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Ecological determinants of rotifer vertical distribution in a coastal karst lake (Vrana Lake, Cres Island, Croatia)

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Abstract: Vrana Lake is a coastal karst lake on Cres Island within the eastern Adriatic coast. It appears to have formed as a cryptodepression on karstified carbonate rocks, and is filled with fresh water. It is classified as an oligotrophic hydrosystem and serves as a natural water supply reservoir (max. depth 74.5 m; surface area 5.5 km^2; water volume 220 × 10^6 m^3). The aim of this study was to assess the influence of seasonally and spatially varying ecological conditions (i.e., thermal stratification, dissolved oxygen, orthophosphate and chlorophyll *a* concentrations) on the vertical distribution of the rotifer plankton community in this geomorphologically and hydrologically specific coastal lake. The rotifer community was surveyed monthly over a one year period. During the study period, a total of 21 rotifer taxa were identified. Among them *Ascomorpha* spp. (including *A. ecaudis, A. ovalis* and *A. saltans*), *Filinia terminalis, Keratella cochlearis, Synchaeta* gr. *tremula-oblonga* and *Polyarthra vulgaris* prevailed, representing 92% of the total rotifer abundance. Measured seasonal and spatial patterns of the rotifer assemblage along a vertical profile of Vrana Lake were considerably affected by temperature, food availability and biotic (competition, predation) interactions in the zooplankton community.

Key words: coastal lakes; karst lakes; thermal stratification; macrofilter-feeder rotifers; microfilter-feeder rotifers; competition

Introduction

According to hydrological and ecological findings, Vrana Lake is classified as an oligotrophic and monomictic Mediterranean coastal karstic lake (Petrik 1960; Bonacci 1993; Bukvić et al. 1997; Ternjej & Tomec 2005; Habdija et al. 2007). There were several reasons for the present ecological study of the rotifer zooplankton community within Vrana Lake. Firstly, coastal lakes are widespread in the Mediterranean area and are recognized worldwide as hotspots of aquatic fauna biodiversity (Blondel & Aronson 1999; Schallenberg et al. 2003). It is well known that rotifers play an important role in water quality assessment (Gannon & Stemberger 1978; Pejler 1983, 1995), and thus our objective was to analyze the seasonal and spatial rotifer distribution patterns and rotifer interactions in relation to environmental conditions in the lake. Secondly, many recent studies have investigated the relationship between physical and chemical lake stratification and rotifer communities within different lake environments (Bērziņš & Pejler 1989a, b; Oehms & Seitz 1992; Miracle & Alfonso 1993; Jersabek 1995; Pejler 1995; Kobayashi 1997; Plenković et al. 1998; Fernandez-Rosado & Lucena 2001; Galkovskaya et al. 2006), but little attention in this regard has been given to ecological interactions within coastal and karst lakes. Thirdly, considering that competition among zooplankton groups (rotifers, cladocerans, copepods) is often induced by limiting food resources (DeMott 1989; Armengol-Diaz et al. 1993; Baião & Boavida 2000; Conde-Porcuna et al. 2002; Kirk 2002), we examined whether sharing of resources affected the outcome of vertical distribution of the observed rotifer species in the lake.

The aim of the present study was to evaluate the seasonal and spatial distribution patterns of five predominant rotifer taxa: *Ascomorpha* spp., *Filinia terminalis* (Plate, 1886), *Keratella cochlearis* (Gosse, 1851), *Synchaeta* gr. *tremula-oblonga sensu* Ruttner-Kolisko (1974) and *Polyarthra vulgaris* Carlin, 1943 in a coastal karst lake, with an emphasis on reviewing the diversity of rotifer feeding groups along a vertical profile in the lake (Pourriot 1977; Karabin 1985). We analysed (a) the interactions between rotifers and spatio-temporal variations in physical-chemical conditions (i.e., thermal stratification, dissolved oxygen, orthophosphate and chlorophyll *a* concentrations) along a vertical profile at the deepest part of the lake; (b) the relationship between rotifer functional feeding groups and their food availability; and (c) rotifer-related biotic interactions within the lake. We expected that seasonal changes in dissolved oxygen and orthophosphate, and their vertical stratification, would significantly depend on the thermal stratification of the lake and the activity of plankton community, respectively. We further anticipated that the diversity of rotifer feeding groups along the vertical profile of the lake would be influenced by

