Ann. Limnol. - Int. J. Lim. 48 (2012) 161–175
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DOI: 10.1051/limn/2012005

Available online at:
www.limnology-journal.org

Submerged macrophytes as a habitat for zooplankton development in two reservoirs of a flow-through system (Papuk Nature Park, Croatia)

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Received 10 January 2011; Accepted 18 October 2011

Abstract – In order to determine the influence of lentic habitats and macrophyte stands on the plankton development and seston flux, an investigation of zooplankton was carried out in the karst Jankovac flow-through system (Papuk Nature Park, Croatia). The system was characterized by low abundance (1–116 ind.L^{-1}) and high diversity of identified zooplankton. Eighty-six taxa were recorded, comprising 57 rotifers, 15 cladocerans, 8 copepods and 6 members of other groups of organisms. The spatial oscillations of environmental parameters and biocoenosis assemblage revealed statistically significant differences between lotic and lentic habitats, as well as between vegetated and non-vegetated stations. These differences mainly respond to higher concentration of food resources and zooplankton/zooseston abundance and biomass in lentic, especially vegetated, habitats. This is also proved by results of principal component analysis (PCA), which suggested that the main drivers of development of the planktonic community were the food resources and the avoidance of flow velocity. Accordingly, shoreline areas with submerged macrophyte stands of *Hippuris vulgaris* L. were the most productive parts, represented by highest zooplankton abundance, biomass and biodiversity. Flow velocity significantly affected crustaceans assemblage, so that higher abundances of the larger cladocerans and copepods were achieved in vegetated stations with low flow velocity, while rotifers showed to be rheotolerance organisms. On the other hand, the longitudinal discontinuum of the stream channel by two man-made reservoirs could offer new habitats to enrich seston with organic particles and bioseston. The results of our study pronounce the need for further monitoring of this hydrosystem, especially considering biodiversity and microhabitats conservation.

Key words: Rotifers / cladocerans / copepods / karst stream / seston flux

Introduction

Freshwater ecosystems are often affected by different anthropogenic disturbances, which are mainly manifested through pollution, flow regime alteration, *e.g.* damming and, consequently, habitat destruction (Lair, 1980; El-Shabrawy and Dumont, 2003; Castro *et al.* 2005). Longitudinal discontinuities in running waters, such as lateral dams, reservoirs or riverine lakes can be a source of plankton (Lair and Reyes-Marchant, 1997; Basu *et al.*, 2000; Špoljar *et al.*, 2007b; Zimmermann-Timm *et al.*, 2007). These lentic areas in a flow-through system play a role in organic matter production that latter on serves as food supplies for downstream benthic organisms (Sandlund, 1982; Hart and Finelli, 1999; Špoljar *et al.*, 2007b).

Slow-flowing inshore habitats provide favourable conditions for development of extensive beds of aquatic macrophytes outside the mainstream channel (Basu *et al.*, 2000). Macrophyte stands have multiple effects on aquatic ecosystems, such as reducing sediment suspension, preservation of physical stability of the littoral zone, reducing erosion processes, nutrient concentration and ameliorating eutrophication symptoms such as water turbidity (Horppila and Nurminen, 2005; Estlander *et al.*, 2009). Also, macrophytes offer food supplies as well as refuge for zooplankton species from pelagial predators (Burks *et al.*, 2001a; Kuczyńska-Kippen and Nagengast, 2006; Estlander *et al.*, 2009). The availability of macrophytes as food resources and refuge depends on various factors

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including plant architecture, size and density of plant patches, and also, on the predators that these plants host (Jeppesen *et al.*, 1997; Kuczyńska-Kippen, 2005; Meerhoff *et al.*, 2007). Seeking daytime refuge from visual predator, *i.e.* fish, in shallow lakes, zooplankton shifts into the littoral vegetated area presenting diel horizontal migrations (Gliwicz and Rykowska, 1992; Lauridsen and Lodge, 1996; Meerhoff *et al.*, 2006). In the littoral zone, zooplankton can be confronted with invertebrate predators including odonates, notonectids, dytiscid beetles and water mites, which exert a strong predation impact on zooplankton populations (Beklioglu and Jeppesen, 1999; Burks *et al.*, 2001b; Meerhoff *et al.*, 2007; González-Sagrario *et al.*, 2009).

Our study was undertaken in the Jankovac Stream (Papuk Nature Park, Croatia), struck by anthropogenic hydromorphological impact that resulted in two reservoirs. As a consequence, lentic stretches occupy the majority of the stream length and consist of two man-made reservoirs covered by submerged vegetation, while lotic stretches are represented by the spring and waterfall area. In such a flow-through system, the existing seston (rheoseston) consists of organic dead or alive, and inorganic particles of both autochtonous and allochtonous origin (Breitig and von Tümpling 1982; Špoljar *et al.*, 2007b). Zooseston represents its faunistic component. The majority of the particles and organisms in seston originate from the benthos (bed or periphyton) and/or the plankton (from upstream reservoirs). Thus, seston importance manifests as food resource for downstream benthic communities (Descy, 1993; Špoljar *et al.*, 2007b; Zimmermann-Timm *et al.*, 2007) and organisms dispersion (Sertić Perić *et al.*, 2011).

In this study, we attempted to analyse the development of zooplankton community in reservoirs of a submountain flow-through system and its influence on downstream seston flux. Our survey considers primarily rotifers, cladocerans and copepods assemblages in two reservoirs in relation to two main factors: presence or absence of (a) macrophyte stands and (b) flow velocity. Thus, we anticipated that water current and possible fish predation more affect cladoceran's and copepod's shift to the littoral zone than rotifer's. Accordingly, we expected that rotifers, as rheotolerant organisms, would have substantial contribution to the downstream seston flux. The objectives of this study were to determine: (1) the influence of reservoirs on the development of the zooplankton community in the flow-through system; (2) the importance of shoreline macrophyte habitats for the zooplankton assemblages and (3) the influence of hydrological features on the seston flux.

Study area

This investigation was conducted in the Jankovac Stream situated on sedimentary rocks in the Papuk Nature Park, Croatia (Fig. 1). Jankovac is a small, approximately 700 m long, flow-through system in a submountain area at 475 m asl. (45°31'07"N, 17°41'11"E) in which two hydrologically different habitats, *i.e.* lentic and lotic, alternate. Across the longitudinal profile, the stream is mostly surrounded by deciduous forest at a distance of 10 to 2 m, from mouth to spring, respectively. The main hydromorphometric features as well as the macrophyte composition of the study area and sampling stations are summarized in Table 1. The lotic stretches are represented by the rheocrene spring and adjacent hypocrenal area (JS sampling station) and the Skakavac waterfall over a tufa barrier that, at the same time, represents the mouth of the Jankovac Stream (JW sampling station). The majority of the streambed is lentic, which has shaped two man-made reservoirs. The stream inflows to the first reservoir (R1) after approximately 60 m of flow over a moss-covered bed. This reservoir is separated from the second one (R2) by a 2-m high bank, and water flows through a small connection between these reservoirs. Both reservoirs are polymictic with a maximum depth of 2 m and characterized by low phosphate (R1 0.02 ± 0.009 mg PO_4^{3-}-P.L^{-1}, R2 0.02 ± 0.01 mg PO_4^{3-}-P.L^{-1}, $N_{R1,R2} = 12$) and higher nitrate (R1 1.10 ± 0.17 mg NO_3^--N.L^{-1}, R2 1.0 ± 0.2 mg NO_3^--N.L^{-1}, $N_{R1,R2} = 12$) concentrations. The reservoirs are not usually frozen in the winter or just thin ice cover appears sporadically during December to February. Transparency through the entire water column enables the growth of submerged macrophytes, *Potamogeton natans* L. and *Hippuris vulgaris* L., the latter mostly contributes to the coverage of reservoir's bottom. The littoral zones of both reservoirs are covered with narrow discontinued belt of emergent macrophyte species such as *Carex* sp., *Scirpus* sp., *Iris pseudacorus* L. and *Typha latifolia* L. Two different habitats can be identified within the reservoirs: non-vegetated (R1N and R2N) and vegetated (R1M and R2M) areas. The outflow of the second reservoir is channelled and leads to the Skakavac waterfall (JW) which flows into the Kovačica stream and thereby belongs to Drava River watershed area.

