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Impact of Environmental Variables and Food Availability on Rotifer Assemblage in the Karstic Barrage Lake Visovac (Krka River, Croatia)

key words: karstic riverine lake, rotifer density and diversity, macrofilter-feeder rotifer, microfilter-feeder rotifer

Abstract

We evaluated the impact of 18 environmental variables (physico-chemical, nutrients, food resources) on rotifer assemblage in the sub-Mediterranean karstic barrage Lake Visovac. In terms of the space-time distribution the highest density of rotifers was noted in the summer period (average 386 ind/l, relative annual abundance 62%), and in the epilimnetic layer (average 309 ind/l, relative annual abundance 58%). A total of 41 rotifer taxa belonging to 22 genera and 14 families were identified. Three rotifer species: *Gastropus stylifer*, *Synchaeta tremula* and *Trichocerca birostris* were dominant and perennial during the annual investigation. Pearson's product-moment correlations and canonical correlation analysis suggest that temperature, pH values, alkalinity, chemical oxygen demand and chlorophyll *a* concentration significantly influenced rotifer density. According to rotifer food collection and selection, in Visovac Lake macrofilter-feeders predominated, and microfilter-feeders were in a minority.

1. Introduction

Many recent studies have established the relationship between the plankton community density and diversity and limnological characteristics of different water body types, for instance: floodplains (de Azevedo and Bonecker, 2003), backwaters (Arora and Mehra, 2003), riverine lakes (Eckert and Walz, 1998; Walz and Welker, 1998; Fernández-Rosado and Lucena, 2001), karstic lakes (Habdija *et al.*, 1993; Miracle and Alfonso, 1993; Rodrigo *et al.*, 2000).

Lake Visovac is a lentic dilatation of the Krka River and is bounded by two barriers with impressive waterfalls, Roški slap to the north and Skradinski buk to the south. With respect to the origin of the lake basin, Visovac Lake belongs to a group of karstic barrage lakes (Hutchinson, 1957). Water flowing through the karstic area precipitates calcite (limestone), which creates different sedimentary forms, one of them being barriers.

According to field investigations and experimental laboratory studies provided by many authors, rotifer distribution in lakes is related to both abiotic factors, such as temperature (Bçrzinš and Pejler, 1989; Watanabe, 1992), oxygen content (Miracle and Armengol-Díaz, 1995), pH values (Bērzinš and Pejler, 1987), light intensity (Saunders-Davies, 1989), and to biotic factors, such as food availability (Pourriot, 1977; Gilbert and Bogdan, 1981; Bogdan and Gilbert, 1987; Arndt, 1993; Habdija *et al.*, 1993), exploitative

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competition (Gilbert, 1985; 1990; Kirk, 1991), interference competition (Gilbert and Stemberger, 1985; Burns and Gilbert, 1986) and predation (Stemberger and Gilbert, 1985).

According to Kirk (2002), rotifers show a gleaner-opportunistic trade-off. With such characteristics, they are able to adapt quickly to changing and fluctuating physico-chemical and hydrological conditions, which exist in barrage lakes. Thus, in freshwater communities rotifers make up more than 50% of zooplankton productivity (Herzig, 1987; Walz, 1995) and are an essential component in the freshwater plankton food web. Because of their high food and assimilation efficiency and high reproductive rate, the role of the rotifers is very important in organic matter cycling and energy flow in the freshwater plankton community (Ruttner-Kolisko, 1972; Pourriot, 1977; Gilbert and Bogdan, 1981; Bogdan and Gilbert, 1987; Sanders *et al.*, 1989; Arndt, 1993; Fernández-Rosado and Lucena, 2001).

Until this study, performed in 1995–1996, no specific study had been carried out on the zooplankton of Visovac Lake. The only existing available data relate to occasional samples. We evaluate our hypothesis in a few directions: (i) seasonal and temporal rotifer community structure in the karstic barrage Lake Visovac is related to temperature and factors responsible for the water buffer system; (ii) rotifer community structure depends on food availability; (iii) rotifer community structure in Visovac Lake is characteristic of riverine lakes in the karstic Mediterranean area.

2. Materials and Methods

2.1. Study Site

The investigation was carried out in the area of the Krka National Park (Croatia), located in the SW Dinarid mountains, 22 km from the Adriatic coast. The most important rock of this area is the Quaternary sediment travertine. The Krka River rises NE of Knin: it is a sinking river, 72 km in length, with a watershed area of 270 km^2 in winter and 187 km^2 in summer. In the south, Visovac Lake is fed from the left bank Čikola River, the largest tributary of the Krka River.

The investigated vertical profile K1 was situated close to the left bank of the lake, between Cape Jelinjak and Peralište Bay (Fig. 1, Table 1). In this area, lake depth is 25 m.

2.2. Methods

We considered physico-chemical variables, and rotifer density in their spatial and temporal distribution. In the temporal distribution, we distinguished four seasons: spring (April–June), summer (July–September), autumn (October–December), winter (February, March). The samples for January were not collected.

2.2.1. Zooplankton Collection and Counting

Zooplankton samples were collected monthly, from April 1995 until March 1996, between 9 and 11 hours GMT, using an electric immersed pump (Omega, Q = 50 l/min) from a boat. Water was pumped

Table 1. Morphometric data of Lake Visovac.

Altitude (m)	32
Surface area (km^2)	7.9
Maximum length (km)	13.5
Maximum width (m)	750
Maximum depth (m)	25

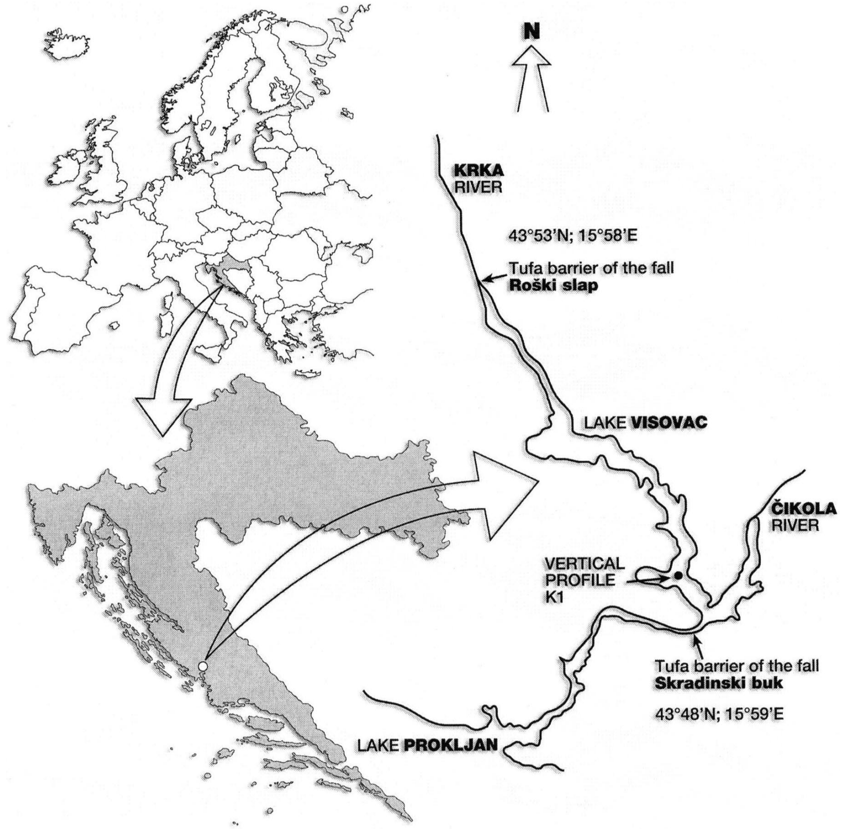


Figure 1. Location of the study area with the investigated vertical profile marked K1.

from the depths of 1, 2, 5, 10, 15 and 20 m. Throughout the investigated period, we collected 66 water samples. From all the depths, volumes of 30 l were filtered through a 36 μm mesh net. The samples were kept cool and transported to the laboratory in 200 ml bottles.

Identification was carried out on living material, which was later fixed in 4% formaldehyde. Rotifers were identified according to VOIGT and KOSTE (1978) up to species or genus level, and enumerated using a Sedgewick-Rafter cell under an inverted microscope Opton-Axiovert 35. Bdelloidea were counted, but not identified. The densities of *Polyarthra dolichoptera* and *P. vulgaris* were aggregated as one category because of the difficulties in distinguishing these close species during the counting.

2.2.2. Abiotic Variables

The general chemical parameters of the water, such as alkalinity, total hardness, soluble reactive phosphorous (SRP) or orto-phosphate (PO_4^{3-}-P), total phosphorous (TP) and total nitrogen (TN) were analysed according to APHA (1985). Particulate phosphorous (PP) was obtained as the difference between TP and SRP. Ammonium was determined spectrophotometrically by the method of WAGNER (HRN ISO, 1984), while nitrite was determined by the method with sulphanilic acid and α-naphtylamine, and nitrate by dimethyphenol (HOELL, 1968). In the present study, the ammonium (NH_4-N), nitrite (NO_2-N) and nitrate (NO_3-N) concentrations were aggregated and considered as dissolved inorganic nitrogen (DIN).

A field spectrophotometer (HACH, Model DR2000) was used for the spectrophotometric measurement and field instruments were employed for the determination of the values of temperature and the oxygen concentrations (WTW OXI 96), pH (Model MA 5750) and electrical conductivity (Model MA 5950).

Data for discharge were obtained from the State Meteorological and Hydrological Service.

Water transparency was determined by Secchi disc.

2.2.3. Food Resources

According to their food-collecting mechanisms and the size of food particles, rotifers can be classified with respect to feeding types (KARABIN, 1985). Species of the first type feed partly or exclusively on bacteria-detritus suspension and nanophytoplankton (particles ≤20 μm), and constitute the microfilter-feeders, for instance: *Anuraeopsis fissa*, *Keratella cochlearis*, *Filinia longiseta*, *Keratella quadrata*. Species of the second type feed on nanophytoplankton too, but mainly on net algae (filamentous algae, dinoflagellates), and sometimes on animal food as well (particles 20 to ≥50 μm) and represent macrofilter-feeders: species of the genera *Trichocerca*, *Synchaeta*, *Polyarthra*, *Ascomorpha*, *Gastropus*. Predator species were represented by *Asplanchna priodonta* in a low density, and for this reason this trophic group will not be considered in this study.

