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Spatial and temporal variability of hyporheic invertebrate community within a stream reach of the River Bača (W Slovenia)

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Abstract. We studied spatio-temporal distribution of hyporheic invertebrate community at the stream-reach scale in the River Bača on three sampling occasions (January, March, May) in 2005. On each sampling occasion, invertebrates were collected from the shallow hyporheic zone (RB1; depth 30-60 cm, 3 replicates), and deeper hyporheic zone (RB2; depth 60-90 cm, 2 replicates) in the river bed, and adjacent gravel bar (GB; depth 60-90 cm, 3 replicates) using Bou-Rouch piston pump. Concurrently, temperature, conductivity and oxygen were measured in the surface water and in hyporheic water at each sampling station. Differences in hyporheic community between dates and habitats were analysed by using two-way ANOVA (dates and habitats as fixed factors) and explored by principal component analysis (PCA). Altogether, 21,657 specimens from 63 taxa were collected. Cyclopoida juveniles, *Leuctra* sp. (Plecoptera), Chironomidae (Diptera), *Acanthocyclops vernalis* (Fischer, 1853) and *Diacyclops languidus* (G. O. Sars, 1863) were the most abundant in the samples. Two-way ANOVA showed significant differences between habitats (RB1 and GB), but no differences between dates when using taxonomic richness as dependent variable. No differences between habitats and dates were calculated when invertebrate densities were applied. PCA of hyporheic invertebrate data showed a gradient in community composition from shallow hyporheic zone (RB1) to deeper hyporheic zone (RB2) and gravel bar (GB). The differences were most probably due to different sediment composition in the studied habitats and less frequent disturbances due to floods in deeper layers and lateral gravel bars.

Key words: stream reach, hyporheic zone, invertebrates, distribution, community composition, spatial and temporal distribution

Izvleček. PROSTORSKO-ČASOVNA SPREMENLJIVOST ZDRUŽBE NEVRETENČARJEV V HIPOREIKU REKE BAČE (Z SLOVENIJA) – V letu 2005 je bila opravljena raziskava združbe nevretenčarjev v hiporeiku reke Bače, kjer smo opazovali prostorsko-časovno spremenljivost združbe nevretenčarjev v 3 vrstah habitatov. Nevretenčarje smo vzorčili iz globine 30 – 60 cm (RB1; 3 podvzorci) in iz globine 60 – 90 cm (RB2; 2 podvzorca) v rečni strugi ter v obrežnem prodišču iz globine 60-90 cm (GB; 3 podvzorci) v januarju, marcu in maju 2005. Merili smo tudi temperaturo vode, prevodnost in vsebnost kisika. Za testiranje razlik v številčnosti nevretenčarjev in številu taksonov med habitatoma (RB1, GB) in datumi smo uporabili dvosmerno analizo variance z vrsto habitata in datumom kot glavnima faktorjema. Sestavo združb med posameznimi habitati in datumi smo primerjali s pomočjo multivariatne analize glavnih komponent (PCA). V hiporeiku reke Bače smo nabrali 21.657 osebkov iz 63 taksonov. Najbolj številčni so bili predstavniki zgodnjih razvojnih stadijev rakov ceponožcev (Cyclopoida, Copepoda), ličinke vrbnic (*Leuctra* sp.) in trzač (Chironomidae) ter 2 vrsti ceponožnih rakov, *Acanthocyclops vernalis* (Fischer, 1853) in *Diacyclops languidus* (G. O. Sars, 1863). Dvosmerna analiza variance je pokazala razlike med RB1 in GB v številu taksonov, medtem ko razlik med datumi ni bilo. Številčnost nevretenčarjev ni bila značilno različna ne med habitati in ne med datumi. Analiza glavnih komponent (PCA) je pokazala gradient v sestavi združbe od plitvega hiporeika (RB1) do globljega hiporeika (RB2) in obrežnega prodišča (GB), najverjetneje zaradi različne strukture sedimenta v izbranih habitatih in bolj pogostih motenj (mešanje sedimenta) zaradi visokih voda v plitvejših slojih hiporeika.

Ključne besede: rečni odsek, hiporeik, nevretenčarji, porazdelitev, sestava združbe, prostorska spremenljivost, časovna spremenljivost

Introduction

The term hyporheic biotope was first used in the late 50s and described as the interstitial habitat beneath a stream, bordered by the surface water above and by true groundwater below (Orghidan 1959, Schwoerbel 1961). However, investigations of fauna in sediments along the river banks have longer tradition (Karaman 1935, Chappuis 1942, Angelier 1953). Later, the hyporheic zone was more precisely defined as the saturated interstitial spaces below the stream bed and adjacent stream banks that contain some proportion of channel water (White et al. 1993). Recently, it has been shown by several authors that many rivers exchange water with their subsurface aquifers at a range of scales (Packman & Bencala 2000), both vertically into the hyporheic zone sensu stricto below the stream and laterally into the parafluvial zone below the banks and floodplain. Surface water down-wells into the sediments and travels for some distance through the saturated sediments before upwelling into the stream again. During its hyporheic journey, the downwelling water mixes with groundwater, and its chemical composition is further altered by biogeochemical processes typically mediated by microbial biofilms on sediment particles (Boulton et al. 1998).

Hyporheic zone is inhabited by a diverse array of invertebrate assemblages. In the areas where downwelling of river water occurs, the sediments are well-oxygenated, rich in labile carbon, and harbour primarily organisms from benthic origin. With increasing residence time below the riverbed, hyporheic water becomes less oxygenated, biogeochemical processes become reductive, and the hyporheic fauna becomes dominated by groundwater species (Gibert et al. 1994, Brunke & Gonser 1997). The hyporheic zone is a site of spawning and egg incubation for some salmonid species (Geist & Dauble 1998), as well as a nursery site for some insect taxa, such as Leuctridae (Plecoptera) and Heptageniidae (Ephemeroptera) (Malard et al. 2003). The hyporheic sediment pores can act as a refuge for invertebrates during periods of drought (Williams 1977, Wood et al. 2010), and can be regularly used by early instars of benthic insects as a refuge against strong currents (shear stress) (Schwoerbel 1964).