From vertebrate predators newts and fish were presented. Newts were dominated by species *Lissotriton vulgaris* (L.) and less by *Ichthyosauras alpestris* (Laurenti) and *Triturus carnifex* (Laurenti). According to the ichthyological survey conducted during 2006 across the water bodies in Nature Park Papuk, in Jankovac Stream only lamprey, *Lamperta planeri* Bloch, and brown trout, *Salmo trutta* L., with 25 and 75% in abundance, respectively, were identified (Mrakovčić *et al.*, 2008). Detailed ichthyological examinations have not been conducted during field sampling, because these reservoirs belong to a protected area.

Materials and methods

Samples were collected on a monthly basis from May to October 2008. According to the currently accepted conception of seston, all our samples could be considered as zooseston, but we divided them into two groups. In lentic stretches, *i.e.* reservoirs, we considered samples as

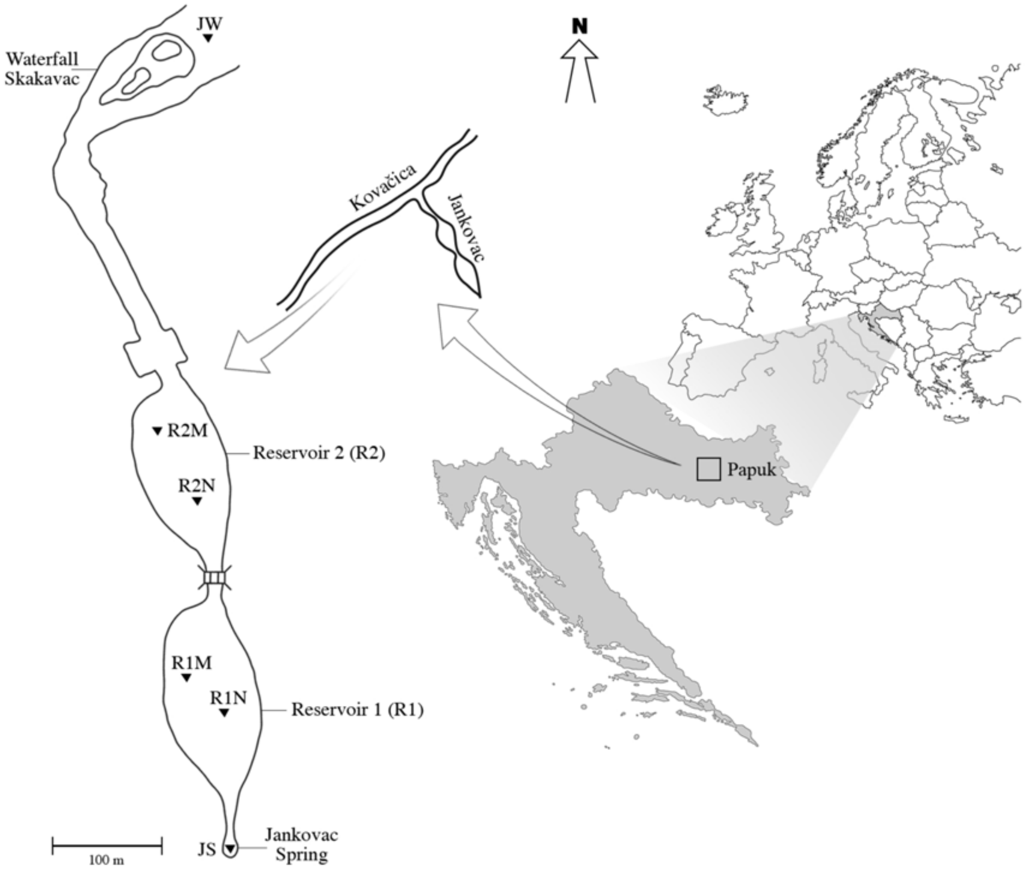

Fig. 1. Map of the Jankovac Stream flow-through system with sampling stations investigated marked.

zooplankton which were collected from two different habitat types, vegetated (R1M and R2M) and non-vegetated (R1N and R2N). In lotic stretches, *i.e.* spring and waterfall, we considered samples as zooseston, which were taken from the spring station as inflow (JS) and from the waterfall station (JW) as the outflow of seston flux. In this study, difference between zooplankton and zooseston is terminological, but not methodological.

From each station, 50 L of water were filtered through a plankton net (26 µm mesh; 6 months × 6 sites × 3 replicates = 108 samples). The samples were kept cool and transported to the laboratory in 200 mL bottles. A mean of triplicate was used as a single data point for a given date and site for further data analyses. Zooplankton/zooseston identification was carried out on live materials, which were later fixed in 4% formalin. The diversity and abundance in zooplankton/zooseston were assessed considering three groups of organisms: Rotifera, Cladocera and Copepoda. Rotifers were identified to the species or genus level according to Voigt and Koste (1978). Bdelloidea were counted, but not identified. Most crustaceans belonged to Cladocera and Copepoda and were identified to the genus or species level using the identification keys of Margaritora (1983) and Einsle (1993), while Ostracoda were not identified. Turbellaria, Nematoda, Gastrotricha, Oligochaeta, Tardigrada, Hydrachnidia and Ostracoda were not identified to the lower taxonomic level, but were classified as a heterogenic group of organisms. For quantitative analysis, the entire sample was counted using a Petri dish under an Opton-Axiovert 35 inverted microscope.

Biomass (dry weight, DW) of rotifers, cladocerans and copepods in seston was calculated according to the length–weight relationship for up to 30 randomly selected specimens per taxon (Dumont *et al.*, 1975; Malley *et al.*, 1989). Biomass in the heterogenic group of organisms was determined after being oven dried at 104 °C. Measurements were carried out on up to 20 randomly selected specimens per taxon. We considered specimens from the genera *Alona*, *Bosmina*, *Ceriodaphnia*, *Chydorus*, *Disparalona* and *Pleuroxus*, as small bodied (length 500 µm to 1 mm) and species from genera *Daphnia, Sida* and *Simocephalus* as large bodied (length > 1–6 mm).

The following parameters were measured *in situ*: temperature, dissolved oxygen concentration (WTW OXI 96), pH (WTW 330i), conductivity (HACH sension 5) and flow velocity (P600 flow meter, DOSTMANN electronic GmbH). For analyses of chemical parameters and chlorophyll *a* (Chl *a*), 3 L of non-filtered water was collected in bottles from each study site as the zooseston/zooplankton samples (6 months × 6 sites × 1 sample = 36 samples). Total alkalinity was measured by acidimetry with methyl orange as an indicator and nitrates were quantified using the sodium salicylate method (Höll, 1986). The stannous chloride method was used for the measurement of phosphate according to APHA (1985).

Table 1. Main morphometric features and macrophyte composition of the sampling stations on Jankovac Stream, Papuk Nature Park. WRT, water residence time.

