

Meiofauna constitute a considerable portion of invertebrate drift among moss-rich patches within a karst hydrosystem

Mirela SERTIĆ PERIĆ, Tvrtko DRAŽINA, Maria ŠPOLJAR, Ines RADANOVIĆ, Biserka PRIMC & Ivan HABDIJA

University of Zagreb, Faculty of Science, Department of Biology, Rooseveltov trg 6, 10000 Zagreb, Croatia;
 e-mail: msertic@zg.biol.pmf.hr

Abstract: Aiming to establish the most frequent invertebrate taxa in drift at the small spatial scale within a moss-rich karst tufa-precipitating hydrosystem, we sampled drift among microhabitats differing in substratum type and flow conditions along a tufa barrier-cascading lotic reach. Additionally, we addressed the question of the contribution and the potential significance of meiofauna within the overall invertebrate drift at the small spatial scale. During the study period, a total of 60 invertebrate taxa were recorded in the drift. Six of these taxa belonged to the annelid/arthropod meiofauna and they represented 35% of total drift density. Macroinvertebrates found in drift were represented mainly by larval insects. The composition of the most abundant taxa in total drift was as follows: *Alona* spp. (Cladocera 26.7%), *Riolus* spp. (Coleoptera: Elmidae 13.2%), *Simulium* spp. (Diptera: Simuliidae 12.2%), Enchytraeidae (Oligochaeta 10.4%), Hydrachnidia (6.3%), Orthocladinae (Diptera: Chironomidae 3.9%) and Naididae (Oligochaeta 3.6%). Faunal drift densities and amounts of transported particulate matter (PM) were highest at the fast-flowing sites located at the barriers and lowest at the slow-flowing sites within pools. Similarly to the seasonal amounts of transported PM, faunal drift was lowest in winter, and peaked in autumn and in late spring/early summer. Correlation between flow velocity and PM-faunal drift densities suggested a significant effect of the dislodged PM, though a minor influence of discharge and flow velocity on faunal drift. We suggest that the small-scale habitat heterogeneity and the respective feeding and refugial strategies of the fauna, as well as faunal passive dislodgement initiated by the shear forces of the flow were the most important drivers of observed drift patterns.

Key words: words drift; macroinvertebrates; meiofauna; habitat patchiness; Plitvice Lakes; flow velocity

Introduction

Drift – the downstream movement of the organisms driven by flow – is one of the most important and most studied transport phenomena in stream ecology (reviews by Waters 1972; Müller 1974; Brittain & Eikeland 1988). As a mechanism of continuous re-distribution of stream biota, drift is considered to be an important factor that affects changes in stream benthic community composition, energy flow and habitat heterogeneity in all lotic hydrosystems (e.g., O’Neill 1976; Frissell et al. 1986; Wallace & Webster 1996; Palmer & Poff 1997; Yarnell et al. 2006). It includes both passive and active movements of fauna (Mackay 1992) and enables organisms to escape predators or unfavorable environmental conditions, colonize new habitats and/or move among different habitat patches (Townsend & Hildrew 1976; Peckarsky 1980; Brittain & Eikeland 1988; Humphries 2002).

Thus far, most drift studies have been focused on macroinvertebrate patterns in various stream types and over a large range of spatio-temporal scales (e.g., Elliott & Tullett 1977; Cellot 1989; Rader & McArthur 1995; Ramirez & Pringle 1999, 2001; Jacobsen & Bojsen 2002; Robinson et al. 2002). However, little is known about

the contribution of zooplankton, microscopic zoobenthos and meiofauna in drift, especially at the small spatial scale (Sandlund 1982; Palmer 1992; Swan & Palmer 2000; Špoljar et al. 2007). An insight into the faunal drift patterns at the small spatial scales could contribute to understanding the interactions among species’ life histories, behavior and dispersion, community dynamics, habitat characteristics, aspects of disturbance, and overall patch dynamics (Minshall 1988; Pringle et al. 1988; Lancaster 1999; Swan & Palmer 2000; Winemiller et al. 2010).

Meiofauna refer to benthic animals collected by the usage of a standardized mesh size ranging from 50–1000 μm (Giere 2009; Schroeder et al. 2012). Their size range partially overlaps with macroinvertebrate sizes, i.e., with early life stages of many macroinvertebrates. While mature macroinvertebrates are generally larger than 1000 μm (Cummins 1975; Rosenberg & Resh 1993), their early stages are mostly retained by 125–250 μm meshes (Hauer & Resh 2007). However, most stream ecologists consider as macroinvertebrates all individuals that reach macro sizes in their mature stages (Hauer & Resh 2007). Meiofauna is traditionally classified as permanent (taxa of meiofaunal dimensions even as adults, e.g., rotifers, copepods, cladocer-

ans, some oligochaetes) and temporary (taxa growing into macrofauna in later life cycle stages, e.g., chironomids) meiofauna. Furthermore, they are classified as interstitial, burrowing and epibenthic meiofauna, as they could live between, within or on the stream substratum, respectively (Giere 2009). The largest numbers of meiofaunal taxa are epibenthic, inhabiting in-stream vegetation, wood, or leaves, and have a patchy distribution (Palmer et al. 2007). The ways of meiofaunal taxa dispersal are still rather unknown (Swan & Palmer 2000; Robertson 2002).

Karst is a complex landscape that encompasses a variety of geomorphic features formed by dissolution, erosion and/or deposition of soluble rocks, including limestone and dolomite (Ford & Williams 2007). Karst streams are distributed worldwide (e.g., Southeast Asia, South Africa, Central America, Southwest Australia, Mediterranean basin), but they are underrepresented in the literature regarding their hydrological and environmental, as well as their ecological and biodiversity dimensions (World Bank 2008). Karst streams of the Balkan Peninsula (i.e., in the Dinaric region along the eastern Adriatic) are characterized by tufa formation from calcium carbonate precipitation (Ford & Pedley 1996). Tufa formations (i.e., lakes, underwater barriers, waterfalls, cascades and channels) considerably increase stream spatial heterogeneity providing extensive small-scale variations in hydromorphological habitat conditions and community assemblage (Habdija et al. 1994; Sertić Perić et al. 2011). Small-scale spatial heterogeneity within karst tufa-depositing streams is greatly enhanced by the presence of moss-rich patches (Habdija et al. 2004; Sertić Perić et al. 2011). Moss microhabitats increase the streambed stability by their ability to trap and retain various food particles and ensure in-stream refugial zones for many macroinvertebrates and meiofauna (Suren 1991, 1992a, b; Vlčková et al. 2002; Heino & Korsu 2008). Although organisms developed characteristic adaptations preventing them from being washed out of the sheltering substratum, water-column transport is an inevitable and important mean of their dispersal (Giller & Malmqvist 1998; Giere 2009).

The main objectives of the present paper were: (a) to establish the most frequent invertebrate taxa in drift, and (b) to assess the contribution of permanent versus temporary meiofauna to invertebrate drift among hydromorphologically different microhabitats (patches) within a moss-rich study reach in a karst tufa-precipitating hydrosystem. Specifically, we aimed to: (i) determine taxonomic and size structure of the invertebrates found in drift at selected microhabitats; and (ii) identify the principal drivers that influenced the observed drift patterns at the small spatial scale. Initially this study was not designed to investigate the meiofaunal drift, but to trace the small-scale macroinvertebrate drift patterns. However, during processing of our drift samples, we observed that besides numerous macroinvertebrates, our drift nets (214 µm mesh size) had caught a large numbers of meiofauna. Being aware that our sampling methodology did not allow catching

the total existing meiofauna, but only the anellid and arthropod specimens larger than 214 µm in size, in this paper we addressed the question of the contribution and the potential significance of meiofauna within the overall invertebrate drift at the small spatial scales. We presumed that small-scale variations in flow conditions and moss patchiness play a dominant role in generating distributional patterns of macro- and meiofaunal community assemblages within karst and tufa-precipitating hydrosystems, respectively.

Material and methods

Study reach

Plitvice Lakes National Park (44°53' N, 15°37' E), Croatia, lies within the karst region of the NW Dinarid Mountains (Fig. 1). Besides dense surrounding forests of beech, fir and spruce, the Park encompasses 16 consecutive oligotrophic lakes mutually separated by transverse tufa barriers, though connected by waterfalls, cascades, channels and fast flowing streams, thus forming a cascading barrage hydrosystem. The lake cascade system is aligned in a south-north direction, descending from an altitude of 636 to 503 m a.s.l. over a distance of 8.2 km. It is divided into two clusters – the Upper Lakes situated on impermeable dolomite and the Lower Lakes placed in a narrow limestone canyon.

This research was carried out within the Upper Lakes between the Veliki Burget and Kozjak lakes. The 15-m long study reach was located immediately downstream of the Veliki Burget outlet. It consisted of a lotic stretch containing two consecutive shallow pools separated by a tufa barrier. The study reach was segmented into six sampling sites (microhabitats): P1, B-R1, PP, P2a, P2b and B-R2 (Fig. 1, Table 1). The distance between individual sampling sites was about 3 m, enabling the small-scale assessment of drift. Depending on their position within the study reach and distance from each tufa barrier, the sampling sites differed in flow conditions, depth and substratum composition (Table 1). Detailed description of the study reach and sampling sites is set out in previous paper by Sertić Perić et al. (2011).

