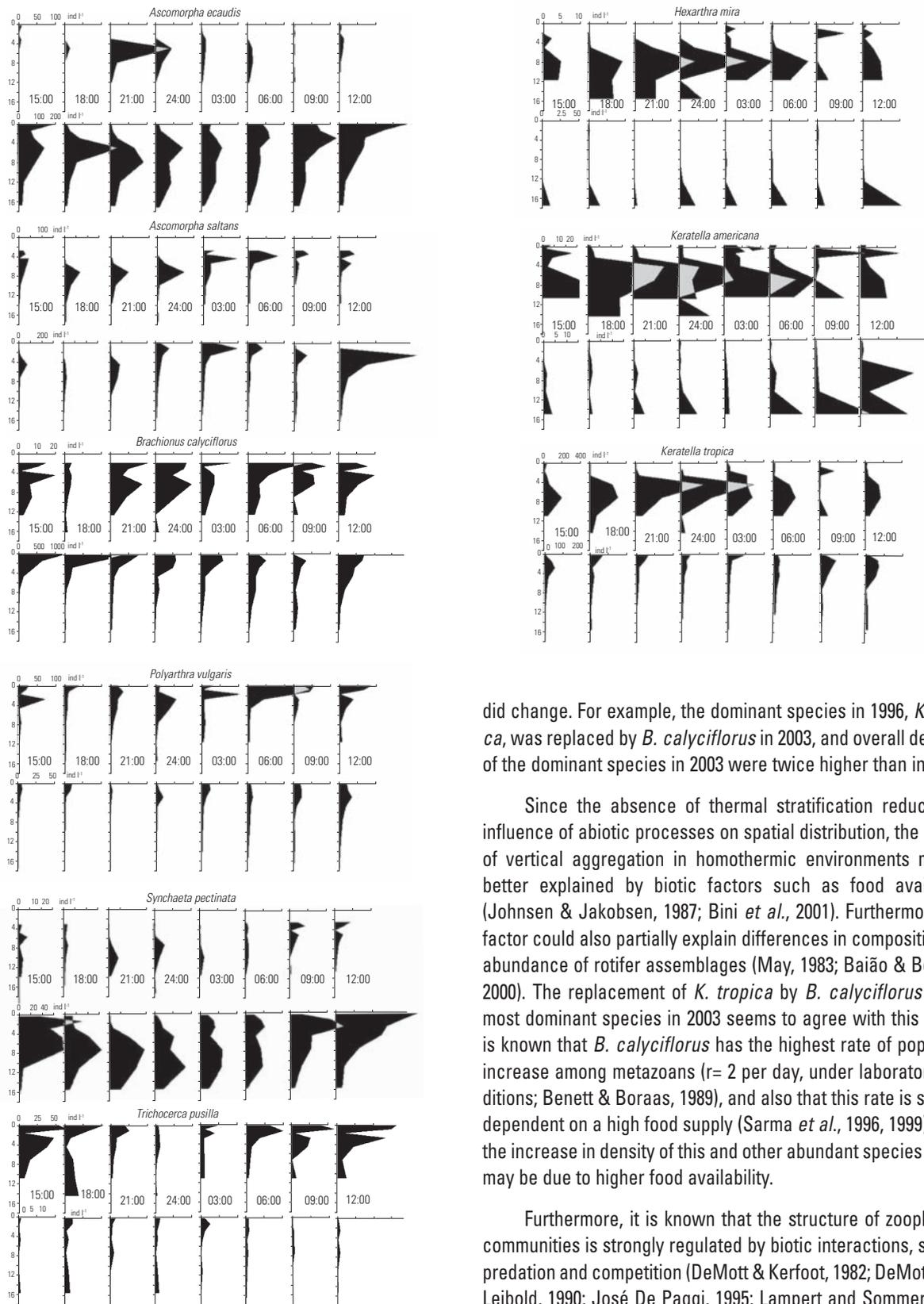
Fig. 3. Vertical distribution of the main rotifer species of Laguna Escondida, Mexico along two diel cycles. In each case, 1996 is the upper panel and 2003 the lower. Vertical axes refer to depth, in meters.

did change. For example, the dominant species in 1996, *K. tropica*, was replaced by *B. calyciflorus* in 2003, and overall densities of the dominant species in 2003 were twice higher than in 1996.

Since the absence of thermal stratification reduces the influence of abiotic processes on spatial distribution, the degree of vertical aggregation in homothermic environments may be better explained by biotic factors such as food availability (Johnsen & Jakobsen, 1987; Bini *et al.*, 2001). Furthermore, this factor could also partially explain differences in composition and abundance of rotifer assemblages (May, 1983; Baião & Boavida, 2000). The replacement of *K. tropica* by *B. calyciflorus* as the most dominant species in 2003 seems to agree with this idea. It is known that *B. calyciflorus* has the highest rate of population increase among metazoans (r= 2 per day, under laboratory conditions; Benett & Boraas, 1989), and also that this rate is strongly dependent on a high food supply (Sarma *et al.*, 1996, 1999). Thus, the increase in density of this and other abundant species in 2003 may be due to higher food availability.

