

FRESHWATER REEFS AS MESOHABITATS FOR THE ASSESSMENT OF DIEL INVERTEBRATE DRIFT PATTERNS

MIRELA SERTIĆ PERIĆ^{1*}, RENATA MATONIČKIN KEPČIJA²,
INES RADANOVIĆ³, BISERKA PRIMC⁴ & IVAN HABDIJA⁵

¹Department of Biology, Faculty of Science, University of Zagreb, Rooseveltov trg 6, 10 000 Zagreb, Croatia (E-mail: msertic@biol.pmf.hr; phone: +385 1 4877 705; <https://orcid.org/0000-0002-4744-7884>)

²Department of Biology, Faculty of Science, University of Zagreb, Rooseveltov trg 6, 10 000 Zagreb, Croatia (E-mail: rmatonic@biol.pmf.hr; <https://orcid.org/0000-0002-4408-0845>)

³Department of Biology, Faculty of Science, University of Zagreb, Rooseveltov trg 6, 10 000 Zagreb, Croatia (E-mail: iradan@biol.pmf.hr; <https://orcid.org/0000-0003-3239-0536>)

⁴Department of Biology, Faculty of Science, University of Zagreb, Rooseveltov trg 6, 10 000 Zagreb, Croatia (E-mail: bprimc@biol.pmf.hr)

⁵Department of Biology, Faculty of Science, University of Zagreb, Rooseveltov trg 6, 10 000 Zagreb, Croatia (E-mail: ihabdija@biol.pmf.hr)

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Freshwater reefs (known as tufa barriers) are special karst features recognized for highly heterogeneous habitat structures, complex hydrogeological features, and unique macrozoobenthos drift (downstream dispersal) patterns. Our study objective was to investigate diel and seasonal drift patterns between barriers and pools, both composed of moss-rich and fishless mesohabitat types, aligned on a small spatial scale within the karst, tufa-precipitating Plitvice Lakes hydrosystem. We monthly sampled drift at the two mesohabitat types (barriers and pools) during midday and dusk and examined quantitative and qualitative drift compositions, including drifting invertebrates, moss, and associated particulate organic and inorganic matter (APOIM). Barriers displayed higher invertebrate drift densities than those of pools. The same pattern was observed for moss and APOIM. At both mesohabitat types, invertebrate drift showed peak but highly variable densities during late spring and summer (mean >100 individuals m⁻³), whereas during late winter and early spring the drift densities were 5-fold lower than those densities. The nonmetric multidimensional scaling analysis revealed that invertebrate drift seasonality was influenced by seasonal drift patterns of aquatic moss and moss-dwelling invertebrate taxa. Adult and/or larval *Riolus* spp. and larval *Hemerodromia* spp. were found to be the most significant for the separation of midday and dusk within the NMDS ordination of barriers and pools. At barriers, midday drift densities of invertebrates, moss, and APOIM were higher than the respective dusk records. Within pools, invertebrate drift was largely aperiodic. We suggest that increased midday and/or aperiodic drift are a consequence of the lack of fish between barrier- and pool-mesohabitats. Our results further indicated that aquatic invertebrates inhabiting fast-flowing barriers and slow-flowing pools mostly exhibit "passive drift" mediated by transport agents such as water flow and dislodged aquatic vegetation. The observed spatio-temporal drift patterns are also likely influenced by ontogenetic shifts in drift periodicity (i.e., shifts depending on the development stage and morphological characteristics of the individual taxa) as well as benthic distribution of moss-dwelling invertebrate taxa.

* corresponding author

We can conclude that biotic (vs. abiotic) controls of drift are likely minimized in the fishless case of the freshwater reefs and associated barrier–pool sequences within Plitvice Lakes hydrosystem.

Keywords: aquatic invertebrates; drift periodicity; dispersal; karst; flow velocity

Sertić Perić, M., Matonićkin Kepčija, R., Radanović, I., Primc, B. & Habdija, I.: Slatkovodni grebeni kao mezostaništa za utvrđivanje dnevnih obrazaca drifta beskraljeznjaka. *Nat. Croat.*, Vol. 29, No. 2, 185-203, 2020, Zagreb.

Slatkovodni grebeni (*engl.* freshwater reefs; poznati kao sedrene barijere) posebnost su krša, a poznati su po jako heterogenim staništima, složenim hidrogeološkim značajkama i jedinstvenim obrascima drifta (nizvodnog rasprostranjivanja) makrozoobentosa. Cilj našeg istraživanja bio je istražiti dnevne i sezonske obrasce drifta između barijera i ujezerenih dijelova toka, koji predstavljaju različite tipove mezostaništa bogatih mahovinom, ali bez riba, na maloj prostornoj skali unutar krškog sedrotvornog hidrosustava Plitvičkih jezera. Mjesečno smo uzorkovali drift na dva tipa mezostaništa (barijere i ujezerenja) tijekom podneva i sumraka, ispitujući kvantitativni i kvalitativni sastav drifta, uključujući beskraljeznjake, mahovinu i pridružene čestice organske i anorganske tvari (APOIM). Barijere su bilježile veće gustoće drifta beskraljeznjaka nego ujezereni dijelovi toka. Isti obrazac uočen je za mahovinu i APOIM. U oba tipa mezostaništa, beskraljeznjaci su pokazali izrazito visoke, ali vrlo promjenjive gustoće drifta tijekom kasnog proljeća i ljeta (u prosjeku > 100 jedinki m⁻³), dok su tijekom kasne zime i ranog proljeća gustoće drifta bile peterostruko niže. Analiza nemetričkog višedimenzionalnog skaliranja (NMDS) otkrila je da na sezonske obrasce drifta beskraljeznjaka utječe sezonsko otplavlivanje vodenih mahovina i pridruženih im beskraljeznjaka. NMDS analizom je utvrđeno da su odrasli i/ili ličinački stadiji svojite *Riolus* spp. te ličinke svojite *Hemerodromia* spp. najznačajnije utjecale na razlike između podnevnih i sumračnih gustoća drifta na barijerama i u ujezerenim dijelovima toka. Na barijerama su podnevne gustoće drifta makrozoobentosa, mahovina i APOIM bile više od gustoća drifta u uzorcima sakupljenima u sumrak. Unutar ujezerenih dijelova toka, drift beskraljeznjaka je u velikoj mjeri bio aperiodičan. Sugeriramo da je porast podnevnog i / ili aperiodičnog drifta posljedica nedostatka riba između barijera i ujezerenih dijelova toka. Naši rezultati nadalje su pokazali da vodeni beskraljeznjaci koji nastanjuju barijere (brze dijelove toka) i ujezerenja (spore dijelove toka) uglavnom pokazuju „pasivni drift“ posredovan čimbenicima važnima za transport tvari i organizama unutar vodenih tokova, poput protoka vode i otplavlivanja vodene vegetacije. Na promatrane prostornovremenske obrasce drifta vjerojatno utječu i ontogenetski pomaci u periodičnosti drifta (tj. pomaci koji ovise o stupnju razvoja i morfološkim obilježjima pojedinih svojti), kao i bentoska raspodjela pojedinih svojti beskraljeznjaka unutar mahovine. Možemo zaključiti da je u područjima slatkovodnih grebena i pridruženih slijedova barijera i ujezerenih dijelova toka unutar hidrosustava Plitvičkih jezera, utjecaj biotičkih čimbenika na obrasce drifta minimalan u odnosu na snažan utjecaj abiotičkih čimbenika.