Localities	JS	R1		R2		JW
Coordinates		45°31'09"N; 17°41'11"E		45°31'14"N; 17°41'09"E		
Area (m^2)		9240		5317		
$Length_{max}$ (m)	61	168		130		
$Width_{max}$ (m)	3	52		51		
z_{max} (m)	0.25	1.9		1.95		0.7
Height (m)						32
Total volume (m^3)		8.8×10^4		6.8×10^4		
WRT (day)		4.4		3.4		
Sampling stations	JS	R1N	R1M	R2N	R2M	JW
Habitat specification	Lotic	Lentic	Lentic	Lentic	Lentic	Lotic
Flow velocity ($m.s^{-1}$)	0.91 ± 0.69	0.16 ± 0.10	Stagnant	0.14 ± 0.088	Stagnant	1.38 ± 1.03
Habitat description	Small pool (z_{mean} = 0.15 m, Ø 1.5 m) on the cave entrance, *cca.* 3 m after spring, and before hypocrenal area	Reservoir, non-vegetated	Reservoir, vegetated	Reservoir, non-vegetated	Reservoir, vegetated	Small pool (z_{mean} = 0.5 m, Ø 1.5 m), after waterfall and bryophyte covered barrier, on the stream mouth
Bottom granulometry	Sand, detritus	Mud	Mud	Mud	Mud	Boulders, tufa
Bed and macrophyte coverage %	Thin layer of sediment	Non-vegetated	*Potamogeton natans* (25%), *Hippuris vularis* (50%)	Non-vegetated	*H. vularis* (60%)	Thin layer of sediment

Phytoplankton and particulate organic matter (POM) were considered as food resource for the main zooplanktonic groups as well as for benthic organisms. Chl *a* concentration was estimated by ethanol extraction by Nusch (1980) and was used as an indicator of algal biomass. For DW and ash-free dry weight (AFDW) estimation, an additional 3 L of water was first filtered (Schleicher & Schuell White Ribbon 589/2, ashless quantitative filter paper), then dried at 104 °C and ashed at 600 °C/6 h (6 months × 6 sites × 1 sample = 36 samples). DW was considered as the amount of total suspended matter (TSM), while AFDW was considered as an indicator of detritus or POM. The flux (kg/d) of TSM, POM and zooseston DW biomass was estimated as the product of related amounts and discharge.

The field data for the morphometric features of the sampling stations and flow velocity were used for the calculation of discharge and water residence time (WRT; Kalff, 2002). Macrophyte coverage (%) was estimated from the ratio of transect length occupied by a particular macrophyte to total transect length in each reservoir (Lau and Lane, 2002).

Prior to statistical analysis, all abiotic and biotic data were logarithmically transformed [log $(x + 1)$] and their normality was checked using Shapiro–Wilk's test. As this test suggested the data did not follow a normal distribution, a non-parametric Kruskal–Wallis test (comparison among multiple independent samples for environmental parameters and biotic components) or a Mann–Whitney *U* test (comparison between two independent samples for environmental parameters and biotic components) were used. Data were correlated using Spearman rank. For Kruskal–Wallis test, the *post-hoc* multiple comparison of average ranks was provided. The provided analyses reflected seasonal oscillations among, *i.e.* spring (May, June), summer (July, August) and autumn (September, October), as well as among investigated months, but no statistically significant differences were observed, except for temperature, nitrates and orthophosphates. Therefore, environmental parameters and biotic components were considered only through the spatial oscillations. For an explanation of the relationships between the abundance/seston flux of the dominant zooplankton/zooseston taxa and environmental variables (flow velocity/discharge, conductivity, pH, Chl *a* and AFDW), a multivariate method, the principal component analysis (PCA) was used. The interactions between biota and environmental parameters were presented by plotting the correlations of variables with the extracted PCA axes. For statistical data analyses, STATISTICA software package was used (StatSoft©).

Table 2. Minimum, maximum and mean values with noted statistically significant differences among investigated sampling stations for (a) environmental conditions and (b) biocoenosis diversity, abundance and biomass (Kruskal–Wallis test, df = 5, $N = 36$), with accompanied results of *post-hoc* multiple comparison test. Abbreviations: TSM, total suspended matter; POM, particulate organic matter; DW, dry weight; AFDW, ash-free dry weight.

	Mean ± SD	Min	Max	H	P	Multiple comparison test
(a) Environmental conditions						
Flow velocity ($m.s^{-1}$)	0.62 ± 0.34	0.01	1.50	25.33	***	JS, JW > R1N, R1M, R2N, R2M
Temperature (°C)	15.21 ± 3.86	9.40	21.60	10.69	ns	
Dissolved oxygen ($mg.L^{-1}$)	11.39 ± 2.40	7.48	16.90	2.90	ns	
Conductivity ($\mu S.cm^{-1}$)	461.19 ± 29.63	388.00	521.00	25.17	***	JW < JS, R1N
pH	7.78 ± 0.30	7.23	8.43	24.82	***	JW > JS, R1N
Free CO_2 ($mg.CO_2.L^{-1}$)	8.46 ± 4.00	2.20	17.60	19.72	**	JS > R2M, JW
Alkalinity (mg $CaCO_3.L^{-1}$)	243.29 ± 14.29	205.00	275.00	25.18	***	JW < JS, R1N, R1M; R2N < JS
Nitrates, NO_3^--N ($mg.L^{-1}$)	1.12 ± 0.28	0.72	1.77	17.65	**	JS > R2N, R2M, JW
Orthophosphates, $PO4_3^-$-P ($mg.L^{-1}$)	0.03 ± 0.01	0.01	0.06	2.18	ns	
Chl *a* ($\mu g.L^{-1}$)	1.07 ± 1.15	0.01	4.32	17.23	**	JS < R1M, R2N, R2M
TSM (DW $mg.m^{-3}$)	9.18 ± 29.42	0.97	174.60	19.64	**	JS < R1M, R2M
POM (AFDW $mg.m^{-3}$)	6.09 ± 28.40	0.25	171.20	22.11	***	JS < R1M, R2M; R1N < R1M; R1M > R2M
(b) Biocoenosis diversity, abundance and biomass						
Biodiversity (taxa number)	13.92 ± 6.78	1.00	28.00	18.89	**	JS < R1M
Rotifers ($Ind.L^{-1}$)	10.40 ± 14.22	0.11	73.21	20.39	***	JS < R1M, R2N, JW
Cladocerans ($Ind.L^{-1}$)	3.51 ± 11.13	0.01	59.36	16.72	**	JS < R1M; R1M > R2N
Copepods ($Ind.L^{-1}$)	2.51 ± 5.09	0.01	23.64	24.24	***	JS < R1M, R2M
Total zooseston ($Ind.L^{-1}$)	16.71 ± 24.76	0.11	122.36	24.24	***	JS < R1M, R2M, JW
Rotifers ($\mu g.L^{-1}$)	1.59 ± 2.74	0.01	12.14	20.86	***	JS < R2N, R2M
Cladocerans ($\mu g.L^{-1}$)	20.51 ± 57.41	0.01	300.50	18.26	**	JS < R1M
Copepods ($\mu g.L^{-1}$)	5.18 ± 11.24	0.01	52.33	22.54	***	JS < R1M, R2M
Total zooseston ($\mu g.L^{-1}$)	33.35 ± 67.60	0.01	357.03	18.61	**	JS < R1M, R2M

*$P < 0.05$; **$P < 0.005$; *** $P < 0.001$

Results

Environmental parameters in the Jankovac flow-through system

Among the sampling stations, significant differences were observed for the majority of measured parameters except for temperature, dissolved oxygen and orthophosphate (Table 2a). Across the longitudinal profile, the temperature was lowest (10.95 ± 2.15 °C), but the concentration of dissolved oxygen was the highest (12 ± 2.5 mg $O_2 .L^{-1}$) at JS. Higher oxygen concentrations were also observed in the vegetated areas of both reservoirs with higher photosynthetic activity of submerged macrophytes (R1M 12 ± 2.9 mg $O_2.L^{-1}$; R2M 11.8 ± 2.8 mg $O_2.L^{-1}$), but these differences were not significant ($P > 0.05$). As expected, temperature showed significant seasonal differences (Kruskal–Wallis test, $N = 36$, $H = 16.90$, $P = 0.002$) with higher values in summer and autumn (*post-hoc* test, $P = 0.0001$).

