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# BENTHIC MACROINVERTEBRATE COMMUNITIES CHANGE ALONG A KARSTIC BARRAGE-LAKE SYSTEM

**Sanja Sviben[1], Renata Matoničkin Kepčija[1], Marina Vilenica[2,*], Ivančica Krulik[1], Vlatka Mičetić Stanković[3], Petar Kružić[1] & Mladen Kučinić[1]**

[1]University of Zagreb, Faculty of Science, Department of Biology, Horvatovac 102a, 10 000 Zagreb, Croatia (e-mails: sanjasviben@gmail.com; renata.matonickin.kepcija@biol.pmf.hr; ivancica.krulik@biol.pmf.hr; petar.kruzic@biol.pmf.hr; mladen.kucinic@biol.pmf.hr)

[2]University of Zagreb, Faculty of Teacher Education, Trg Matice Hrvatske 12, 44250 Petrinja, Croatia (e-mail: marina.vilenica@ufzg.hr)

[3]Croatian Natural History Museum, Demetrova 1, 10000 Zagreb, Croatia (e-mail: vlatka.micetic-stankovic@hpm.hr)

**Sviben, S., Matoničkin Kepčija, R., Vilenica, M., Krulik, I., Mičetić Stanković, V., Kružić, P. & Kučinić, M.: Benthic macroinvertebrate communities change along a karstic barrage-lake system. Nat. Croat., Vol. 33, No. 1., 105-121, 2024, Zagreb.**

Barrage-lake systems are a rare natural phenomenon with specific ecological characteristics that are greatly affected by tufa formation. Our main goal was to investigate benthic macroinvertebrate communities and their longitudinal variations within the lakes arranged in cascades in the Dinaric karst hydrosystem. Each lake within the Plitvice Lakes system studied presented with a distinct community, showing the effects of the barrage-lake system on the macroinvertebrates in these lakes. We observed a downstream decrease in taxa richness, abundance and Shannon diversity index along the longitudinal profile of the studied barrage-lake system. This pattern is most probably a result of decreased organic matter and increased tufa deposition. Overall, our results suggest that the hydrosystem studied represents a sequence of sediment sinks in which lakes retain and accumulate organic matter and fauna. Therefore, each lake acts as a filtering screen and consequently appears to be a small ecosystem. Each lake has its own community characteristics, regardless of the fact that water flows from one lake to the next, connecting them and creating very similar abiotic conditions in each lake along the system.

**Key words:** Dinaric karst, tufa deposition, barrage lakes, retention effect, macrozoobenthos

**Sviben, S., Matoničkin Kepčija, R., Vilenica, M., Krulik, I., Mičetić Stanković, V., Kružić, P. & Kučinić, M.: Zajednice bentičkih makrobeskralješnjaka u kaskadnom jezerskom sustavu. Nat. Croat., Vol. 33, No. 1., 105-121, 2024, Zagreb.**

Kaskadni jezerski sustavi rijedak su prirodni fenomen obilježen specifičnim ekološkim značajkama na koje uvelike utječe stvaranje sedre. Glavni cilj ovog rada bio je istražiti zajednice bentičkih makrobeskralješnjaka i njihove razlike duž kaskadnog jezerskog kompleksa u hidrološkom sustavu Dinarskog krša. Svako jezero unutar istraživanog dijela kompleksa Plitvičkih jezera ima specifičnu zajednicu bentičkih makrobeskralješnjaka, što je posljedica učinka kaskadnog sustava jezera na makrozoobentos. Uzduž longitudinalnog profila jezerskog kompleksa zabilježeno je smanjenje bogatstva svojti, brojnosti jedinki i Shannonovog indeksa raznolikosti, što je vjerojatno posljedica smanjenja količine organske tvari i povećanja taloženja sedre. U ovakvim kaskadnim jezerskim sustavima jezera zadržavaju i akumuliraju organsku tvar i faunu zbog čega je svako jezero naseljeno specifičnim zajed-

*Corresponding author

nicama makrobeskralješnjaka, bez obzira na to što voda teče iz jednog jezera u drugo, povezuje ih i osigurava vrlo slične abiotičke uvjete u svakom jezeru duž istraživanog jezerskog sustava.