Despite the extensive faunistic research of groundwater invertebrates in Slovenia over the past decades, the ecology of interstitial habitats along the rivers remains poorly investigated, especially in comparison to those in karst aquifers. Invertebrate communities living in different groundwater habitats of the River Sava in southern Slovenia and northern Croatia were investigated from 1960-70 (Meštrov 1960, Meštrov et al. 1983). In the late 1970s, comprehensive studies of the invertebrate community from interstitial habitats were conducted in the River Sava (at Ljubljansko polje) (Sket & Velkovrh 1981). Two decades later, intensive ecological studies of interstitial habitats were performed on four rivers, tributaries of the River Sava, flowing in the south and southeastern part of Ljubljansko Barje (Mori 2004, Dole-Olivier et al. 2009). Recently, the ecology of hyporheic biofilm (Simčič & Mori 2007) and the impacts of gravel extraction on the hyporheic invertebrates of the River Bača, a tributary of the River Soča, have been studied (Simčič & Mori 2007, Mori et al. 2011).

In this paper we present the composition and spatio-temporal dynamics of hyporheic invertebrate community at the stream-reach scale in the pre-alpine gravel-bed River Bača with the aim to compare assemblages inhabiting shallow (RB1) and deeper (RB2) hyporheic zone in the river bed and those from adjacent gravel bar (GB), and discuss the importance of hydrology and river bed geomorphology in shaping the hyporheic invertebrate community.

Materials and methods

The study was carried out within a 20 m long reach of the pre-alpine River Bača (W Slovenia, the River Soča catchment). The study site is located 2.5 km before the river confluence with the River Idrijca, where a 100 m long gravel bar is extending along the right side of the stream channel. The width of the channel was 5 m and additional 5 m belonged to the gravel bar. The River Bača has pluvio-nival discharge regime, with maximum discharge rates in autumn. The predictability of discharge rates is relatively low, especially for October and November. The mean annual discharge was 7.1 m^3/s for the 1961 – 1990 period, and 6.6 m^3/s for the 1991 – 2004 period (Environment Agency RS). The maximum and minimum mean daily discharges for 13 years period were 38.7 and 2.6 m^3/s, respectively. The substrate is highly permeable, composed mainly of gravel and pebble.

In this paper, the results of three sampling campaigns carried out at three different dates (i.e. in January, March and May 2005) are presented (Fig. 1). On each sampling occasion, a mobile steel pipe (Ø 45 mm) with a perforated distal end (apertures in a length of 30 cm, diameter of holes were 10 mm) was inserted into the river sediments at six sampling stations. Three samples were taken from the depths between 30 and 60 cm (shallow hyporheic zone - RB1) in the river bed, and three from adjacent gravel bar, from a depth between 60 and 90 cm (GB). Two samples were taken at the same sampling stations as RB1, but from the depths between 60 and 90 cm (deeper hyporheic zone – RB2). The samples from RB2 were not collected in January 2005 due to technical problems, and one of the RB2 samples was not collected in March and May because the sediments were too shallow at the most downstream RB1 station to insert the steel pipe deeper than 60 cm into the sediments. Sampling stations at RB1 were approximately 5 m apart in a line along the river flow, while stations at GB were parallel to RB1. At each sampling station (n=8), 10 litre mixtures of water, sediment and invertebrates were extracted using a piston pump fixed on a mobile steel pipe (Bou & Rouch 1967). Invertebrates and organic matter were removed from the sample by elutriating and filtering the water through a hand net (mesh size 100 µm), stored in PVC bottles in 4% formaldehyde solution and transported to the laboratory for processing. After collecting the biological samples, oxygen (WTW Multiline P4, CellOx 325), temperature and conductivity (WTW Multiline P4, TetraCon 325) of the surface water and hyporheic water in the steel pipes were measured. In the laboratory, the biological samples were sorted and invertebrates counted and identified to the species where possible (Rivosecchi 1984, Studeman et al. 1992, Einsle 1993, Janetzky et al. 1996, Graf & Waringer 1997, Meisch 2000, Zwick 2004).

Physical and chemical measurements and invertebrate densities and taxonomic richness were compared between different sampling occasions and between RB1 and GB, using two-way analysis of variance (ANOVA) with habitats (RB1, GB) and dates (January, March, May) as fixed factors. Data were normalized by log10(x+1) (T, conductivity, oxygen, invertebrate density) and by $\sqrt{(x+3/8)}$ (taxonomic richness) transformations. Data from the deeper hyporheic zone (RB2) were not included in the above analyses due to lacking data from January sampling campaign. Principal component analysis (PCA) on log (x+1) transformed invertebrate abundances was carried out to examine the variation in community composition between habitats and dates. The CANOCO software package was applied (ter Braak & Šmilauer 2002).

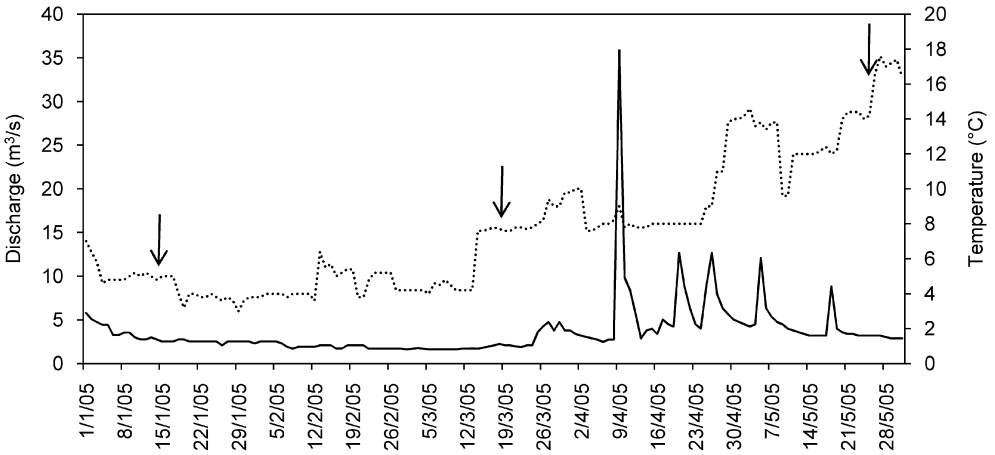

Figure 1. Mean daily discharge (solid line) and surface water temperatures (dashed line) in the River Bača from January to May 2005. Arrows indicate the sampling dates.
Slika 1. Srednji dnevni pretoki (neprekinjena črta) in temperature površinske vode (pikčasta črta) v reki Bači, merjeni od začetka januarja do konca maja 2005. Puščice označujejo datume vzorčenja.