Flow velocity was obviously higher in lotic (JS and JW) than in lentic (R1N, R1M, R2N and R2M) stations. The parameters indicating the water-buffering capacity, free CO_2, alkalinity and conductivity showed negative, while pH showed positive longitudinal gradient. Most of these results were caused by the differences between JS and JW, as confirmed by *post-hoc* test (Table 2a).

Nitrates (Kruskal–Wallis test, $N = 36$, $H = 13.29$, $P = 0.001$) and orthophosphates (Kruskal–Wallis test, $N = 36$, $H = 10.86$, $P = 0.004$) showed significant seasonal differences, as a consequence of higher *vs.* lower concentrations of nitrates and orthophosphates in spring, respectively (*post-hoc* test, $P < 0.05$). Also, markedly higher concentrations of nitrates were found in JS (1.59 ± 0.11 mg NO_3^--$N.L^{-1}$) compared to the other stations (Table 2a). The results of statistical analysis suggested that concentrations of food items, algae (Chl *a*) and detritus or POM, significantly differed along the longitudinal profile with pronounced higher values in lentic vegetated stations (Table 2a). POM shared from 21 to 33% in TSM, except for R1M, where its portion was 76%.

Between the reservoirs R1 and R2, environmental parameters did not differ significantly (Mann–Whitney U test, $P > 0.05$, $N_{R1,R2} = 12$). Increase of POM concentration from non-vegetated to vegetated stations in both reservoirs as well as Chl *a* concentration in R1 gave rise to statistically significant differences (Mann–Whitney U test, $P < 0.05$, $N_{R1N,R1M} = 6$) shown in Table 3.

Zooseston in the Jankovac flow-through system

The results of the statistical analyses suggested that zooseston abundance, biomass and biodiversity were significantly different in the longitudinal profile of the system. This was the case for the main investigated organism groups (Table 2b). The abundance (1–116 $ind.L^{-1}$) and biomass (0.1–357 $\mu g.DW.L^{-1}$) of

Table 3. Results of Mann–Whitney U test ($N_{\mathrm{R1N,\ R1M,\ R2N,\ R2M}} = 6$) present primary significant differences between non-vegetated and vegetated stations for dominant taxa and main zooseston groups in reservoirs R1 and R2 in Jankovac flow-through system. Abbreviations: Chl *a*, chlorophyll *a* concentration; POM, particulate organic matter; AFDW, ash-free dry weight.

	R1N Mean ± SD	R1M Mean ± SD	*Z*	*P*	R2N Mean ± SD	R2M Mean ± SD	*Z*	*P*
Chl *a* (μg.L^{-1})	0.7 ± 0.3	2.0 ± 1.6	−2.40	*	1.5 ± 1.5	1.4 ± 1.1	−0.16	ns
POM (AFDW mg.m^{-3})	0.6 ± 0.4	32.8 ± 67.9	−2.72	**	0.6 ± 0.3	1.3 ± 0.8	−2.24	*
Colurella spp. (Ind.L^{-1})	0.1 ± 0.1	0.3 ± 0.2	−2.32	**	0.2 ± 0.1	0.2 ± 0.1	0.16	ns
Lepadella patella (Ind.L^{-1})	0.2 ± 0.2	0.6 ± 0.4	−2.32	**	0.2 ± 0.1	0.3 ± 0.3	−0.48	ns
Cladocerans (Ind.L^{-1})	0.7 ± 0.8	14.0 ± 22.8	−2.50	**	0.1 ± 0.2	6.1 ± 12.5	−1.28	ns
Cladocerans large-bodied (Ind.L^{-1})	0.1 ± 0.2	0.7 ± 0.5	−2.72	**	0.0 ± 0.0	0.4 ± 0.6	−1.34	**
Copepods (Ind.L^{-1})	0.4 ± 0.4	8.3 ± 4.5	−2.80	**	0.5 ± 0.7	5.7 ± 9.2	−2.16	ns
Macrocyclops spp. (Ind.L^{-1})	0.0 ± 0.1	0.5 ± 0.2	−2.88	***	0.0 ± 0.1	0.2 ± 0.3	−1.75	ns
Nauplii (Ind.L^{-1})	0.1 ± 0.1	0.7 ± 0.2	−2.88	***	0.1 ± 0.1	0.5 ± 0.5	−1.60	ns
Total zooseston (Ind.L^{-1})	5.1 ± 2.1	41.3 ± 40.7	−2.80	**	10.3 ± 5.5	20.2 ± 23.3	−0.48	**
Copepods (μg.L^{-1})	0.6 ± 0.7	21.2 ± 17.2	−2.80	**	0.5 ± 1.0	8.4 ± 12.5	−2.16	ns
Taxa number	14.5 ± 3.3	20.8 ± 5.6	−2.17	**	14.3 ± 4.8	15.5 ± 4.0	−0.40	ns

*$P < 0.05$; **$P < 0.005$; ***$P < 0.001$

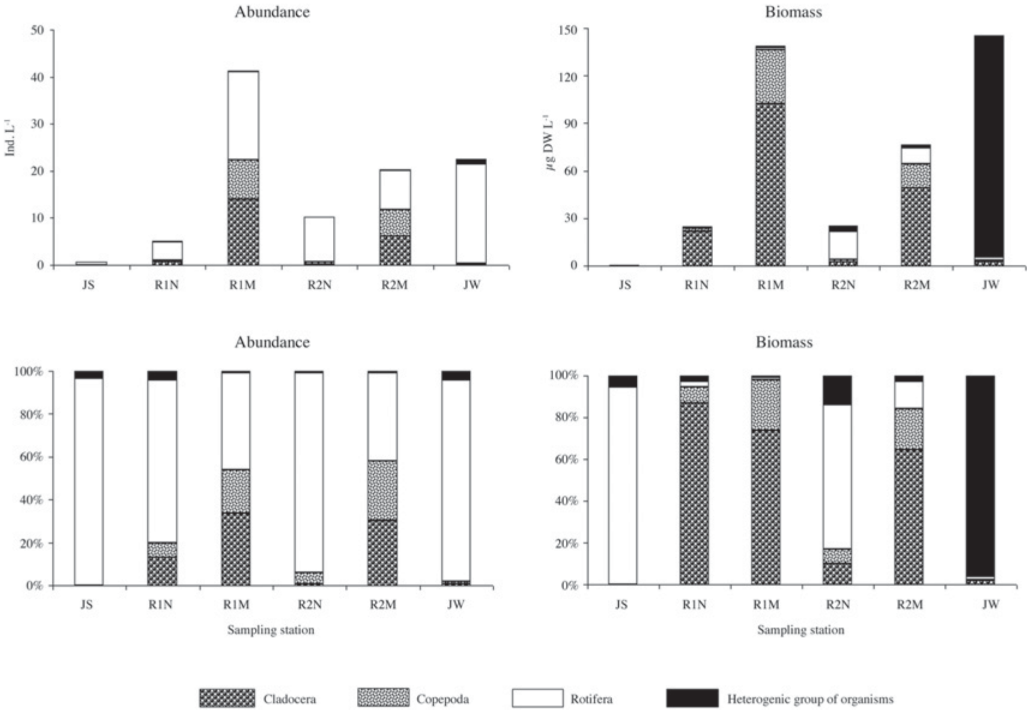

Fig. 2. Mean and relative abundance and biomass of Cladocera, Copepoda, Rotifera and heterogenic group of organisms in the investigated sampling stations of Jankovac Stream. Legend: JS, Jankovac Spring; R1N, Reservoir 1, non-vegetated area; R1M, Reservoir 1, vegetated area; R2N, Reservoir 2, non-vegetated area; R2M, Reservoir 2, vegetated area; JW, Jankovac Waterfall.

zooseton in all sampling stations of the Jankovac Stream were generally low, while zooseston biodiversity was high (Fig. 2). Altogether, 86 taxa were identified, 57 rotifers, 15 cladocerans, 8 copepods and 6 members of a heterogenic group of mostly benthic organisms (Table 4). Higher biodiversity was measured in vegetated (R1M 64 taxa and R2M 47 taxa) than in other stations (Tables 2b and 3).