Physical and chemical parameters

Water temperature, dissolved oxygen (WTW OXI 96), conductivity, total dissolved solids (TDS) (Hach Sension 5) and pH (WTW 330i) were measured *in situ* in the middle of the study reach on each sampling occasion using respective probes. On each sampling date, one additional water sample (2 L) was collected for laboratory analyses of valuable tufa-related site descriptors: alkalinity, total water hardness, nitrite, nitrate, *o*-phosphate (APHA 1985) and total chemical oxygen demand (COD) (Deutsches Institut für Normung 1986). Daily discharge data (Q) (Fig. 2) were obtained from the gauging station of the State Meteorological and Hydrological Service located at Kozjak Lake, 200 m downstream and nearest to our study site. The instream morphological features were determined visually (habitat/substratum type) or by assessment measurements (channel depth) at the site of interest.

Drift sampling design

Two-hour drift samples were collected monthly at each site from October 2006 to September 2007, with the exception of August 2007. At each site three samples at three cross-sectional depths were taken simultaneously. Exceptions were sites 1 and 2 where only a single drift sample could be taken

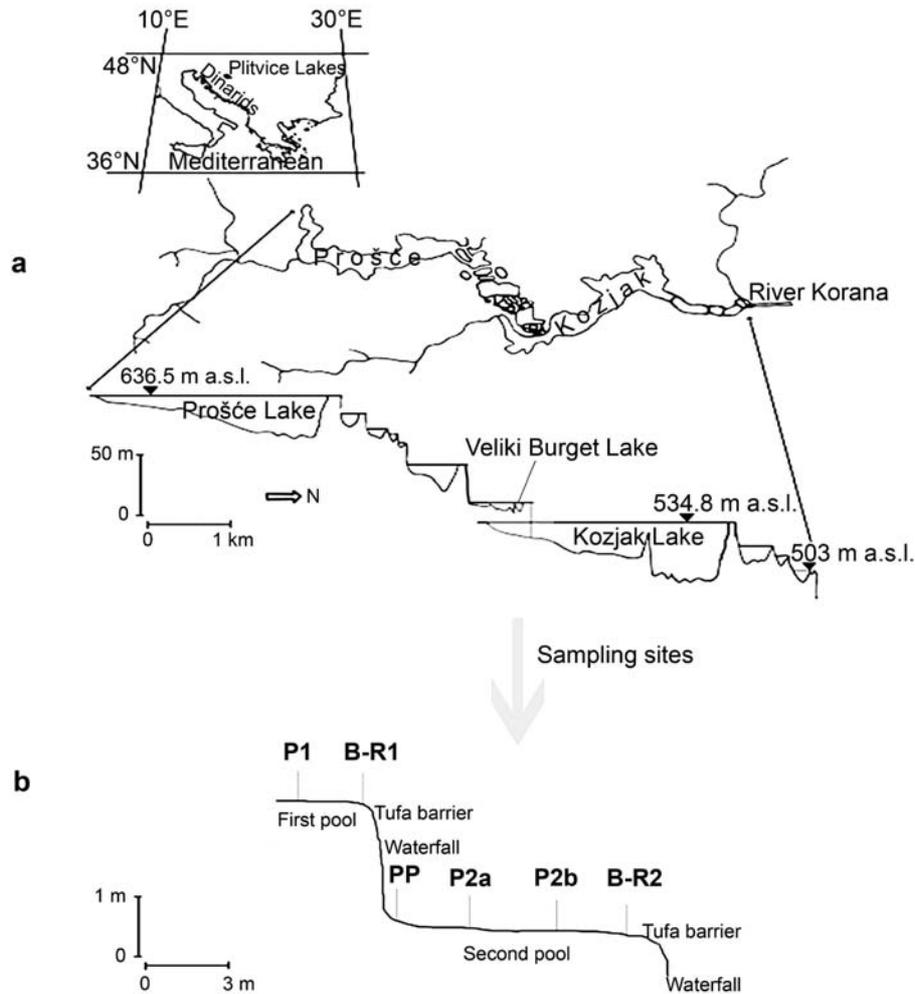


Fig. 1. Location of study area with the ground- and side-plan of Plitvice barrage lakes (modified after Špoljar et al. 2007) and location of the study reach (shadowed) (A); Schematic spatial presentation of the six sampling sites along the study reach (B).

due to inadequate width and depth. As a result, we had unequal sample sizes across sampling sites. Drift samplers were cylindrical plastic tubes (50 cm long, inner diameter 7.5 cm; aperture 44.2 cm²) fitted with a 1.5 m long net (mesh-size 214 μm). On each sampling date, the samples were taken twice a day (at midday and dusk). At the aperture of each sampler after the initial hour of sampling the flow velocity (FV) was measured (P600, Dostmann electronic GmbH) to standardize drift variables per unit volume (m⁻³) (Smock 2007). Through the applied methodology, we aimed to compromise among multiple constraints of differing flow velocities along the study reach (i.e., net clogging, variations in sampled volume) (Faulkner & Copp 2001) and to mitigate the effects of diel drift periodicity (Elliott 1969).

Laboratory procedures

Sample contents were preserved in 4% formaldehyde solution. In the laboratory, invertebrates and moss fragments were separated from each sample. Invertebrates were identified to the lowest possible taxonomic level (genus in most cases; subfamily for Chironomidae; family for Oligochaeta, Copepoda, Collembola, and early insect larval stages; mites were grouped as Hydrachnidia) using a stereomicroscope (Zeiss Stemi 2000-C) and available taxonomic keys and species descriptions (Knoz 1965; Margaritora 1983; Amoros 1984; Schmedtje & Kohmann 1988; Nilsson 1996, 1997;

Waringer & Graf 1997; Di Sabatino et al. 2000; Tachét et al. 2000; Bauernfeind & Humpesch 2001; Sundermann & Lohse 2004; Zwick 2004). Each individual was measured (excluding antennae and terminal cerci) to the nearest 0.01 mm, using an ocular micrometer, to determine total body length. Through the identification and measuring procedure, it was detected that meiofauna constituted a considerable portion of drift. Individuals up to 1000 μm in length that remain within this size range throughout their entire life cycle were classified as “permanent meiofauna” (i.e., *Alona* spp., *Alonella* spp., *Chydorus* sp., Cyclopoida gen. sp., Harpacticoida gen. sp. and Hydrachnidia gen. sp.) (Galassi et al. 2002; Giere 2009; Schroeder et al. 2012), while the individuals larger than 1000 μm during their entire life span, and taxa smaller than this size threshold, but known to reach macro sizes in their mature stages (i.e., Oligochaeta, Amphipoda and insect larvae/pupae/adults) were classified as “temporary meiofauna” + “macrofauna”, respectively (Hauer & Resh 2007). *Daphnia* sp. was designated as planktonic (e.g., Galassi et al. 2002).

Subsequently, samples were sieved through nested nets (1 mm and 50 μm mesh size) to separate coarse (>1 mm; CPOM) and fine (1 mm to 50 μm; FPOM) particulate organic matter (POM) size-fractions. Due to the usage of 214 μm drift-nets, the material < 214 μm may have been lost already during the sampling, so we actually separated

Table 1. Hydromorphological features of the investigated sampling sites (microhabitats) during the study period.

	Sampling site (microhabitat)					
	P1	B-R1	PP	P2a	P2b	B-R2
Habitat type	Pool	Run	Plunge pool	Pool	Pool	Run
Flow velocity (m s ⁻¹)	0.17 (± 0.11) ^{C,D,E}	1.09 (± 0.52) ^A	0.28 (± 0.098) ^C	0.09 (± 0.048) ^E	0.16 (± 0.079) ^D	0.46 (± 0.18) ^B
Depth (m) (min – max)	0.40–0.45	0.25–0.30	0.80–1.05	0.50–0.65	0.50–0.65	0.50–0.60
Substratum type	Silt-laden tufa + moss	Porous tufa blocks + moss	Tufa gravel	Tufa sand + moss	Tufa sand + moss	Porous tufa blocks + moss
Moss cover (relative coverage)	f	a	r	o	o	a

Explanations: Capital letters beside flow velocity (mean ± SD) indicate the formation of homogenous groups among the sampling sites according to Unequal N HSD *post-hoc* test ($\alpha = 0.01$). Abbreviations: a – abundant, f – frequent, o – occasional, r – rare.

a FPOM fraction between 214 µm and 1 mm. After separation, moss stems and POM size-fractions were dried at 104 °C for 36 hours, weighed, ashed at 400 °C for 4 hours and reweighed to estimate ash-free dry mass (AFDM) for moss (MD) and POM size-fractions within each sample. Total particulate organic matter (TPOM) was calculated as the sum of moss, CPOM and FPOM values. The remaining content after ashing was estimated as the amount of total particulate inorganic matter (TPIM). Since it was observed that mosses included much bound tufa, inorganic residuals remained after ashing moss stems were expressed as “moss-attached” tufa (MAT).

Data analysis

For seasonal and annual variation of physical and chemical characteristics we calculated the coefficient of variation (CV) for each measured variable. For each sampling date, we assessed taxonomic composition of the drift at each site as the abundance (i.e., drift density) and the proportion of each taxon in the total drifting invertebrates at the site.

Prior to statistical analyses, Shapiro-Wilk’s assessment of normality was applied. Where necessary and appropriate (i.e., FV, TPOM, TPIM, MD and CPOM), data were transformed ($\sqrt{\quad}$, $\sqrt[3]{\quad}$ or $\log_{10}(x + 1)$), to ensure conformance to an approximately normal distribution. Spatial differences in FV, TPOM, TPIM, MD and CPOM were tested using one-way analysis of variance (ANOVA) (site as factor). Alternatively, when transformations did not improve normality (i.e., FPOM, MAT and total drifting invertebrates data), the non-parametric Kruskal-Wallis test was employed. When significant differences were identified by ANOVA and/or Kruskal-Wallis tests, Unequal N HSD (Tukey’s HSD method modified for unequal sample sizes) and analogue non-parametric multiple comparison *post-hoc* tests were used to establish which sites along the study reach differed significantly from one another ($\alpha = 0.01$).