**Ključne riječi:** dinarski krš, taloženje sedre, kaskadna jezera, retencijski učinak, makrozoobentos

## INTRODUCTION

Despite the considerable amount of research on the process of freshwater carbonate precipitation and tufa formation (e.g. Srdoč *et al.*, 1985; Emeis *et al.*, 1987; Chafetzet *et al.*, 1991; Ford & Pedley, 1996; Bellinzoni *et al.*, 2003), the components involved in these processes are still the subject of research. Generally, tufa is a porous sedimentary rock typical of carbonate rich areas where the spring waters appear supersaturated with calcium carbonate. Restoring the chemical equilibrium, some of the calcium carbonate is precipitated from the solution (Golubić, 1969; Riding, 1991). This results in tufa deposition, and the initiation of this process appears to be result of three factors – the biological, geological and chemical (micro) environments (Emeis *et al.*, 1987; Ford & Pedley, 1996). Organisms have an inevitable role (Chafetz *et al.*, 1994) since they provide a substrate for calcite nucleation which accelerates tufa deposition (Kempe & Emeis, 1985; Merz-Preiss & Ridding, 1999; Matoničkin Kepčija *et al.*, 2006). A wide range of organisms is associated with tufa, as it is a suitable substratum that provides shelter and food in the form of encrusted algae and detritus for invertebrates (Pentecost, 2005). Nevertheless, intensive carbonate deposition and encrustation create unfavorable conditions for these organisms (Golubić, 1969; Emeis *et al.*, 1987), which could have negative effects on macroinvertebrate abundance and community structure (Rundio, 2009). Many invertebrates, especially insects, have evolved peculiar adaptations which enable them to exist in these extreme conditions (Pentecost, 2005).

Tufa deposits are quite common, yet the development of tufa dams which lead to the differentiation of a river profile into a series of lakes and waterfalls is a rare phenomenon (Golubić, 1969). As a result of this process, barrage-lake systems are formed, such as the Ruidera Pools Natural Park (Spain), Plitvice Lakes National Park (Croatia), d'Immouzer and Ida du Tanane (Marocco), Turner Falls (USA) and tufa springs in Queensland (Australia) (Ford & Pedley, 1996). In a stream containing tufa dams, organic matter tends to accumulate, resulting in tight spirals, delaying nutrient loss (Pentecost, 2005). So far, the effects of the dams have not been investigated in terms of nutrient retention (Pentecost, 2005), however, a significant decrease in the organic matter downstream the Plitvice Lakes barrage-system in Croatia has already been observed (Obelić *et al.*, 2005; Horvatinčić *et al.*, 2006; Miliša *et al.*, 2006). Also, according to the developmental scheme of a barrage system proposed by Golubić (1969), tufa deposition should be increasing downstream. For now, Plitvice Lakes are the only barrage system confirming both these hypotheses (Srdoč *et al.*, 1985) which makes them very interesting in the context of ecological research.

The Plitvice Lakes are a karstic hydrosystem with well-defined hydrobiological (Golubić, 1969, Emeis *et al.*, 1987), hydrological (Petrik, 1958), mineralogical (Stoffers, 1975), chemical (Kempe & Emeis, 1985; Frančišković-Bilinski *et al.*, 2004) and ecological (Šegulja & Hršak, 1994; Habdija *et al.*, 2004; Miliša *et al.*, 2014) characteristics. In this study, we aimed to determine whether the organisms within the tufa barrage system would show distinctive quantitative or qualitative downstream patterns. Macrozoobenthos provides an excellent opportunity to address this type of question in community ecology due to its interactions with tufa. Despite the increasing amount of research conducted in the area of Plitvice Lakes National Park (NP) during the last two decades (e.g. Popijač & Sivec, 2009; Ivković *et al.*, 2012, 2014; Šemnički *et al.*, 2012; Kučinić *et al.*, 2008; Ivković & Pont, 2016; Vilenica *et al.*, 2014; 2017; Mičetić Stanković *et al.*, 2019), macroinvertebrates within the lakes have not yet been investigated in detail. Previous studies were mainly focused on the organisms living on the barriers where calcium precipitation is very pronounced due to water splashing and aeration (e.g. Špoljar *et al.*, 1994; Primc-Habdija *et al.*, 2001; Miliša *et al.*, 2006; 2014). Thus, we sampled the littoral zone, which in comparison to other lake zones supports larger and more diverse populations of benthic invertebrates (Wiederholm, 1984) due to substrate heterogeneity (Strayer, 1985). Having in mind the complexity of barrage systems, the main goals of this study were to determine: a) benthic macroinvertebrate community composition and its seasonal variations within the lakes, b) influence of different substrate types on the abundance and distribution of benthic macroinvertebrates and c) quantitative and qualitative patterns of benthic macroinvertebrates downstream the barrage-lake system of the Plitvice Lakes.