Rotifers prevailed in abundance (from 40 to 97%) in all the investigated stations. In lentic stations, crustaceans prevailed in biomass, except for R2N, where rotifers dominated (Fig. 2). The heterogenic group of organisms had the highest biomass in the lotic station JW, at the outflow of Jankovac Stream (Fig. 2). Considering the lifestyle, in the six investigated stations, 60% of the taxa were semi-planktonic, 36% euplanktonic and the remaining, only 1%, belonged to benthic organisms (Table 4).

Zooplankton community in lentic habitats

Reservoir 1

In this reservoir, proximate to the stream inflow and prolonged WRT contrary to R2, significantly higher taxa

Table 4. Taxa presence on the investigated stations of Jankovac Stream. Abbreviations: LS, life style; B, benthic organisms; EP, euplanktonic organisms; SP, semi-planktonic organisms.

	JS	R1N	R1M	R2N	R2M	JW	LS		JS	R1N	R1M	R2N	R2M	JW	LS
Rotifera								Cladocera							
Ascomorpha ecaudis (Perty, 1850)				*			EP	*Alona guttata* (Sars, 1862)					*	*	SP
Asplanchna brightwelli (Goose, 1850)			*	*		*	EP	*Bosmina longirostris* (O. F. Müller, 1776)		*					EP
Asplanchna girodi (De Guerne, 1888)			*				EP	*Ceriodaphnia quadrangular* (O. F. Müller, 1785)			*				EP
Bdelloidea	*	*	*	*	*	*	B	*Chydorus ovalis* (Kurz, 1875)			*			*	EP
Brachionus diversicornis (Daday, 1883)						*	SP	*Chydorus sphaericus* (O. F. Müller, 1776)		*					EP
Cephalodella catellina (Müller, 1786)				*			SP	*Chydorus* sp.			*		*		EP
Cephalodella forficata (Ehrenberg, 1832)				*	*		SP	*Daphnia curvirostris* (Eylmann, 1887)			*				EP
Cephalodella gibba (Ehrenberg, 1832)		*	*	*	*	*	SP	*Daphnia longispina* (O. F. Müller, 1776)					*		EP
Colurella obtuse (Gosse, 1886)	*	*	*	*	*	*	SP	*Daphnia magna* (Straus, 1820)		*	*	*	*		EP
Colurella uncinata (O.F. Müller, 1773)	*	*	*	*	*	*	SP	*Daphnia pulex* (Leydig, 1860)			*		*		EP
Cyrtonia tuba (Ehrenberg, 1834)			*	*	*	*	SP	*Disparalona* sp.			*				SP
Dicranophorus spp.			*				SP	*Pleuroxus laevis* (Sars, 1862)		*	*	*	*		EP
Diplois sp.			*		*		SP	*Pleuroxus uncinatus* (Baird, 1850)			*	*	*	*	EP
Euchlanis dilatata (Ehrenberg ,1832)		*	*		*	*	EP	*Sida crystalline* (O. F. Müller, 1776)						*	SP
Filinia longiseta (Ehrenberg, 1834)				*	*		EP	*Simocephalus vetulus* (O. F. Müller, 1776)			*	*	*	*	SP
Filinia longiseta limnetica (Zacharias, 1893)			*		*		EP	Copepoda							
Keratella cochlearis (Gosse, 1851)		*	*	*	*	*	EP	*Canthocamptus staphylinus* (Jurine, 1820)					*		SP
Keratella quadrata (O. F. Müller 1786)		*	*			*	EP	*Eucyclops macrurus* (Sars, 1863)			*				EP
Lecane clara (Bryce, 1892)					*		SP	*Eucyclops serrulatus* (Fischer, 1851)			*		*	*	EP
Lecane closterocerca (Schmarda, 1859)		*	*	*	*	*	SP	*Eudiaptomus gracilis* (Sars, 1863)		*	*				EP
Lecane cornuta (Müller, 1786)			*				SP	*Macrocyclops albidus* (Jurine, 1820)		*			*		EP
Lecane elongata (Harring & Myers, 1926)		*	*				SP	*Macrocyclops fuscus* (Jurine, 1820)		*	*	*	*	*	EP

Table 4. (*Contd.*)

	JS	R1N	R1M	R2N	R2M	JW	LS		JS	R1N	R1M	R2N	R2M	JW	LS
Lecane flexilis (Gosse, 1886)		*	*				SP	*Macrocyclops* sp.						*	EP
Lecane haliclysta (Harring & Myers, 1926)			*		*		SP	*Megacyclops viridis* (Jurine, 1820)			*				EP
Lecane luna (Müller, 1776)	*	*	*	*	*	*	SP	Ostracoda			*	*	*	*	SP
Lecane lunaris (Ehrenberg, 1832)		*	*	*	*	*	SP	Nematoda	*	*	*		*	*	B
Lecane spp.		*	*	*	*	*	SP	Gastrotricha							
Lepadella patella (O. F. Müller, 1786)	*	*	*	*		*	SP	*Chaetonotus hystrix* (Metschnikoff, 1865)		*		*		*	B
Lepadella rhomboides (Gosse, 1886)			*				SP	Oligochaeta						*	B
Lindia sp.					*		SP	Hydrachnidia			*	*	*		B
Monommata longiseta (Müller, 1786)		*		*			SP	Tardigarda							
Monommata caudata (Myers, 1930)			*				SP	*Macrobiotus* sp.					*		B
Monommata sp.					*		SP								
Mytilina mucronata (O. F. Müller, 1773)			*	*	*		SP								
Mytilina ventralis (Ehrenberg, 1832)			*		*	*	SP								
Notholca acuminata (Ehrenberg, 1832)		*	*	*	*	*	EP								
Notommata aurita (Müller, 1786)			*			*	SP								
Squatinella mutica (Ehrenberg, 1832)			*				SP								
Squatinella rostrum (Schmarda, 1846)		*	*				SP								
Synchaeta oblonga (Ehrenberg, 1831)				*			EP								
Synchaeta pectinata (Ehrenberg, 1832)			*	*	*	*	EP								
Testudinella patina (Hermann 1783)						*	SP								
Trichocerca bicristata (Gosse, 1887)					*	*	SP								
Trichocerca brachyura (Gosse, 1851)		*				*	SP								
Trichocerca capucina (Wierzejski & Zacharias, 1893)		*	*				EP								
Trichocerca cavia (Gosse, 1886)		*					SP								

Table 4. (*Contd.*)

	JS	R1N	R1M	R2N	R2M	JW	LS
Trichocerca collaris (Rousselet, 1896)			*				SP
Trichocerca longiseta (Schrank, 1802)			*	*	*	*	SP
Trichocerca musculus (Hauer, 1937)			*		*		SP
Trichocerca porcellus (Gosse, 1851)		*	*	*	*	*	SP
Trichocerca relicta (Donner, 1950)			*		*		SP
Trichocerca vernalis			*	*	*	*	SP
Trichocerca weberi (Jennings, 1903)			*				SP
Trichocerca sp.			*			*	SP
Trichotria pocillum (*O.F.* Müller, 1776)		*	*				SP
Trichotria tetractis (Hauer, 1936)		*	*	*	*	*	EP
Wierzejskiella velox (Wiszniewski, 1932)		*					SP

number was recorded in vegetated, R1M, than the non-vegetated, R1N station, 60 and 33 taxa, respectively (Tables 3 and 4). Rotifers, particularly the genera *Lecane* (8 taxa) and *Trichocerca* (11 taxa), had the highest contribution to the biodiversity in the vegetated area. Figure 2 shows that zooplankton abundance was dominated by rotifers (R1N 78%; R1M 45%), while cladocerans dominated the zooplankton biomass (R1N 60%; R1M 73%). Also, Figure 2 shows a positive shift in the abundance of all the investigated groups of organisms from non-vegetated to the vegetated stations, where abundance of cladocerans, copepods and total zooplankton significantly increased in the vegetated station, R1M (Table 3).