Ključne riječi: vodeni beskraljeznjaci; periodičnost drifta; rasprostranjivanje; krš; brzina strujanja vode

INTRODUCTION

Freshwater reefs, also known as tufa barriers, are special karst features that can be found in karst barrage hydrosystems worldwide (e.g., Plitvice Lakes National Park, Croatia; Ruidera National Park, Spain; Caerwys, Lathkill and Wye valleys, UK; Band-e-Amir National Park, Afghanistan; Turner Falls Park, USA) (FORD & PEDLEY, 1996; PEDLEY, 1992). They appear as deposits of inorganic (i.e., calcite) and organic material (e.g., moss, leaf litter, branches, fine detritus) inhabited by many living organisms (e.g., periphyton, meiofauna, macroinvertebrates) (PEDLEY, 1992; PENTECOST, 2005). They actually represent natural dams (i.e., barriers), which may create a series of waterfalls, cascades, and interconnecting waterways and pools (ZHANG *et al.*, 2001), resulting in different hydromorphological habitat features at various spatio-temporal scales. Due to the high habitat complexity, freshwater reefs have been recognized as important habitats for a range of organisms, and as a major dispersal link connecting barrage lake

communities, i.e., as regions of pronounced dispersal by downstream drift for many invertebrate taxa (SERTIĆ PERIĆ *et al.*, 2011, 2014, 2015).

Drift is strongly affected by environmental and/or biotic settings, which can change on various spatio-temporal scales (IMBERT & PERRY, 2000; RAMÍREZ & PRINGLE, 2001; SERTIĆ PERIĆ *et al.*, 2011). Spatial drift patterns mostly depend on the spatial distribution of benthic communities, habitat type, patchiness and physical and chemical properties, and the degree to which organisms are able to move between different patches and scales (BRITAIN & EIKELAND, 1988; FONSECA, 1999; HANSEN & CLOSS, 2007; BROOKS *et al.*, 2017). Temporal drift fluctuations are greatly influenced by diel and seasonal light, temperature, precipitation and flow conditions, aquatic and riparian vegetation features as well as biotic interactions including predation and competition, and organisms' life history strategies (e.g., HUHTA *et al.*, 2000; RAMÍREZ & PRINGLE, 2001; SERTIĆ PERIĆ *et al.*, 2011). Macroinvertebrate drift can be: i) "passive", if the organisms accidentally detach from the substrate due to hydraulic stress or other environmental conditions (disturbances) causing flushing of the individuals from the stream bottom; (ii) "active", if organisms deliberately detach from the substrate aiming to leave or reach specific habitat(s); (iii) "catastrophic" (or "mass") drift, defined as a rapid increase in passive drift; (iv) "constant" drift, defined as continuously occurring passive drift of low numbers of individuals (NAMAN *et al.*, 2016).

Diel differences in invertebrate drift patterns have mainly been attributed to active drift, i.e., to behavioral cues occurring as a predator-avoidance-mechanism (ALLAN, 1978; FLECKER, 1992; HUHTA *et al.*, 2000). Most invertebrate taxa demonstrate increased nocturnal drift, which is mainly related to: 1) pre-contact avoidance of visually hunting (i.e., day-active) predators, and/or 2) post-contact invertebrate response caused by tactile benthic (i.e., night-active) predators (HUHTA *et al.*, 2000 and references therein). The foraging activity of both invertebrate and vertebrate predators may increase nocturnal invertebrate drift, whereas the absence of predators may result in mainly diurnal and/or aperiodic drift (LANCASTER, 1990; FLECKER, 1992; HUHTA *et al.*, 1999, 2000; HAMMOCK *et al.*, 2012).

The drift studies previously conducted in the karst, tufa-precipitating UNESCO-protected NP Plitvice Lakes (Croatia) have indicated that fine-scale spatial invertebrate drift patterns are notably affected by seasonal shifts in aquatic moss cover associated with changes in water temperature and hydrochemistry (SERTIĆ PERIĆ *et al.*, 2011, 2014, 2015). In that context, the downstream flow-mediated transport of moss could serve as an important mechanism in dispersing invertebrates and transporting particulate organic and inorganic matter within tufa-precipitating systems (SERTIĆ PERIĆ *et al.*, 2011, 2014). The previous findings have primarily built on abiotic controls of invertebrate drift, whereas the present study investigates the diel drift periodicity (i.e., potential biotic controls of drift) within the tufa-precipitating barrage hydrosystem of Plitvice Lakes. These lakes harbor several native and non-native fish species (e.g., trout, chub: see *Study system and sampling sites* for details) that could potentially affect the diel invertebrate drift patterns (i.e., active/behavioral drift).

We aimed to investigate whether biotic controls of drift are minimized in the fishless case of the freshwater reefs and associated barrier-pool sequences within Plitvice Lakes hydrosystem. Thus, our study goal was to compare temporal (i.e., seasonal and diel) drift patterns between two types of mesohabitats (see also MADDOCK, 1999), i.e., fast-flowing barriers (or freshwater reefs) and slow-flowing pools, located at a small

spatial scale along a short lotic reach within the Plitvice Lakes hydrosystem. By examining the quantitative and qualitative invertebrate drift composition and the associated particulate organic and inorganic matter (APOIM) between barriers and pools throughout the annual cycle, we shaped our results as a comparison of (a) spatial drift patterns between two mesohabitat types (barriers and pools) and (b) temporal (seasonal and diel) drift patterns at these mesohabitat types. The results of the present study could be relevant not only for the freshwater reef frameworks but also for other studies on freshwater ecology dealing with fishless barrier–pool and moss-rich hydrosystems.

MATERIALS AND METHODS

Study system and sampling sites

We conducted this study in the Croatian National Park (NP) Plitvice Lakes (44°53' N, 15°37' E), located in the inland mountain region of Croatia, within the Dinaric Karst region (Fig. 1). The entire lake area is densely shaded by beech (*Fagus silvatica* L.), manna ash (*Fraxinus ornus* L.), fir (*Abies alba* Mill.) and spruce (*Picea abies* (L.) H.Karst.). Because of their specific geological, hydrological and biological features, Plitvice Lakes were declared a national park in 1949 and have been an UNESCO World Heritage Site since 1979. The NP is famous for a particular form of a porous calcareous precipitate (i.e., tufa) that shapes a chain of 16 oligotrophic lakes, and interconnecting lotic stretches and tufa barriers. The lake chain descends from an altitude of 636 to 503 m a.s.l. over a distance of 8.2 km and is divided into two clusters: (1) the Upper Lakes situated on poorly permeable dolomite and (2) the Lower Lakes placed in a narrow canyon composed of very permeable limestone. The formation and physical, chemical and biological properties of the lakes and associated tufa features greatly depend on the interaction between water temperatures, pH, mineral composition, ion saturation levels (i.e., carbonate biochemistry), and resident organisms (SRDOČ *et al.*, 1985; GOLUBIĆ *et al.*, 2008).