## METHODS

### Study area

The Plitvice Lakes are located in the karstic region of the NW Dinaric Mountains in Croatia (Fig. 1). This natural system is composed of 16 barrage-lakes where water flows from one lake to the next over tufa barriers, which are the main factor in creating waterfalls and cascades (Ford & Pedley, 1996). Water splashes in the waterfalls, stimulating the extraction of carbon dioxide and sedimentation of calcium carbonate from the water. The overall result is the growth of tufa barriers, causing a rise in the water level (Zwicker & Rubinić, 2005). The lakes receive water from the two main suppliers, Bijela rijeka and Crna rijeka rivers, which join into the Matica River, and two tributaries, the Rječica and Plitvica streams. The altitude of the area ranges between 636 and 503 m a.s.l. The lake system is 9.05 km long and because of its geomorphological features, it is divided into 12 upper and four lower lakes (Riđanović & Božičević, 1996). Upper lakes are located in a dolomite valley while lower lakes flow through a rudist limestone canyon, where the last lake drains into the karst lowland Korana River (Riđanović & Božičević, 1996).

In our study, we investigated four lakes: Prošće, Ciginovac, Kozjak and Kaluđerovac. Their characteristics are given in Tab. 1. The first three lakes, Prošće, Ciginovac and Kozjak, are part of the upper section while the fourth, Kaluđerovac Lake, is a part of the lower section. Prošće is the first lake in the barrage system. Progressive filling with sediment and aquatic vegetation was recorded there 40 years ago (Iveković, 1971). At the outlet, water from the Prošće Lake flows partially into Ciginovac Lake and partially into Okrugljak Lake. Some of the water that flows into Ciginovac Lake is probably drained under the ground through the very porous tufa barrier (Beraković, 2005). Kozjak Lake is the last in the string of upper lakes. It is the largest lake, and its deepest point is 46 m, which makes it also the deepest lake in the hydrosystem. Except for a few perennial streams and temporary flows, the watercourse that mostly affects the water regime of Kozjak Lake is the Rječica Stream (Iveković, 1971). Kaluđerovac Lake is specific because of its pronounced tufa deposition, greater than that of other lakes.