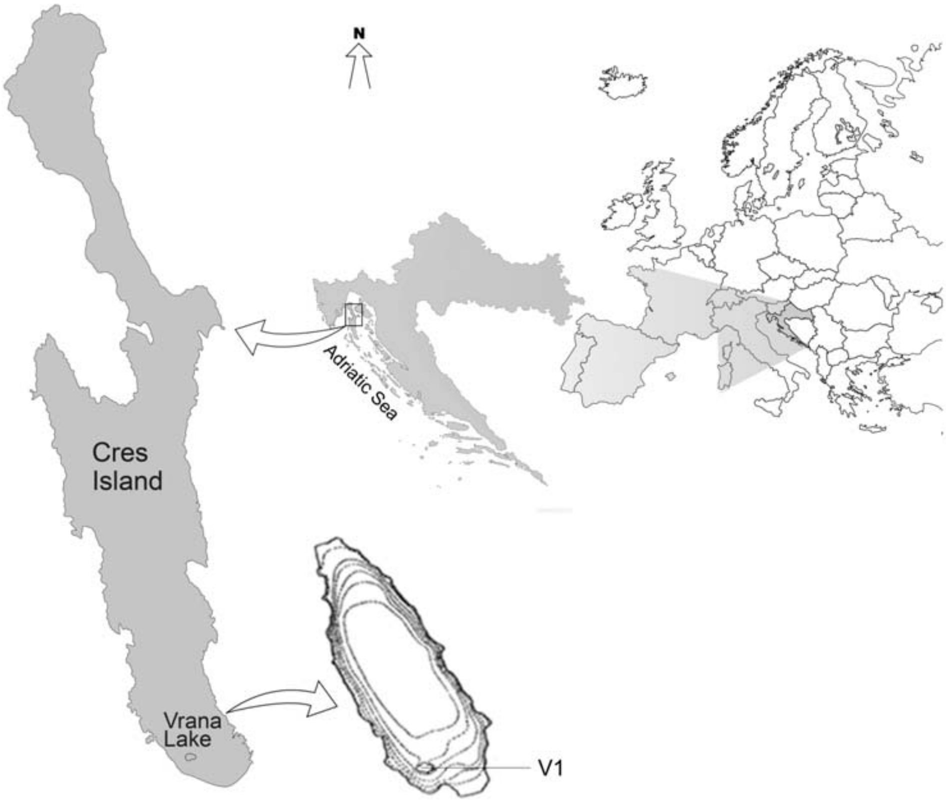

Fig. 1. Position of Vrana Lake and the location of the vertical profile V1 at the deepest part of the lake.

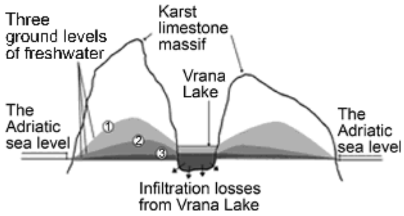

Fig. 2. Hydrogeological position and characteristics of Vrana Lake. Numbers 1, 2 and 3 indicate the three ground levels of freshwater.

food availability and biotic interactions within the zooplankton assemblage.

Material and methods

Study site and sampling
The present study was conducted on the Mediterranean coastal karst lake, Vrana Lake (44°50′13″ N, 14°24′47″ E), situated on Cres Island within the eastern Adriatic coast (Fig. 1). Cres Island is almost entirely composed of carbonate and dolomite rocks from the Cretaceous and Eocene periods. Vrana Lake is a cryptodepression formed on karstified carbonate rocks. The average annual lake water level is about 13 m above the Adriatic Sea level and the bottom of the depression is at 61.5 m below the mean sea level (Fig. 2). Main morphometric features of the lake are as follows: 5.5 km maximum length, 1.5 km width, 74.5 m depth, around 5.5 km^2 surface area, on average holding 220 × 10^6 m^3 of fresh water. From an ecological and biological standpoint based on water chemistry (Habdija et al. 2007), and the community structure of zooplankton (Bukvić et al. 1997; Tomec et al. 2002; Ternjej & Tomec 2005) and phytoplankton (Tomec et al. 2002), the lake is classified as an oligotrophic hydrosystem.