We used chlorophyll *a* concentration data as an indicator of the phytoplankton component, which is the main food for macrofilter-feeders. For microfilter-feeders we used data on heterotrophic bacteria and chemical oxygen demand, $COD_{(KMnO4)}$, as an indicator of organic matter.

For the calculation of chlorophyll *a* (Chl *a*) ethanol extraction was used according to NUSCH (1980). Heterotrophic bacteria were analysed by the spread plate method, after serial dilution of samples. Colony forming units (CFU) were counted after incubation at 22°C/72 h (APHA, 1985). Chemical oxygen demand (COD) was measured by the oxidation of dissolved organic matter, in a sample of a known volume, using $KMnO_4$ (results expressed as mg O_2/l).

2.2.4. Data Analysis

Species diversity (H') was calculated by the Shannon-Wiener's index (SHANNON and WEAVER, 1949). The index of domination was evaluated according to KOWNACKA and KOWNACKI (1972):

$$d_{a1} = a_1 100/a_n \times n/N$$

where d_{a1} = domination index for species a_1, a_1 = average density for species a_1, a_n = average density of total number of individuals for specific depth or season, n = number of samples with species a_1, N = total number of samples.

For estimating the correlation between rotifer density and independent variables (environmental variables and food availability), Pearson product-moment correlation coefficients were estimated throughout.

Nonparametric Kruskal-Wallis (for correlation between many independent variables) and Mann-Whitney U test (for correlation between two variables) were used for establishing the significant differences between the temporal (spring, summer, autumn, winter) and spatial distribution (epilimnion, metalimnion, hypolimnion) of rotifer density. The similarity among lakes in temperate and Mediterranean karstic area according to dominant rotifer species was determinated using cluster analysis. The tree clustering and complete linkage methods were based on Euclidean distance as a distance measure. For Pearson's product-moment correlation coefficients, cluster analysis and nonparametric tests, STATISTICA package was employed (copyright©StatSoft).

For an explanation of the relationship between rotifer assemblage (densities of the 14 most abundant taxa) and environmental variables (temperature, oxygen content, pH, alkalinity, conductivity, free CO_2, Chl *a*, COD) a multivariate method, canonical correspondence analysis, CCA (TER BRAAK and VERDONSCHOT, 1995) was used. Rotifer density was logarithmically transformed [log (x + 1)] and centred prior to the analysis. Ordination axes represent the linear relationship between the dependent (rotifer density) and independent variables (physico-chemical factors). CCA was performed using PC-ORD, Multivariate analysis of ecological data, version 4 (MCCUNE and MEFFORD, 1999).

3. Results

3.1. Environmental Conditions

Water temperature. According to the annual cycle of thermal stratification, Lake Visovac has a monomictic regime (Fig. 2a). Vertical mixing began in November and lasted until March. A thermocline becomes established from June to October, with a maximum vertical difference of ca. 4 °C. During the year, water temperature varied as follows: spring 9.3–21.2 °C; summer 14.2–23.4 °C; autumn 18.3–9.4 °C; winter 6.5–10.5 °C. Maximum and minimum temperatures were 23.4 and 6.5 °C at the surface and lake bottom, respectively. The maximum difference in temperature between epilimnion and the hypolimnion was in August (9.2 °C).

Dissolved oxygen. During the winter and spring, the lake is well oxygenated, and concentrations of dissolved oxygen varied between 9 to 11 mg/l through the whole water column (Fig. 2b). In the summer, surface layers were still well oxygenated, apart from oxygen declines in the hypolimnetic layer. In August and September, we found a severe depletion near the bottom (around 1 mg O_2/l). At the beginning of the mixing period in autumn, oxygen concentrations were homogeneous through the whole water column (9 to 10 mg/l).

pH values and alkalinity. Water pH values ranged from neutral to slightly alkaline (7.3 to 8.2.). From April to October pH values were higher in the epilimnion than in the deeper layers and ranged from 7.9 to 8.2. During the clear water season pH decreased from 8.1 to 7.3 (Fig. 2c). Alkalinity values were mostly around 200 mg $CaCO_3$/l, and varied between 186 to 236 mg $CaCO_3$/l (Fig. 2d).

CO^2. From the epilimnion to the hypolimnion, the values of free CO_2 increased (Fig. 2e). Mean values of free carbon dioxide were 4.4 mg/l in the epilimnion and 10.6 mg/l in the hypolimnion.

Conductivity. Water conductivity fluctuated between 390 to 578 μS/cm (Fig. 2f). In the superficial water layer average conductivity values were slightly lower (500.4 μS/cm) than in the deeper layers (519.3 and 514.8 μS/cm). A significantly positive correlation was recorded between conductivity and nitrate salts ($r = 0.46$; $p = 0.00009$).

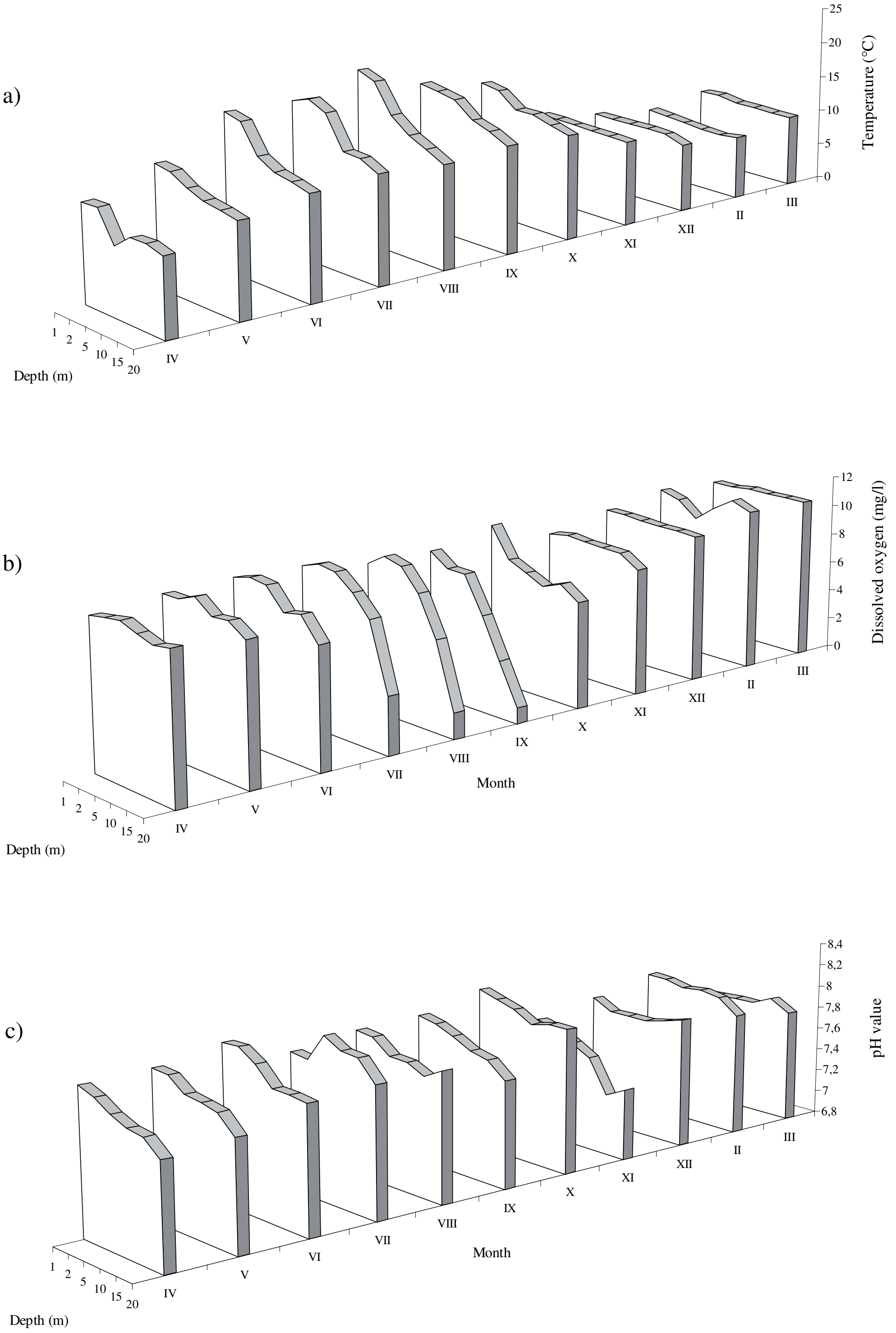
Discharge. Figure 3a shows daily discharge in the investigation period, which ranged from 13 to 306 m^3/s. The lowest mean seasonal discharge value was measured for the summer period (25 m^3/s).

Transparency. Secchi-disc transparency fluctuated between 2.5 to 8 m. There were higher average values in the summer/winter period than in autumn/spring (Fig. 3b).

3.2. Nutrients

Annual fluctuations of soluble reactive phosphorus (SRP), particulate phosphorus (PP) and total phosphorus (TP) are shown in Figures 4a–c. The concentrations of SRP were very low and ranged from 0.003 to 0.01 mg/l (without values at 20 m depth in June). Starting at the minimum during the clear water season in April, concentrations of SRP increased until August and decreased afterwards. For TP, lower values were also recorded in the epilimnion (mean 0.18 mg/l) and higher in the deeper water layers (mean 0.20 mg/L for both). The lowest concentrations, close to 0.01 mg/l were recorded in April and May, before phytoplankton and zooplankton growth. Higher mean concentrations of TP in the whole water column were recorded in the period from June to August (mean 0.27 mg/l). Spatial and temporal distribution for PP was the same as for TP.