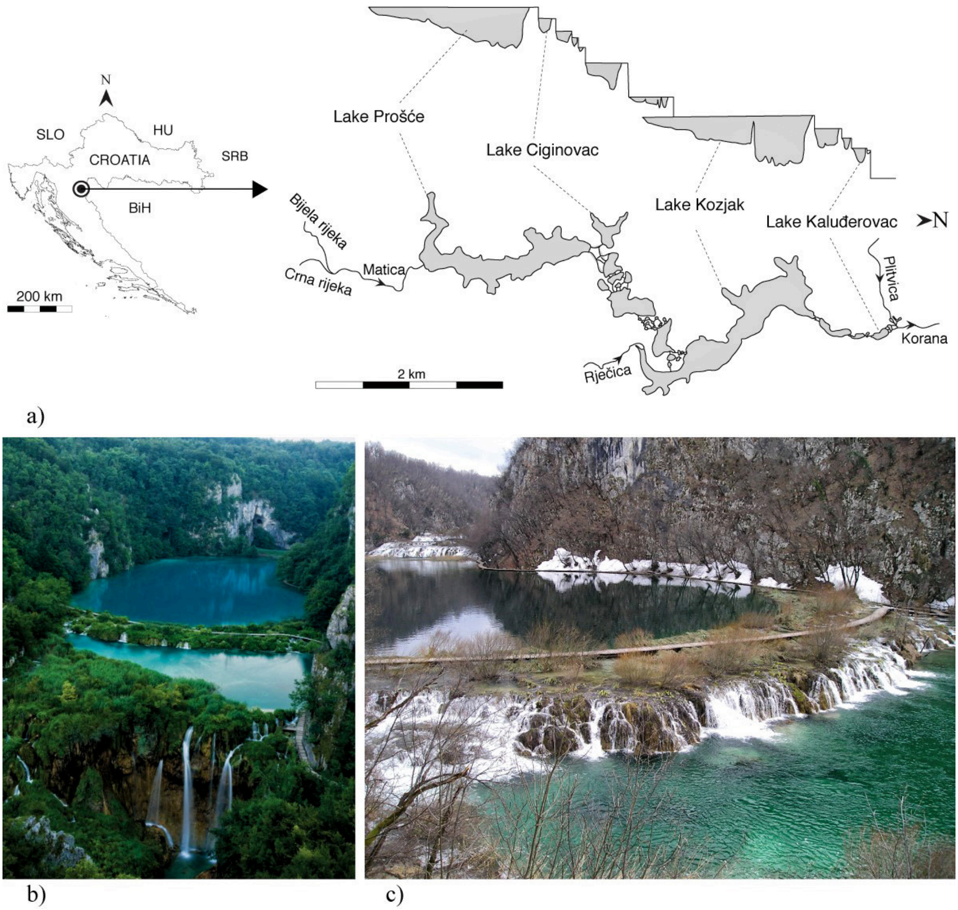


**Fig. 1.** a) Study area and location of the sampling sites, b) and c) Lakes divided by tufa barriers in Plitvice Lakes barrage-system. (Photo: P. Kružić and R. Matoničkin Kepčija).

Biologically induced calcite precipitation is probably enhanced due to the increase in primary production (Horvatinčić *et al*., 2008).

## Sampling protocol

At each lake, one littoral station was selected near forested banks at depth not more than one metre. To determine macroinvertebrate abundance and taxa richness, samples were collected monthly from April 2007 to March 2008. Sampling points were characterized with respect to the most dominant substrates (Tab. 1) in the littoral zone of each lake. In Prošće Lake, we sampled *Chara* sp. and mosaic substrate sand/leaf litter, and in Ciginovac Lake cobbles and leaf litter were sampled. In the Kozjak Lake, macroinvertebrate communities were sampled on *Chara* sp. and leaf litter. The algae were sampled over a period of only eight months, as it vanished during October, November, December and January, when it was replaced with sandy substrate. Thus, during those four months, sand was sampled instead. In Kaluđerovac Lake, we sampled only the

**Tab. 1.** Main characteristics of the four studied lakes in the Plitvice Lakes barrage-system (P = Prošće, C = Ciginovac, Ko = Kozjak, Ka = Kaluđerovac).

| Lake characteristics | P | C | Ko | Ka |
|---|---|---|---|---|
| Elevation (m a.s.l.) | 637 | 620 | 534 | 505 |
| Mean depth (m) | 37 | 11 | 46 | 13 |
| Length (m) | 2100 | 470 | 2350 | 225 |
| Width (m) | 180-400 | 120 | 135-670 | 70-100 |
| Surface area (km$^2$) | 0.68 | 0.07 | 0.83 | 0.02 |
| Dominant riparian vegetation: | | | | |
| *Fagus sylvatica* L. | + | + | + | |
| *Carpinus betulus* L. | | | | + |
| Substrate type: | | | | |
| *Chara* sp. | + | | + | |
| Cobbles | | + | | |
| Leaf litter | | + | + | |
| Sand | | | + | |
| Cobbles/Leaf litter | | | | + |
| Sand/leaf litter | + | | | |

mosaic combination of two substrates, leaf litter and cobbles. To equalize the area sampled in each lake, we collected duplicates of microhabitat with leaf litter and cobbles in Kaluđerovac Lake during each sampling event.