According to Kruskal-Wallis test applied to monthly measurements within individual sites, there were no significant differences in flow velocities among sampled cross-sectional depths ($P = 0.078$ – 0.97) during the study period. As well, no significant differences between midday and dusk total macroinvertebrate drift were observed (Kruskal-Wallis test, $P = 0.38$ – 0.98). Because of the observed non-significant trends, all measurements and drift samples taken at individual sites were averaged for each site.

To test for temporal variability of flow velocities and drift variables (TPOM, TPIM, MD, CPOM, FPOM, MAT, total drifting invertebrates), the Friedman’s ANOVA, a non-parametric equivalent of repeated measures ANOVA was used. Kendall’s concordance coefficient (the degree to which

multiple measurements of the same variable are similar at different microhabitats) was calculated simultaneously with the Friedman’s ANOVA. The range of Kendall’s concordance coefficient (τ) varies from 0 to 1. Values closer to 1 represent a better agreement in the rankings of the variables among cases (i.e., microhabitats).

Spearman’s rank correlation analysis was applied to determine the relationship among selected environmental variables (Q, FV, MD, CPOM, FPOM, TPIM) and drift densities of the most frequent invertebrate taxa found in drift. Statistical analyses were performed using Statistica software package (StatSoft Inc. 2007).

Results

Physical and chemical characteristics of the study reach
Sampling sites, in general, differed in substratum type and flow conditions, respectively (Figs 1, 2, Table 1). A significant difference in flow velocity was observed among sites ($F_{5,148} = 43.45$, $P < 0.001$). Barrier sites (B-R1 and B-R2) had the fastest flows, pool sites (P1, P2a and P2b) had the slowest flows, while sampling site located in a plunge pool below a waterfall (PP) had moderate flow (Table 1). According to Unequal N HSD *post-hoc* test, all sampling sites differed significantly from each other in flow ($P < 0.01$). An exception was sampling site P1, which significantly differed only from sites B-R1 and B-R2 ($P < 0.001$) (Table 1). During the study period, flow velocity varied the most (CV = 67%) at the head of the study reach (i.e., site P1) located near the lake outlet. Conversely, the lowest flow variability (CV = 35%) was observed for site PP (Fig. 2).

Repeated monthly measurements of flow velocity at the six sampling sites were not significantly different ($P = 0.61$). Kendall’s concordance coefficient indicated a lack of agreement in the rankings of the monthly flow measurements among microhabitats ($\tau = 0.14$). Flow was less variable among microhabitats only in autumn ($\tau = 0.96$, $P < 0.01$) (Fig. 2), as also shown by the respective low FV variation coefficients (autumn CV = 5%, other season CV = 21 – 27%) and by the discharge data (Fig. 2). The most stable discharge was observed in autumn (CV = 14.6%). In contrast, spring was the season with the most variable (CV = 45.8%) and peaking discharges (Fig. 2). The highest mean discharge was

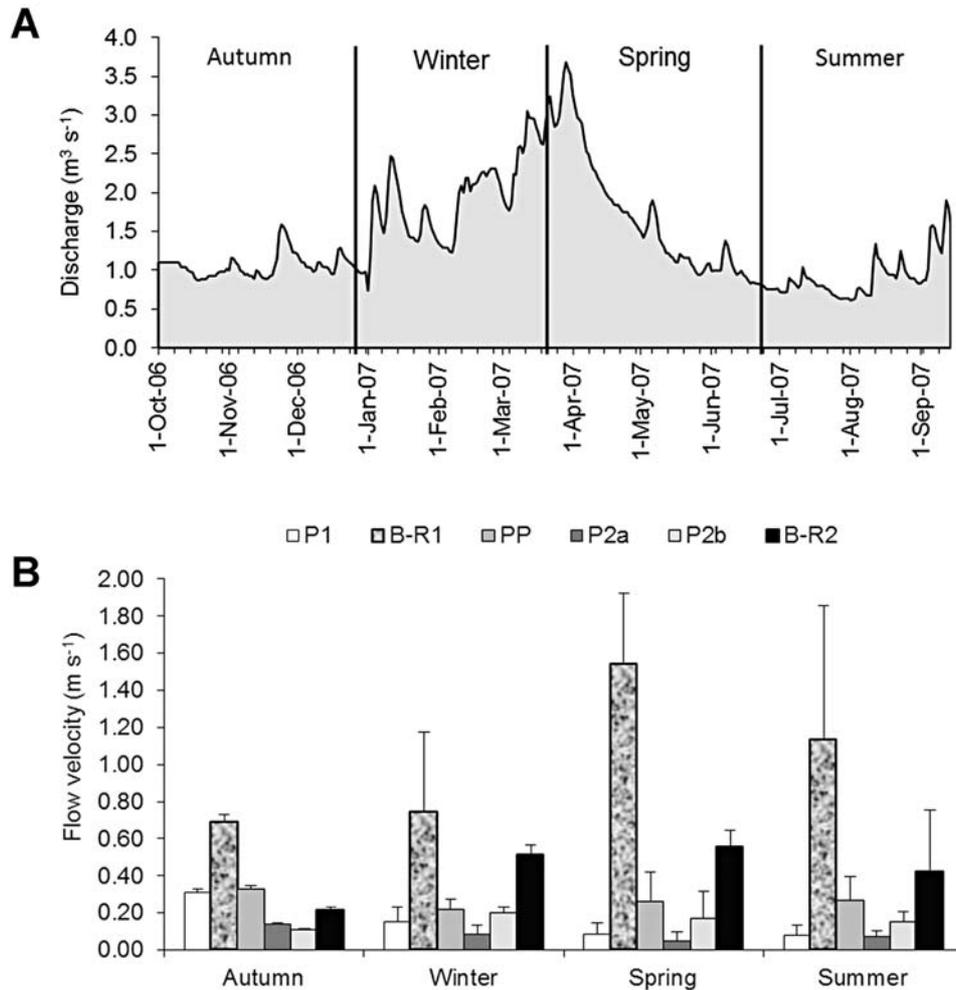


Fig. 2. Discharge hydrograph during the study period (October 2006 – September 2007). Daily discharge data were obtained from the gauging station of the State Meteorological and Hydrological Service located at Kozjak Lake (A); Mean (\pm SD) flow velocities at six sampling sites during the study period (B).

Table 2. Physical and chemical characteristics of the study system during experimental period.

Physical-chemical variable	Min–max	Mean	SD	CV (%)
Water temperature ($^{\circ}$ C)	4.0–22.4	11.7	6.1	52.1
O ₂ (mg L ⁻¹)	8.5–18.7	12.8	3.4	26.5
O ₂ (%)	93.0–159.0	125.6	23.5	18.7
COD _{KMnO₄} (mg O ₂ L ⁻¹)	0.04–1.67	0.45	0.48	107.1
pH	8.16–8.34	8.25	0.05	0.6
Alkalinity (mg CaCO ₃ L ⁻¹)	195.0–215.0	204.9	5.3	2.6
Total water hardness (mg CaCO ₃ L ⁻¹)	204.7–250.6	214.7	13.4	6.3
N-NO ₂ ⁻ (μ g L ⁻¹)	0.73–35.50	6.59	9.90	150.3
N-NO ₃ ⁻ (μ g L ⁻¹)	1.00–32.16	11.79	10.76	91.3
P-PO ₄ ³⁻ (μ g L ⁻¹)	1.00–3.34	1.63	0.94	57.4
Conductivity (μ S cm ⁻¹)	346–384	371	12.5	3.4
TDS (mg L ⁻¹)	166.6–184.0	179.1	6.0	3.4
Q (m ³ s ⁻¹)	0.775–2.755	1.457	0.609	41.8

Explanations: SD – standard deviation; CV – coefficient of variation.

recorded in March, while minimal discharges were evident during summer, reaching the lowest mean in July (Table 2). *Post-hoc* tests suggested that discharge was significantly different among all seasons ($P < 0.001$).

Most physico-chemical measures showed differences between the colder (autumn, winter) and warmer

(spring, summer) seasons. Seasonal trends of measured physico-chemical parameters are briefly summarized in Table 2.

Particulate matter in drift samples

The mean contributions of the measured PM frac-

Table 3. Content of the measured particulate matter (PM) components (expressed as % of total particulate organic matter, TPOM, and total particulate inorganic matter, TPIM) found in drift at individual sites during the study period.