Water and plankton samples were collected at monthly intervals over a one year period during 1996 (with the exception of January 1996). Samples were taken in triplicate with a 5-litre Van Dorn sampler from multiple depths (1, 5, 10, 20, 30, 40, 50 and 65 m) at one vertical profile (V1) located at the deepest part of the lake (Fig. 1). In total, we collected 264 plankton samples (11 months × 8 depths × 3 replicates). The samples were concentrated by filtration using a plankton net (36-µm mesh size) and preserved with 4% formaldehyde. Afterwards, organisms from each sample were identified and enumerated in 5 subsamples using a Sedgewick-Rafter cell (1 mL) using an Opton-Axiovert 35 inverted microscope. Rotifers were determined to the species or genus level (Koste 1969, 1978, 1980; Ruttner-Kolisko 1972, 1974, 1980, 1989; Hofmann 1974; Pontin 1978; Schaber & Schrimpf 1984; Sanoamuang 1993). Identified rotifer taxa were sorted into functional feeding groups according to their food-collecting mechanism and the size of food particles (Dumont 1977; Pourriot 1977; Karabin 1985).

Temperature and dissolved oxygen were measured *in situ* using a field oxymeter (WTW OXI 96), and water transparency was assessed by Secchi disc. Oxygen values for March and September are missing due to hardware/software malfunction of the oxymeter. Orthophosphate concentration was determined according to APHA methodology (1985). Chlorophyll *a* (*CHL*) content served as an indicator of phytoplankton biomass (i.e., algae), which is considered the main food source for macrofilter-feeder rotifers (Karabin 1985, Špoljar et al. 2005), and was analysed by ethanol extraction according to Nusch (1980). Regression analysis was

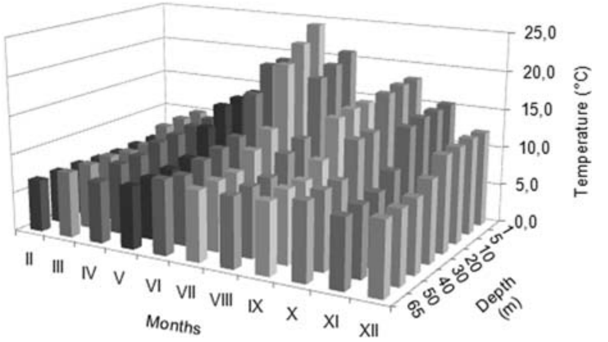

Fig. 3. Thermal stratification of Vrana Lake during the study period.

carried out using Statistica software (StatSoft Inc. 2001).

Results and discussion

Environmental conditions

Detailed description of the physical-chemical features of Vrana Lake is presented by Tomec et al. (2002). During the present study, Secchi disc transparency varied between 11 and 17 m, which is very high and also in concordance with values measured at some other deep oligotrophic lakes, for instance Lake Stechlin (Padisák et al. 1997). Our data of vertical water temperature regime corroborate previous findings that reported Vrana Lake as a monomictic lake (Petrik 1960; Bonacci 1993; Bukvić et al. 1997). The temperature regime was characterized with the beginning of thermal stratification in late spring, complete thermal stratification during summer, and isothermal conditions with temperatures below 7 °C after winter overturn (Fig. 3). The mean temperature of the summer epilimnion (from surface to a depth of 10 m) was 23 °C, while the mean temperature was 10.7 °C in the hypolimnion (depths of 20 to 65 m). A thermocline was established at depths of 10 to 20 m, with a thermal gradient of 7.7 °C m^{-1}.

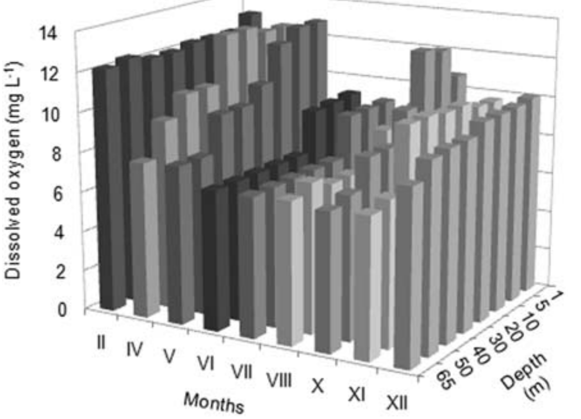

Fig. 4. Vertical stratification of dissolved oxygen in Vrana Lake during the study period. Missing March and September values are due to hardware/software malfunction of the oxymeter.