Annual fluctuation of nitrogen salts are shown in Figures 5a–e. They were more concentrated in the hypolimnion, particularly the reduced nitrogen forms, ammonium and nitrites.


a)
Temperature (°C)
0
5
10
15
20
25
Depth (m)
1
2
5
10
15
20
IV
V
VI
VII
VIII
IX
X
XI
XII
II
III
b)
Dissolved oxygen (mg/l)
0
2
4
6
8
10
12
Depth (m)
1
2
5
10
15
20
IV
V
VI
VII
VIII
IX
X
XI
XII
II
III
Month
c)
pH value
6,8
7
7,2
7,4
7,6
7,8
8
8,2
8,4
Depth (m)
1
2
5
10
15
20
IV
V
VI
VII
VIII
IX
X
XI
XII
II
III
Month

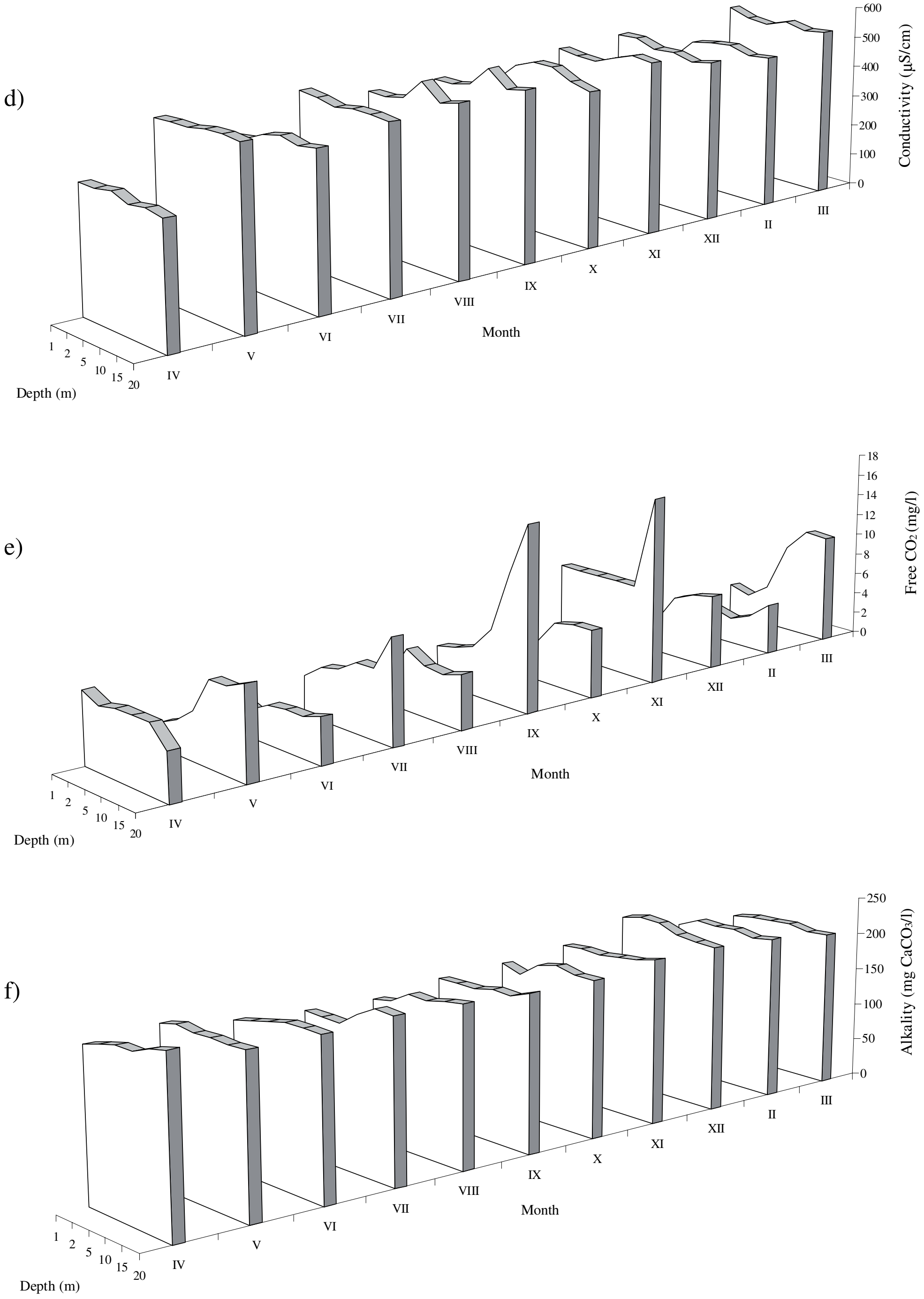


Figure 2. Environmental variables along the vertical profile K1 in Visovac Lake. Temperature (a), dissolved oxygen (b), pH-values (c), alkalinity (d), free CO_2 (e), conductivity (f).

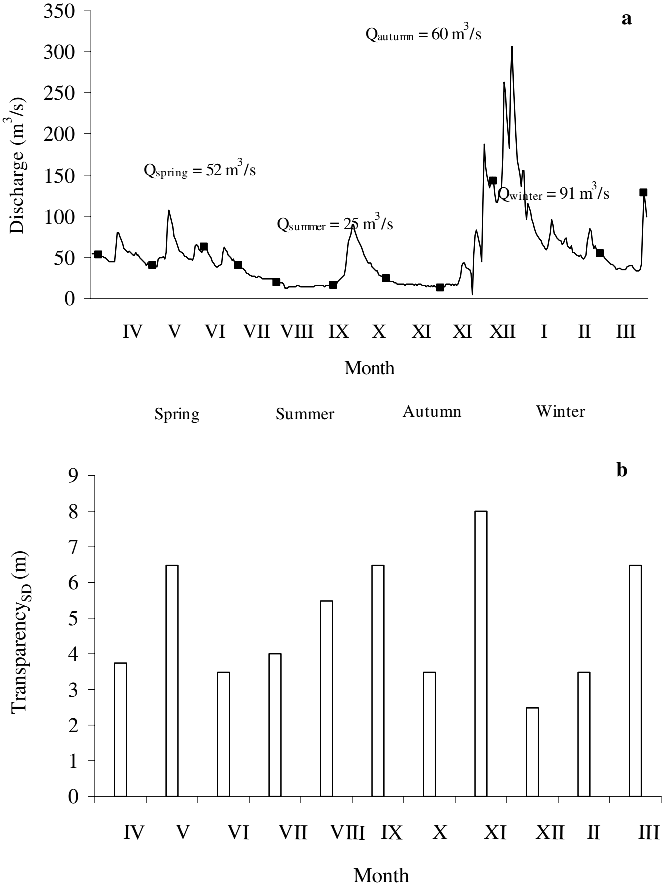


Figure 3. Daily changes in discharge in the riverine Visovac Lake during the investigation period with mean values for spring, summer, autumn and winter (a). Quadrangles mark sampling dates. Transparency$_{SD}$ of water along the vertical profile K1 (b).

3.3. Food Availability

Chl *a* concentrations in Visovac Lake were in general below 0.005 μg/l (Fig. 6a). The maximum Chl *a* value was observed at the beginning of autumn, reaching ca 0.007 μg/l, but the highest concentrations of Chl *a* were measured in spring in the superficial layers (average 0.002 μg/l).

Annual values of $COD_{(KMnO4)}$ varied between 2 to 6 mg O_2/l. Two COD peaks, 9 and 11 mg O_2/l, were recorded in surface layers during the clear water season (Fig. 6b).

Average CFU values were lower in spring and summer (93 CFU/ml) than in the autumn and winter period (287 and 320 CFU/ml) (Fig. 6c). The highest number of bacteria was near the bottom, at a depth of 20 m (annual average 283 CFU/ml).