			P1	B-R1	PP	P2a	P2b	B-R2	
TPOM/TPIM component			% of TPOM						
MD	Autumn	MEAN	8.2	34.3	24.5	24.5	26.5	27.8	
		SD	2.6	28.6	18.7	23.1	16.0	25.3	
	Winter	MEAN	0.5	9.4	13.3	14.0	15.2	22.0	
		SD	0.8	8.4	14.8	12.1	9.0	5.7	
	Spring	MEAN	10.2	15.9	9.2	1.8	21.7	18.0	
		SD	4.6	9.5	6.1	3.7	14.1	7.2	
	Summer	MEAN	6.3	6.9	18.6	9.1	10.0	11.3	
		SD	3.9	2.8	17.1	5.6	6.2	5.9	
	TOTAL	MEAN	7.7	36.6	15.6	4.7	17.0	18.5	
		SD	10.8	76.3	19.9	6.5	14.3	20.8	
	CPOM	Autumn	MEAN	69.6	59.5	58.1	45.8	52.0	61.0
			SD	17.6	27.0	21.4	28.9	17.5	25.5
Winter		MEAN	68.5	79.5	67.8	36.6	48.0	58.9	
		SD	23.8	13.6	25.5	7.8	12.3	6.4	
Spring		MEAN	71.9	53.5	61.3	43.9	40.5	62.0	
		SD	9.7	17.0	9.6	10.1	13.7	9.5	
Summer		MEAN	46.5	75.5	58.3	48.7	56.3	69.1	
		SD	15.7	3.6	18.6	4.0	22.0	10.4	
TOTAL		MEAN	73.0	55.6	72.6	53.2	58.6	68.2	
		SD	75.5	45.7	93.6	83.5	92.4	79.8	
FPOM		Autumn	MEAN	22.2	6.2	17.4	29.8	21.5	11.1
			SD	15.0	2.3	15.0	18.7	5.4	8.2
	Winter	MEAN	31.0	11.0	19.0	49.3	36.8	19.1	
		SD	24.7	5.3	11.4	7.1	12.4	5.7	
	Spring	MEAN	17.9	30.6	29.5	54.3	37.9	20.1	
		SD	7.7	10.4	10.9	12.6	18.8	8.2	
	Summer	MEAN	47.2	17.6	23.1	42.2	33.7	19.6	
		SD	19.6	0.9	16.1	7.9	16.6	11.0	
	TOTAL	MEAN	19.3	7.9	11.9	43.0	24.6	13.2	
		SD	22.3	5.0	5.7	27.3	13.9	10.8	
				% of TPIM					
	MAT	Autumn	MEAN	3.2	20.4	1.3	1.6	4.9	4.7
SD			2.0	32.6	1.0	1.8	2.9	2.2	
Winter		MEAN	1.2	1.3	1.6	2.9	2.4	4.9	
		SD	2.1	1.0	1.7	2.4	1.4	2.7	
Spring		MEAN	2.7	1.0	1.0	0.2	3.4	3.1	
		SD	0.3	0.8	1.0	0.4	2.6	1.3	
Summer		MEAN	2.0	2.7	4.5	3.2	1.8	1.4	
		SD	1.9	3.6	6.9	2.9	1.0	0.9	
TOTAL		MEAN	3.0	37.1	0.8	0.6	2.9	3.0	
		SD	4.0	74.6	0.5	0.8	3.0	2.8	

Explanations: Shadowed values indicate seasonal and annual (TOTAL) maximums of each measured TPOM/TPIM component. Acronyms stand for the contents of: moss (MD), coarse particulate organic matter (CPOM), fine particulate organic matter (FPOM), moss-attached tufa (MAT). SD – standard deviation.

tions (MD, CPOM, FPOM and MAT) to the respective TPOM/TPIM categories at each sampling site are shown in Table 3.

Particulate matter (PM) content in drift samples varied considerably among sampling sites (TPOM $F_{5,299} = 43.28$, $P < 0.001$; TPIM $F_{5,299} = 28.13$, $P < 0.001$). The observed spatial variation of the measured PM drift variables resulted in high standard deviations of the mean monthly and the mean annual (total) values of the TPOM and TPIM components, respectively

(Table 3). Most measured PM drift variables were highest at and upstream the barriers – at sites B-R1, P2b and B-R2 ($P < 0.01$). According to the statistical analysis results, site P1, in general, accumulated similar PM quantities in drift as sites PP and P2a which had the lowest drift densities and were grouped as one homogeneous group in *post-hoc* tests ($\alpha = 0.01$).

Total moss content (MD) was highest at site B-R1 (Table 3). At the other two barrier sites (P2b, B-R2) and in the plunge pool below the waterfall (PP)

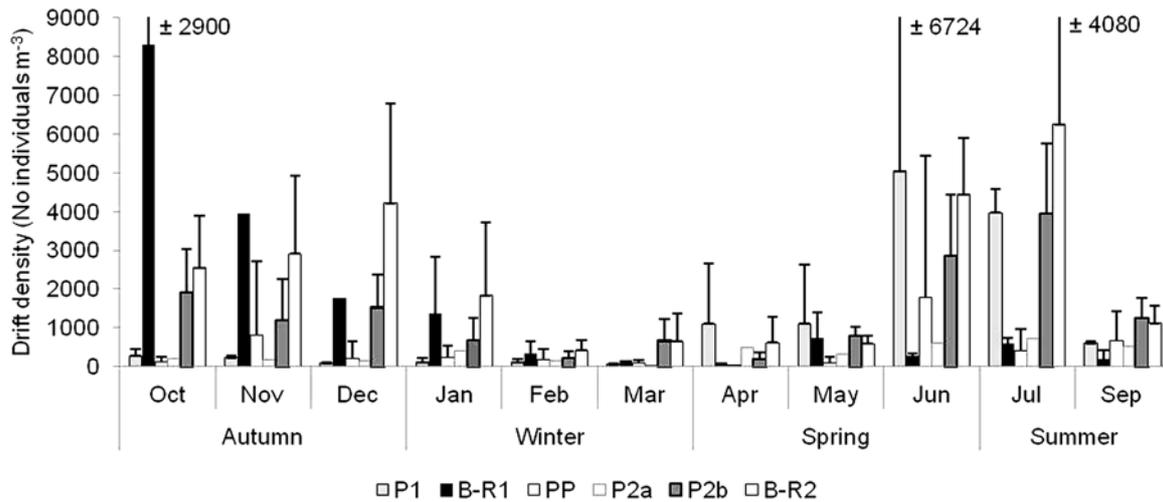


Fig. 3. Total drifting invertebrates (mean \pm SD) for the six sampling sites during the study period.

it was nearly twofold lower, while at slow-flowing sites (P1, P2a) the total moss content was five- to nine-fold lower. CPOM constituted most of the TPOM accumulated in drift at all six sites ($> 53\%$ at each site). During the study period FPOM amounts were two- to four-fold higher at pool-situated sites (P1, P2a, P2b), than at barrier sites (B-R1, B-R2) and beneath the waterfall (PP) (Table 3). MAT followed the trend shown by moss. At all sites except site B-R1 it represented 0.8–3.0% of TPIM. At site B-R1, a large amount of MAT corresponded ($N = 20$; $R = 0.97$, $P < 0.001$) to the large moss content at the site (Table 3).

Regarding temporal trend, minimal amounts of TPOM ($1.69 \pm 1.46 \text{ g m}^{-3}$) and TPIM ($12.35 \pm 10.05 \text{ g m}^{-3}$) in drift samples were observed in winter (February) and maximal amounts ($8.05 \pm 13.21 \text{ g m}^{-3}$ of TPOM; $194.91 \pm 448.79 \text{ g m}^{-3}$ of TPIM) were observed in autumn (October). Friedman’s ANOVA did not yield statistically significant temporal differences either for TPOM ($P = 0.22$) or for TPIM ($P = 0.10$). Associated Kendall’s concordance coefficients indicated a lack of agreement in the rankings of the monthly measurements of TPOM ($\tau = 0.22$) and TPIM ($\tau = 0.26$) among microhabitats. The same statistical trend was recorded for temporal data sets of CPOM ($\tau = 0.28$; $P = 0.074$), FPOM ($\tau = 0.17$; $P = 0.41$) and MAT ($\tau = 0.26$; $P = 0.12$). Only MD showed significant temporal differences ($\chi^2 (N = 6, \text{df} = 10) = 19.47$, $P = 0.035$), although it did not show a consistent pattern among microhabitats ($\tau = 0.32$). Extreme peaks of moss content in drift were observed at barrier site B-R1 in October and November when moss accounted for 66.6% and 23.7% of TPOM at the site, respectively.

Invertebrate drift densities and taxonomic composition
Density of drifting invertebrates across the entire sampling period differed significantly among sites ($H (5, N = 305) = 112.55$, $P < 0.001$) (Fig. 3). Total mean drift densities were lowest at sites P2a ($346 \pm 364 \text{ ind. m}^{-3}$) and PP ($418 \pm 1286 \text{ ind. m}^{-3}$). Increased drift densi-

ties were observed at the head of the study reach – at site P1 ($1153 \pm 2282 \text{ ind. m}^{-3}$) and at the barrier B-R1 ($1566 \pm 2589 \text{ ind. m}^{-3}$). The highest numbers of invertebrates in drift during the study period were found at the exit of the study reach – at sites P2b ($1387 \pm 1401 \text{ ind. m}^{-3}$) and B-R2 ($2351 \pm 2509 \text{ ind. m}^{-3}$).

Friedman’s ANOVA evidenced temporal differences in faunal drift ($\chi^2 (N = 6, \text{df} = 10) = 30.30$, $P < 0.001$) and Kendall’s concordance coefficient indicated some degree of agreement in the rankings of the monthly measurements among microhabitats ($\tau = 0.51$). Winter months February ($232 \pm 119 \text{ ind. m}^{-3}$) and March ($277 \pm 298 \text{ ind. m}^{-3}$) showed the lowest mean drift densities (Fig. 3). In contrast, the highest invertebrate drift densities were observed in October ($2221 \pm 3141 \text{ ind. m}^{-3}$), June ($2500 \pm 1969 \text{ ind. m}^{-3}$) and July ($2647 \pm 2418 \text{ ind. m}^{-3}$). During the autumn sampling occasions, remarkable peaks of invertebrate drift densities at barrier sites B-R1 and B-R2 were observed (Fig. 3). In the late spring and early summer, peak drift densities were recorded at the entrance and exit of the study reach (sites P1, P2b and B-R2).

A total of 60 invertebrate taxa were recorded in drift during the study period (Table 4). Six of these taxa belonged to permanent meiofauna (*Alona* spp., *Alonella* spp., *Chydorus* sp., Cyclopoida gen. sp., Harpacticoida gen. sp. and Hydrachnidia gen. sp.), one taxon (*Daphnia* sp.) was planktonic, while the remaining taxa (53 taxa) belonged to temporary meiofauna and macrofauna (i.e., Insecta, Amphipoda). The insect taxa were mainly larval, although some were also found in pupal and/or imago stages (Table 4).