Results

Mean water temperatures over sampling periods were 4.8 - 14.5°C (surface), 5 - 14.4°C (RB1), 6.4 - 14°C (RB2) and 5.5 - 16°C (GB) respectively (Fig. 2a) and were significantly different between dates (two-way ANOVA; $F = 3.88$, $p < 0.001$), but not between RB1 and GB. Mean conductivity of the surface water was 265 - 279 µS/cm, of the shallow river bed (RB1) 268 – 282 µS/cm, of the deeper river bed water (RB2) 266 – 279 µS/cm, and of gravel bars (GB) 282 – 290 µS/cm (Fig. 2b). Mean oxygen concentrations were 11.7 – 13.8 mg/l in the surface water, 9.0 – 12.2 mg/l in RB1, 11.6 – 12.8 mg/l in RB2 and 8.2 – 9.8 mg/l in GB (Fig. 2c). Two-way ANOVA did not show significant differences in conductivity and oxygen concentrations between habitats RB1 and GB, and dates.

Altogether, 21,657 specimens from 63 taxa were collected (Tab. 1). Juveniles of Cyclopoida, *Leuctra* sp. (Plecoptera), Chironomidae (Diptera), *Acanthocyclops vernalis* (Fischer, 1853) and *Diacyclops languidus* (G. O. Sars, 1863) (Crustacea, Copepoda) were the most abundant taxa in the samples. Eleven groundwater taxa were collected, with *Diacyclops languidoides* (Lilljeborg, 1901) being the most abundant among them. Mean densities ($n=3$) over the sampling occasions were in RB1 556 - 650 specimens/10 l, in RB2 1,316 - 2,960 specimens/10 l, and in GB 479 - 1,308 specimens/10 l (Fig. 3a). Mean taxonomic richness ($n=3$) varied from 8.7 – 14.3 taxa 10/l in RB1, from 14.0 – 17.5 taxa/10 l in RB2, and from 18.0 – 21.7 taxa/10 l in GB (Fig. 3b). Two-way analysis of variance revealed significant difference in taxonomic richness between RB1 and GB ($p < 0.001$, $F = 4.74$), but not in density, as well as there was no impact of sampling dates on taxonomic richness or density.

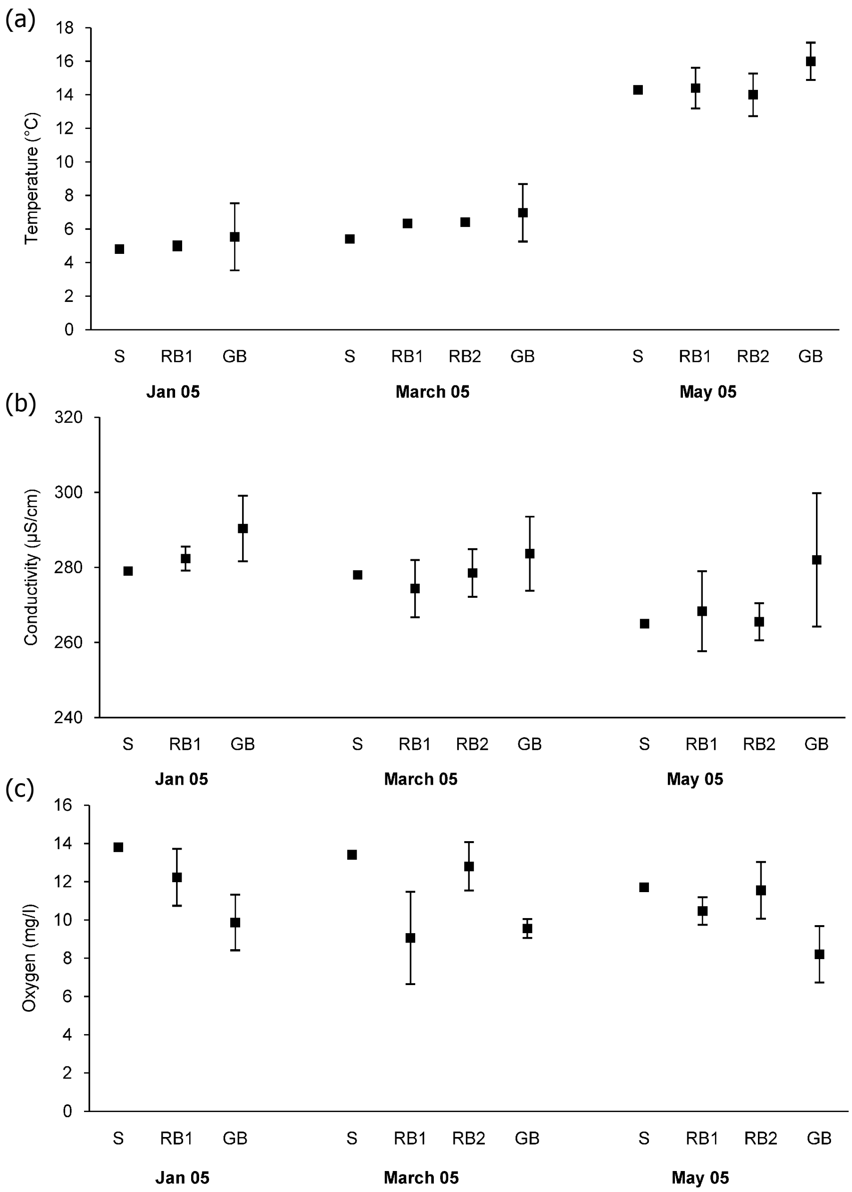

Figure 2. Mean temperatures **(a)**, conductivity **(b)** and oxygen concentrations **(c)** (±SE) of surface and hyporheic water measured during invertebrate sampling. RB1 – shallow hyporheic zone (30 – 60 cm); RB2 – deeper hyporheic zone (60 – 90 cm); GB – gravel bars (60 – 90 cm). RB1, GB, n=3; RB2, n=2.