Furthermore, it is known that the structure of zooplankton communities is strongly regulated by biotic interactions, such as predation and competition (DeMott & Kerfoot, 1982; DeMott, 1989; Leibold, 1990; José De Paggi, 1995; Lampert and Sommer, 1997). Moreover, habitat segregation would be an important mechanism that allows the coexistence of potential competitors (Schoener, 1974; Leibold, 1990, 1991). In Laguna Escondida *A. ecaudis* and

Table 2. Amplitude and type of migration of the dominant rotifer species in Laguna Escondida, Mexico, in the two sampling dates.

| Species | Amplitude (m) and type of migration | | | |
	1996		2003	
Ascomorpha ecaudis	4.19	normal	4.29	reversed
Ascomorpha saltans	4.90	reversed	5.18	normal
Brachionus calyciflorus	2.05	not clear	3.12	not clear
Hexarthra mira	6.42	not clear	2.95	twilight ?
Keratella americana	3.28	reversed ?	5.90	not clear
Keratella tropica	2.45	not clear	1.79	not clear
Polyarthra vulgaris	2.52	reversed	1.72	not clear
Synchaeta pectinata	5.73	reversed	6.14	reversed
Trichocerca pusilla	2.65	not clear	3.53	not clear
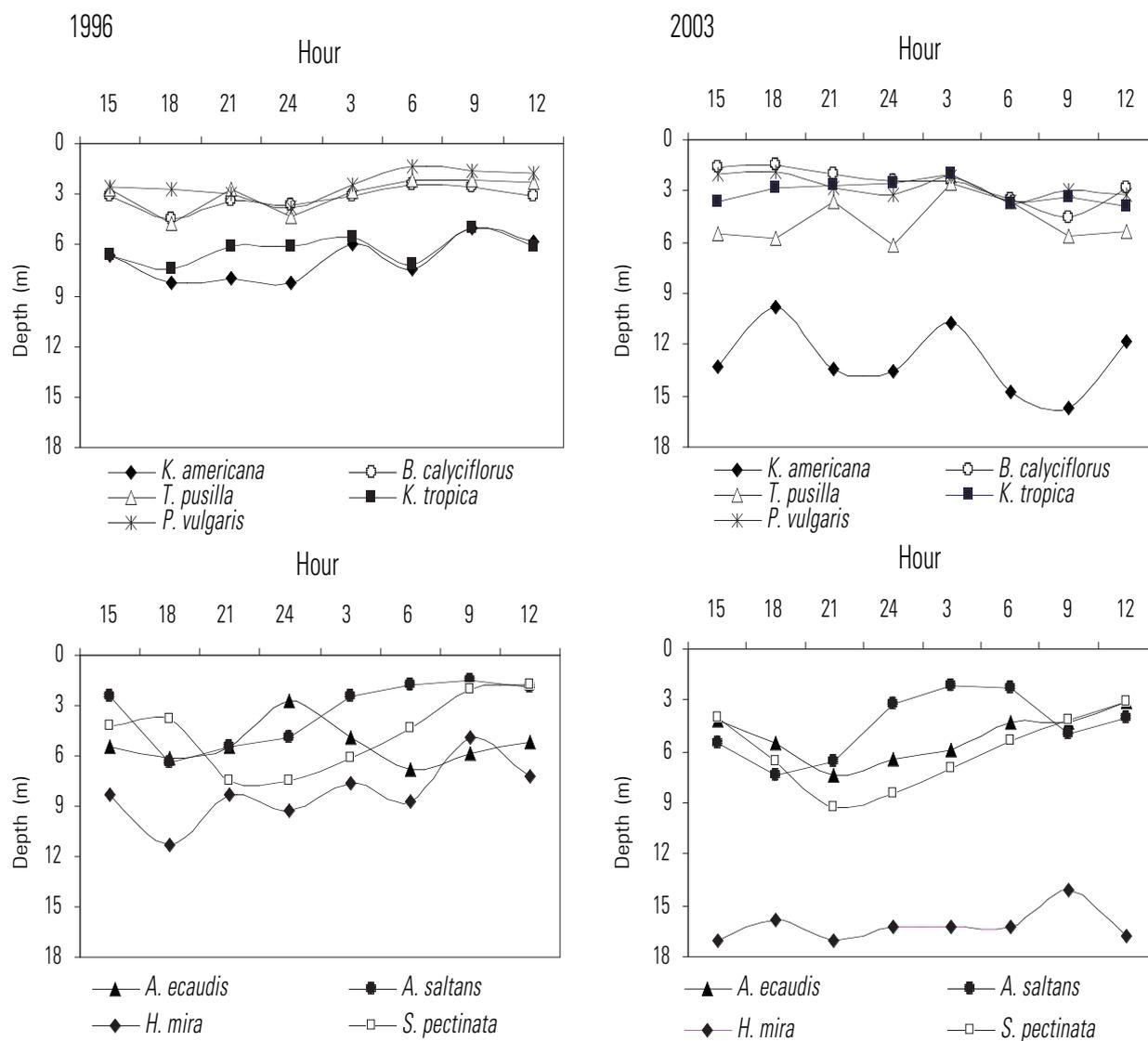
Fig. 4. Mean residence depth of dominant rotifer species of Laguna Escondida, Mexico in two diel cycles (1996 and 2003).