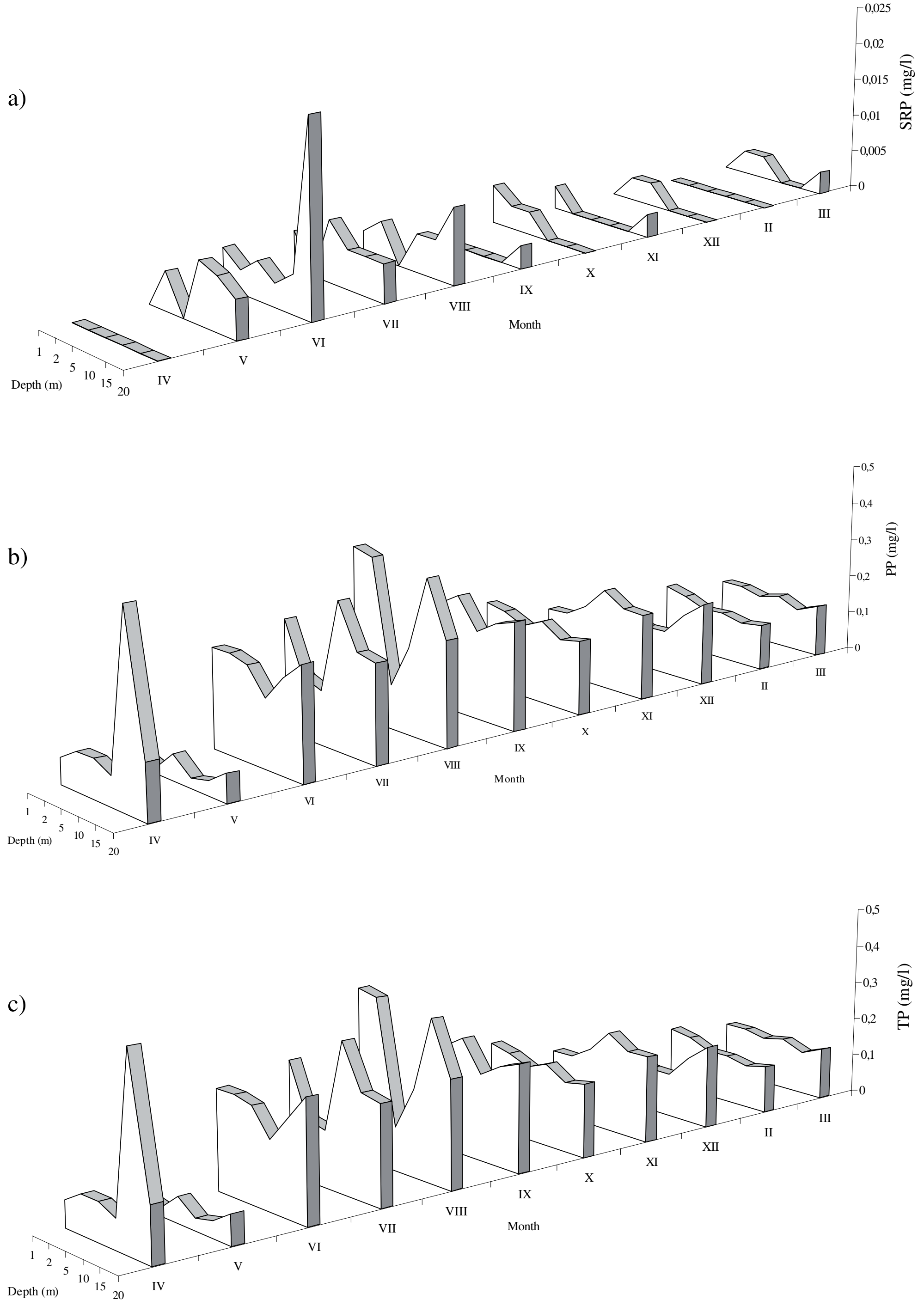
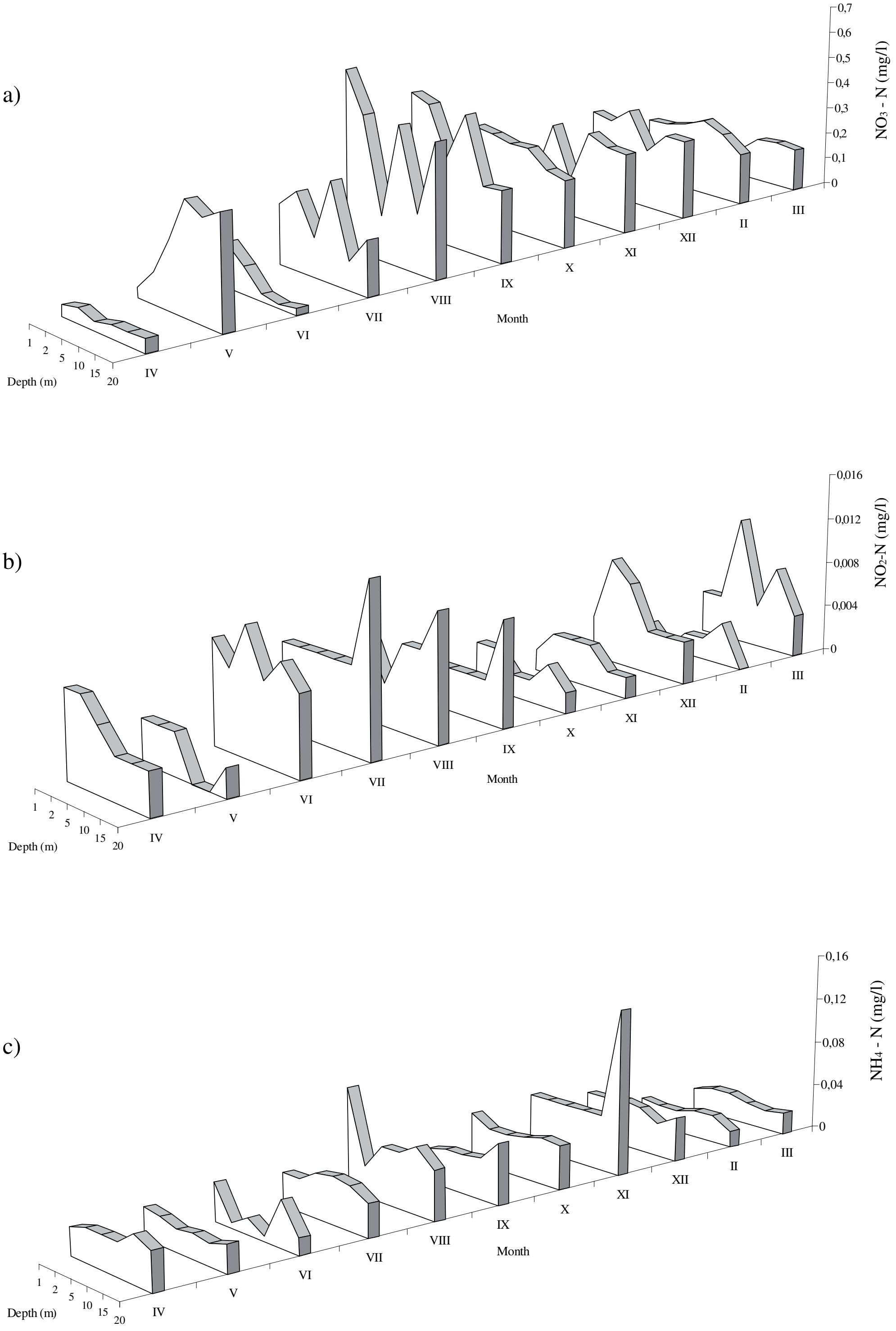


Figure 4. Available nutrients: SRP (a), PP (b) and TP (c) along the vertical profile K1 in Visovac Lake.


a)
0,7
0,6
0,5
0,4
0,3
0,2
0,1
0
NO3 - N (mg/l)
1
2
5
10
15
20
Depth (m)
IV
V
VI
VII
VIII
IX
X
XI
XII
II
III
Month
b)
0,016
0,012
0,008
0,004
0
NO2-N (mg/l)
1
2
5
10
15
20
Depth (m)
IV
V
VI
VII
VIII
IX
X
XI
XII
II
III
Month
c)
0,16
0,12
0,08
0,04
0
NH4 - N (mg/l)
1
2
5
10
15
20
Depth (m)
IV
V
VI
VII
VIII
IX
X
XI
XII
II
III
Month

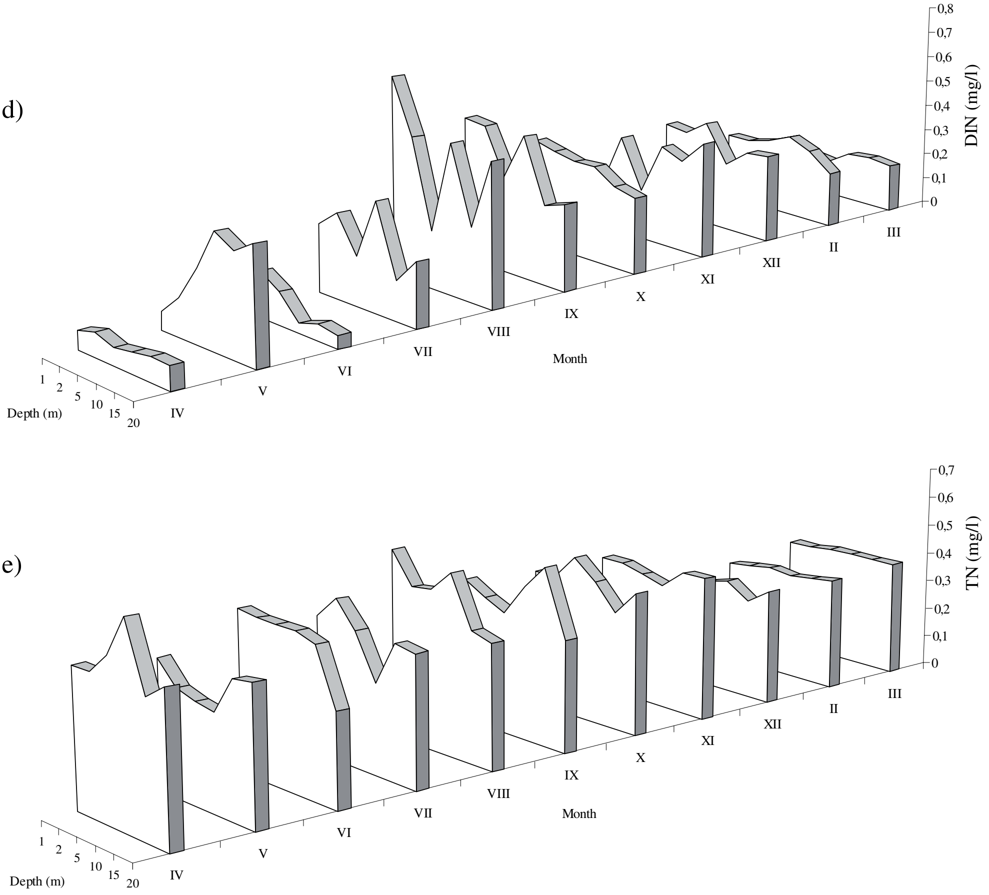


Figure 5. Available nutrients: NO_3-N(a), NO_2-N(b), NH_4-N(c), DIN (d) and TN (e) along the vertical profile K1 in Visovac Lake.

3.4. Species Diversity and Density

During the year-round study on the vertical profile K1, a total of 41 rotifer taxa belonging to 22 genera and 14 families were identified (Table 2). The highest number of species was recorded in the family Brachionidae (7). The Shannon-Wiener diversity index (H´) ranged from 0.5 to 4 (Fig. 7). The highest species diversity was reached in early spring and in winter, when rotifer density was the lowest. In the summer period the density of two species (*Gastropus stylifer*, *Trichocerca birostris*) was very high, and H´ values were the lowest. Rotifer density was significantly negatively related with H´ values ($r = -0.86$; $p = 0.0006$), and was slightly positively related with the number of species ($r = 0.6$; $p = 0.05$).