The NP harbors native populations of the brown trout (*Salmo trutta* Linnaeus, 1758), and many non-native fish species such as the rainbow trout (*Oncorhynchus mykiss* (Walbaum, 1792)), the common minnows (*Phoxinus phoxinus* (Linnaeus, 1758)), the European chub (*Squalius cephalus* (Linnaeus, 1758)), the Danubian loach (*Cobitis elongatoides* Bacescu & Maier, 1969) and the common rudd (*Scardinius erythrophthalmus* (Linnaeus, 1758)). The fish inhabit the large lakes within the NP, whereas the short lotic sequences and barriers within the NP are mainly fishless (TALER, 1958; Z. MARČIĆ, unpubl. data). The two native European crayfish species, *Astacus astacus* (Linnaeus, 1758) and *Austropotamobius torrentium* (Schrank, 1803) also inhabit the NP waters, including the barriers (MAGUIRE *et al.*, 2013). Tufa barriers within the NP are overgrown by the moss-rich vegetation belonging to the alliance *Cratoneurion commutati* Koch 1928, which is common to carbonate springs of montane and subalpine belts of Europe (ALEGRO *et al.*, 2019).

Our study area was located within the Upper Lakes, between lakes Veliki Burget (553 m a.s.l.; area: 1 ha; depth: 5 m) and Kozjak (535 m a.s.l.; area: 81.5 ha; depth: 47 m). It is c. 10 m long stretch placed closely downstream of the Lake Veliki Burget consisting of two tufa barriers and a shallow pool in-between (Fig. 1C). Water within the study area flows over the first barrier (i.e., sampling site B1), creates c. 1 m-high waterfall and feeds the shallow pool (i.e., sampling sites P1, P2), which ends up with another barrier

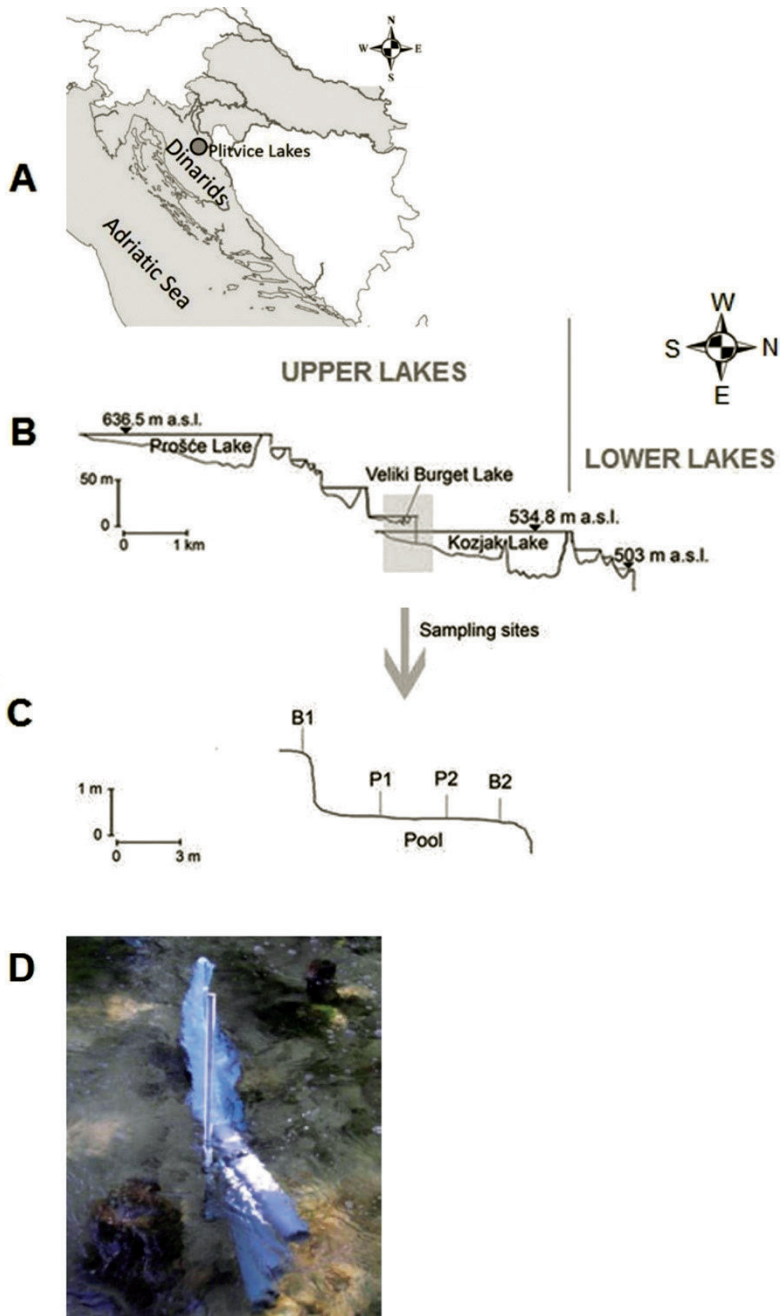


Fig. 1. (A) Location of the study system (NP Plitvice Lakes) with the (B) cross-section of the barrage lakes (modified after ŠPOLJAR *et al.*, 2007) and position of the study site (shadowed); the vertical line denotes the boundary between the Upper and Lower Lakes; (C) schematic spatial arrangement of the four sampling sites along the study site; (D) a photo of the drift-samplers set at three different depths within the water column during sampling.

(i.e., sampling site B2) and a series of waterfall cascades that finally repel down to the Lake Kozjak. The four sampling sites (B1, B2, P1 and P2) were chosen to represent replicate units of the two differing mesohabitat types, i.e., barriers (B; fast-flowing mesohabitats) and pools (P; slow-flowing mesohabitats). The distance between the individual sampling sites was c. 3–4 m, enabling the small-scale assessment of drift.

General sampling design

Field sampling was conducted monthly over a one-year period from October 2006 to September 2007, with the exception of August 2007, when there was a high tourist inflow into the NP and it was hard to reach our sampling sites. On each field visit in the middle of the study site, spot measures for water temperature and dissolved oxygen (OXI 96, WTW GmbH, Weilheim, Germany), pH (330i, WTW GmbH, Weilheim, Germany) and conductivity (Sension 5, Hach, Loveland, Colorado, USA) were taken with the portable field meters. A 1-L water sample also was collected for chemical analysis in the laboratory. The critical tufa-related water parameters were determined following the standard procedures: alkalinity, total water hardness, nitrate-N (NO_3^- -N) and ortho-phosphate-P (PO_4^{3-} -P) according to APHA (1985), and total chemical oxygen demand according to DEUTSCHES INSTITUT FÜR NORMUNG (1986), using potassium-permanganate method ($\text{COD}_{\text{KMnO}_4}$). Daily discharge records were obtained from the State Meteorological and Hydrological Service gauging station at Lake Kozjak (c. 1800 m downstream of our study site, at 533 m a.s.l.). The in-stream morphological features were determined visually (mesohabitat/substratum type) or by channel transect measurements (channel depth) at the individual sampling sites.

On each sampling date at each sampling site, drifting benthic invertebrates and associated organic and inorganic matter (i.e., APOIM) were collected using drift samplers, i.e., cylindrical plastic tubes (50-cm long, inner diameter 7.5 cm; aperture 44.2 cm^2) fitted with a 1.5-m long net (mesh-size 214 μm). At each site, we took 2-h drift samples twice a day (i.e., at midday and dusk, having an equal interval between the two samples) to enable the assessment of diel drift periodicity. Three samples at three cross-sectional depths (41 ± 3 cm, 30 ± 4 cm, 17 ± 3 cm) of the water column were taken simultaneously (Fig. 1D), except at site B1 where only a single drift sample could be taken due to inadequate width and depth of the channel. At the aperture of each sampler, after the initial hour of sampling, the flow velocity was measured (flow velocity meter P600, Dostmann electronic GmbH, Wertheim-Reicholzheim, Germany) to standardize drift variables per unit volume (m^3). Samples were preserved in situ in a 4% formaldehyde solution (i.e., 10% formalin).