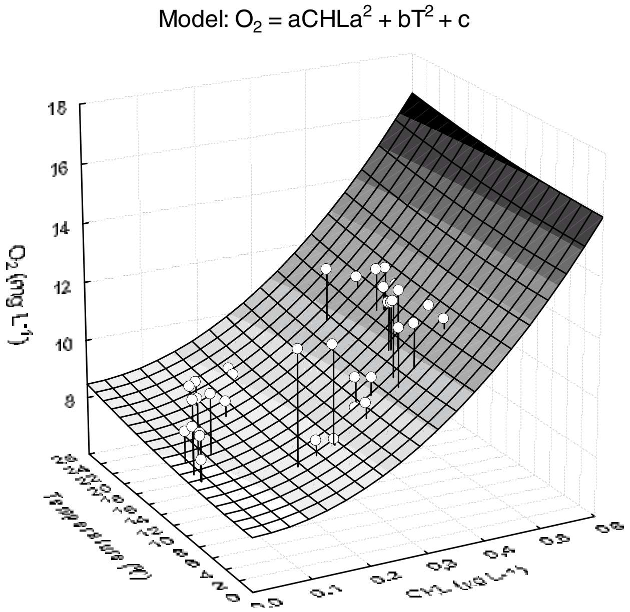

Fig. 5. The relationship between O_2-concentration (O_2), chlorophyll *a* (CHL) and temperature (T) according to multiple regression analysis.

Vertical stratification of dissolved oxygen indicated an orthograde oxygen distribution during the summer, and an increasing trend in dissolved oxygen in the epilimnion during the spring and autumn (Fig. 4). In the epilimnion and metalimnion, dissolved oxygen varied between 10 and 15 mg L^{-1} and the lowest oxygen concentrations (between 7 and 8 mg L^{-1}) were found in the hypolimnion. We assumed that dissolved oxygen (O_2) depended only on temperature (T), but in the first step of a regression analysis using a quadratic model $O_2 = aT^2 + bT + c$, the results showed that there was no significant correlation between these two variables ($R = 0.086$, $P > 0.05$, df = 61, $n = 64$). Further analysis revealed statistically significant results for oxygen concentration and chlorophyll *a* content and indicated that the relationship (O_2)–(CHL) is well fitted by the quadratic model $O_2 = aCHL^2 + bCHL + c$ ($R = 0.72$, $P < 0.05$, df = 69, $n = 72$). The second step of the regression analysis considered dissolved oxygen versus temperature and chlorophyll *a*. It revealed a scatter plot of multiple regression ($O_2 = aCHL^2 + bT^2 + c$; $R = 0.78$, $P < 0.05$, df = 60, $n = 62$) and indicated that oxygen concentration increases with an increase in chlorophyll *a* content and temperature (Fig. 5). Based upon prior lake research (Wetzel 1983; Lampert & Sommer 1997; Knappe et al. 2004), it was found that increasing values of temperature and light intensity initiate increases in biotic activity, essentially photosynthesis by phytoplankton, and consequently caused the increase in dissolved oxygen concentration. In contrast, due to increased organic matter accumulation in the boundary hypolimnetic layer, microbial activity increases oxygen consumption which could ultimately lead to hypoxic conditions (Wetzel 1983).

For the assessment of food (i.e., algae) availability for the predominant rotifer taxa, it was impor-

Table 1. Spatial and temporal distribution of the total number of rotifers (ind. L^{-1}) from multiple depths (1, 5, 10, 20, 30, 40, 50 and 65 m) at the sampled vertical profile located at the deepest part of the lake.

Month	Depth (m)								
	1	5	10	20	30	40	50	65	Average
II	12.92	20.00	5.87	16.53	27.64	26.93	34.00	23.00	20.86
III	10.00	20.00	21. 9	19.56	26.00	34.21	33.00	26.00	24.11
IV	12.80	1.00	6.00	15.00	26.90	34.21	34.58	22.00	19.06
V	2.27	5.01	4.71	9.90	26.69	34.40	34.58	27.56	18.14
VI	15.02	19.20	21.87	25.24	63.91	28.27	29.00	29.10	28.95
VII	0.56	0.71	0.80	0.89	3.38	3.29	3.40	15.00	3.50
VIII	1.69	8.44	20.18	21.33	39.30	20.98	17.59	21.51	18.88
IX	0.36	0. 42	0.77	0.75	9.00	10.00	0.87	17.00	5.54
X	0.36	30.00	0.77	0.75	0.95	0.77	0.87	13.00	5.93
XI	31.64	75.98	82.25	71.45	129.00	19.82	19.60	22.67	56.55
XII	1.33	1.24	1.96	1.87	2.58	2.16	2.50	14.00	3.46
Average	8.09	18.16	14.52	16.66	32.31	19.55	19.09	20.99	18.63