S. pectinata, that are of similar size and share the same feeding strategy (both are raptors that suck out the cytoplasm of their preys: Nogrady *et al.*, 1993; Ruttner-Kolisko, 1974), showed DVM patterns suggesting they would avoid interspecific competition by means of space-time segregation (Fig. 4).

The rotifers of Laguna Escondida share the water column with crustacean zooplankters like the copepods *Thermocyclops inversus* Kiefer, 1936, and *Tropocyclops prasinus* (Fischer, 1860), and the cladocerans *Moina micrura* Kurz, 1874, and *Daphnia parvula* Fordice,1901, which also migrate (Torres-Orozco & Estrada-Hernández, 1997). Therefore, interference or exploitative competition between rotifers and some of these species would be expected. Regarding predation, the lake is inhabited by important populations of poecillid fishes of the genera *Xiphophorus*, *Poecilia*, *Heterandria* and *Priapella,* as well as some species of *Astyanax* and *Cichlasoma* (Torres-Orozco & Estrada-Hernández, 1997) that, indeed, can prey on rotifers. Thus, the presence of these predators could also play a significant role in the rotifers' population dynamics.

The three basic types of migration, i.e., nocturnal or "normal" migration, twilight migration, and reversed migration (Hutchinson, 1967), were recognized in the diel vertical movements of dominant rotifers (Fig. 4; Table 2). Nevertheless, some species showed important differences in their migration patterns. Thus, *Ascomorpha ecaudis* changed its migratory movements from a normal type in 1996 to a reversed type in 2003. Although less clearly, *A. saltans* showed also a shift but in this case from a reversed type in 1996 to the normal type in 2003. Even though the migration patterns of some species were not easily assignable to a certain type, in most cases they appeared to be of the reversed type. In *Synchaeta pectinata*, the reversed type of migration was clear and consistent in both years (Fig. 4).

In the preferential position (i. e. MRD's) of rotifers along the water column, three different species categories could be recognized: a) species with relatively small vertical movements in the upper water column (e.g. *B. calyciflorus*, *P. vulgaris* and *T. pusilla*), b) species with noticeable movements between the middle and upper portions of the water column (e.g.: *Ascomorpha ecaudis*, *A. saltans* and *S. pectinata*) and, c) species with variable vertical displacements associated to deeper waters (e.g.: *H. mira* and *K. americana*, mainly in 2003). However, our results show that each species' habitat is a dynamic feature that may change with time. Examples are *H. mira* and *K. americana*, whose preferential positions moved to higher depths in 2003, or of *T. pusilla* and *K. tropica* that, although remaining in the same category, changed significantly their MRD in the two studied years. It is noteworthy that in contrast with Armengol and Miracle (2000), who found *H. mira* in the well-oxygenated surface waters of a Spanish lake, we in 2003 found this species inhabiting water layers close to the bottom, where oxygen levels were the lowest recorded (3.2 ± 0.57 mg l^{-1}).

The migration amplitudes observed for some species also differed from those reported in other lakes. Armengol and Miracle (2000), for example, found relatively low values for *A. saltans*, *H. mira* and *S. pectinata* (2.0, 2.5 and 1.3 m, respectively), whereas we observed notably higher values for these species (see Table 2). In addition, for *S. pectinata* they reported a normal migration type while, in our study, it was a clearly reversed one.

In summary, when comparing rotifer assemblages from different years with similar abiotic conditions, important differences became discernible in: a) the absolute population densities, b) the species dominance ranking, c) the preferential position of specific species in the water column, d) the relationship between such preference and the abiotic factors and, e) the types and amplitudes of their migrations. So, our working hypothesis was not supported by our data. The behavioral plasticity observed herein could be better explained with arguments of biological nature, but there are required further research efforts to unveil the actual role of biological interactions in the structuring of rotifer communities.

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