Slika 2. Srednje vrednosti temperature (a), prevodnosti (b), in vsebnosti kisika (c) (±SE) v vzorcih površinske vode in vode, ki se je pretakala v hiporeiku med vzorčenjem nevretenčarjev. RB1 – plitev hiporeik (30 – 60 cm); RB2 – globlji hiporeik (60 – 90 cm); GB – prodišče (60 – 90 cm). RB1, GB, n=3; RB2, n=2.

Table 1. List of invertebrates collected in the hyporheic zone of the River Bača on three sampling occasions in 2005. RB1 – shallow hyporheic zone (30 – 60 cm); RB2 – deeper hyporheic zone (60 – 90 cm); GB – gravel bars (60 – 90 cm). Mean abundances (No. of specimens in 10 l) are shown for each habitat. RB1 and GB, n=9; RB2, n=4. Taxa in **bold -** stygobionts (i.e. groundwater taxa).

Tabela 1. Seznam nevretenčarjev, ugotovljenih v hiporeiku reke Bače januarja, marca in maja 2005. RB1 – plitev hiporeik (30 – 60 cm); RB2 – globlji hiporeik (60 – 90 cm); GB – prodišče (60 – 90 cm). Za posamezne habitate so prikazane povprečne abundance (št. osebkov v 10 l). RB1, GB, n=9; RB2, n=4. **Poudarjeni taksoni -** stigobionti (t.j. podzemni taksoni).

Taxa	Total number of specimens	RB1	RB2	GB
Cyclopoida juveniles	10012	185.8	1281.3	357.2
Leuctra sp.	3194	29.0	212.8	231.3
Chironomidae	1601	150.2	14.8	21.1
Acanthocyclops vernalis (Fischer, 1853)	1565	57.8	190.8	31.3
Diacyclops languidus (G. O. Sars, 1863)	1389	36.1	200.3	29.2
***Diacyclops languidoides* (Lilljeborg, 1901)**	**607**	**21.1**	**38.8**	**29.1**
Cladocera navpliji	571	8.2	77.3	20.9
Baetoidea (Baetidae+Siphlonuridae)	513	11.3	33.3	30.9
Acarina	448	46.2	4.3	1.7
Oligochaeta	310	9.4	22.8	14.9
Nematoda	246	17.1	7.3	7.0
Acanthocyclops gmeineri Pospisil, 1989	231	8.7	31.5	3.0
Siphlonurus sp.	201	8.4		13.9
Harpacticoida juveniles	120	1.1	1.8	11.4
Taeniopterygidae	91	10.1		
Tipulomorpha	90	3.2	3.3	5.3
Bryocamptus minutus (Claus, 1863)	69		0.3	7.6
Hydridae	65			7.2
Rotatoria	42		10.5	
Bryocamptus zschokkei (Schmeil, 1893)	36	0.2	0.3	3.7
***Bathynella* sp.**	**27**	**3.0**		
Ceratopogonidae	25	1.3	0.5	1.2
***Parastenocaris gertrudae* Kiefer, 1968**	**25**	**1.1**		**1.7**
Habroleptoides sp.	20	0.7		1.6
Echinocamptus pilosus (Van Douwe, 1911)	12	0.3	1.3	0.4
***Bryocamptus pygmaeus* (Sars, 1863)**	**11**	**0.3**	**0.8**	**0.6**
***Parastenocaris nolli alpina* Kiefer, 1960**	**11**	**1.2**		
Dryopoidea	10	0.8		0.3
Simulidae	10	0.2	0.5	0.7
Bryocamptus dacicus (Chappuis, 1923)	9		0.8	0.7
Polycentropodidae	9	0.8		0.2
***Bryocamptus typhlops* (Mrázek, 1893)**	**8**		**0.8**	**0.6**
Epactophanes richardi Mrázek, 1893	8		0.3	0.8
Gastropoda	8	0.6	0.3	0.2
Candoninae juveniles	7			0.8
***Proasellus* sp.**	**6**	**0.2**		**0.4**
***Speocyclops* sp.**	**6**	**0.7**		
Athericidae	4		0.5	0.2
Diacyclops sp.	4	0.4		
Beraidae	3		0.3	0.2
Scirtidae	3	0.1		0.2
Rhitrogena sp.	2	0.1		0.1

Taxa	Total number of specimens	RB1	RB2	GB
Sericostomatidae	2	0.1		0.1
Amphinemoura sp.	2	0.2		
Hydropsychidae	2	0.2		
Philopotamidae	2		0.5	
Ephemera sp.	2			0.2
Ephemerella sp.	2			0.2
Moraria varica (Graeter, 1911)	2			0.2
Brachyptera sp.	1	0.1		
Cyclops vicinus Uljanin, 1875	1	0.1		
Gammarus sp.	1	0.1		
Limnephilidae	1	0.1		
Rhyacophilidae	1	0.1		
Turbellaria	1	0.1		
Alona rectangula Sars, 1862	1		0.3	
Chydorus sphaericus (O.F. Müller, 1785)	1		0.3	
Psychomyidae	1		0.3	
Alona costata Sars, 1862	1			0.1
Candona candida (Müller, 1776)	1			0.1
***Fabaeformiscandona breuli* (Paris, 1920)**	**1**			**0.1**
Heptageniidae	1			0.1
Nemoura sp.	1			0.1
Total number of specimens	**21657**			
Number of taxa	**63**			