Laboratory procedures

In the laboratory, invertebrates (i.e., macrofauna and meiofauna) 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, Collembola and early insect larval stages; mites were grouped as Hydrachnidia) using a stereomicroscope (Stemi 2000-C, Carl Zeiss, Jena, Germany) and available taxonomic keys (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 & HUMPECH, 2001; ZWICK, 2004).

After removing the organisms and moss, the sample remains were sieved through nested sieves (1-mm and 50- μm mesh size) to separate particulate organic matter (POM) size-fractions, i.e., coarse (>1 mm; CPOM) and fine (1 mm to 50 μm ; FPOM) fractions. Due to the usage of 214- μm drift-nets, the material < 214 μm may not have been collected during sampling, so the label FPOM actually refers to a FPOM fraction between 214 μm and 1 mm, and CPOM to coarse particulates excluding (excl.) moss. After separation, moss and POM size-fractions were dried at 104°C until constant weight, ashed at 400°C for 4 hours and reweighed to estimate moss, CPOM and FPOM as ash-free dry mass (AFDM; g m^{-3}) within each sample. The sample contents of moss, CPOM and FPOM that remained after ashing were summed and estimated as the amount of total inorganic matter (TIM).

Data analysis

The number of individuals, AFDM of moss, CPOM, FPOM and TIM mass accumulated in drift nets during sampling were used to calculate the drift density, and to express drift contents per unit volume (m^3). The following equations were used for the calculation of drift densities (СМОСК, 2006):

$$\text{Invertebrate drift density} = N / [(t) (P) (v) (3600 \text{ s h}^{-1})]$$

$$\text{Density of moss, organic and inorganic matter in drift} = m / [(t) (P) (v) (3600 \text{ s h}^{-1})],$$

where N is a number of individuals (invertebrates) in the collected sample, t is sampling duration in hours [h], P is drift sampler aperture area [m^2], v is water flow velocity [m s^{-1}], and m is AFDM of moss, CPOM, FPOM and TIM mass [g].

A Mann–Whitney U -test was used for analyzing differences in drift densities between the two mesohabitat types (i.e., barriers vs. pools) and times of the day (midday vs. dusk) (ZAR, 1984). Friedman's ANOVA, coupled with multiple comparison post-hoc test, was performed to test the differences between the repeated monthly measurements of the selected parameters (Statistica 9.1, StatSoft, Inc., Tulsa, Oklahoma, USA). Kendall's concordance coefficient (τ) was calculated simultaneously with the Friedman's ANOVA to assess the agreement of the repeated monthly measurement drift trends between midday and dusk ($\tau = 1$ indicates complete concordance of the trends; $\tau = 0$ indicates no concordance).

To visualize the spatial and temporal drift patterns and the effects of mesohabitat types, season, midday–dusk differences, and environmental parameters (i.e., physical and chemical water parameters, moss and POM content within drift samples) on the observed invertebrate drift patterns, we used nonmetric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarities of drift community composition in PC-ORD 5.0 (McCUNE & MEFFORD, 2006). Symbols plotted within the NMDS ordination diagrams denote samples distributed in the NMDS space according to invertebrate taxa drift densities and their relation to selected environmental variables. The NMDS analysis in PC-ORD also provides r -values representing correlation coefficients between each axis and each (environmental and drift) variable in the final ordination space. The r -values are used to assess which variable is more responsible for the differences observed in the gradient created by the final ordination (e.g., Axis 1, Axis 2). We $\log(x+1)$ -transformed all data before the ordination analysis.

RESULTS

Physical and chemical, hydromorphometric and invertebrate assemblage overview of the study site

Ranges of the water physical and chemical parameters during the present study are presented in Tab. 1. A more detailed overview of the physical and chemical characteristics of the study system is given in SERTIĆ PERIĆ *et al.* (2011). According to daily discharge records obtained from the State Meteorological and Hydrological Service, average water discharge during the present study was $1.4 \text{ m}^3 \text{ s}^{-1}$ (range: $0.8 - 2.8 \text{ m}^3 \text{ s}^{-1}$; coefficient of variation, CV = 42%). The two mesohabitat types (fast-flowing barriers and slow-flowing pools) differed in their flow conditions and substratum composition (Tab. 2). Water depth ranged from 25–30 cm at the site B1, 50–60 cm at the site B2, and 50–65 cm at the sites P1 and P2.

Tab. 1. Physical and chemical characteristics of the study site from October 2006 to September 2007. Abbreviations: SD – standard deviation, CV – coefficient of variation (expressed in percentage), MIN – MAX – minimal to maximal values measured during the study period.

Physical and chemical variables	MEAN \pm SD	CV	MIN – MAX
Water temperature ($^{\circ}\text{C}$)	11.7 ± 6.1	52	4.0 – 22.4
O_2 (mg L^{-1})	12.8 ± 3.4	27	8.5 – 18.7
$\text{COD}_{\text{KMnO}_4}$ ($\text{mg O}_2 \text{ L}^{-1}$)	0.45 ± 0.48	107	0.04 – 1.67
pH	8.25 ± 0.05	0.6	8.16 – 8.34
Alkalinity ($\text{mg CaCO}_3 \text{ L}^{-1}$)	204.9 ± 5.3	3	195.0 – 215.0
Total water hardness ($\text{mg CaCO}_3 \text{ L}^{-1}$)	214.7 ± 13.4	6	204.7 – 250.6
$\text{NO}_3^- \text{-N}$ ($\mu\text{g L}^{-1}$)	11.8 ± 10.8	91	1.0 – 32.2
$\text{PO}_4^{3-} \text{-P}$ ($\mu\text{g L}^{-1}$)	1.6 ± 0.9	57	1.00 – 3.34
Conductivity ($\mu\text{S cm}^{-1}$)	371 ± 12.5	3	346 – 384

Tab. 2. Hydromorphometric characteristics of the investigated mesohabitat types from October 2006 to September 2007. Abbreviations: *n* – sample size (i.e., number of flow velocity measurements), SD – standard deviation, CV – coefficient of variation, MIN – MAX – minimal to maximal values measured during the study period. Asterisks indicate significant difference between the two mesohabitat types regarding the flow velocity (based on Mann–Whitney *U*-test): ****p* < 0.0001.