Macroinvertebrates were collected using a D-frame net sampler with a surface area of 0.1 m$^2$ and mesh size 500 µm. Sampled substrates were carefully washed in the field. Material was placed in plastic containers and preserved in 96 % ethanol. In the laboratory, 24 hours after sampling, material was transferred to 80 % ethanol. Macroinvertebrates were sorted, counted, identified under a stereomicroscope and stored in 70 % ethanol. According to the identification keys (e.g. Engblom, 1996; Meinander, 1996; Nilsson *et al*., 1996; Gerken & Sternberg, 1999; Waringer & Graf, 1997; 2011; Bauernfeind & Humpesch, 2001; Hölzel, 2002; Jäch & Brojer, 2006) benthic macroinvertebrates were identified to the lowest possible taxonomic level with a focus on insect larvae.

Analysis of physico-chemical water properties was conducted according to the procedures in APHA (1998). The following physico-chemical water properties were measured at each sampling event: water temperature, dissolved oxygen concentration (using an oximeter (WTW Oxi 330/SET), pH (using a pH-meter (WTW ph 330), conductivity (using a conductometer (WTW LF 330)), nutrients (nitrate levels (by chromotropic acid method), nitrites (by sulfanilic acid and 1-Naphthylamine in the colorimetric method), ortho-phosphates (by the molybdophosphoric acid method) and ammonia (by salicylic acid)). Although the ortho-phosphate and nitrite levels were measured during the entire study period, the sensitivity of the method was too low for their detection.

## Data analysis

The benthic macroinvertebrate abundance, taxa richness and Shannon diversity index were calculated for each investigated lake.

To examine similarities in benthic macroinvertebrate communities between different lakes and different substrates, NMDS analyses were conducted. The analyses were based on the monthly samples and were conducted using a Bray-Curtis resemblance coefficient. Prior to analysis, all data were log(X+1)-transformed. Samples without macroinvertebrate records were excluded from the analyses. Shannon diversity and NMDS analyses were performed in the software package PRIMER 6 (Clarke & Gorley, 2006).

## RESULTS

### Physico-chemical water properties

Mean water temperature ranged between 11.6°C in Prošće Lake and 14.2°C in Kozjak Lake. Mean concentration of dissolved oxygen in water ranged between 9.8 mg $L^{-1}$ in Kozjak Lake and 11.6 mg $L^{-1}$ in Prošće Lake. Mean value of pH was 8.2 in Prošće and Ciginovac lakes, and 8.4. in Kozjak and Kaluđerovac lakes. Conductivity ranged between 366 μS $cm^{-1}$ in Kaluđerovac Lake and 405 μS $cm^{-1}$ in Prošće Lake. Mean concentration of nitrates in water ranged between 0.5 mg $L^{-1}$ in Kaluđerovac Lake and 0.8 mg $L^{-1}$ in Prošće Lake. Mean concentration of ammonia was higher in Kaluđerovac Lake (0.06 mg $L^{-1}$) than in the other three lakes (Tab. 2).

**Tab. 2.** Physico-chemical water properties measured from April 2007 to March 2008 in the four lakes of the Plitvice Lakes barrage-system presented as mean values ± SD.