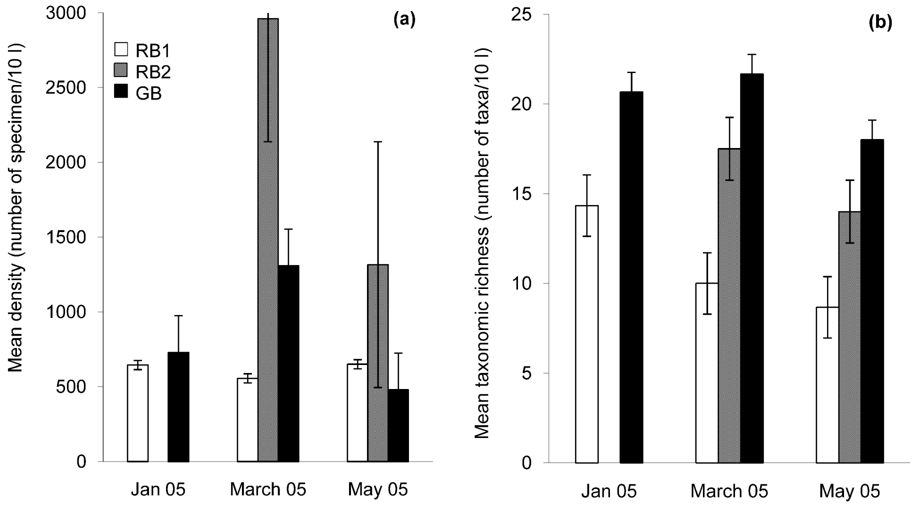

Figure 3. Mean densities **(a)** and taxonomic richness **(b)** (±SE) of the samples collected in January, March and May 2005. RB1 – shallow hyporheic zone (30 – 60 cm); RB2 – deep hyporheic zone (60 – 90 cm); GB – gravel bars (60 – 90 cm). RB1, GB, n=3; RB2, n=2.

Slika 3. Srednje vrednosti številčnosti osebkov (a) in število taksonov (b) (±SE) v vzorcih, nabranih v januarju, marcu in maju 2005. RB1 – plitev hiporeik (30 – 60 cm); RB2 - globlji hiporeik (60 – 90 cm); GB – prodišče (60 – 90 cm). RB1, GB, n=3; RB2, n=2.

The most abundant taxa (Cyclopoida, *Leuctra* sp.) had different spatio-temporal patterns (Fig. 4a, b). Cyclopoida (Copepoda) were the most abundant in March in all three habitats (RB1 - 476 individuals 10/l; RB2 – 2,477 individuals/10 l; GB – 856 individuals/10 l). In general, their densities were higher in RB2 and GB than in RB1 during all sampling occasions. *Leuctra* sp. (Plecoptera) densities were much lower than densities of Cyclopoida with the highest values in January in GB (403 individuals/10 l). In March, their densities were lower than in January, but densities in RB2 (206 individuals/10 l) and GB (255 individuals/10 l) were higher than in RB1 (17 individuals/10 l). In May, densities in RB2 (217 individuals/10 l) were the highest, followed by RB1 (53 individuals/10 l) and GB (35 individuals/10 l).

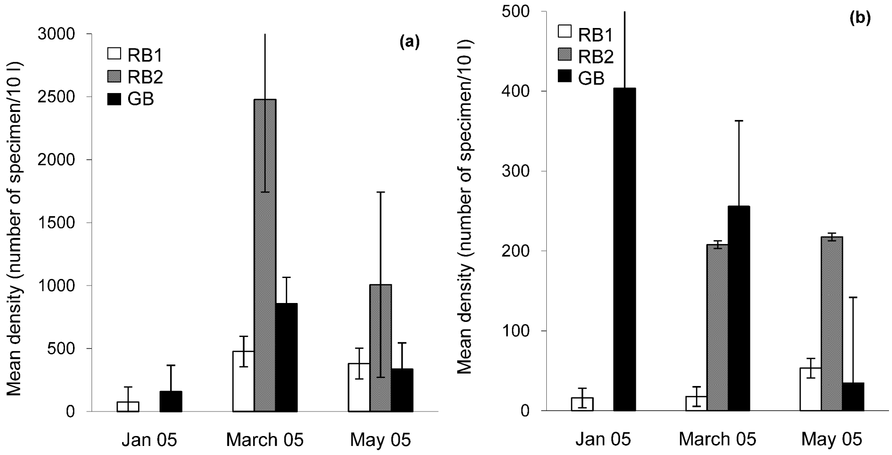

Figure 4. Mean densities of Cyclopoida **(a)** and *Leuctra* sp. **(b)** (±SE) of the samples collected in January, March and May 2005 (RB1, GB, n=3; RB2, n=2).

Slika 4. Srednje vrednosti številčnosti ceponožnih rakov (Cyclopoida) **(a)** in predstavnikov rodu *Leuctra* sp. (Plecoptera) **(b)** (±SE) v vzorcih, nabranih v januarju, marcu in maju 2005 (RB1, GB, n=3; RB2, n=2).

PCA explained 40.3% of the variance in the data by the first two ordination axes. PCA ordination resulted in the clustering of the RB1 and GB samples into two relatively distinct groups, while the samples from RB2 were grouped between them. A within-habitat variability of the invertebrate community was relatively high, but the lowest in January. The samples from RB1 were associated with higher densities of Chironomidae and *D. languidus*, while the samples from GB were the most distinct from the other two groups due to the presence of Baetoidea and *D. languidoides* (Fig. 5).