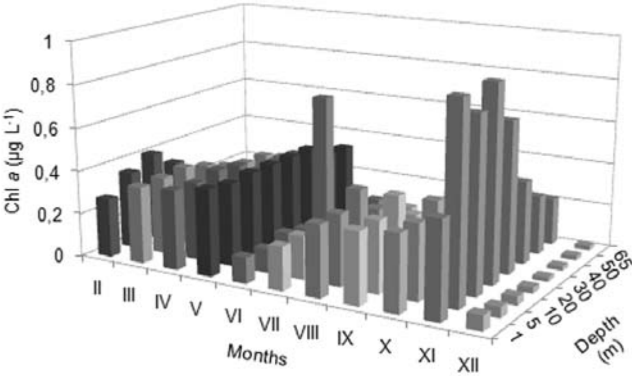

Fig. 6. Temporal dynamics and vertical stratification of chlorophyll *a* (Chl *a*) in Vrana Lake during the study period.

tant to establish factors influencing the spatio-temporal variations of chlorophyll *a* (Fig. 6). Considering vertical thermal stratification, the highest concentration of chlorophyll *a* was recorded in the epilimnion. Seasonally, the highest epilimnetic values of chlorophyll *a* were observed during spring (0.27 µg L^{-1} to 0.41 µg L^{-1}) and autumn (0.33 µg L^{-1} to 0.90 µg L^{-1}), whereas lowest values occurred in summer (0.11 µg L^{-1} to 0.20 µg L^{-1}). Observed winter chlorophyll *a* concentrations were below 0.07 µg L^{-1} along the entire vertical profile. According to Ternjej & Tomec (2005), *Ceratium hirundinella* and species of genera *Cyclotella*, *Dynobryon* and *Peridinium* were the dominant phytoplankton of Vrana Lake. Using the derived quadratic model ($P\text{-}PO_4 = aCHL^2 + bO_2^2 + c$) for the relationship among orthophosphate ($P\text{-}PO_4$), chlorophyll *a* (CHL) and dissolved oxygen concentration (O_2), we confirmed our assumptions ($R = 0.78$, $P < 0.05$, df $= 61$, $n = 64$) that, besides other environmental factors, phytoplankton activity (measured as chlorophyll *a*) significantly depended on orthophosphate content and *vice versa.* The same effect was reported by other authors for different lake types in the temperate zone (Lampert et al. 1986; Christensen et al. 1995; Špoljar et al. 2005; Habdija et al. 2007).

Rotifer distribution

A total of 21 rotifer taxa were identified during the study period. Based on the average of 264 collected plankton samples and considering their abundance, rotifer species were divided in the two groups. Predominant rotifer taxa were *Keratella cochlearis* (36.6%), *Synchaeta* gr. *tremula-oblonga* (24.3%), *Filinia terminalis* (14.3%), *Polyarthra vulgaris* (10.5%) and *Ascomorpha* spp. (5.1%), including the species *Ascomorpha ecaudis* Perty, 1850*, A. ovalis* Carlin, 1943 and *A saltans* Bartsch, 1870. Mentioned *Ascomorpha* spp. were distinguishable as separate species, but in this study they were considered at the genus level. All above mentioned species represented 92% of the total rotifer abundance (Fig. 8); (2) Subdominant rotifer taxa *Asplanchna priodonta* (Gosse, 1850), *Brachionus quadridentatus* Hermann, 1783, *Gastropus stylifer* Imhof, 1891, *Hexarthra* sp., *Kellicottia longispina* (Kellicott, 1879), *Keratella quadrata* (Müller, 1786), *Notholca squamula* (Müller, 1786), *Synchaeta pectinata* Ehrenberg, 1832, *Testudinella patina* (Hermann, 1783), and two indeterminate semiplanktonic species of the genera *Colurella* and *Lecane* represented 8% of the total rotifer abundance in the samples. They were either found in low densities or appeared during short periods.