The total number of taxa found in the drift each month varied from 31 (February) to 46 (May), with the permanent meiofauna representing from 8% (October) to 14% (June) of total drift diversity. Permanent meiofauna presented as well a considerable portion (35%) of total drift density among sites across the entire study period, comprising from 15% (B-R1) to 56% (P1) of the total drift density at the individual sites (Fig. 4).

Table 4. Total number and body lengths (mean \pm SD) of individuals captured in drift at six sampling sites along the study reach during the study period.

CLASS/ORDER/Family	Subfamily/Genus/Species	P-Meio/T-Meio/Macro/Pl	Drift density	Body length
			(Ind. m ⁻³)	(mm)
OLIGOCHAETA				
Enchytraeidae	Enchytraeidae gen. sp.	T-Meio+Macro	35177	2.23 \pm 0.94
Lumbriculidae	Lumbriculidae gen. sp.	Macro	6012	3.92 \pm 1.59
Lumbricidae	<i>Eiseniella tetraedra</i> (Savigny, 1826)	Macro	883	9.23 \pm 4.96
Naididae	Naididae gen. sp.	T-Meio+Macro	12114	1.51 \pm 0.62
AMPHIPODA				
Gammaridae	<i>Gammarus</i> sp.	Macro	572	4.34 \pm 2.29
CLADOCERA				
Chydoridae	<i>Alona</i> spp.	P-Meio	90137	0.78 \pm 0.10
	<i>Alonella</i> sp.	P-Meio	21	0.51 \pm 0.02
	<i>Chydorus</i> sp.	P-Meio	605	0.42 \pm 0.15
Daphniidae	<i>Daphnia</i> sp.	Pl	2062	0.69 \pm 0.21
COPEPODA				
Cyclopoida	Cyclopoida gen. sp.	P-Meio	4962	0.71 \pm 0.30
Harpacticoida	Harpacticoida gen. sp.	P-Meio	545	0.77 \pm 0.18
ARACHNIDA				
Hydrachnidia	Hydrachnidia gen. sp.	P-Meio	21356	0.48 \pm 0.17
COLLEMBOLA				
Isotomidae	Isotomidae gen. sp.	Macro	758	1.35 \pm 0.48
EPHEMEROPTERA				
Baetidae	<i>Baetis</i> sp.	Macro	1785	2.97 \pm 1.89
Caenidae	<i>Caenis</i> sp.	Macro	1344	1.87 \pm 0.61
Ephemeridae	<i>Ephemera danica</i> (Müller, 1764)	Macro	31	11.75 \pm 8.84
	<i>Ephemera</i> sp.	Macro	24	5.72 \pm 2.09
Ephemerellidae	<i>Ephemerella notata</i> (Eaton, 1887)	Macro	204	2.09 \pm 0.67
Heptageniidae	<i>Rhitrogena</i> sp.	Macro	1255	3.24 \pm 1.16
Leptophlebiidae	<i>Paraleptophlebia</i> sp.	Macro	5582	3.49 \pm 1.73
ODONATA				
Calopterygidae	<i>Calopteryx</i> sp.	Macro	166	3.15 \pm 2.35
Gomphidae	<i>Onychogomphus forcipatus</i> (L., 1758)	Macro	768	3.93 \pm 2.92
PLECOPTERA				
Leuctridae	<i>Leuctra</i> sp.	Macro	885	3.21 \pm 2.04
Nemouridae	<i>Protonemura</i> sp.	Macro	4292	2.33 \pm 1.12
	<i>Nemoura</i> sp.	Macro	496	2.90 \pm 1.24
	<i>Amphinemura</i> sp.	Macro	390	2.97 \pm 1.36
Perlodidae	<i>Besdolos imhoffi</i> (Pictet, 1841)	Macro	12	8.50 \pm 0.00
COLEOPTERA				
Elmidae	<i>Riolus</i> spp. (L + I)		44524	
	L	Macro	38265	1.90 \pm 0.32
	I	Macro	6259	1.89 \pm 0.17
Scirtidae	<i>Elodes</i> sp.	Macro	7799	2.24 \pm 0.68
	<i>Cyphon</i> sp.	Macro	980	2.12 \pm 0.68
DIPTERA				
Athericidae	<i>Ibisia marginata</i> (F., 1781)	Macro	836	4.23 \pm 1.67
Ceratopogonidae	Ceratopogonidae gen. sp. (L + P)		3284	
	L	Macro	2708	3.29 \pm 1.26
	P	Macro	576	2.52 \pm 0.23
Chironomidae	Orthoclaadiinae gen. sp.	T-Meio+Macro	13032	2.40 \pm 0.86
	Tanypodinae gen. sp.	T-Meio+Macro	3545	2.78 \pm 1.04
	Tanytarsini gen. sp.	T-Meio+Macro	2632	1.94 \pm 0.60
	Chironomini gen. sp.	T-Meio+Macro	1301	1.81 \pm 0.67
	Chironomidae gen. sp. (L + P + I)		1225	
	L	T-Meio+Macro	53	2.35 \pm 0.20
	P	Macro	1097	2.59 \pm 0.43
	I	Macro	75	2.26 \pm 0.01
Dixidae	<i>Dixa</i> sp.	Macro	497	1.99 \pm 0.74
	Dixidae gen. sp. (I)	Macro	130	3.31 \pm 0.01
Empididae	<i>Hemerodromia</i> spp.	Macro	9697	1.67 \pm 0.40
Psychodidae	Psychodidae gen. sp.	Macro	57	2.01 \pm 0.91
	<i>Jungia</i> sp.	Macro	8	3.00 \pm 0.00
Simuliidae	<i>Simulium</i> spp. (L + P)		41163	
	L	Macro	40457	2.23 \pm 0.62
	P	Macro	707	3.06 \pm 0.35
	<i>Prosimulium</i> spp.	Macro	756	3.21 \pm 0.97
TRICHOPTERA				
Beraeidae	<i>Beraemyia</i> sp.	Macro	31	2.46 \pm 0.39
Hydropsychidae	<i>Hydropsyche</i> sp.	Macro	6910	3.49 \pm 1.08

Table 4. (continued)

CLASS/ORDER/Family	Subfamily/Genus/Species	P-Meio/T-Meio/Macro/Pl	Drift density	Body length
			(Ind. m ⁻³)	(mm)
Hydroptilidae	<i>Oxyethira</i> sp.	Macro	996	1.52 ± 0.52
	<i>Hydroptila</i> sp.	Macro	16	2.00 ± 0.01
	<i>Orthotrichia</i> sp.	Macro	856	1.59 ± 0.49
	<i>Agraylea</i> sp.	Macro	379	1.23 ± 0.25
	<i>Tricholeiochiton</i> sp.	Macro	125	0.97 ± 0.17
Lepidostomatidae	<i>Lepidostoma</i> sp.	Macro	32	4.85 ± 0.49
Limnephilidae	<i>Limnephilus</i> sp.	Macro	9	2.00 ± 0.02
Philopotamidae	<i>Wormaldia</i> sp.	Macro	723	4.03 ± 1.65
Polycentropodidae	<i>Polycentropus</i> sp.	Macro	118	3.35 ± 1.28
	<i>Plectrocnemia conspersa</i> (Curtis, 1834)	Macro	99	5.02 ± 2.09
Psychomyiidae	<i>Tinodes</i> sp.	Macro	875	2.55 ± 0.75
Ptilocolepidae	<i>Ptilocolepus</i> sp.	Macro	12	1.20 ± 0.01
Rhyacophilidae	<i>Rhyacophila</i> spp.	Macro	2201	3.23 ± 1.70
Sericostomatidae	<i>Sericostoma</i> sp.	Macro	21	1.90 ± 0.26

Explanations: Insect taxa identified are primarily larval (unless indicated otherwise in parentheses, i.e., below the taxon name). Abbreviations: L – larvae; P – pupae; I – imago; P-Meio – permanent meiofauna; T-Meio – temporary meiofauna; Macro – macrofauna; Pl – plankton members.