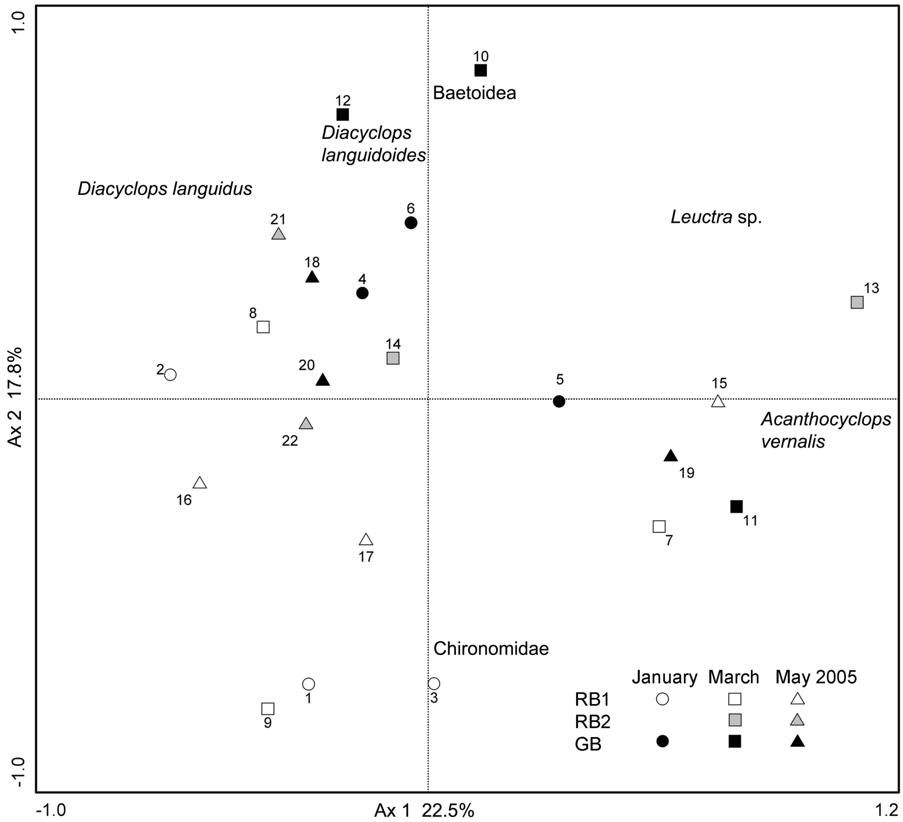

Figure 5. PCA ordination diagram of first two axes indicating the grouping of samples collected from three habitat types in the hyporheic zone of the River Bača on three sampling occasions (RB1, RB2, GB; January, March, May 2005).
Slika 5. Ordinacijski diagram za prvi dve osi analize glavnih komponent (PCA), ki prikazuje grupiranje vzorcev, nabranih v treh različnih tipih habitatov in v treh sezonah (RB1, RB2, GB; januar, marec, maj 2005) v hiporeiku reke Bače.

Discussion

Despite low food availability (Simčič & Mori 2007), low mean annual water temperatures and occasional extremely high autumn peaks in discharge (Mori et al. 2011), a diverse array of invertebrate taxa was collected from the hyporheic zone in the River Bača, with Cyclopoida juveniles (Copepoda) (46%) and early instars of *Leuctra* sp. (15%) and Chironomidae (7%) being the most abundant. Cyclopoida have often been reported as a major component of hyporheos (Boulton et al. 1992, Hunt & Stanley 2003), and *Leuctra* sp. spend early larval developmental stages deep in the hyporheic zone (Sivec 2003). Chironomidae and Leuctridae have been found to occur in high relative abundances in the River Bača benthos as well (Environment Agency RS 2007). Juvenile Copepoda stages dominated in the hyporheic zone of the glacial Roseg River, Switzerland (72% of all individuals), where harsh environmental conditions, such as low temperatures (below 4ºC), shape the community composition (Malard et al. 2003). In rivers that are subjected to frequent fluctuations in discharge, frequent modification of river bed and high loads of suspended sediment, the biota is adapted to cope with such conditions and therefore express greater persistence, resistance and rate of recovery than less variable systems (Poff & Ward 1990). In the streams experiencing frequent disturbance, highly mobile species and species that have ability to reproduce quickly and have short generation times (r-selected) prevail (Townsend 1989). The mobility is needed to move into refugia before and during floods and to recolonize vacated areas after a disturbance (Townsend & Hildrew 1994). Resilient lotic communities include substantial proportions of mayflies (Baetidae, Leptophlebiidae, and occasionally Heptageniidae), multi-voltine black flies (Simuliidae), browser and gatherer Chironomidae and Hydropsychine caddisflies (Mackay 1992). The proportion of stygobionts in the hyporheic zone is low in such streams (Fowler & Death 2001). Those statements are in accordance with our results, where insect larvae (*Leuctra* sp., Chironomidae) prevailed in the samples, and stygobionts were present in low numbers.

Data on temperature, conductivity and oxygen concentrations showed little differences between the surface water and the water flowing through river bed and gravel bars sediments. Those parameters can be used to indirectly measure the influence of the surface water in the river bed sediments (White et al. 1987) and for the estimation of the hydraulic conductivity. Small differences in those parameters between the three habitats and surface water indicate good hydraulic connectivity and fast subsurface-surface exchanges of the water in the hyporheic zone of the River Bača. The subsurface-surface exchanges of the water have direct consequences on the physical, chemical and biological patchiness in the hyporheic zone (Dole-Olivier 1998). Those exchanges are controlled mainly by discharge rates and hydrological regime (Datry et al. 2007), and the sediment size and composition (Hunt & Stanley 2003). Oxygen concentrations were relatively high during all measurements. In well sorted and coarse river bed sediments, oxygen concentrations are normally high (Bretschko 1991, Stanford et al. 1994) and hypoxia (< 3 mgO_2/l) is not a limiting factor for animals.

Despite the similarity in temperature, conductivity and oxygen concentrations of RB1, RB2 and GB habitats, distinct communities were collected by means of taxonomic richness and community composition. Densities were not significantly different between RB1 and GB, but were higher in GB than in RB1 on two out of three sampling occasions (January, March).