In the non-vegetated station (R1N) cladocerans were represented by small-bodied species, *e.g. Bosmina longirostris*, while the vegetated station (R1M) was notably dominated by large-bodied cladocerans, *i.e. Simocephalus vetulus* (Table 3). Copepods, represented mainly by nauplii and adults of *Macrocyclops fuscus,* also significantly increased their abundance in the vegetated area (Table 3). Rotifers contributed mostly in abundance of the non-vegetated (75%) and vegetated (43%) station. However, the difference in rotifer abundance, between vegetated and non-vegetated stations were not significant (Mann–Whitney U test, $P > 0.05$, $N_{\mathrm{R1N,R1M}} = 6$; Fig. 2). On the taxa level, semi-planktonic species from the genus *Colurella* and the species *Lepadella patella* achieved significantly higher abundance in R1M than in R1N (Table 3).

Reservoir 2

In this reservoir with shorter WRT compared to R1, non-vegetated (R2N) and vegetated (R2M) stations contained 33 and 46 taxa, respectively (Table 3). In spite of the higher abundance of large-bodied cladocerans, *i.e. S. vetulus*, in the vegetated than in non-vegetated station, a significant difference in the abundance was not established (Mann–Whitney U test, $P > 0.05$, $N_{\mathrm{R2N,R2M}} = 6$). Copepods were mostly represented by nauplii and less by adults of *M. fuscus*. Abundance and biomass of the copepods were significantly higher ($P < 0.05$) in the vegetated station, R2M (Fig. 2, Table 3). In non-vegetated station, R2N, rotifers prevailed in abundance (97%) and biomass (63%), but in relation to vegetated stations it was not significant (Mann–Whitney U test, $P > 0.05$, $N_{\mathrm{R2N,R2M}} = 6$).

In order to assess the interactions between environmental parameters and the main planktonic taxa in the reservoirs R1 and R2, a PCA was run. The first two axes explain 82% of the variance (Fig. 3). Axis 1 explains 56% of the variance and is negatively correlated with flow velocity and conductivity, while it is positively correlated with food resources (algae and detritus) and pH value. This axis explains the majority of interactions and according to the axis all investigated taxa were negatively affected by flow velocity. On the other hand, the concentration of food resources, detritus (POM) and algae

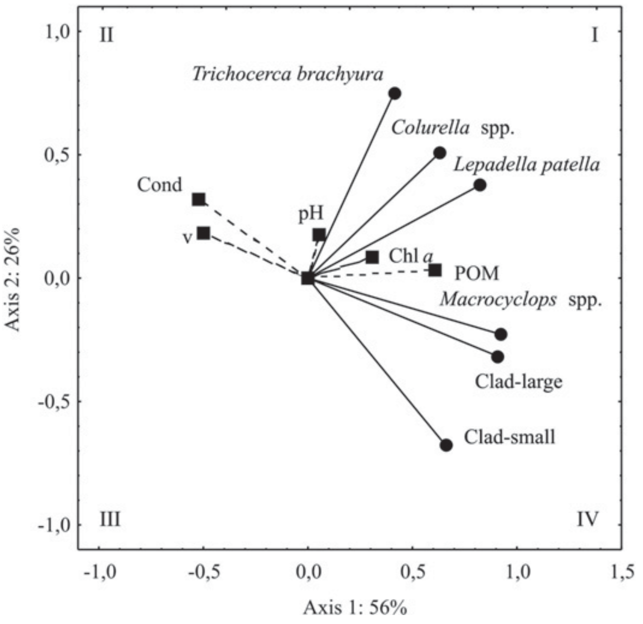

Fig. 3. PCA plot of the main zooplankton taxa abundance against environmental variables. Abbreviations by alphabetic order: Chl *a*, chlorophyll *a* concentration; Clad-large, large-bodied Cladocera; Clad-small, small-bodied Cladocera; Cond, conductivity; POM, particulate organic matter; v, flow velocity. Roman numerals mark quadrants.

(Chl *a*), had positive effects on all the taxa, and were higher in vegetated stations. These results are in concordance with the distribution of stations R1M and R2M in quadrants I and IV of PCA plot. Axis 2 explains 26% of the variance and positively correlates with flow velocity and conductivity. These interactions classified taxa as rheotolerant, rotifers, and rheointolerant, cladocerans and copepods. Moreover, it is in agreement with spatial prevalence of rotifers and crustaceans in R1M quadrant I and in R2M quadrant IV, respectively.

Seston flux on the longitudinal profile

The flux of TSM was highly related ($r = 0.83$; $P < 0.05$, $N = 36$) to the flux of particulated organic matter (POM). The latter was positively influenced by zooseston flux ($r = 0.38$, $P < 0.05$, $N = 36$). Figure 4 shows oscillations of TSM, POM and zooseston flux along the longitudinal profile of the system. These oscillations were significantly different between the stations (Kruskal–Wallis test, $H_{\mathrm{TSM}} = 16.1$, $P = 0.007$; $H_{\mathrm{POM}} = 16.3$, $P = 0.006$; $H_{\mathrm{zooseston}} = 18.1$, $P = 0.003$; $N = 36$). TSM and POM fluxes achieved their peaks in R1M, while zooseston DW peaked in JW. Accordingly, the contribution of zooseston in POM flux increased along the longitudinal profile. Such a contribution was negligible in spring (JS), while it varied downstream from 3 to 30% in lentic habitats and reached a maximum of 57% in JW. It is assumed that a drift in the benthic organisms exhibited prominent contribution in zooseston flux at JW ($r = 0.64$, $P < 0.05$, $N = 36$).

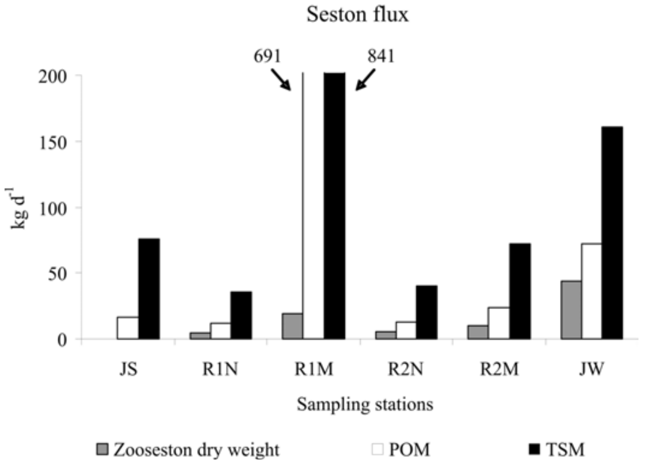

Fig. 4. Flux of the zoosenton dry weight biomass, POM and TSM along the Jankovac Stream longitudinal profile. Legend: JS, Jankovac Spring; R1N, Reservoir 1, non-vegetated area; R1M, Reservoir 1, vegetated area; R2N, Reservoir 2, non-vegetated area; R2M, Reservoir 2, vegetated area; JW, Jankovac Waterfall.