Figure 8 presents spatial and temporal distribution of the most common rotifer genera in Visovac Lake. Most of the taxa were euplanktonic, belonging to 12 genera (*Anuraeopsis*, *Ascomorpha*, *Asplanchna*, *Collotheca*, *Filinia*, *Gastropus*, *Keratella*, *Notholca*, *Polyarthra*, *Pompholyx*, *Synchaeta*, *Trichocerca*), and 9 genera were semiplanktonic (*Brachionus*, *Cephalodella*, *Colurella*, *Euchlanis*, *Lecane*, *Mytilina*, *Monommata*, *Testudinella*, *Tricho-*

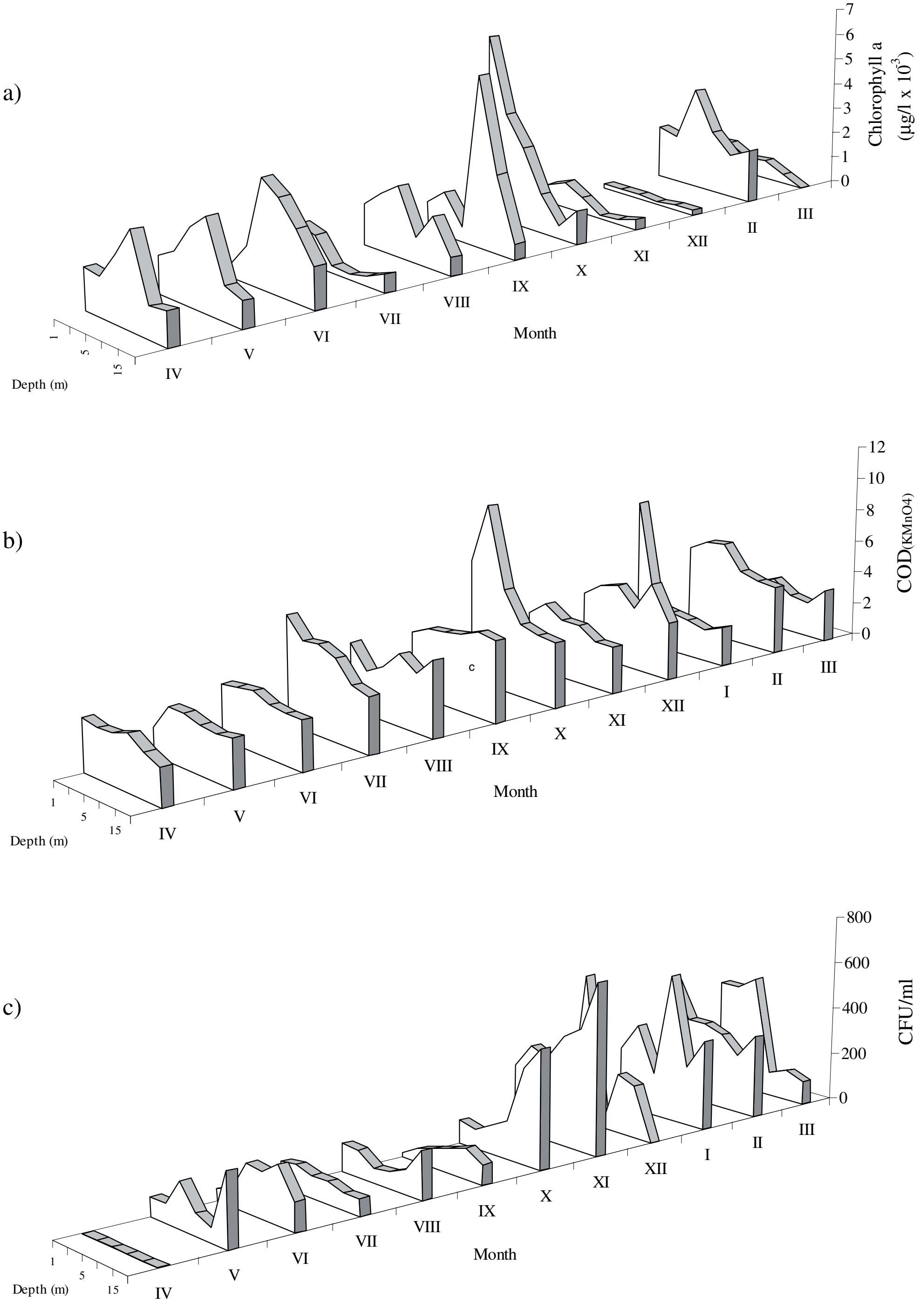


Figure 6. Food resources: Chl *a* (a), COD (b), CFU (c) in Lake Visovac along the vertical profile K1.

Table 2. Rotifer taxa recorded in Lake Visovac

Family: BRACHIONIDAE
Anuraeopsis fissa (Gosse, 1851)
Brachionus angularis Gosse, 1851
Brachionus quadridentatus Hermann, 1783
Keratella cochlearis (Gosse, 1851)
Keratella quadrata (Mueller, 1786)
Notholca acuminata (Ehrb., 1832)
Notholca foliacea (Ehrb., 1838)

Family: EUCHLANIDAE
Euchlanis dilatata Ehrb., 1832

Family: MYTILINIDAE
Mytilina ventralis (Ehrb., 1832)

Family: TRICHOTRIDAE
Trichotria pocillum (O. F. M., 1776)
Trichotria tetractis (Ehrb., 1830)

Family: COLURELLIDAE
Colurella obtusa (Gosse, 1886)
Colurella uncinata (O. F. M. 1773)
Lepadella ehrenbergi (Perty, 1850)
Lepadella patella (O. F. M., 1786*)*

Family: LECANIDE
Lecane flexilis (Gosse, 1889)
Lecane luna (Mueller, 1776)
Lecane lunaris (Ehrb., 1832)

Family: NOTOMMATIDAE
Cephalodella gibba (Ehrb., 1832)
Cephalodella spp.
Monommata aequalis (Ehrb., 1832)

Family: TRICHOCERCIDAE
Trichocerca birostris (Minkiewicz, 1900)
Trichocerca elongata (Gosse, 1886)
Trichocerca sp.

Family: GASTROPODIDAE
Ascomorpha ecaudis Perty, 1850
Ascomorpha ovalis (Bergendahl, 1892)
Gastropus stylifer Imhof, 1891

Family: SYNCHAETIDAE
Polyarthra dolichoptera Idelson, 1925
Polyarthra vulgaris Carlin, 1943
Synchaeta pectinata Ehrb., 1832
Synchaeta stylata Wierzejski, 1893
Synchaeta tremula (O. F. M., 1786)

Family: ASPLANCHNIDAE
Asplanchna priodonta Gosse, 1850

Family: TESTUDINELLIDAE
Testudinella patina (Hermann, 1783)
Pompholyx complanata Gosse, 1851

Family: FILINIIDAE
Filinia longiseta (Ehrb., 1834)

Family: COLLOTHECIDAE
Collotheca mutabilis (Hudson, 1885)

tria). Species of semiplanktonic genera were present in very low densities, while euplanktonic genera accounted for most of the rotifer density.

In temporal distribution, rotifers reached the peak of their density in the summer period (average for summer period 386 ind/l), and remained high in autumn (average 382 ind/l). Without *Synchaeta*, autumnal maximum of rotifers in the epilimnion reached only half of their summer values (average 191 ind/l). At the beginning and end of the annual cycle, in spring and winter, the density of rotifers was low, with average values of 22 and 15 ind/l, respectively. During the investigation period the highest rotifer densitiy was observed in October, at a depth of 1 m, 4574 ind/l, and densities higher than a thousand individuals per litre were noted twice: at a depth of 2 m in August, 1606 ind/l and in October, 1477 ind/l (Fig. 9a). During the rest of the annual cycle rotifer density varied from 0.3 ind/l (February) to 806 ind/l (August).

In spatial distribution during the year-round study, rotifer relative abundance reached a maximum in the epilimnion (58%). In deeper water layers, their relative abundance decreased, in water layer between 10 and 15 m depth to 32%, and downwards to 10%.

According to the Kruskal-Wallis test, there were no significant differences in the spatial distribution of rotifer density. In seasonal distribution, rotifer densities were significantly dif-

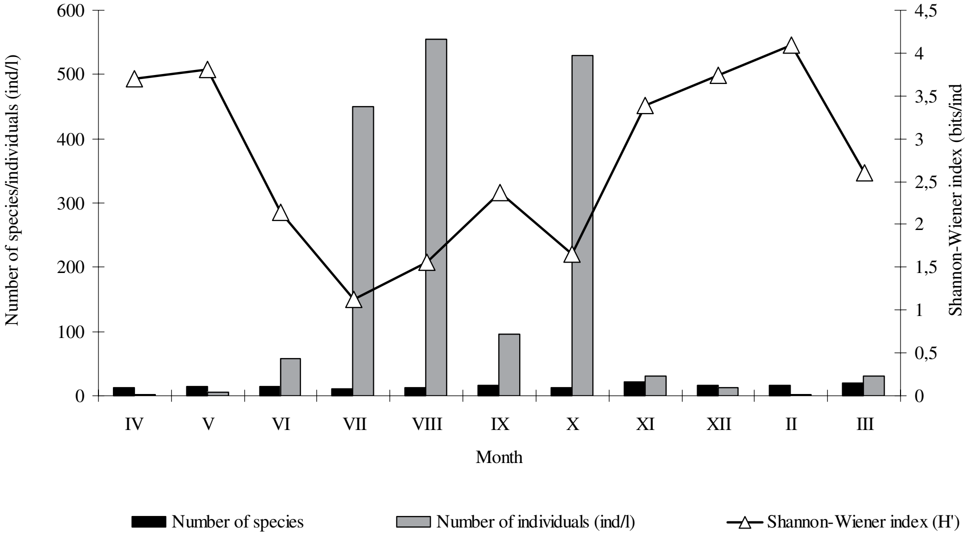


Figure 7. Recorded variation between species diversity index (H′), number of rotifer species and density (average density for vertical profile, each month).