The annual trends in rotifer vertical distribution are shown in Table 1. During the study period, the average number of rotifers was 19 ind. L^{-1} ($n = 264$). Contrary to the epilimnion, rotifers reached higher abundances in the metalimnion and hypolimnion. In spring, rotifer density increased gradually along the vertical profile, reaching a maximum in the hypolimnion. In early summer (June), pronounced rotifer abundances (15–64 ind. L^{-1}) along the entire vertical profile were observed, most probably due to the reduced density of competitive crustaceans (Tomec et al. 2002). Unlike the

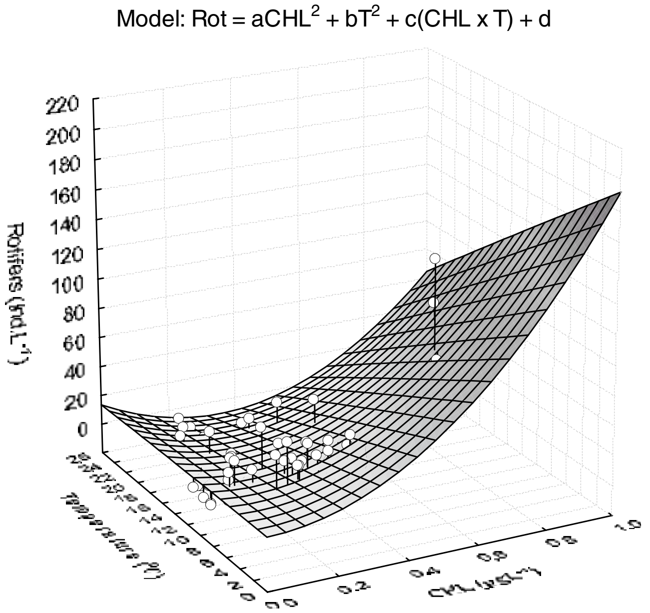

Fig. 7. Changes in the total number of rotifers (ROT) as influenced by thermal stratification (T) and chlorophyll *a* (CHL).

observed June trend, an obvious decrease in rotifer densities in July, October and December was likely due to higher crustacean population densities (Tomec et al. 2002).

According to temperature and oxygen preferences, predominant rotifers detected in Vrana Lake can be classified into three groups: (1) cold-stenotherm rotifers tolerating a wide range of dissolved oxygen and preferring temperatures below 10 °C: *F. terminalis* (Hofmann 1987; Ruttner-Kolisko 1989); (2) rotifers with thermopreferences above 10 °C and high oxygen content requirements (above 8 mg O_2 L^{-1}): *A. ovalis* and *A. saltans* (Bērziņš & Pejler 1989a, b); and (3) rotifers showing a wide temperature and oxygen tolerance range: *Synchaeta* gr. *tremula-oblonga* (Fernandez-Rosado & Lucena 2001), *P. vulgaris* (Bērziņš & Pejler 1989a, b), *K. cochlearis, A. ecaudis* (Mikschi 1989). Also, our findings suggested that *F. terminalis* was a cold-stenotherm species; it continuously inhabited the deepest layers of hypolimnion. The species of genus *Ascomorpha* occurred in the well-oxygenated epilimnion during the summer, while other species showed wider temperature tolerances (Fig. 8).

The above discussed seasonal and spatial trends in rotifer distribution were presumably a consequence of the interaction among coexisting rotifers, their environmental conditions and food availability (Morales-Baquero et al. 1994; Stelzer 1998, 2006; Lampert et al. 2003; Weithoff 2004). By using a regression model: $ROT = aCHL^2 + bT^2 + c\ (CHL \times T) + d$, we confirmed that the total number of rotifers (ROT) significantly depended on the thermal stratification of the lake (T) and chlorophyll *a* concentration (CHL) ($R = 0.75$, $P < 0.05$, df = 69, $n = 72$) (Fig. 7).