Passing through the lentic habitats, seston flux resulted in a significant increase of the phytoplankton (Chl *a*), cladocerans, copepods as well as euplanktonic organisms (Table 5a). Opposed to the inflow station (JS), at the outflow station (JW) significantly higher values of phytoplankton biomass (Chl *a*), suspended POM, biomasses of euplanktonic, semi-planktonic and benthic organisms, and consequently total zooseston biomass were measured (Table 5b).

The PCA plot of interactions between the environmental parameters and the organisms in seston flux explained 65% of the variance (Fig. 5). Both axes (1 and 2) positively correlated with discharge, biomass of rotifers and heterogenic group, mainly benthic organisms and thus, concordantly resulted in increase of benthic organisms in seston flux. The biomass of the main zooseston groups as representatives of different life styles, negatively correlated with discharge and positively with food resources (AFDW and Chl *a*), consequently explaining axis 1 (Fig. 5).

Discussion

The results of our study revealed scarcity of zooseston, but a wide spectrum of diversity caused by the prominent presence of rotifers in a submountain karst flow-through system. In reservoirs, zooplankton achieved higher diversity, abundance and biomass in vegetated than in non-vegetated areas. There, rotifers dominated in non-vegetated, while crustaceans dominated in vegetated stations. Statistical analyses suggested that zooplankton abundances in reservoirs were negatively affected by flow velocity and positively by food resources. Thus, seston flux consisted of rheotolerant zooplankton organisms, *i.e.* rotifers, and from drifted benthic organisms and bdelloid

Table 5. Significant differences in seston flux (a) between lotic and lentic stretches and (b) inflow and outflow station in Jankovac Stream flow-through system analysed by Mann–Whitney *U* test. Abbreviations: Q, discharge; Chl *a*, chlorophyll *a* concentration; POM, particulate organic matter; TSM, total suspended matter.

Flux (kg.d^{-1})	Lotic Mean ± SD	Lentic Mean ± SD	*Z*	*P*
(a) Differences in discharge and seston flux between lotic ($N = 12$) and lentic ($N = 24$) stretches				
Q (m^3.d^{-1})	22398.4 ± 24572.1	28043.4 ± 29680.6	4.2	***
TSM	2.3 ± 1.4	12.6 ± 35.8	1.8	*
Cladocera biomass	17640.6 ± 40405.2	320205.6 ± 613732.0	− 2.1	**
Copepoda biomass	8496.5 ± 8496.5	116576.1 ± 172771.5	− 2.7	**
Euplanktonic organisms biomass	48177.6 ± 61658.9	1114901.4 ± 1864333.9	− 3.5	***
(b) Differences in discharge and seston flux between inflow (NJS = 6) and outflow (NJW = 6) station				
Chl *a*	4296.9 ± 4117.0	36766.9 ± 26053.9	− 2.7	*
Total zooseston biomass	0.1 ± 0.1	72.4 ± 113.9	− 2.7	**
POM	16.1 ± 8.5	44.3 ± 39.3	− 2.1	*
Rotifera biomass	1900.2 ± 2968.2	36856.9 ± 26798.0	− 2.7	**
Benthic organisms biomass	543.7 ± 1331.7	66.3 × 108 ± 143.8 × 108	− 3.1	**
Euplanktonic organisms biomass	21196.8 ± 51039.3	75158.4 ± 63339.5	− 2.2	**
Semi-planktonic organisms biomass	264.4 ± 619.3	217267.2 ± 367320.9	− 2.9	**

*$P < 0.05$; **$P < 0.005$; *** $P < 0.001$

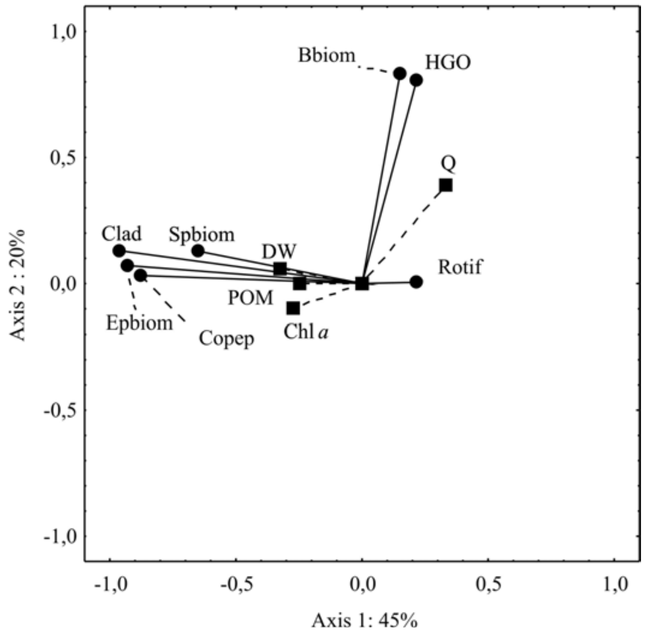

Fig. 5. PCA plot shows flux of the main groups in zooseston against environmental variables. Abbreviations: Q, discharge; Chl*a*, chlorophyll *a* concentration; POM, particulate organic matter; DW, dry weight; Clad, Cladocera biomass; Copep, Copepoda biomass; Rotif, Rotifera biomass; HGO, heterogenic group organisms biomass; Bbiom, benthic organisams biomass; Epbiom, euplanktonic organisms biomass; Spbiom, semi-planktonic organisms biomass.

rotifers, which are less susceptible to water current than cladocerans, as suggested by PCA.

The exclusive characteristics of Jankovac flow-through system are the elevated nitrate concentrations and the abundant stands of the submerged macrophyte *H. vulgaris* in the two man-made reservoirs. Also, recent tufa deposition on Skakavac barrier indicates the low trophic state required for calcite precipitation (Srdoč *et al.*, 1985; Špoljar *et al.*, 2008). Higher nitrate levels can be explained by the proximity of a spring where nitrate-rich groundwater rises, which is common for spring waters, especially in the karst area (Malard *et al.*, 1997). Nitrates declined in vegetated reservoirs probably due to macrophytes utilization causing significant downstream nitrate depletion.

The habitats of *H. vulgaris* are on the list of endangered species in Croatia (Nikolić and Topić, 2005). As the structural complexity is a main driver of biodiversity, more complex habitats generally contain more species (Van de Meutter *et al.*, 2008). In Jankovac Stream, man-made reservoirs disrupt longitudinal continuum of running water and represent insurmountable barrier particularly for benthic macroinvertebrates (Bednarek and Hart, 2005). However these new habitats represent *inocula* of plankton abundance and diversity (Lair and Reyes-Marchant, 1997; Zimmermann-Timm *et al.*, 2007). Regarding hydrogeomorphology, the Jankovac reservoirs are comparable to the Plitvice Lakes. First, both hydrosystems are situated in sedimentary karst rocks and second, the lentic stretches dominate over lotic (Špoljar *et al.*, 2007a, b). Furthermore, in both hydrosystems, high biodiversity has been established (Plitvice Lakes: 66 rotifer and 23 crustacean taxa; Jankovac reservoirs: 57 rotifer and 26 crustacean taxa). This high biodiversity in two small Jankovac reservoirs can be explained by the presence of high percentage of submerged macrophytes with complex habitat architecture, *i.e. H. vulgaris*. This is in accordance with the findings of other authors (Duggan *et al.*, 2001; Kuczyńska-Kippen, 2005; Cazzanelli *et al.*, 2008), who confirmed higher biodiversity in complex macrophyte stands. In Plitvice Lakes, the bottom is mostly covered with *Chara* spp., a complex habitat genus. Unfortunately, investigation or published data about zooplankton within its stands are not available. We hypothesise that submerged *Chara* stands promote diversity together with bryophyte communities on tufa barriers (Špoljar *et al.*, 2007b; Sertić Perić *et al.*, 2011). Moreover, in Jankovac Stream, lotic stretches are also covered with bryophyte, which is assumed to contribute to species diversity (Špoljar *et al.*, 2012).