	Mesohabitat type		
		B (barrier)	P (pool)
		Fast flowing tufa barrier	Pool between the two tufa barriers
Flow velocity (m s^{-1})***	<i>n</i>	85	132
	MEAN \pm SD	0.61 ± 0.40	0.12 ± 0.08
	CV	67%	68%
	MIN – MAX	0.11 – 1.97	0.01 – 0.42
Substratum type/ bottom cover		Well-developed moss cover, predominantly <i>Cratoneurum commutatum</i> (Hedw.) Roth. and <i>Rhynchostegium riparioides</i> (Hedw.) Card.	Tufa sand with sporadic moss mats

In total, we found 60 invertebrate taxa in drift during the study — all of them were found at barriers, but only 44 of them were found at both habitat types. The detailed list of taxa and the total numbers of individuals captured in drift during the study period are provided in SERTIĆ PERIĆ *et al.* (2014). The 13 taxa occurring only at barriers were cladoceran *Alonella* sp., and larval representatives of Trichoptera (*Plectrocnemia* spp., *Limnephilus* spp., *Lepidostoma* sp., *Sericostoma* sp., *Beraeamyia* sp., *Agraylea* sp., *Hydroptila* sp., *Ptilocolepus* sp., *Tricholeiochiton* sp.), Ephemeroptera (*Ephemera danica* Muller, 1764, *Ephemerella notata* Eaton, 1887) and Plecoptera (*Besdolus imhoffi* (Pictet, 1841)). The dominant invertebrates in drift at both mesohabitat types during the entire study were cladoceran *Alona* spp. (534 ± 1043 [= mean \pm SD] individuals [hereafter called "ind." m⁻³, $n = 131$), Oligochaeta (210 ± 400 ind. m⁻³, $n = 288$), and larval stages of dipteran *Simulium* spp. (215 ± 223 ind. m⁻³, $n = 169$) and coleopteran *Riolus* spp. (178 ± 188 ind. m⁻³, $n = 180$). The observed standard deviations of the means resulted from the seasonal peaks in the faunal drift, i.e., summer peak of *Alona* spp. (2236 ± 352 ind. m⁻³, $n = 34$), and autumn peaks of *Simulium* spp. (387 ± 118 ind. m⁻³, $n = 51$), *Riolus* spp. (257 ± 191 ind. m⁻³, $n = 52$) and Oligochaeta (168 ± 105 ind. m⁻³, $n = 95$).

Spatial drift patterns (barriers vs. pools)

Considering the entire study period, barriers displayed significantly higher invertebrate drift densities in comparison to pools (Mann–Whitney *U*-test, $p < 0.0001$; Figs. 2 and 3). The same pattern also was observed for moss, CPOM (excl. moss) and TIM, whose respective amounts at barriers were in average 5-, 3.5- and 4.5-fold higher than in pools (Mann–Whitney *U*-test, $p < 0.0001$; Figs. 2 and 3). FPOM in drift also reached higher amounts at barriers, but at the lower significance level (Mann–Whitney *U*-test, $p < 0.05$).

During the entire study period, the measured drift parameters yielded very high coefficient of variation (CV), ranging between 90% (observed for FPOM) and 328% (observed for invertebrate drift density). Both CV extremes were observed at barriers, indicating that barriers withstand larger temporal oscillations in drift than pools (Fig. 3). Temporal or monthly difference was not detected for invertebrate drift density, moss, and FPOM in barriers and for invertebrate drift density in pools with a marginal significance (Tab. 3). According to Friedman's ANOVA results (Tab. 3), the moss and FPOM patterns were associated with late autumn and winter (i.e., October to January) peaks of moss and FPOM in drift at barriers, which contrasted their 3- to 6-fold lower late-spring (i.e., May, June) amounts in drift (Fig. 3B, D).

The NMDS based on the invertebrate drift densities and selected environmental variables revealed contrasts in drift composition between barriers and pools (Fig. 4). The mesohabitat types were separated along NMDS axis-2, with barrier sites inclining towards higher numbers of larval simuliid blackflies (*Simulium* spp.; $r = 0.68$), coleopteran *Riolus* spp. ($r = 0.61$) and *Elodes* spp. ($r = 0.55$), and cladoceran *Alona* spp. ($r = 0.51$) individuals in drift. The NMDS further revealed that the observed invertebrate drift patterns at barriers and pools were mostly influenced by amounts of drifting TIM ($r = 0.45$) and CPOM excl. moss ($r = 0.42$) that correlated with NMDS axis-2 (Fig. 4).

Temporal (seasonal and diel) drift patterns at the two mesohabitat types (barriers vs. pools)

At both mesohabitat types, invertebrate drift showed peak, but highly variable densities in late spring and during summer (i.e., June, July), averaging > 100 ind. m⁻³

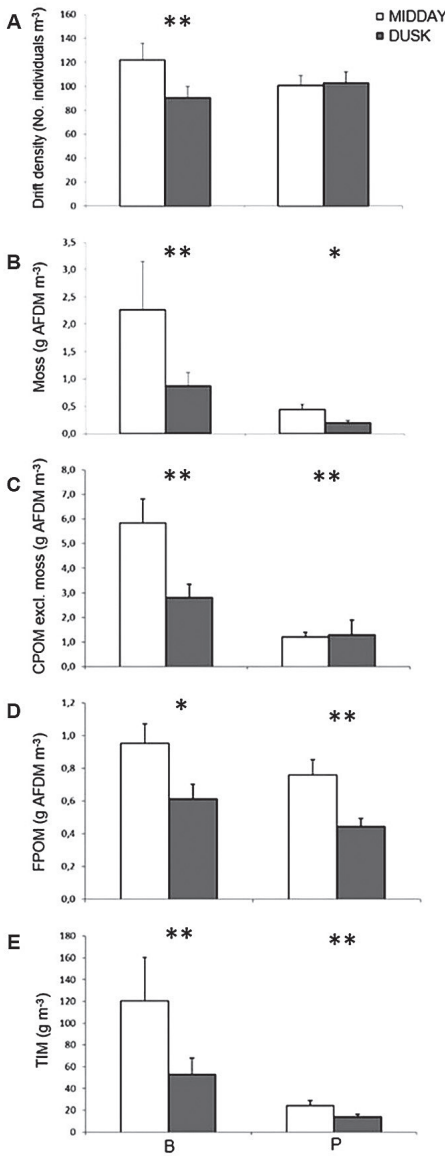


Fig. 2. (A) Mean (+ SE, i.e., standard error) amounts of drifting invertebrates and (B-E) associated particulate organic and inorganic matter (APOIM) found in midday and dusk drift samples taken at the two mesohabitat types (B – barriers, P – pools) from October 2006 to September 2007. For parameter abbreviations see Tab. 3. Asterisks indicate significant differences between midday and dusk based on Mann-Whitney *U*-test: * $p < 0.05$, ** $p < 0.01$. Note different scaling of y-axes.