According to Pourriot (1977) and Karabin (1985), food distribution is one of the most important mediators in niche occupation by rotifers. We suggest that food supplies for rotifers in the study lake were constrained by the access of three main food sources: (1) nanophytoplankton, (2) bacteria-detritus suspension, and (3) large net algae (Dumont 1977; Pourriot 1977; Karabin 1985). According to the same authors and our analysis, the dominant rotifers in Vrana Lake appeared to constitute the following functional feeding groups: (a) microfilter-feeders (sedimentors; consumers of bacteria-detritus suspension) represented by *K. cochlearis* and *F. terminalis* that achieved 51% of the total rotifer abundance, and (b) macrofilter-feeders (raptors) divided as large raptors (consumers of nanophytoplankton and net algae over 50 µm in size) represented by *Synchaeta* gr. *tremula oblonga* (24% of the total), and small raptors (consumers of nanophytoplankton and net algae of 20–30 µm in size) represented by *P. vulgaris* (11% of the total). According to Gilbert & Bogdan (1981), species of the genus *Polyarthra* and some species of the genus *Synchaeta* could be considered as food specialists that prefer consumption of larger flagellate *Cryptomonas*, while the Gastropodidae *Ascomorpha* species mostly feed on dinoflagellates, green algae (Dumont 1977) and Chrysomonades (Pourriot 1965; Ruttner-Kolisko 1972).

As an explanation of spatio-temporal rotifer distribution, we also considered rotifer-crustacean interactions – competition and predation (Devetter 1998; Brandl 2005). Rotifers mostly are in interference or exploitative competition with cladocerans (Wickham & Gilbert 1980; Fernandez-Rosado & Lucena 2001). They also are part of predator-prey relationships, as they are shown to be prey for copepods (Stemberger & Gilbert 1987) or predators of other rotifers and ciliates (Stemberger & Gilbert 1984). According to Bukvić et al. (1997) and Tomec et al. (2002), four copepods, *Cyclops abyssorum* G.O. Sars, 1863, *Macrocylops distinctus* (Richard, 1887), *Macrocyclops albidus* (Jurine, 1820) and *Megacylops viridis* (Jurine, 1820), and three cladocerans, *Daphnia longispina* (O.F. Müller, 1776), *Diaphanosoma brachyurum* (Lievin, 1848) and *Bosmina longirostris* (O. F. Müller, 1776) dominate the crustacean zooplankton of Vrana Lake.

Spatio-temporal separation of microfilter-feeder rotifers (*K. cochlearis* and *F. terminalis*) could be explained by their temperature preference, food availability and competitive interactions with crustaceans (Hofmann 1987; Kirk 2002; Żurek 2006). During the study period, the cold-stenotherm species *F. terminalis* was restricted to the hypolimnetic layer, most probably feeding on bacteria-detritus suspension from upper euphotic layers. Eurythermal sedimentator species *K. cochlearis* achieved higher abundances in the winter-spring period because it is less dependent on autotrophic production (Ruttner-Kolisko 1974). According to Tomec et al. (2002), we assume that the appearance of competitive microfilter-feeder crustaceans (i.e., *B. longirostris, D. brachyurum*) in spring suppressed *K. cochlearis* in deeper water layers, resulting in its higher abundance in the metalimnion and hypolimnion.