Densities in RB2 were on both sampling occasions (March, May) higher from those in GB and RB1. Taxonomic richness was the highest in gravel bars (GB), followed by that in deeper hyporheic zone (RB2), and in the shallow hyporheic zone (RB1). This is most probably due to the fact that shallow hyporheic zone (up to 60 cm) is more often exposed to the frequent sediment replacements occurring during floods. Disturbances caused by drastic variations in flow have been considered as one of the most important factors regulating the structure of lotic invertebrate communities in whole (Reice 1985), as well as affecting hyporheic communities (Olsen & Townsend 2005). It was proposed by intermediate disturbance hypothesis that biodiversity is the highest when disturbance is neither too rare nor too frequent (Connell 1980). In our case we studied habitats that are often disturbed by smaller floods (RB1 - shallow hyporheic zone) and consequently had lower taxonomic richness than habitats (RB2, GB) that are rarely disturbed by large scale floods, which occur every few years. Additional reasons for lower taxonomic richness in RB1 could be due to higher shear stress than in deeper and adjacent layers. In benthic habitats, invertebrates often aggregate in areas of the streambed characterized by low shear stress (Robertson et al. 1995). Similarly, hyporheic invertebrates could accumulate in areas with lower hydraulic conductivity (slower interstitial flow rates), which are in deeper sediments and gravel bars. The amounts of finer sediments (< 5 mm) extracted by piston pump were higher in gravel bars and deeper sediments than in shallow hyporheic zone in the River Bača (Mori et al. 2011). Consequently, the hydraulic conductivity is lower in deeper layers and GB. This provides a diverse array of more favourable microhabitats than those from shallow hyporheic zone, where water flows faster through coarser grained interstitial spaces. Moreover, the food availability is probably higher in that kind of micro-spaces. When patch quality was manipulated (amount of microbial and fungal biomass and production) in the hyporheic zone, invertebrate abundances increased greatly in high quality areas (Swan & Palmer 2000). The analysis of community composition across three habitats showed that juvenile Cyclopoida and Chironomidae prevailed in RB1, while together with *Leuctra* sp., juvenile Cyclopoida, *D. languidus* and *A. vernalis* dominated in RB2 and juvenile Cyclopoida and *Leuctra* sp. in GB. In deeper, more stable hyporheic zone with lower hydraulic conductivity meiofauna dominate, whereas in more dynamic, coarse grained shallow hyporheic zone representatives of pioneering groups, such as Chironomidae, prevail. The importance of sediment grain size, hydrological exchange patterns and sediment stability for hyporheic invertebrate communities have been shown previously by several other researchers (Creuzé des Chatelliers 1991, Gibert et al. 1994, Olsen and Townsend 2003). The spatio-temporal dynamics of invertebrate community depends not only on environmental conditions, but also on annual life cycles of individual taxa, which result in different temporal patterns. Cyclopoida showed a peak in abundances in March, while *Leuctra* sp. peaked in January. However, no significant differences in total density and taxonomic richness between dates were calculated.

The interpretations of all the above observations need to be taken carefully due to small number of samples (n=22), lack of January samples for RB2 and only three sampling dates. Still, we can conclude that invertebrate community in hyporheic zone of the River Bača exhibits high spatial heterogeneity due to heterogeneous sediment composition and complex hydraulic patterns across the studied habitats, and shows moderate temporal variation over sampling dates mainly due to specific annual life cycles of individual taxa.

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References

Angelier E. (1953): Recherches écologique et biogéographiques sur la faune des sables submergés. Archs. Zool. Exp. Gen 90: 37-161.

Bou C., Rouch R. (1967): Un nouveau champ de recherches sur la faune aquatique souterraine. C.R. Acad. Sci. Paris 265: 396-370.

Boulton A.J., Valett H.M., Fisher S.G. (1992): Spatial distribution and taxonomic composition of the hyporheos of several Sonoran Desert streams. Arch. Hydrobiol. 125: 37-61.

Boulton A.J., Findlay S., Marmonier P., Stanley E.H., Valett H.M. (1998): The functional significance of the hyporheic zone in streams and rivers. Ann. rev. ecolog. syst. 29: 59-81.

Bretschko G. (1991): Bed sediments, groundwater and stream limnology. Verh. Int. Ver. Limnol. 24: 1957-1960.

Brunke M., Gonser T. (1997): The ecological significance of exchange processes between rivers and groundwater. Freshwat. Biol. 37: 1-33.

Chappuis P.A. (1942): Eine neute Methode zur Untersuchung der Grundwasserfauna. Acta Sci. Math. Nat. Univ. Kolozsvar 6: 3-7.

Connell J.H. (1978): Diversity in tropical rain forests and coral reefs. Science 199: 1302–1310.

Creuzé des Chatelliers M. (1991): Geomorphological processes and discontinuities in the macrodistribution of the interstitial fauna. A working hypothesis. Int. Ver. Theor. Angew. Limnol. 24: 1607-1612.

Datry T., Larned S.T., Scarsbrook M.R. (2007): Responses of hyporheic invertebrate assemblages to large-scale variation in flow permanence and surface-subsurface exchange. Freshwat. Biol. 52: 1452-1462.

Dole-Olivier M.-J. (1998): Surface water–groundwater exchanges in three dimensions on a backwater of the Rhône River. Freshwat. Biol. 40: 93-109.

Dole-Olivier M.J., Castellarini F., Coineau N., Galassi D.M.P., Martin P., Mori N., Valdecasas A., Gibert J. (2009): Towards an optimal sampling strategy to assess groundwater biodiversity: comparison across six European regions. Freshwat. Biol. 54: 777-796.

Einsle U. (1993): Crustacea: Copepoda: Calanoida und Cyclopoida. Gustav Fischer Verlag, Stuttgart, 208 pp.

Environment Agency RS (2007): Izvajanje monitoringa za ekološko stanje vodotokov v letu 2007. Bentoški nevretenčarji v vodotokih. http://www.arso.gov.si/vode/podatki/bn_2007.pdf, Environmental Agency RS: 109.

Fowler J., Death R.G. (2001): The effect of environmental stability on hyporheic community structure. Hydrobiol. 445: 85-95.

Geist D.R., Dauble D.D. (1998): Redd site selection and spawning habitat use by fall chinook salmon: the importance of geomorphic features in large rivers. Environ. manage. (N.Y.) 22: 655-669.

Gibert J., Danielopol D.L., Stanford J.A. (1994): Groundwater Ecology. Academic Press, New York, 570 pp.

Graf W., Waringer J. (1997): Atlas der Osterreichischen Kocherfliegen larven. Facultas Universitetverlag, Wien, 286 pp.