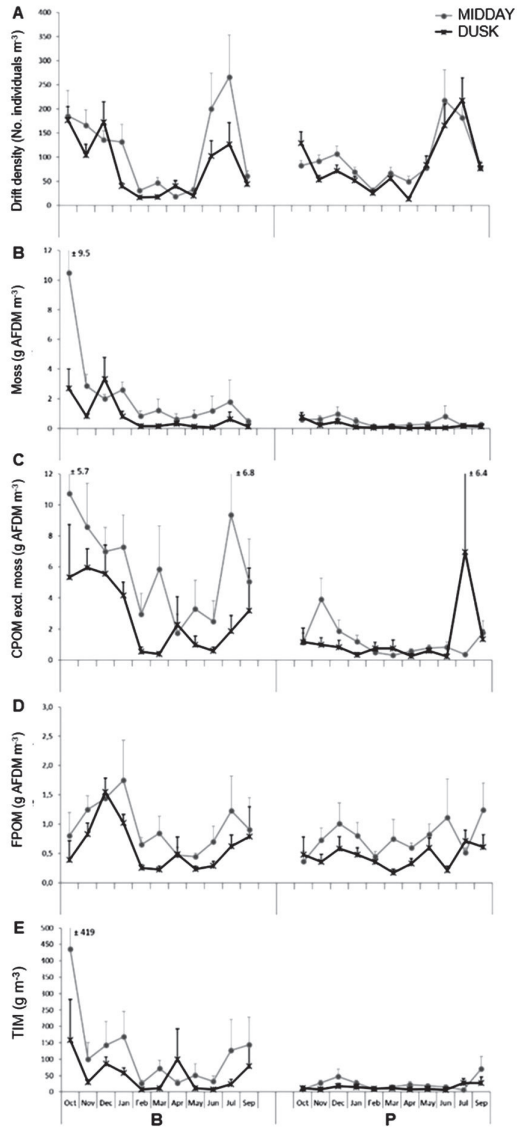


Fig. 3. Temporal (monthly and diel) dynamics of the measured drift parameters from October 2006 to September 2007. Data represent mean (+ SE, i.e., standard error): (A) invertebrate drift densities and (B-E) amounts of associated particulate organic and inorganic matter (APOIM) recorded in monthly midday and dusk drift samples at the two mesohabitat types (B – barriers, P – pools). Note different scaling of y-axes. For parameter abbreviations and statistical differences between individual months and times of the day refer to Tab. 3.

Tab. 3. Statistical analysis results for selected drift parameters at the two differing mesohabitat types (refer to Fig. 3). Abbreviations: CPOM excl. moss – coarse particulate organic matter excluding moss, FPOM – fine particulate organic matter, TIM – total inorganic matter, χ^2 – Friedman’s ANOVA results, τ – Kendall’s concordance coefficient. Bolded and italicized *p*-values indicate results of marginal significance ($\alpha = 0.05$).

	Barriers (B)			Pools (P)		
	χ^2	<i>p</i>	τ	χ^2	<i>p</i>	τ
Drift parameters Invertebrate drift density	18.09	0.054	0.90	17.82	0.058	0.89
Moss	17.73	0.059	0.89	13.64	0.19	0.68
CPOM excl. moss	15.55	0.11	0.78	11.64	0.31	0.58
FPOM	17.91	0.057	0.90	11.27	0.34	0.56
TIM	16.09	0.097	0.80	11.09	0.35	0.55

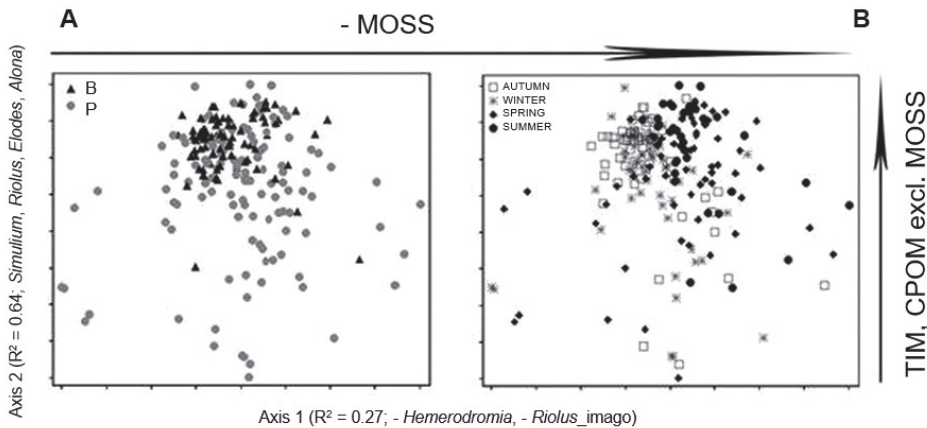


Fig. 4. NMDS ordination diagram (stress = 0.17) revealing the most significant (A) spatial and (B) temporal interactions and grouping patterns of the total drift samples ($n = 210$) collected from October 2006 to September 2007; (A) grouping of the sampled mesohabitat types (B – barriers, P – pools); (B) grouping of the seasons. The most influential environmental variables for the ordinations are given along arrows, and the most affected invertebrate taxa are indicated besides the axes names. A negative sign before a taxon/environmental variable name indicates a negative relationship of that taxon’s density (or variable amount) along that axis. For parameter abbreviations see Tab. 3.

(Fig. 3A). The peak drift densities significantly differed (Friedman’s ANOVA, $p \leq 0.05$) from the respective late winter/early spring (i.e., February to April) densities, which were *c.* 5-fold lower at both mesohabitat types. At the barriers, the late spring/summer drift peak was less pronounced at dusk than at midday, and the late winter/early spring drift was lower and more stable compared to pools (Fig. 3A). The most abundant taxa in drift during June and July at both mesohabitat types were cladoceran *Alona* sp. (1618 ± 123 ind. m^{-3} , $n = 34$), larval coleopteran *Riolus* spp. (259 ± 80 ind. m^{-3} , $n = 38$), dipteran *Simulium* spp. (247 ± 71 ind. m^{-3} , $n = 36$), Hydrachnidia (201 ± 100 ind. m^{-3} , $n = 33$), and oligochaetes from family Naididae (163 ± 22 ind. m^{-3} , $n = 13$). Several invertebrate taxa were also found abundant (> 100 ind. m^{-3}) at both mesohabitat types in autumn (October and November), i.e., dipteran *Simulium* spp. (298 ± 12 ind. m^{-3} , $n = 34$), larval *Riolus* spp. (273 ± 113 ind. m^{-3} , $n = 35$), and oligochaetes belonging to families Lumbricu-

lidae (312 ± 209 ind. m^{-3} , $n = 14$), Enchytraeidae (267 ± 211 ind. m^{-3} , $n = 19$) and Naididae (161 ± 1 ind. m^{-3} , $n = 25$). The autumn increase in drift densities of these taxa were coupled with a slight increase of overall drift densities in autumn months (Fig. 3A).

The main seasonal differences were depicted as separation of spring and summer vs. autumn and winter along NMDS axis-1 (Fig. 4). The observed grouping of seasons was associated with drift density decreases of larval empidid dipterans *Hemerodromia* spp. ($r = -0.51$) and adult coleopterans *Riolus* spp. ($r = -0.46$) during spring and summer. As revealed by the NMDS analysis, the invertebrate drift seasonality was further coupled with a decrease of moss ($r = -0.32$) in drift during spring and summer (Fig. 4).

In general, for most measured parameters, drift was higher during the day, and significant differences between midday and dusk at both mesohabitat types were proven (Fig. 2). An exception was invertebrate drift within pools, which did not yield significant diel differences (Fig. 2A). Monthly records of all measured drift parameters showed a high degree of concordance between midday and dusk (Fig. 3, Tab. 3). However, according to the Kendall's coefficient (τ) values, the concordance was slightly more pronounced at the barriers ($\tau \geq 0.78$) than within pools ($\tau \geq 0.55$).

At barriers, all drift parameters were ≤ 3 -fold higher during the midday compared to the dusk (Mann-Whitney U -test, $p < 0.05$; Fig. 2). Within pools, the means of moss, TIM and FPOM in drift were ≤ 2.5 -fold higher (Mann-Whitney U -test, $p < 0.05$) during the midday, whereas CPOM excl. moss (Mann-Whitney U -test, $p < 0.01$) and invertebrates (Mann-Whitney U -test, $p > 0.05$) reached slightly higher quantities during the dusk (Fig. 2).