Reservoir and macrophyte habitats as a zooplankton source

Flow velocity and WRT have been established as the key factors in the development of a plankton community in the running waters (Basu and Pick, 1996; Obertegger *et al.*, 2010). In accordance to this, our results suggest that lentic habitats of the Jankovac flow-through system ensure the development of higher phytoplankton biomass and significant prevalence of semi-planktonic and euplanktonic small-bodied species, especially rotifers. Other authors noted the positive relationships between WRT and development of phytoplankton and zooplankton, *i.e.* rotifers and crustaceans (Basu and Pick, 1996; Walz and Welker, 1998; Rennella and Quiros, 2006; Obertegger *et al.*, 2007).

Our results showed an increase of zooplankton diversity, abundance and biomass in vegetated area with lower current in comparison with non-vegetated area with higher current. Several mechanisms can explain the horizontal (non-vegetated *vs.* vegetated) distribution of zooplankton assemblages in reservoirs. First, non-uniform zooplankton distribution can be explained by different adaptations to water current. According to the PCA plot, we presumed that in Jankovac reservoirs, small- and large-bodied cladocerans, as well as *Mesocyclops* avoid water current and belong to the group of rheointolerant organisms prevalent in the littoral vegetated zone, while rotifers belong to the group of rheotolerant organisms prevalent in the non-vegetated mainstream zone. Resistance of rotifers to water current in field and laboratory conditions has been attributed to their rapid heterogenetic reproduction, short generation time and less-susceptible fecundity in comparison with crustaceans as well as their resistance against sedimentation, which is contrary to larger-bodied organisms such as cladocerans (Stemberger and Gilbert, 1985; Węglenska and Ejsmont-Karabin, 1994; Holst *et al.*, 1998; Burger *et al.*, 2002; Sluss *et al.*, 2008). Copepods are capable of avoiding water current due to fast movements or better handle turbulent conditions than cladocerans, but arguments also exist that they are sensitive to hydraulic stress (Lair and Reyes-Marchant, 1997; Eriksson, 2002; Sluss *et al.*, 2008). The significantly higher abundance/biomass of cladocerans, copepods and total zooseston in vegetated littoral stations of Jankovac reservoirs could be explained by the effect of a "zone of retentiveness" or a "storage zone" (Schiemer *et al.*, 2001; Baranyi *et al.*, 2002), where extended WRT allows zooplankton to grow and reproduce, and results in higher plankton abundance (Reynolds *et al.*, 1991; Vadebouncoeur, 1994; Welker and Walz, 1998; Akbulut, 2004; Zimmermann-Timm *et al.*, 2007).

Second, higher diversity, abundance and biomass of zooplankton in vegetated than in non-vegetated stations can be due to macrophyte coverage that provides more favourable habitat for zooplankton than open water because of the following: diverse habitats, richness of food quality and quantity, refuge from pelagial predators and competitors, and water movement (Bukvić *et al.* 1998; Basu *et al.*, 2000; Burks *et al.*, 2001a; Kuczyńska-Kippen and Nagengast, 2006). In our study, the PCA results confirm that all taxa included in the analysis, positively correlated with phytoplankton (Chl *a*) and suspended detritus particles (POM) as food resources, and that corresponded to the higher abundance in vegetated sampling stations. Similar results were obtained by Basu *et al.* (2000) in St. Lawrence River fluvial lakes, where zooplankton densities were higher in littoral zones than in the mainstream, and the plankton abundance was much higher in littoral macrophyte beds than in non-vegetated areas. Furthermore, we presumed that high percentage of macrophyte coverage and a shallow littoral zone induce the development and domination of semi- planktonic species as also established in *Myriophyllum* covered Budzyńskie Lake in Wielkopolski National Park, Poland (Kuczyńska-Kippen, 2003).

Third, biotic interactions, predation and competition increased under lentic conditions and decreased impact of losses due to advection (Baranyi *et al.*, 2002). Opposite gradient in abundance ratio between rotifers and crustaceans in non-vegetated *vs.* vegetated area, could be explained by the biotic interactions. According to field observation and literature data (Mrakovčić *et al.*, 2008), in Jankovac reservoirs, trout (*S. trutta*) is the main visual predator in non-vegetated area. It probably caused escape into vegetated areas and consequently higher abundance and biomass of large-bodied cladocerans and copepods in such habitats. Trout not only are known as opportunistic feeders that rely on benthic prey but also are partly planktivorous and could reduce large-bodied crustaceans, due to the size-selective predation (Fitzmaurice, 1979; Winder *et al.*, 2003; Schabetsberger *et al.*, 2006). Predation by newts, according to the literature, has weak impact on crustaceans, and there are more references about coexistence between newts and large crustaceans due to newts low digestion rate (Schabetsberger *et al.*, 1996, 2006; Jersabek *et al.*, 2001). Moreover, the higher relative abundance of rotifers in the non-vegetated compared to the vegetated areas could be a result of other biotic interactions, for instance competition with crustaceans (Bogdan and Gilbert, 1987; Cazzanelli *et al.*, 2008) and avoidance of tactile predators, *i.e.* insect larvae, in the litoral zone (Burks *et al.*, 2001b; Meerhoff *et al.*, 2007; González-Sagrario *et al.*, 2009).

Seston advection

Quantitative and qualitative seston structure is relevant as food resources for downstream benthic community (Habdija *et al.*, 2004; Špoljar *et al.*, 2007b) and organisms' dispersion (Sertić Perić *et al.*, 2011). According to the data presented, the inflow station, JS, adjacent to spring was characterized by poor production and represented the initial state for downstream inoculation of seston with plankton and benthos. Downstream flux through the reservoirs implicated the remarkable enrichment of organic matter (POM and zooseston biomass), which originated mostly in vegetated stations and could be comparable to inshore influence on the fluvial lakes of the St. Lawrence River (Basu *et al.*, 2000). In the vegetated lentic stations in Jankovac system, higher POM concentrations peaked prevalently from residuals of macrophyte stems, higher macroinvertebrate abundance and leaf litter. We presumed that the higher amount of organic matter on outflow, at JW, was a mixture of POM and benthic organisms from upstream bryophyte-covered bottom over the barrier and plankton enrichment through highly vegetated reservoirs (Sandlund, 1982; Suren, 1991). We consider substantial rotifer's abundance on the outflow station (JW), as *sucus* of specimens from reservoirs and drifting of benthic species, particularly bdelloids (Špoljar *et al.*, 2007b).

The hydromorphological differences of Jankovac Stream channel maintained many microhabitats and seston biodiversity in a small-scale pattern, flowing from almost the uninoculated spring over bryophyte covered lotic stretches, towards reservoirs and finally over the bryophyte covered tufa barrier as Skakavac Waterfall. Results of this study indicate that hydrological features (flow velocity and WRT) and food resources (algae and detritus) mainly influenced zooseston longitudinal and horizontal assemblages within a flow-through system. Our results indicated that zooplankton horizontal assemblage could be shaped by the impact of biotic factors in submerse macrophyte covered reservoirs. Also, in our study, we included rotifers, which are often neglected in freshwater biotic interactions. Thus, the influence of biotic interactions, pelagial and littoral predation on horizontal distribution of zooplankton in reservoirs required elucidation and could be the objective of further investigation. High biodiversity on the invertebrate level and specific microhabitats on relatively small area deserve further investigation and monitoring and communication with the management in terms of appropriate protection and conservation.

Acknowledgements. This study was funded by the Papuk Nature Park and project 11900000001205 of the Ministry of Education, Science and Sport, Republic of Croatia. We thank the personnel of Papuk Nature Park for their help in administrative and field support during this investigation. We appreciate helpful and constructive comments of two anonymous referees for improvement of this manuscript.

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