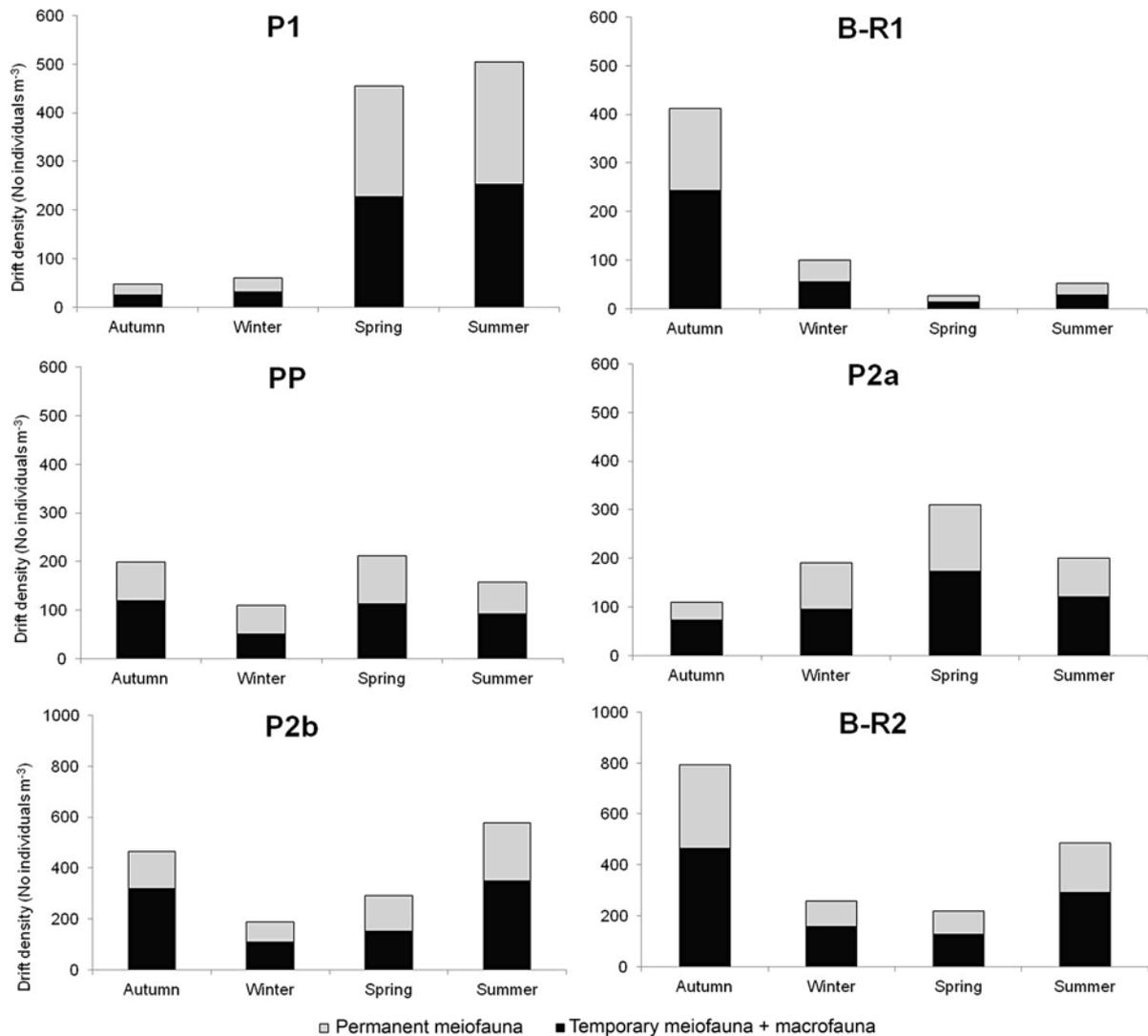


Fig. 4. Total drift densities of permanent meiofauna and temporary meiofauna + macroinvertebrates during the study period at individual sampling sites. Note scaling of axes.

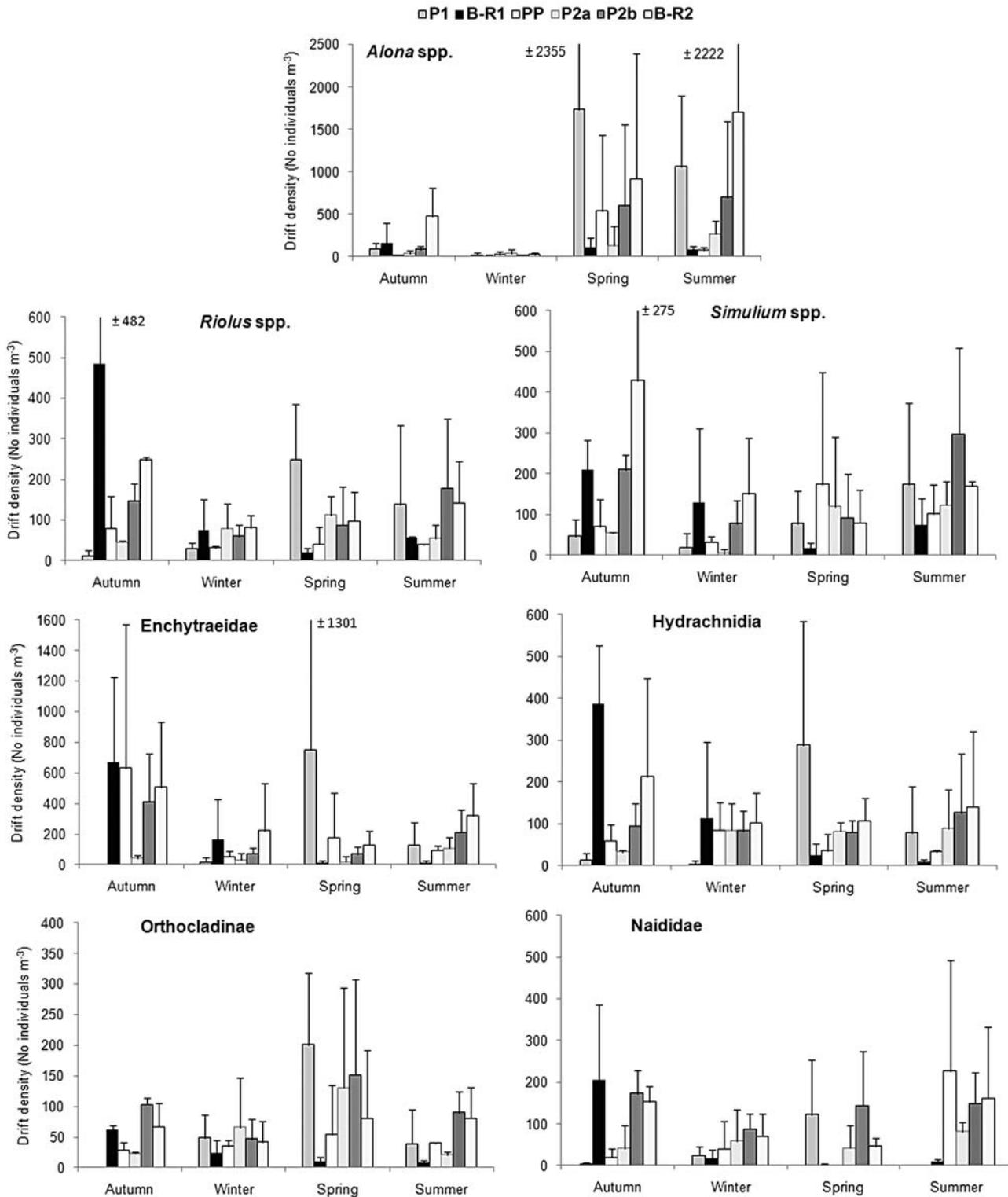


Fig. 5. Seasonal changes in drift densities of the most frequent drift taxa along the study reach during the study period. Note scaling of axes.

The most abundant drift taxa (i.e., those found in drift with $> 10,000 \text{ ind. m}^{-3}$ across the study period, occupying more than 3.5% of total drift density, respectively) are listed in Table 4, and their drift densities are shown in Fig. 5. Cladocerans, mainly represented by larval and adult *Riolus* spp. (13.2% of total drift density), larval and pupal *Simulium* spp. (12.2%) and Enchytraeidae (10.4%). Less abundant though common taxa in drift were Hy-

P1, PP, P2a, P2b and B-R2). They constituted 26.7% of total drift density. At the same time, with approximately twofold lower shares in total drift, subdominant drift taxa were represented by larval and adult *Riolus* spp. (13.2% of total drift density), larval and pupal *Simulium* spp. (12.2%) and Enchytraeidae (10.4%). Less abundant though common taxa in drift were Hy-

Table 5. Spearman rank correlation coefficients describing the association among densities of the most frequent invertebrate families in drift, measured PM drift parameters (MD, CPOM, FPOM, TPIM) and hydrological parameters (FV, Q) within all six sampling sites during the study period ($n = 305$).

Drift taxa	Family	MD	CPOM	FPOM	TPIM	FV	Q
Oligochaeta	Enchytraeidae	0.62***	0.50***	0.47***	0.56***	0.26***	-0.18**
	Lumbricidae	0.42***	0.38***	0.29***	0.41***	0.24***	-0.02 n.s.
	Lumbricullidae	0.43***	0.34***	0.23***	0.34***	0.16**	-0.08 n.s.
	Naididae	0.57***	0.44***	0.45***	0.47***	0.06 n.s.	-0.12*
Cladocera	Daphnidae	0.08 n.s.	0.14*	0.13*	0.13*	0.11 n.s.	0.09 n.s.
	Chydoridae	0.48***	0.46***	0.43***	0.38***	0.10 n.s.	-0.42***
Arachnoidea	Hydrachnidia	0.63***	0.50***	0.50***	0.54***	0.09 n.s.	-0.16**
Coleoptera	Elmidae	0.72***	0.57***	0.55***	0.61***	0.06 n.s.	-0.30***
	Scirtidae	0.67***	0.50***	0.45***	0.55***	0.27***	-0.10 n.s.
Diptera	Chironomidae	0.60***	0.53***	0.53***	0.54***	0.03 n.s.	-0.30***
	Simuliidae	0.67***	0.57***	0.51***	0.56***	0.20***	-0.33***
PM parameter							
MD		–	0.74***	0.63***	0.77***	0.27***	-0.08 n.s.
CPOM		0.74***	–	0.81***	0.84***	0.14*	0.01 n.s.
FPOM		0.63***	0.81***	–	0.78***	-0.09 n.s.	0.04 n.s.
TPIM		0.77***	0.84***	0.78***	–	0.16**	0.09 n.s.

Explanations: Marked correlations are significant at: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; n.s. – not significant.

drachnidia (6.3%), Orthocladinae (3.9%) and Naididae (3.6%). All other taxa represented 0.0025–2.9% of total drift (Table 4).

The most frequent taxa in drift, *Alona* spp., reached peak densities in spring and summer months, and this trend was most obvious near the lake outlet (i.e., at site P1) and at the lower-most site B-R2 (Fig. 5). Subdominant, though common taxa in drift (*Riolus* spp., *Simulium* spp., Enchytraeidae, Hydrachnidia, Orthocladinae and Naididae) reached highest densities in autumn at barriers B-R1 and B-R2, and at upstream-barrier site P2b. Another peak of those taxa in drift was observed in spring and summer at the head (i.e., at site P1) and at the exit of the study reach (i.e., at sites P2b and B-R2). Following the trend of total drift densities (Fig. 3), there was an obvious decrease in most frequent taxa drift densities at barrier site B-R1 during the warm seasons, compared to autumn and winter. An opposite trend was observed for the site P1 located near the lake outlet (Fig. 5).