The NMDS analysis conducted on separate (i.e., barrier vs. pool) data sets revealed a clear separation of midday and dusk (i.e., clear diel differences) at both barriers and pools (Fig. 5). As depicted in the NMDS ordination, midday at the barriers was mostly associated with increased drift densities of larval empidid dipteran *Hemerodromia* spp. ($r = 0.51$), as shown along NMDS axis-1, and larval coleopterans *Riolus* spp. ($r = -0.89$) and *Elodes* spp. ($r = -0.65$), cladocerans *Alona* spp. ($r = -0.71$), and water mites (Hydrach-

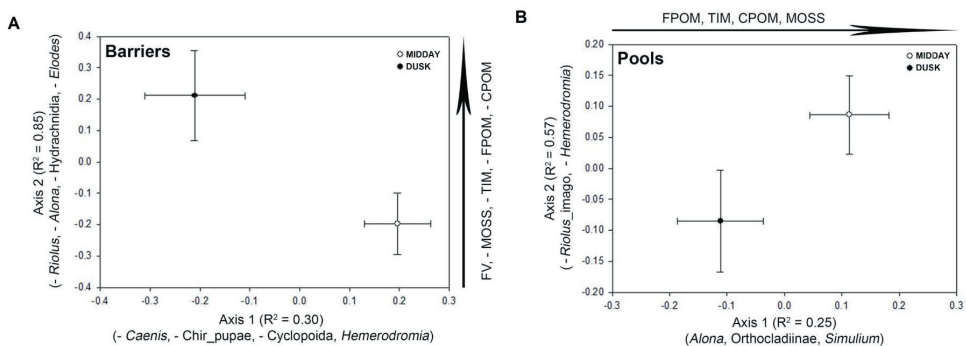


Fig. 5. NMDS ordination plot based on midday and dusk drift densities of the invertebrate taxa at the two mesohabitat types: (A) barriers (stress = 0.17; $n = 85$) and (B) pools (stress = 0.19; $n = 125$) from October 2006 to September 2007. Error bars are standard errors, illustrating temporal variability in invertebrate densities based on monthly measurements within each mesohabitat type. For parameter abbreviations see Tab. 3, whereas FV stands for flow velocity. For additional explanations, refer to the caption of Fig. 4.

nidia; $r = -0.70$), as shown along NMDS axis-2. Considering other measured drift parameters, during the midday at barriers were mostly recorded lower flow velocities (FV; $r = 0.69$) and higher moss ($r = -0.60$), TIM ($r = -0.57$), FPOM ($r = -0.56$) and CPOM excl. moss ($r = -0.55$) amounts in drift (Fig. 5A). Also within pools, the NMDS results indicate that the diel drift pattern was driven by an increase in FPOM, TIM ($r = 0.39$ for both), CPOM excl. moss ($r = 0.37$) and moss ($r = 0.31$) during the midday (Fig. 5B). However, the pool-NMDS- r -values of the environmental variables were *c.* twofold lower than at barriers, indicating that their influence on invertebrate drift patterns within pools were weaker. Flow velocity effect within pools was not proven significant. As indicated along NMDS axis-2, the slight increase of nocturnal invertebrate drift within pools (Fig. 2A) was mostly coupled with higher numbers of drifting *Riolus* spp. adults ($r = -0.42$) and larval *Hemerodromia* spp. ($r = -0.37$) during the dusk (Fig. 5B). NMDS axis-1 indicated that relatively high midday drift within pools was mostly driven by increased number of cladoceran *Alona* spp. ($r = 0.60$), Orthoclaadiinae chironomids and blackflies (*Simulium* spp.) ($r = 0.47$ both) in drift (Fig. 5B).

DISCUSSION

Effects of mesohabitat and seasonal shifts on invertebrate drift

Results of the present study indicate that freshwater reefs are loci of intense day drift of invertebrates and APOIM within tufa-depositing hydrosystems. Our barrier (i.e., fast-flowing) sites displayed significantly higher drift densities of the measured drift parameters (i.e., invertebrates, moss, CPOM excl. moss, FPOM and TIM) in comparison to pools (i.e., slow-flowing sites), as shown in the earlier drift studies within the same hydrosystem (SERTIĆ PERIĆ *et al.*, 2011, 2014, 2015). Whereas some previous drift studies suggested that low invertebrate drift densities within pools result from low flow velocities throughout the pools (MARTIN & KNIGHT, 1989; LANCASTER *et al.*, 2011; BROOKS *et al.*, 2017), the earlier studies within our hydrosystem evidenced that there was no significant correlation between flow velocity and the amount of drift (SERTIĆ PERIĆ *et al.*, 2011, 2014, 2015). Conversely, a highly significant positive correlation between the amounts of moss and other measured drift parameters was indicated (SERTIĆ PERIĆ *et al.*, 2011). Such correlations suggested that drift patterns within the studied hydrosystem are greatly influenced by seasonal changes in aquatic vegetation (i.e., moss-covered tufa substrate), and its efficiency to trap particles and organisms.

However, we could not completely neglect the flow effect on the observed drift patterns within the studied hydrosystem. Although the extensive moss cover at the barriers provides plenty of food and safe shelter (i.e., protection from predators and detrimental flow conditions) for benthic invertebrates (e.g., SUREN, 1992; MILIŠA *et al.*, 2006; DRAŽINA *et al.*, 2013), the barrier flow conditions likely exceed the physical durability of moss, so they easily get flushed from the barrier streambed together with associated particles and organisms (BULL, 1979). Considering our observations of peak drift densities of moss and FPOM at barriers during late autumn and early winter, we suggest that aquatic moss within our study system is most vulnerable to flow alterations during periods of vegetation die-off in temperate regions. The autumn moss peak can also result from the increased moss fragility caused by high contents of tufa precipitated on moss substrate at that time of year, due to which the moss can become stiff and more prone to crack (SERTIĆ PERIĆ *et al.*, 2011, 2014). Furthermore, water flow is the primary dispersal mechanism for aquatic mosses (GLIME, 2014). It also might en-

hance the vegetative dispersal of aquatic moss, as it was observed for *Fontinalis anti-pyretica* Hedw. – one of the most common aquatic mosses in temperate regions, whose fragments that detached from the bryophyte stems by water flow evidenced extraordinary powers of regeneration (ARES *et al.*, 2014). Water-mediated downstream transport of moss therefore likely represents an important dispersal mechanism within the Plitvice Lakes hydrosystem – not only for benthic invertebrates, but also for aquatic vegetation and particulate organic substances supporting the food web (cf. SERTIĆ PERIĆ *et al.*, 2011).

Our own flow velocity measurements taken at each sampling occasion during eleven months twice a day, as well as the mean values and standard deviations of the flow velocities (Tab. 2) provide evidence that barriers experience more fluctuations in flow than pool reaches. Barriers within our study are characterized by shallow depths, and fast and turbulent water, which respond more readily to variations in discharge, and could thus exhibit more oscillatory flow than deeper pool areas (NEWBURY & BATES, 2007). As our barrier sites evidenced larger temporal oscillations of most measured drift parameters (i.e., invertebrates, moss and FPOM) than pools, we can conclude that flow alterations have influenced the observed drift patterns, as it has been demonstrated in many drift studies worldwide (e.g., JAMES *et al.*, 2009; CASTRO *et al.*, 2013; MILLER & JUDSON, 2014 and references therein). Similar conclusions were also posed by MILLER & JUDSON (2014) in the study at Flaming Gorge Dam (Utah, USA), where the effects of natural hydropeak cycles and experimental flows on drift patterns were investigated. It was found that the daily amounts of drifting benthic invertebrates increased after the dam flow release, but the drift amounts were even higher if there were two hydropeaks rather than just one. Such results suggested that benthic invertebrates respond more to changes in flow rather than to the absolute flow velocities (MILLER & JUDSON, 2014).