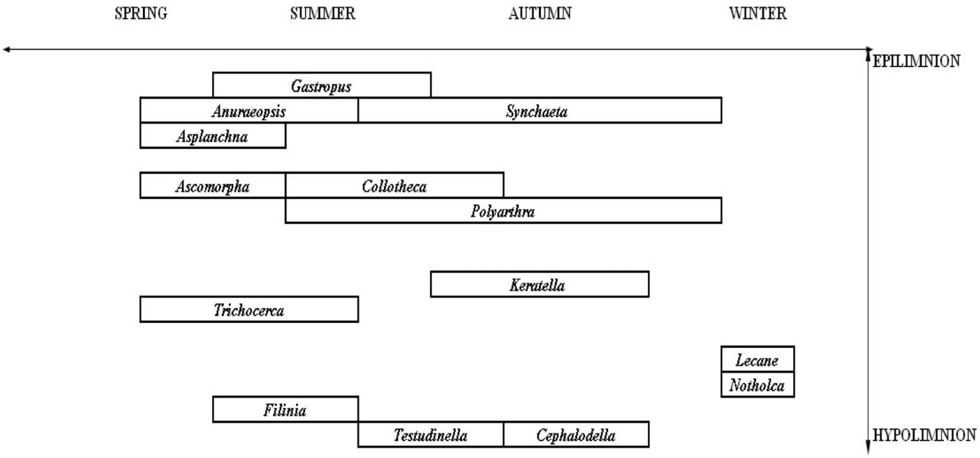
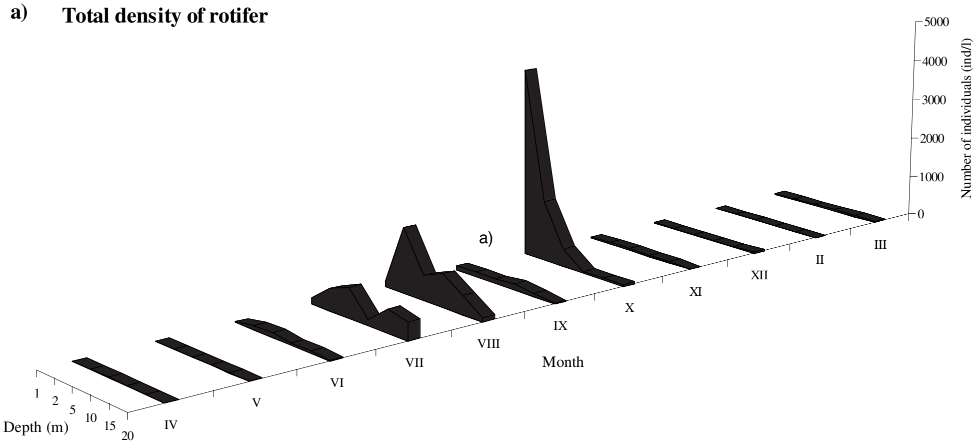


Figure 8. Spatial and temporal distribution of the most common rotifer genera in Visovac Lake.

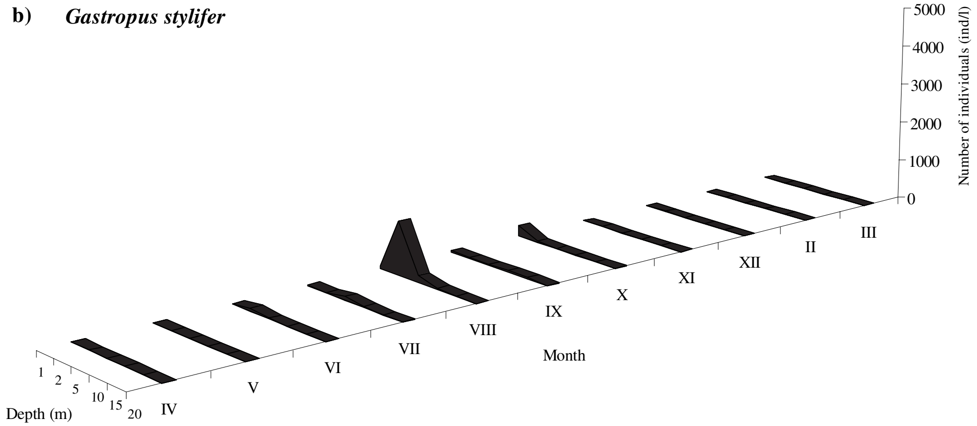
ferent between the seasons (Mann-Whitney U test; $p < 0.05$), except between autumn and winter, when rotifer densities were not significantly different (Mann-Whitney U test; $p = 0.37$).

For estimating the correlation between rotifer density and 18 independent variables, the Pearson product-moment correlation coefficients were estimated throughout (Table 3). Rotifer density was significantly positively related with temperature, pH, Chl *a* and $COD_{(KMnO4)}$, and inversely and significantly related with alkalinity.

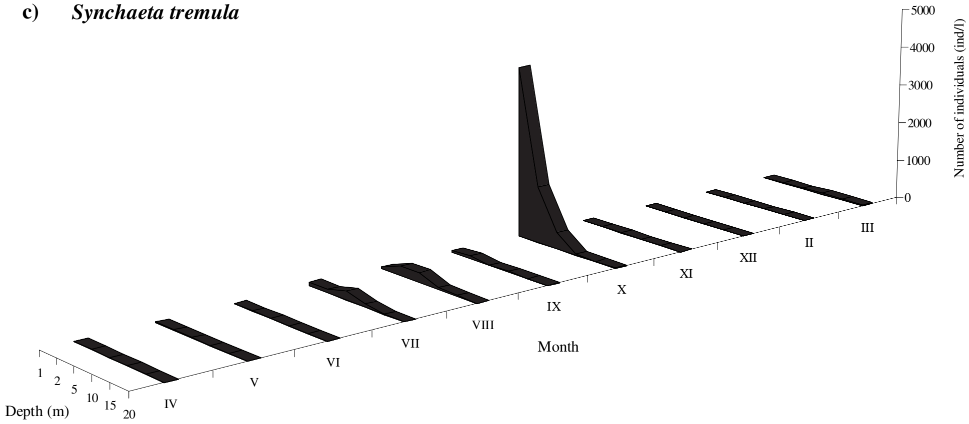
a) **Total density of rotifer**



b) ***Gastropus stylifer***



c) ***Synchaeta tremula***



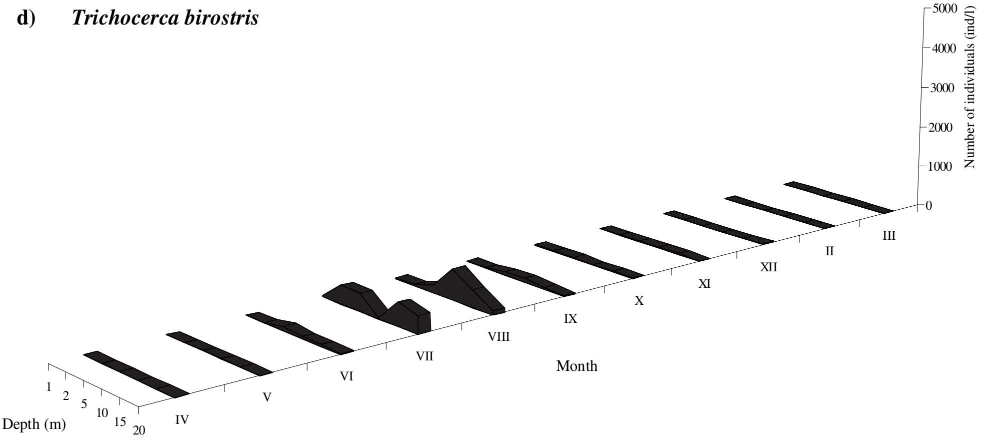

d) *Trichocerca birostris*

Figure 9. Seasonal dynamics of total rotifer density (a) and population density of species *Gastropus stylifer* (b), *Synchaeta tremula* (c) and *Trichocerca birostris* (d).

In relation to temperature, most of the present species were eurythermous (*K. cochlearis*, *K. quadrata*, *A. priodonta, T. birostris*). In spring and autumn *Ascomorpha ecaudis*, *Pompholyx* sp., *Filinia longiseta* and *S. tremula* appeared. In summer appeared warm stenothermous species such as *Anuraeopsis fissa*, *Collotheca mutabilis*, *G. stylifer*, and in winter or early spring cold stenothermous species *Notholca acuminata* and *N. foliacea* (Fig. 8).

In addition, analysis of domination showed that three rotifer species: *Synchaeta tremula*, *Gastropus stylifer* and *Trichocerca birostris*, were perennial and dominant. These species always constituted 85 to 99% of the total rotifer abundance, and we will consider these further.

Gastropus stylifer was characteristic of the epilimnion in the warmer period of the year (Fig. 9b). We argue this for two reasons. Firstly, its highest value of index of domination (43) was reached in the epilimnion in summer. Secondly, the epilimnion was the location for 84% of the total annual density of *G. stylifer*, while downwards its density decreased from 13% to 3%. The highest density of *Gastropus* was reached in August, at a depth of 2 m (1339 ind/l). In autumn, the density of *G. stylifer* was seven times lower than in summer, and in winter, its population density decreased markedly to just a few individuals per litre of lake water. The density of *G. stylifer* was significantly positively associated with temperature ($r = 0.35$; $p = 0.008$) and TP ($r = 0.35$; $p = 0.006$), but significantly negatively related to alkalinity ($r = -0.32$; $p = 0.01$) and hardness ($r = 0.27$; $p = 0.04$).

Synchaeta tremula reached the highest relative abundance in the superficial water layers up to 5 m depth (89% of total annual values) with an annual peak of 4296 ind/l at a depth of 1 m in October (Fig. 9c). Its lowest density was observed in spring. According to the results, this species characterised the superficial water layers in the colder period of the year. For instance, *S. tremula* showed very high values for the index of domination in the epilimnion in autumn (93), and in the deeper water layer in winter (94). Pearson's correlation index suggested a significant positive correlation between *S. tremula* density and Chl *a* ($r = 0.56$; $p = 0.000007$), $\mathrm{COD}_{(\mathrm{KMnO4})}$ ($r = 0.50$; $p = 0.00008$) and pH ($r = 0.29$; $p = 0.03$).

The highest relative abundance of *Trichocerca birostris* was recorded in the deeper water layers (57%). In general, this species is characteristic of the metalimnetic-hypolimnetic layers in the warmer period of the year (Fig. 9d). In spring and summer, very high index of domination was noted for this species (83 to 95) in the metalimnion and hypolimnion. In the summer, the density of *T. birostris* increased and reached its annual maximum in August at the

Table 3. Pearson's product-moment correlation coefficients between rotifer density and limnological parameters.