Drift-environment relationships

In general, Spearman correlation coefficients between observed PM drift parameters (MD, CPOM, FPOM, TPIM) and densities of the most frequent taxa in drift were positive and strongly significant (Table 5). Among the PM drift parameters, MD showed the highest positive correlations with the observed faunal densities ($R > 0.50$, $P < 0.001$). Flow velocity yielded low positive ($0.02 < R < 0.30$) but rarely significant correlation coefficients with nearly all (PM and faunal) drift components. Discharge showed weakly negative ($-0.33 < R < -0.02$), rarely significant correlations with most faunal drift parameters, and positive but non-significant

($P > 0.05$) correlations with PM drift components (Table 5). Observed PM drift parameters showed strong and highly significant correlation ($R > 0.60$, $P < 0.001$) between each other (Table 5).

Discussion

Physico-chemical characteristics and habitat patchiness
Small-scale spatial geomorphic and flow differences along our study reach provided hydromorphologically heterogeneous patches suitable for our *in situ* drift study. Observed habitat patchiness is clearly reflected in the spatio-temporal patterns of transported PM and drifting invertebrates.

Karst aquifers are often reported as habitats recognizable by uneven flow/discharge rates (e.g., Legrand & Stringfield 1973; White 1988; Barberá & Andreo 2011; Zhang et al. 2011). However, the variability of subterranean flow in karst aquifers is mostly related to the specific permeability features of the limestone and to the storage capacity of the epikarstic layer, whereas the surface water flow in karst aquifers, pronounced in our cascading lake hydrosystem, is likely more dependent on precipitation and runoff (Ford & Williams 2007). We suggest that temporal changes in flow velocity observed during our study are overridden by the specific alternating sequence of lentic and lotic areas within the barrage Plitvice Lakes hydrosystem. The retentive lake effect likely dampens discharge variation and consequently stabilizes the flow along the entire karst cascading hydrosystem (Špoljar et al. 2007). The effect most likely translates to a smaller scale as well. That suggestion is corroborated by the assessment of annual flow variability along our lotic stretch, which appears to be more

pronounced at slow-flowing sites P1 (CV = 67%), P2a (CV = 53%) and P2b (CV = 50%) than at fast-flowing barrier sites B-R1 (CV = 48%) and B-R2 (CV = 39%) and in plunge pool below the waterfall (CV = 35%).

As previously discussed by Sertić Perić et al. (2011), significant FV spatial variability among our sample sites primarily depended on the fine-scale position of the study sites, and their distance from barriers and associated waterfalls. Water inevitably accelerates approaching a waterfall (e.g., sites B-R1, B-R2), subsequently forms a turbulent pool below the waterfall (e.g., site PP) (Zhang et al. 2001; Chen et al. 2004) and acts as a homogeneous jet retaining its finite velocity for an appreciable distance after entering a wider channel (e.g., sites P1, P2a and P2b) (Vanoni 2006).

Besides small-scale spatial flow heterogeneity, inter-site patchiness was also observed in substratum cover (Table 1). The observed pattern unambiguously indicated the relationship between substratum type and flow velocity. Hydraulically rough in-stream habitats (riffles, splash zone of emergent rocks, turbulent cascades and waterfalls) often offer favorable conditions for rich moss cover (Bowden et al. 2007), as observed along our study reach. Although not measured during this study, we suggest that increased levels of turbulence, shear stress and erosional power may have led to predominantly coarse substratum size in fast-flowing and turbulent reaches (i.e., at sites B-R1, PP and B-R2). In contrast, reduced turbulence and erosional action most likely allowed the deposition of smaller particles and the formation of finer substrata at slow-flowing sites (i.e., sites P1, P2a and P2b) (Giller & Malmqvist 1998; Miliša et al. 2006).

Patterns of particulate matter transport

We suggest that PM content in drift samples at individual sites was a result of transport from near-upstream reaches, as it clearly reflected the type of substratum at each site. High flow velocities at barrier sites (B-R1, B-R2) and turbulence below the waterfall (PP) may have eroded and pushed both coarse and fine particles into the subsequent pool areas (P2a, P2b), where slow flows allowed finer particles to settle (Vogel 1981; Hart & Finelli 1999; Robinson et al. 2004). It is most likely the explanation of the increased FPOM loads in the water column at slow flowing sites (P1, P2a, P2b).

PM content in drift samples at our sampling sites followed a similar curve as flow velocity. These results at first glance suggested that the patterns of drifted PM were primarily influenced by the flow conditions. However, Spearman correlation coefficients between the measured PM variables and flow/discharge did not corroborate this hypothesis. This observation diverges from many previous findings on particle transport that showed a strong positive relationship among hydrological predictors (i.e., discharge, flow velocity, shear stress) and transported PM (Maciolek 1966; Naiman & Sedell 1979; Wilcox et al. 2008). Besides water column/near-bed hydrological conditions, particle transport in streams is greatly affected by initial

benthic material distribution, substratum and channel (geo)morphology, complexity of in-stream retention structures, and biological activity (Cushing et al. 1993; Cordova et al. 2008; Small et al. 2008). It appears that the crucial control mechanism of the in-stream transport capacity is the stream's ability for material retention and resuspension.

The material retention and resuspension processes within our study reach were likely governed by an interaction between the habitat patchiness and local flow conditions along the study reach (Sertić Perić et al. 2011). The retentiveness of the channel was probably modified by the presence of in-stream moss (Suren 1991, 1992a, b), as has been observed for macrophytes (Angradi 1991; Miliša et al. 2006). Because of effective surface area increase, in addition to flow velocity decrease within the mats, moss exhibits a tendency to entangle and accumulate particulate organic and inorganic matter as well as benthic animals (Suren 1991, 1992a, b; Habdija et al. 2000, 2002, 2004; Sertić Perić et al. 2011). During this study, the retentive character of the moss and its vector role in invertebrate and PM dispersal/transport is indicated by highly significant positive correlations between moss and particle/invertebrate densities within drift samples (Sertić Perić et al. 2011).

In our study, the complexity of particle transport regulation was reflected in inconsistent temporal and spatial patterns of the measured drift variables, as shown by Friedman's ANOVA and Kendall's concordance coefficients. We presume that high variations of measured TPOM and TPIM variables observed within individual sites originated due to large temporal differences. The most prominent temporal trend during our study was the autumn peak of PM in drift samples. Those observations diverge from results of seston research within Spanish (Molla et al. 2006) and Pennsylvania (Richardson et al. 2009) streams that evidenced peaking spring/summer PM concentrations, suggesting that spring/summer seston maxima might be a consequence of maximal stream organism activity (i.e., feeding and bioturbation) during warm seasons. In the previous study, Sertić Perić et al. (2011) suggested that the autumn-peaking PM trend derives from the typical seasonal die-back of in-stream vegetation, and increased moss fragility caused by lack of protection by tufa accumulation during colder seasons. Additionally, the PM loads increase in our study could be interpreted by seasonal changes within the deciduous riparian vegetation, and autumnal increase of allochthonous organic matter fall-in, respectively (Richardson et al. 2009).

Faunal drift composition

In our study, drift fauna was composed of diverse insect and non-insect taxa. Larval Ephemeroptera, Simuliidae, Plecoptera and Trichoptera are known to be frequent members of the drift (e.g., Brittain & Eikeland 1988; Waringer 1992; Saltveit et al. 2001; Sertić Perić et al. 2011). During our study, the most abundant insect taxa in the drift were larval and adult *Riolus* spp.

(Coleoptera – Elmidae), larval and pupal *Simulium* spp. (Diptera – Simuliidae) and Orthocladinae (Diptera – Chironomidae). They are all recognized as taxa well adapted to karst environment, tufa-depositing conditions and harsh flow, respectively (Pentecost 2005; Matoničkin Kepčija et al. 2006).

High abundances of permanent meiofauna were found in the drift at all six sampling sites. Permanent and temporary meiofauna play important roles in community and ecosystem processes (Robertson et al. 2000) and many studies have regarded them as important constituents of invertebrate drift (Sandlund 1982; Palmer 1992; Bottazzi et al. 2011; Mori & Brancelj 2011). Stream meiofauna are mostly dominated by rotifers, copepods, nauidid and enchytraeid oligochaetes, nematodes and young chironomids, but often also contain flatworms, gastrotrichs, tardigrades, cladocerans, ostracods, water mites and early instars of insects (Palmer et al. 2007). Meiofaunal composition of our drift samples demonstrates that both temporary and permanent meiofauna comprised a considerable portion of drift along our study reach. However, the applied sampling methodology and the usage of 214 µm mesh size drifts nets allowed us to collect only annelid and arthropod meiofaunal members larger than 214 µm in size. Considering the meiofaunal size range, the observed meiofaunal diversity and drift densities would likely be higher had we used finer-mesh drift nets. A usage of 40 µm – 1 mm meshes would yield more precise estimates of meiofaunal drift, including smaller “microdrift” (e.g., protozoans, rotifers, cladocerans, copepods) (Sandlund 1982; Giere 2009). Nevertheless, even with the larger mesh size we were able to document many meiofaunal taxa and assess their contribution to drift.