Hunt G.W., Stanley E.H. (2003): Environmental factors influencing the composition and distribution of the hyporheic fauna in Oklahoma streams: variation across ecoregions. Arch. Hydrobiol. 158: 1-23.

Janetzky W., Enderle R., Noodt W. (1996): Crustacea: Copepoda: Gelyelloida und Harpacticoida. Gustav Fischer Verlag, Stuttgart, 288 pp.

Karaman S.T. (1935): Die fauna der unterirdischen Dewässer Jugoslawiens. Verh. Int . Ver. Limnol. 7: 46-73.

Mackay R.J. (1992): Colonisation by lotic macroinvertebrates: review of processes and patterns. Can. j. fish aquat. Sci. 49: 617-628.

Malard F., Galassi D., Lafont M., Dolédec S., Ward J.W. (2003): Longitudinal patterns of invertebrates in the hyporheic zone of a glacial river. Freshwat. Biol. 48: 1709-1725.

Meisch C. (2000): Crustacea: Ostracoda Spektrum Akademischer Verlag, Heildelberg, 522 pp.

Meštrov M. (1960): Faunističko-ekološka i biocenološka istraživanja podzemnih voda savske nizine. Biol. Glas. 13: 73-108.

Meštrov M., Stilinović B., Habdija I., Lattinger R., Maloseja Ž., Kerovec M., Čičin-Šain L. (1983): Ekološka svojstva intersticijskih podzemnih voda u odnosu na vodu reke Save. Act. Biol. 48: 5-33.

Mori N. (2004): Interstitial communities of Harpacticoida (Crustacea, Copepoda) in four different river basins from central Slovenia. Master's Thesis. Nova Gorica, School of Environmental Sciences, Nova Gorica Polytechnic, 72 pp.

Mori N., Simčič T., Lukančič S., Brancelj A. (2011): The effect of in-stream gravel extraction in a pre-alpine gravel-bed river on hyporheic invertebrate community. Hydrobiol. 667: 15-30.

Olsen D.A., Townsend C.R. (2003): Hyporheic community composition in a gravel-bed stream: influence of vertical hydrological exchange, sediment structure and physicochemistry. Freshwater Biol. 48: 1363–1378.

Olsen D.A., Townsend C.R. (2005): Flood effects on invertebrates, sediments and particulate organic matter in the hyporheic zone of a gravel-bed stream Freshwater Biol. 50: 839-853.

Orghidan T. (1959): Ein neuer Lebensraum des Unterirdischen Wassers der hyporheischen Biotope. Arch. Hydrobiol. 55: 392-414.

Packman A.I., Bencala K.E. (2000): Modelling subsurface hydrological interactions. In: Jones J. B. & P. J. Mulholland (Eds.), Streams and ground waters. Academic Press, New York, pp. 45–80.

Poff N.L., Ward J.V. (1990): The physical habitat template of lotic systems: recovery in the context of historical pattern of spatio-temporal heterogeneity. Environ. manage. (N.Y.) 14: 629-645.

Reice S.R. (1985): Experimental disturbance and the maintenance of species diversity in a stream community. Oecologia 67: 90-97.

Rivosecchi L. (1984): Ditteri. Guide per il riconoscimento delle specie animali delle acque interne italiane. Stamperia Valdonega, Verona, 176 pp.

Robertson A.L., Lancaster J. Hildrew A.G. (1995): Stream hydraulics and the distribution of microcrustacea: A role for refugia? Freshwater Biol. 33: 469-484.

Schwoerbel J. (1961): Über die Lebensbedingungen und die Besiedlung des hyporheischen Lebensraumes. Arch. Hydrobiol. Suppl. 25: 182-214.

Schwoerbel J. (1964): Die Bedeutung des Hyporheals für die benthischen Lebensgemeinschaften des Fliessgewässers. Verh. Int . Ver. Limnol. 15: 215-226.

Simčič T., Mori N. (2007): Intensity of mineralization in the hyporheic zone of the prealpine river Baca (West Slovenia). Hydrobiol. 586: 221–234.

Sivec I. (2003): Plecoptera. In: Sket B., Gogala M., Kuštor V. (Eds.), Živalstvo Slovenije. Tehniška založba Slovenije, Ljubljana, pp. 290-294.

Sket B., Velkovrh F. (1981): Phreatische Fauna in Ljubljansko Polje (Ljubljana-Ebene, Jugoslawien) – ihre ökologische Verteilung und zoogeographische Beziehungen. Int. J. Speleol. 11: 105-121.

Stanford J.A., Ward J.V., Ellis B.K. (1994): Ecology of the alluvial aquifers of the Flathead river, Montana. In: Gibert J., Danielopol D., Stanford J.A. (Eds.), Groundwater ecology. Academic Press, New York, pp. 367-390.

Studeman D., Landolt P., Sartori M., Hefti D., Tomka I. (1992): Ephemeroptera. Insecta Helvetica, Fauna 9. Imprimerie Mauron & Tinguely & Lachat SA, Friburg, 176 pp.

Swan C.M., Palmer M. (2000): What drives small-scale spatial patterns in lotic meiofauna communities? Freshwater Biol. 44: 109-212.

Ter Braak C.J.F., Šmilauer P. (2002): CANOCO, version 4.5.

Townsend C.R. (1989): The patch dynamic concept of stream community ecology. J. North Am. Benthol. Soc. 8: 36-50.

Townsend C.R., Hildrew A.G. (1994): Species traits in relation to a habitat templet for river systems. Freshwater Biol. 31: 265-275.

White D.S., Elzinga C.H., Hendricks S.P. (1987): Temperature patterns within the hyporheic zone of a Northern Michigan River. J. North Am. Benthol. Soc. 6: 85-91.

Williams D.D. (1977): Movements of benthos during recolonisation of temporary streams. Oikos 29: 306-312.

Wood P.J., Boulton A.J., Little S., Stubbington R. (2010): Is the hyporheic zone a refugium for aquatic macroinvertebrates during severe low flow conditions? Fundam. appl. limnol. 176: 377-390.

Zwick P. (2004): Key to the west palaearctic genera of stoneflies (Plecoptera) in the larval stage. Limnol. 34: 315-348.