Parameters	Number (ind/l)
Temperature	0.37**
Dissolved oxygen	0.04
pH	0.33**
Alkalinity	– 0.31**
Hardness	– 0.20
Conductivity	– 0.02
Dissolved CO_2	– 0.20
Orto-phosphate (SRP)	0.15
TP	0.20
PP	0.19
NH_4	0.08
NO_2^-	0.07
NO_3^-	0.21
DIN	0.22
TN	0.18
COD	0.44***
Chlorophyll *a*	0.50***
Bacteria	– 0.25

** $p < 0.01$; *** $p < 0.001$

depth of 10 m (731 ind/l). Very low density of *T. birostris* was recorded in autumn and winter in the whole water column. The density of *T. birostris* was related significantly positively ($r = 0.35$; $p = 0.0039$) to temperature, TP and nitrates.

Canonical correspondence analysis identified patterns of variation in the rotifer assemblage relative to environmental variables (Fig. 10). Axis 1 explained 17.5% of the species scores. The species-environmental correlation with axis 1 was 0.73. Axis 1 correlated well with oxygen content and temperature. In addition, axis 2 explained 10.2% of the variation in species score and correlated well with temperature, Chl *a*, pH and free CO_2. The species-environmental correlation to axis 2 was 0.80. According to the plot, temperature, pH, Chl *a* and oxygen content are positively related to the densities of species *G. stylifer, A. priodonta* and *S. tremula*. CCA suggested that alkalinity and free CO_2 positively influenced the taxa Bdelloidea, *Cephalodella gibba*, *K. cochlearis*, *Polyarthra dolichoptera/vulgaris*, but negatively influenced *G. stylifer*, *A. priodonta* and *S. tremula*. The direction of the arrow suggested that increase in temperature, pH and Chl *a* negatively affected the density of *K. quadrata*, *S. pectinata*, *N. acuminata* and *N. foliacea*.

3.5. Impact of Food Availability on Rotifer Community

According to the collection and selection of food particles most of the rotifer species were macrofilter-feeders (Fig. 11a). They always contributed up to 60% of the species in the whole water column during the one-year investigation. The three dominant and perennial species, *G. stylifer*, *S. tremula*, *T. birostris,* belong to the macrofilter-feeders group. The space-time distribution of this group was concentrated in the epilimnion, in summer. The annual peak of macrofilter-feeder density (4573 ind/l, in October, at a depth of 1 m) was coincident in 99.9% with the annual peak of total rotifer density and with the annual maxima of *S. tremula*. At that time, this species contributed 96% of the macrofilter-feeder relative abundance. The species *G. stylifer* and *S. tremula* occupied the epilimnetic layer, while

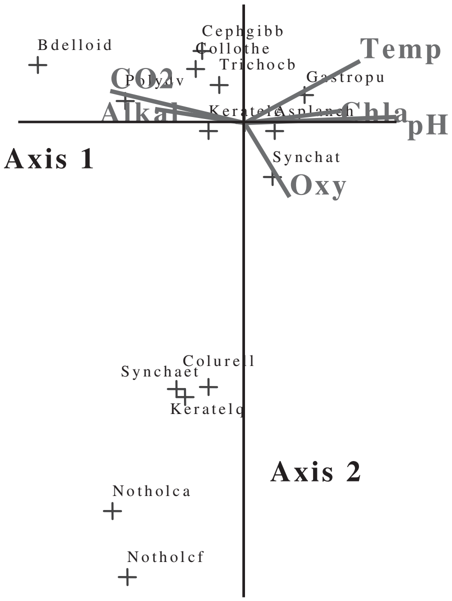


Figure 10. CCA plot of the main zooplankton species against environmental variables. Asplanch = *A. priodonta*; Bdelloid = Bdelloidea; Cephgibb = *C. gibba*; Collothe = *C. mutabilis*; Colurell = *C. obtusa*; Gastropu = *G. stylifer*; Keratelac = *K. cochlearis*; Keratelq = *K. quadrata*; Notholca = *N. acuminata*; Notholcf = *N. foliacea*; Polydv = *P. dolichoptera/vulgaris*; Synchat = *S. tremula*; Synchaet = *S. pectinata*; Trichocb = *T. birostris*.

T. birostris captured the metalimnetic and hypolimnetic layers. As shown in Table 4 the number of macrofilter-feeders is significantly positively related with Chl *a* and $COD_{(KMnO4)}$.

During the annual cycle microfilter-feeder rotifers developed populations in very low densities. Higher density of this ecological group was noted in summer and autumn, with a peak of 11 ind/l, in November at a depth of 2 m (Fig. 11b). The relative abundance of microfilter-feeders was higher in autumn (to 30%), and their density significantly positively correlated to TP, PP and TN (Table 4). *K. cochlearis* was the main rotifer representative of this group in the zooplankton of Visovac Lake.

4. Discussion

4.1. Relationship between the Rotifer Community Structure and Limnological Factors

This study confirmed that rotifers are, in relation to the presence of other constituents of the zooplankton (Protozoa, Cladocera, Copepoda), the most abundant component in different types of water bodies in temperate and Mediterranean area (Mišetić and Sibila, 1979; Habdija *et al.* 1989; Vasconcelos, 1990, Bukvić, 1996, Deimling *et al.* 1997). Comparing rotifer density between Lake Visovac (mean annual value 161 ind/l) and other lakes, we conclude that the density was lower and the dominant species were different, too. For instance, in the warm monomictic Lake Azibo (Portugal), the rotifer density was higher, varied from 220 to 3400 ind/l (Vasconcelos, 1990), and dominant species were *K. cochlearis* and *Po-*

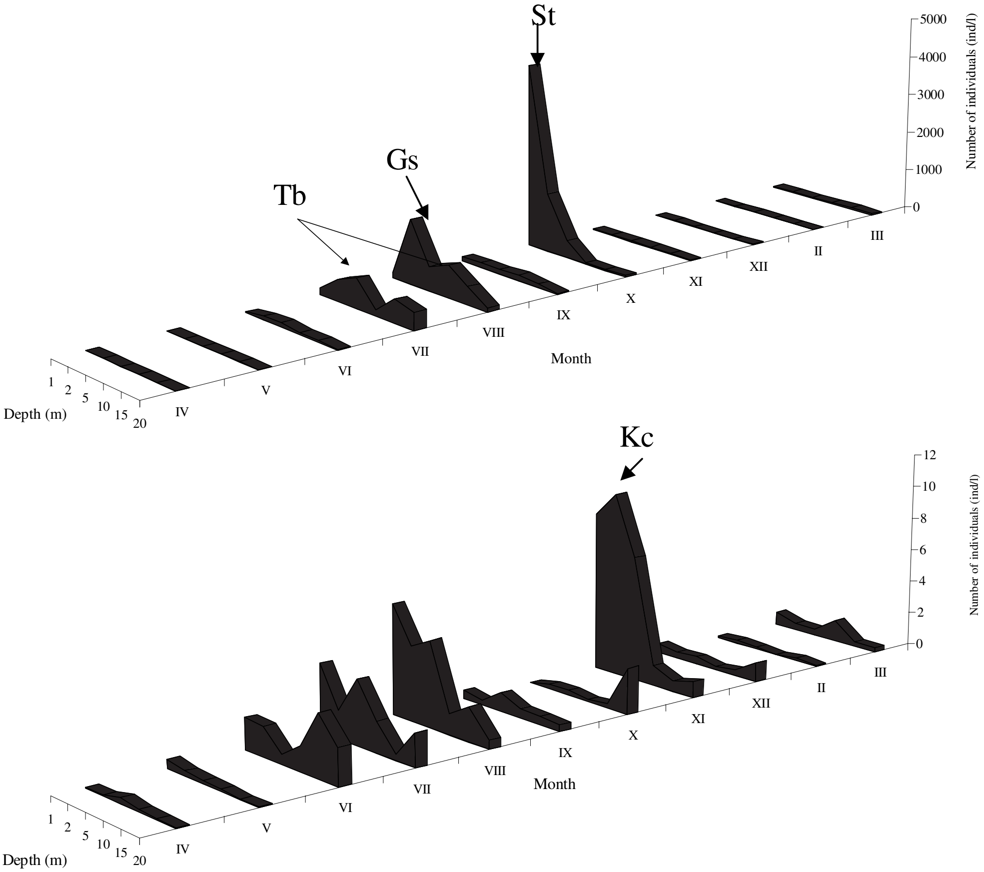


Figure 11. Seasonal changes of population density of macrofilter-feeding (a) and microfilter-feeding rotifers (b) along the vertical profile K1 in Visovac Lake. Gs = *G. stylifer*, Kc = *K. cochlearis*, St = *S. tremula*, Tb = *T. birostris*.

Table 4. Pearson's product-moment correlation coefficients between nutrients and food resources and macrofilter- and microfilter-feeder density.

Food	Macrofilter-feeders	
	r	p
Dissolved organic matter	0.44	0.0007
Chl-*a*	0.52	0.00004
Nutrients	Microfilter-feeders	
TP	0.28	0.04
PP	0.28	0.03
TN	0.46	0.0003

lyarthra sp. In the view of biomass, crustaceans (cladocerans and copepods) had advantage, and their biomass ranged between 0.14 to 517 μg/l (personal communication with Dr. I. Ternjej). They dominated through the annual investigation period on the vertical profile, except in October at 1 m depth when rotifer reached their maximum of density and biomass (155 μg/l).

Temperature and food resources caused rotifer space-time distribution, and that confirmed its significant relationship to these factors. Namely, the highest rotifer density in Visovac Lake was noted in the summer period, in the epilimnetic layer, when temperatures were higher and at the same time high concentrations of food resources occurred (measured as Chl *a*, bacteria and $COD_{(KMnO4)}$). The highest rotifer density in the summer period confirmed the results of other authors who have investigated karstic lakes in the Dinarid area, for instance, Habdija *et al.* (1989) on Plitvice Lakes and Mišetić and Sibila (1979) on Lake Peruča. In our investigation, rotifers reached their annual density maximum in October, at a depth of 1 m (4574 ind/l). We interpret this result firstly by the annual peak of the macrofilter-feeder species *S. tremula*, characteristic of the colder period of the year and secondly, with the annual peak of chlorophyll *a* concentrations. The rapid and extreme increase in the density of one dominant species just once in the year at a single depth could be explained by patchiness (Seda and Devetter, 2000).