Drifting invertebrates showed distinct seasonal and spatial patterns during our study. Seasonality was evident in total numbers of drifting individuals. Similar trends of low winter and high late spring/early summer total drift have been observed for various temperate hydrosystems elsewhere (e.g., Sandlund 1982; Brittain & Eikeland 1988; Waringer 1992; Hansen & Closs 2007). It is likely that drift seasonality reflects seasonal changes in the life cycles of particular taxa (Robinson et al. 2002) and variation in taxonomic composition in the benthos across different types of microhabitat (e.g., Schram et al. 1990; Palmer 1992; Shearer et al. 2003). Accordingly, the autumn drift peak we observed, most obvious at the fast flowing moss-covered (barrier) sites (B-R1, P2b, B-R2), with increased densities of *Riolus* spp., *Simulium* spp., Enchytraeidae, Orthocladinae, Naididae and Hydrachnidia, was probably related to the organisms’ life cycles and the small-scale habitat (i.e., substratum, flow) characteristics. The autumn peaking taxa were predominantly found interwoven with bryophyte stems and rhizoids (Oligochaeta, Hydrachnidia, Coleoptera, Orthocladinae) or attached to floating PM, such as leaf litter (Simuliidae). Those findings are corroborated by correlation data between PM and taxa drift densities, suggesting that dislodged phyto-fragments (i.e., bryophyte-, macrophyte-, ripar-

ian vegetation-fragments) play an important vector role during the downstream transport of organisms (Sertić Perić et al. 2011).

The observed autumnal trend within drifted moss/plant fragments during this study could also be related to faunal feeding behavior. Aquatic vegetation has often been regarded as a habitat-rich environment where organisms efficiently shelter from high flow velocities and forage for food (Suren 1991; Linhart et al. 2002; Bogut et al. 2007; Heino & Korsu 2008). For example, larval Simuliidae often occupy leaves and the parts of submerged plants, as those structures provide a comparatively clean substratum required for simuliid silk pad/hook attachment, allowing them suspension feeding under different flow conditions (Bass 1998). Larval Elmidae (i.e., *Riolus* spp.) moreover have been observed to ingest moss leaves when their primary food (i.e., microorganisms and detritus) becomes short (Nilsson 1996).

Observational and correlation data aroused from our drift samples support many previous reports on Oligochaeta, larval Chironomidae and Cladocera as some of the most abundant invertebrates within the macrophyte and bryophyte stands (Suren 1993; Mastrantuono 1993; Bogut et al. 2007; Špoljar et al. 2012a, b). Different phytal communities support different densities and taxonomic composition of meio- and macrofauna (Suren 1993; Hann 1995; Cheruvilil et al. 2002; Bogut et al. 2007). Suren (1993) found that approximately 12% of the bryophyte fauna in New Zealand streams is comprised of Oligochaeta. In our study, Oligochaeta comprised 15% of the total drift and most of them were found interwoven with bryophytes. Although most of them reach macrofaunal dimensions, some Naididae and Enchytraeidae are recognized as meiofaunal members living as epibenthos in phytal (Giere 2009), inhabiting aquatic macrophytes (Neiff & Caringnan 1997; Phillips 2008) and bryophytes (Sychra et al. 2010), feeding mostly on bacteria and diatoms (Harper et al. 1981; Bott & Borchardt 1999).

Orthocladiinae, abundant in our drift samples especially during warm seasons (Fig. 5), often dominate the fauna of lotic habitats (Nilsson 1996). Moss patches along our study reach might be the source of many drifting Orthocladinae, particularly during warm seasons when nutrient concentrations keep “epiphytic microalgae production at a level sufficient to support large populations of plant-inhabiting chironomid species” (Brodersen et al. 2001). Orthocladiinae are frequently found on submerged plants, but plant tissues are little used as their food source (Soszka 1974). According to Armitage et al. (1995), aquatic vegetation provides a firm substratum in a well-oxygenated environment, allowing diatoms, a major dietary item for most of the Orthocladinae, to grow in abundance. However, it is important to recognize that a variety of factors, including larval size, food quality and sediment composition can influence the motility and the feeding behavior of Chironomidae, including Orthocladiinae (Armitage 1968; Berg 1995; Vallenduuk & Moller Pillot

2007). Regarding the motility, it is known that the first star larvae of most chironomids are more mobile than older larvae; they are mostly free swimming and could crawl on the substrate for only short periods (Vallenduuk & Moller Pillot 2007). Thus, small chironomids are more exposed to the risk of downstream dislodgement, often mentioned as distributional drift (Müller 1973; Williams 1980). This might explain our findings of the numerous young Orthoclaadiinae (i.e., temporary meiofauna members) in spring and summer drift. Contrary, older larvae change location only in response to a shortage of food, heavy disturbance or before pupation (Williams 1989; Lencioni et al. 2002; Grzybkowska et al. 2004, 2006). This might have been the reason for the observed autumn drift peaks of larger Orthoclaadiinae at our barrier sites.

The dominance of *Alona* spp. in drift along our study reach suggests the upstream lake effect, as that epiphytic chydorid cladoceran is often found abundant in the littoral zone of lakes (Jeppesen et al. 1998; Geraldes & Boavida 2004). According to Sakuma et al. (2004) migration is an important factor in the population dynamics of cladocerans such as *Alona*. Frey (1986) described *Alona* as a genus specialized in exploring microhabitats created by submerged stands of macrophytes, reporting that its abundance depends on the structural diversity of the habitat. Other studies evidenced sediment-dwelling (Goulden 1971; Evans 1984) and widely distributed (Chengalath 1982; Tremel et al. 2000) *Alona* species, suggesting that *Alona* abundance is influenced by habitat factors other than macrophyte vegetation (Tremel et al. 2000). We suggest that extensive moss patches along our study reach could recruit many *Alona* individuals, providing adequate food-rich habitat, thus increasing the moss-attached migrating *Alona* abundance. Our “chydorid-MD” correlation data support those suggestions (Table 5).

In general, our results suggest that the observed small-scale drift patterns are considerably influenced by the small-scale substratum differences, and the respective species-specific strategies developed to resist dislodgement. For example, the organisms found numerous within moss (e.g., *Riolus* spp., Hydrachnidia, Oligochaeta) have been observed to have various clinging structures (e.g., hook-like claws) and/or tube-shaped bodies that obviously enable the organisms to entangle and shelter within moss structures (Sertić Perić et al. 2011). However, they were dislodged together with the moss substratum. Smaller organisms (e.g., Hydrachnidia, Harpacticoida, Cyclopoida) mostly known as crawling, burrowing and interstitial (i.e., meiofaunal) lotic fauna (Kowarc 1992; Di Sabatino et al. 2000; Dole-Olivier et al. 2000; Jersabek et al. 2001) were found numerous in drift at the microhabitats containing large amounts of fine sediment (i.e., silt-laden tufa, tufa sand, moss-attached tufa). Although the interstitial fauna is less susceptible to flow disturbances (Robertson 2000), increased flows are proved to reduce their diversity and abundance (Bruno et al. 2009). Flow disturbances do not only disturb the upper-

most substratum layers but could also cause the deeper scouring of the streambed, especially when it comes to extreme flows and sandy substrates (Palmer et al. 1992; Uehlinger & Naegeli 1998 and references therein). As meiofauna are similar in size to sand grains, they could easily get eroded and transported by currents (Palmer et al. 1992).

Drift-environment relationships

If in-stream moss patches are important faunal habitat (cf. Suren 1991, 1992a, b; Habdija et al. 2004) and flow occasionally erodes such patches (Chambers et al. 1991), then it is likely that during our study many stream-dwelling fauna, including numerous meiofauna, were transported via eroded moss. Regardless of weak correlations between drift variables and flow velocity during our study, we suggest that flow influenced the faunal passive entrainment into the water column. Similarly was suggested by Bond & Downes (2003) in an experimental study on eight artificial streams. They evidenced that flow increases alone can disturb benthic fauna, and that neither substratum movement nor suspended sediment increases are necessary to disturb the benthic assemblage. The effects of flow increases most likely depend on the availability of local flow refugia, which allow organisms to avoid shear forces that would otherwise dislodge them from the streambed (Bond & Downes 2003). We suggest that along our study reach moss cover played such refugial role for benthic fauna, mitigating the effects of flow on organism removal.

The weak correlations between drift variables and flow velocity in our study could also be explained by tufa precipitation patterns. Although during this study we did not measure tufa precipitation rates, we did observe moss with visible tufa incrustations (i.e., MAT). According to previous studies at Plitvice Lakes, lower tufa precipitation rates have been recorded during autumn and winter (Srdoč et al. 1985; Matoničkin Kepčija et al. 2006). We suggest that, regardless of flow conditions, the tufa precipitation patterns could affect the moss establishment and occasionally (i.e., during autumn and winter) cause its removal and downstream transport, together with attached material. This theory would be worthy of further investigation. More detailed insights into the tufa-precipitating effects could help us reveal the principal drivers influencing (taxon-specific) drift trends within the Plitvice Lakes hydrosystem and other karst tufa-precipitating hydrosystems as well.

In conclusion the results of our study showed that, besides faunal anatomical-morphological adaptations to resist dislodgement, and active drift initiated by faunal feeding behavior and refugial strategies, drift patterns in this study were most strongly influenced by a complex interaction of (a) habitat heterogeneity (e.g., moss patchiness) and (b) passive dislodgement initiated by the shear forces of the flow. This study also reveals new insights into faunal dispersal at the small spatial scales, especially within complex habitats (i.e., tufa and moss-rich patches), and suggests that drift and phytofragment dislodgement play an important vector-role

in macro- and meiofaunal distribution. Furthermore, we suggest that an insight into the patchiness and transport dynamics of living and non-living material within the Plitvice Lakes hydrosystem could help us understand the uniqueness of tufa-precipitating hydrosystems, and thus contribute to global hydrological, environmental, ecological and conservation-biological understanding of karst environments.

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