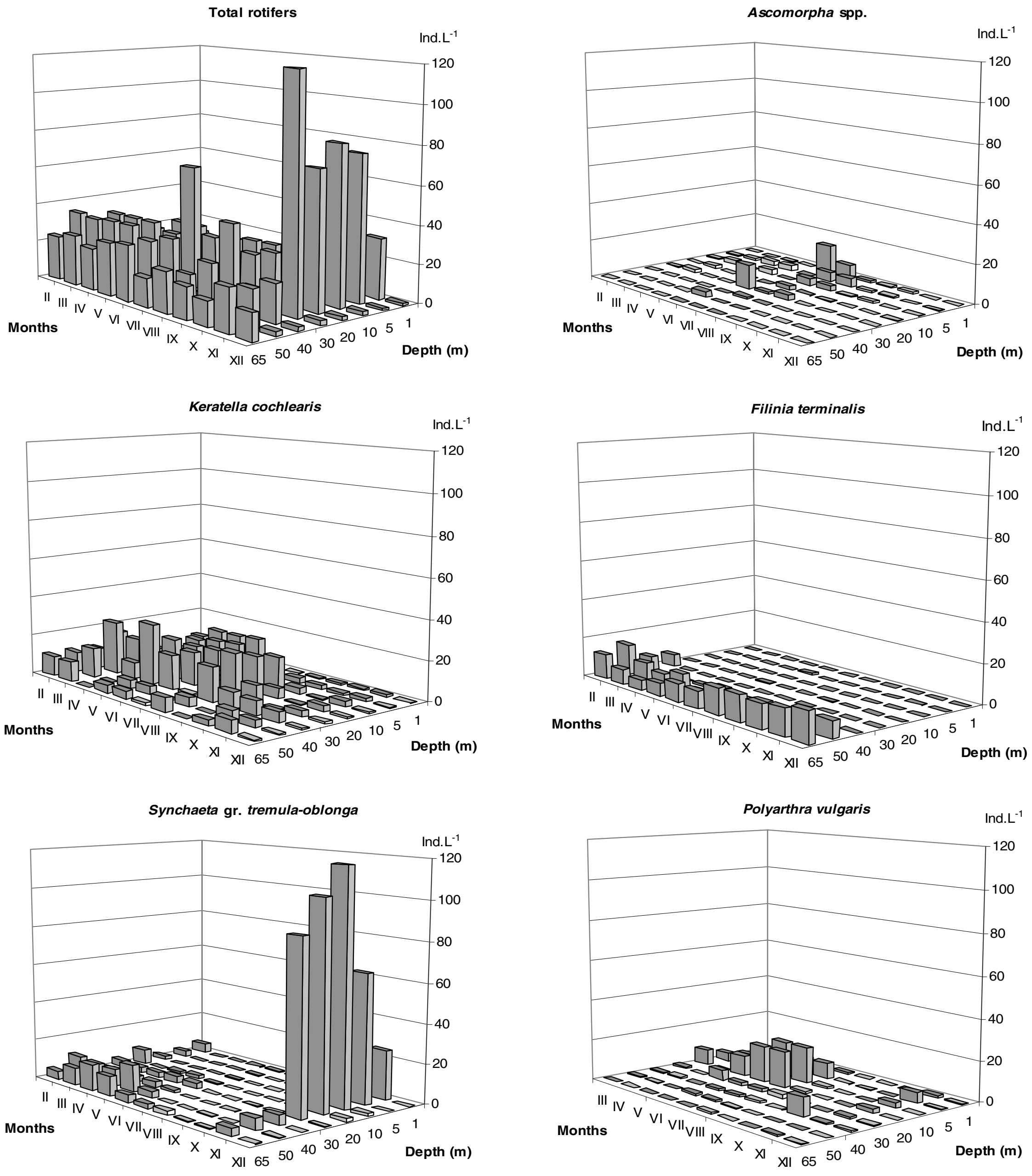

Fig. 8. Seasonal and spatial patterns of the most abundant rotifer taxa.

Spatio-temporal patterns of macrofilter-feeder taxa *Synchaeta, Polyarthra* and specialists *Ascomorpha* spp. (comprising 40% of the total rotifer abundance) may also be explained by exploitative crustacean competition (*sensu* Tomec et al. 2002). This effect was especially obvious in summer on, for example, the *Synchaeta* group which suffered from the pressure of thermophilic crustacean competitors (Fig. 8). After reduction of the crustacean summer competition and gaining a rich food supply (i.e., chlorophyll *a*), *Synchaeta* gr. *tremula-oblonga* reached an annual maximum in November (Fig. 8). *P. vulgaris* and species of the genera *Ascomorpha* coexisted during summer in the epilimnion and metalimnion. The coexistence of these two taxa within the two water layers could be explained by their separate trophic status and different food preferences (Pourriot 1965; Ruttner-Kolisko 1972; Dumont 1977; Gilbert & Bogdan 1981; Stemberger & Gilbert 1985). Furthermore, the summer scarcity of *Polyarthra* and *Synchaeta* species in deeper lake layers could be a consequence of numerous copepod omnivores and predators (*sensu* Tomec et al. 2002), what is in concordance with findings of Devetter (1998) and Brandl (2005).

Considering the results of the present study and previous findings (Walz 1995; Devetter 1998), we suggest that the observed seasonal and spatial patterns of rotifer populations were most likely affected by the thermal stratification of Vrana Lake and, moreover, by food availability and biotic (competition and predation) interactions among zooplankton. Further investigations of rotifer seasonal and spatial distribution within lakes, as well as their coexistence patterns, is of high importance in the assessment of contemporary lake conditions and the detection of anthropogenic disturbance. These data would hence improve the conservation efforts of habitats recognized as hotspots of biodiversity, as is the case for coastal karst lakes.

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