Species diversity in Visovac Lake was higher in the colder period of the year. There are two reasons. Firstly, the lake is the reservoir of the Krka River, and it belongs to a pluvial water regime. More rain causes an increase in water discharge and an input of benthic and semiplanktonic species into the lake, especially in autumn and winter. Secondly, in the summer period, a few species with high densities dominated. Values of Shannon-Wiener diversity index implied that an increase in rotifer density, which caused just a few species, led to decreasing values in the diversity index. By other investigations, diversity is higher in the warmer period of the year in most cases (Guimarães, 1992; Węglenska and Ejsmont-Karabin, 1994).

Out of the range of other environmental factors, it is important to take into consideration the relation between rotifer density and pH values, as one of the indicators of the water buffer system. The basin of Visovac Lake is situated in a karstic area, where we measured higher pH values, from 7.9 to 8.2. These values suggest a significant positive relation between rotifer population density and pH. We confirm this result comparing rotifer species in Visovac Lake with data about rotifer occurrence in relation to pH by Bērziņš and Pejler (1987). That is, in Visovac Lake, 16 rotifer species developed their maximum abundance at $pH \geq 7.0$, and 23 species are tolerant to alkaline conditions.

Discharge is very important factor for riverine lakes. In Visovac Lake rotifer density negatively correlated with discharge ($r = -0.22$), but this relationship was not significant. Such correlation was expected, and is confirmed by other investigators who studied planktonic organisms in the outlet of the lentic into the lotic water (Reynolds, 1988; Vadeboncoeur, 1994; Walz and Welker, 1998). Because of the lack of morphometrical data for the volume of Visovac Lake, we did not calculate water residence time, which is closely connected with discharge. According to literature data, residence time is positively related with plankton density, especially zooplankton, because of its longer generation time (Søbale and Kimmel, 1987; Basu and Pick, 1996). According to our data on Visovac Lake, we could presume that the lowest discharge was in summer, which implies longer water residence time, and higher rotifer density.

Nutrients (SRP, DIN, TP, TN) are not significantly correlated with total rotifer density. For instance, the key nutrients for primary production, SRP, were present in low concentrations (0.003 to 0.03 mg $P\text{-}PO_4^{3-}$). Similar data to those from Visovac Lake were also noted by Habdija *et al.* (1993) in the karstic Lake Kozjak (Plitvice Lakes). Actually, one of the requirements for tufa deposition is a low concentration of dissolved organic matter, <10 mg/l C (Srdoč *et al.*, 1985), which relates to low phosphate concentration.

4.2. Rotifer Community Trophic Structure and Biotic Interactions

Analysing the changes of rotifer trophic structure in Visovac Lake, we concluded that macrofilter-feeders predominated during the whole year, because three dominant species (*G. stylifer*, *S. tremula*, *T. birostris*) belong to this group. These seasonal dynamics can be explained by the seasonal dynamics of Chl *a* which is the indicator of main food resources, phytoplankton, for the macrofilter phytophagous group of rotifers. Moreover, according to KARABIN (1985) macrofilter-feeders are characteristic of oligotrophic lakes, which also tend to confirm our data. Other investigators reported data, which also suggest a positive correlation between Chl *a* concentration and rotifer density (DE MANUEL and JAUME, 1994; MORALES-BAQUERO *et al.*, 1994; VAN DIJK and VAN ZANTEN, 1995). With regard to a positive relationship between Chl *a* concentration and rotifer density, in summer we noted a decline of Chl *a* concentration in the epilimnetic layer (average 0.0014 μg/l), as compared to spring Chl *a* concentration (average 0.0020 μg/l). This result confirms the presence of rotifers grazing on the phytoplankton community, when macrofilter-feeders develop high population densities (MAZUMDER *et al.*, 1992; BUCKA and ŽUREK, 1992). The second example for a possible grazing effect was the rapid biomass decline of the dinoflagellate *Ceratium hirundinella* in August at a depth of 2 m (personal communication with Prof. Dr. PLENKOVIĆ-MORAJ), at the same time as annual peak of dominant species *G. stylifer*.

During the one-year investigation, microfiltrator rotifers were present in a lower abundance than macrofiltrators. The most abundant representative of microfilter-feeders was *K. cochlearis*. Its density increased in the summer, but the relative abundances were increased in the autumn period. At this time, there were tropholytic processes and an increasing quantity of bacteria and detritus.

The density of the microfilter-feeder trophic group suggests a significantly positive relationship with TP, TN and PP. Such results are not surprising, because members of this trophic group feed on bacteria-detritus suspension. The presence of heterotrophic bacteria and detritus suspension also include higher concentrations of different tropholytic states of organic molecules, which are expressed in higher concentrations of TP, TN and PP.

In the plankton community, rotifers interact for space and food resources with other zooplankton groups, primarily with crustaceans (copepods and cladocerans). According to BUKVIC (1996), copepods reached higher density during the summer, ranged between 0.3 to 82 ind/l, while cladocerans developed in less density, 0.3 to 24 ind/l in Visovac Lake. The highest density of crustaceans was also observed in the summer period. Macrofilter-feeding copepods were the most abundant group, with dominant *Eudiaptomus hadzici.* This species, together with different developmental stages of copepods were pressed in deeper water layers. In metalimnion, they were probably in exploitative competition with the rotifer species *Trichocerca.* In the autumnal period, crustaceans reached higher density in epilimnion, while rotifer density decreased, because of their sensitivity to lower temperature and phytoplankton depletion. In spring, microfilter-feeder *K. cochlearis* took over the role of utilisation of detritus and bacteria particles and totally pressured the species *Bosmina longirostris*, while nanophytoplankton fed *Daphnia longispina*. In summer, in deeper layers crustacean microfilter-feeders outcompeted rotifers.

According to the size efficiency theory, most of the species in Visovac Lake are small in size (≤200 μm) and have lower energetic demands, which imply a lower threshold food concentration for their development, in contrast to bigger species (STEMBERGER and GILBERT, 1985). In connection with this, they are able to develop high population densities in a lake with a low nutrient content, for example in oligotrophic lakes.

4.3 Comparisons between Lakes

When we compare the rotifer community structure with the morphometrical, physical and chemical characteristics of Visovac Lake and with other riverine lakes in the Mediterranean area, we can find just a few similar examples. Figure 12 shows the results of cluster analysis between dominant rotifer species presented in some riverine lakes in the temperate and Mediterranean karstic area. The most similar biotopes of riverine lakes in karstic area are Lake Bermejales (depth$_{max}$ 23 m, Spain, Morales-Baquoero *et al.*, 1994) and La Conception Reservoir (depth$_{max}$ 68 m, Spain, Fernandez-Rosando and Lucena, 2001). In these lakes, a similar rotifer community structure with macrofilter-feeder species from genera *Polyarthra*, *Trichocerca* and *Synchaeta* was observed. For instance, riverine lakes in temperate area, Neuendorfer (Germany, depth$_{max}$ 4.5 m, Walz and Welker, 1998) and Mueggelsee (Germany, depth$_{max}$ 8 m, Eckert and Walz, 1998) were distinguished in a cluster analysis in a different group, which suggests a different rotifer community structure in the same type of lakes, but with differences in basin geology and depth.

Our study suggests that food resources connected with temperature and water buffer factors (free CO_2, pH, alkalinity) influenced the rotifer spatial and temporal distribution in the karstic, monomictic barrage Lake Visovac. Rotifer community structure with three dominant species, *Gastropus stylifer*, *Synchaeta tremula* and *Trichocerca birostris*, is characteristic of zooplankton communities in riverine lakes in karstic sub-Mediterranean area. Although it is a riverine lake, there is a lack of significant correlation between rotifer density and discharge. Further studies must be directed towards hydrological factors in the river's drainage area and towards the biotic interactions among the zooplankton components in order to elu-

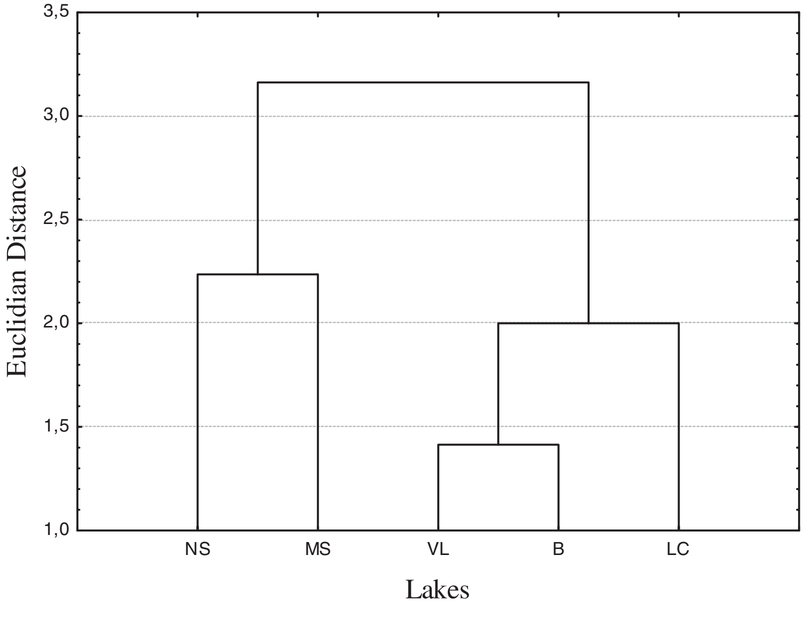


Figure 12. Cluster analysis with regard to dominant rotifer species in the five riverine lakes (Complete linkage, Euclidian distance): NS = Neuendorfer See; MS = Mueggelsee; VL = Visovac Lake; B = Bermejales, LC = La Concepción Reservoir.

cidate the interaction between the biota and the environment in Visovac Lake. In addition, the influence of biota on abiotic factors responsible for calcite precipitation could be object for further studies.

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