The seasonality of drifting invertebrates at both mesohabitat types along our study site was obvious through the conspicuous peak during late spring and summer (i.e., June and July) and less pronounced peak in late autumn and early winter (i.e., October to December), and the contrasting low drift densities during late winter and early spring (i.e., February to April). Similar seasonal patterns have been observed in many other temperate streams (SCHREIBER, 1995; SHEARER *et al.*, 2002; HANSEN & CLOSS, 2007). However, in a piedmont temperate stream in South Carolina, USA, peak drift densities were recorded in early spring and late summer (STONEBURNER & SMOCK, 1979), whereas in a coastal temperate stream, winter drift peaks were observed (LEUNG *et al.*, 2009). In temperate alpine streams, no consistent seasonal pattern of drift was found as it greatly varied among differing alpine stream types (ROBINSON *et al.*, 2002; HIEBER *et al.*, 2003). Our observations of summer and autumn drift peaks (during periods of high primary production in the NP ecosystem, and pronounced moss dislodgement, respectively) support the previous findings suggesting that seasonal drift patterns mostly depend on invertebrate life cycle patterns, food search and supply and/or specific drift behavior (NEALE *et al.*, 2008; SERTIĆ PERIĆ *et al.*, 2011; TONKIN & DEATH, 2013). We could add that the invertebrate drift seasonality greatly depends on the life-cycle phenology of the overall aquatic community assembly (including aquatic vegetation, i.e., moss). As well, it is likely that the seasonal drift patterns in our study system greatly depend on the propensity of individual taxa to be attached to/carried by a certain “drift agent” (e.g., water flow, plant material) at certain life stages.

Effects of diel shifts on invertebrate drift

The significantly increased midday drift observed at our barrier sites is consistent with findings from numerous previous drift surveys conducted within fishless habitats (FLECKER, 1992; SALTVEIT *et al.*, 2001; WINKELMANN *et al.*, 2008). However, in some high altitude and/or tropical fishless streams as well as in arctic streams during polar day periods, drift was found to be largely aperiodic (JACOBSEN & BOJSEN, 2002; HIEBER *et al.*, 2003), i.e., evidencing absence of any significant diel pattern as it was observed within our pool reaches.

Although the NP Plitvice Lakes harbor several fish species such as drift-feeding salmonids and tactile benthic feeders (i.e., cyprinid substrate grubbers) that presumably affected the invertebrate drift patterns, the alternating barrier–pool sequences along our study area were mainly fishless (Z. MARČIĆ, unpub. data). These sequences represent relatively small water bodies accompanied by barriers and waterfalls, and likely act as “natural ecological barriers limiting fish dispersal processes” (MCPHAIL & LINDSEY, 1986; TORRENTE-VILARA *et al.*, 2011). The absence of fish within our study site could thus imply the absence of behavioral drift (i.e., low risk from visual fish predators) and consequently could cause the increased midday and/or aperiodic drift, as observed at our mesohabitats (cf. FLECKER, 1992; HAMMOCK *et al.*, 2012; WORISCHKA *et al.*, 2015).

The increased midday amounts of drifting invertebrates and APOIM observed at both mesohabitat types also could source from the differences in the diel shifts of tufa deposition processes. Tufa deposition is enhanced during the daytime by insolation, temperature rise and consumption of CO₂ due to photosynthesis of submerged aquatic plants (DRYSDALE *et al.*, 2003; LIU *et al.*, 2006). Higher temperatures, accompanied by increased photosynthetic activity of aquatic moss during the daytime might have increased daily tufa (i.e., calcite) precipitation rates along our study site. Considering the concordance between transported moss and other drift parameters at both mesohabitat types and day periods, we suggest that deposited calcite crystals might have outweighed the weak moss stems and increased fragility of the moss, enhancing the removal and downstream transport of moss, APOIM as well as moss-dwelling invertebrates.

Another possible reason for the increased midday drift might be physical disturbance caused by touristic activity within the NP. In past decades, Plitvice Lakes host more than a million of visitors each year (MEE, 2015). The greatest increase in tourist numbers occurs during spring and summer (April to September) (M. VURNEK, personal communication), i.e., at the same period we observed the most prominent invertebrate drift peak. There are studies evidencing that the increased tourist activities might affect habitat quality, abundance and/or even behavior and redistribution of many organisms (MAYAKUN & PRATHEP, 2005; TADESSE & KOTLER, 2012; LAVEN *et al.*, 2015). Thus, it is possible that the numerous tourists visiting Plitvice Lakes during the daytime act as a vast disturbance (e.g., by walking along lake banks and over the lotic sequences) that triggers the increased invertebrate drift of biota inhabiting ‘freshwater reef’ habitats.

Adult and/or larval *Riolus* spp. and larval *Hemerodromia* spp. were found to be the most significant for the separation of midday and dusk within the NMDS ordination of barriers and pools. We suggest that these taxa, i.e., their ontogenetic shifts in drift periodicity and benthic distribution (i.e., shifts depending on the development stage and morphological characteristics of the individual taxa), could have affected the sli-

ghtly increased nocturnal invertebrate drift observed within pools (cf. ELLIOTT, 2008; IVKOVIĆ *et al.*, 2012). Several studies have shown that the downstream drift of the larval and adult riffle beetles (i.e., *Riolus* spp.) occurs chiefly at night (ELLIOTT, 2008), whereas larval Empididae (i.e., *Hemerodromia* spp.) have been described as day drifters (FECHNEY, 1988; SAGAR & GLOVA, 1992). However, as moss has been found as a preferred habitat of larval Empididae (IVKOVIĆ *et al.*, 2012), and larval and adult riffle beetles (i.e., *Riolus* spp.) (NILSSON, 1996; MIČETIĆ STANKOVIĆ *et al.*, 2019), the overlapping drift patterns of these taxa and moss at our barrier sites was not surprising.

Many authors have addressed that drift is “highly patchy” and could greatly vary both spatially and temporally (e.g., TONKIN & DEATH, 2013 and references therein), which is corroborated by the present study. The results of the present study further indicate that aperiodic and/or increased midday drift at the alternating barrier–pool mesohabitats is likely due to a lack of visual fish predators. Thus, the answer to our initial research question is that biotic (vs. abiotic) controls of drift are likely minimized in the fishless case of the freshwater reefs and associated barrier–pool sequences within Plitvice Lakes hydrosystem. Our results also suggest that aquatic invertebrates inhabiting barrier and pool mesohabitats associated to freshwater reefs mostly take advantage of passive drift mediated by transport agents such as water flow and/or dislodged aquatic vegetation (i.e., moss). However, the present study was conducted at only one site within the lake system, i.e., it lacks data from multiple barrier–pool sites. Due to the lack of spatial replication, the results of the present study should be considered with caution, as they could likely not be generalized across the wider fishless barrier–pool and moss-rich hydrosystems. Thus, further investigations are needed to precisely model invertebrate drift in such habitats, and the present study could serve as a good starting point for a more robust drift study within the Plitvice Lakes hydrosystem.

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