| Abiotic parameter | Prošće | Ciginovac | Kozjak | Kaluđerovac |
|---|---|---|---|---|
| Water temperature (°C) | 11.6 ± 7.0 | 12.9 ± 7.7 | 14.2 ± 7.9 | 13.0 ± 7.9 |
| Dissolved oxygen (mg $O_2$ $L^{-1}$) | 11.6 ± 1.7 | 10.9 ± 1.3 | 9.8 ± 1.6 | 10.5 ± 1.7 |
| pH | 8.2 ± 0.5 | 8.2 ± 0.5 | 8.4 ± 0.2 | 8.4 ± 0.1 |
| Conductivity (μS $cm^{-1}$) | 405 ± 28 | 383 ± 256 | 382 ± 39 | 366 ± 22 |
| Nitrates (mg N $L^{-1}$) | 0.8 ± 0.1 | 0.6 ± 0.1 | 0.6 ± 0.2 | 0.5 ± 0.3 |
| Ammonia (mg N $L^{-1}$) | 0.02 ± 0.01 | 0.03 ± 0.02 | 0.02 ± 0.01 | 0.06 ± 0.10 |

### Macroinvertebrate community composition

In all, 16 benthic macroinvertebrate taxa groups were recorded in the studied four lakes (Appendix 1). Altogether 26082 individuals of benthic macroinvertebrates were collected and analysed. Overall, the most abundant macroinvertebrates were Diptera larvae, with Chironomidae as the numerically dominant group. High frequency of Ephemeroptera, especially *Caenis horaria* (Linnaeus, 1758), was recorded only in Prošće Lake. Mollusca, with the most abundant representative *Pisidium* sp., were the second most abundant taxon in Ciginovac Lake, where a high abundance of Isopod *Asellus aquaticus* (Linnaeus, 1758) was also recorded. Macroinvertebrate community compositions of the Kozjak and Kaluđerovac lakes were similar, with Diptera and Oligochaeta as dominant groups.

In the studied lakes, Plecoptera were the least abundant insect group. Ten Odonata taxa and four species of Megaloptera were recorded. Trichoptera larvae were infrequent, but they showed the highest richness with 13 recorded genera. Heteroptera were recorded in a high abundance only in the first lake in the hydrosystem, Prošće Lake. They were also present sporadically in Ciginovac Lake, while they were completely absent from the other two lakes. Abundance of Hirudinea was also decreasing downstream the barrage-lake system, being the most abundant in Prošće Lake and completely absent from Kaluđerovac Lake.

## Seasonal variations in the community composition

Generally, macroinvertebrate abundance was the highest in winter in Prošće Lake, while the lowest value was also recorded in winter, but in Kaluđerovac Lake. During all seasons, Dipteran larvae were a dominant taxon (Fig. 2).

In the upper lakes section (i.e. Prošće, Ciginovac and Kozjak lakes), the abundance of benthic macroinvertebrates was reduced downstream the barrage system during spring and autumn. During summer and winter, a decrease in the abundance was observed along the whole longitudinal profile (Fig. 2).

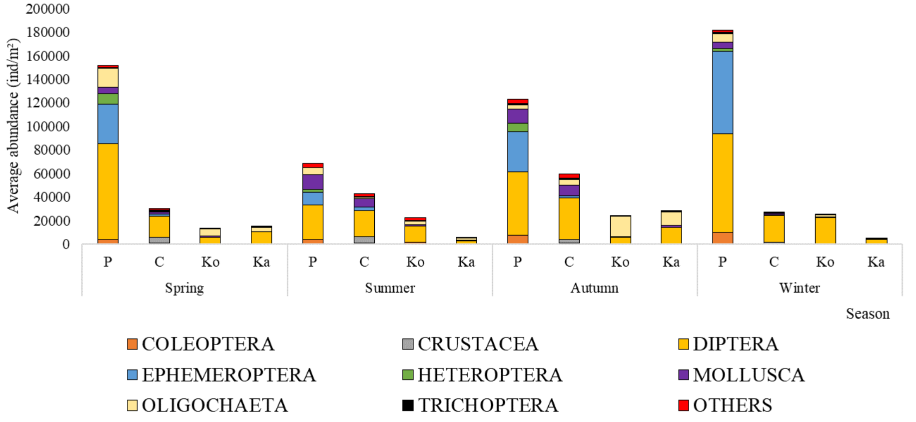


**Fig. 2.** Seasonal variations of the benthic macroinvertebrate communities at investigated sites in the Plitvice Lakes barrage-system. For the abbreviations of the study sites see Tab. 1. Abundance is expresses as number of individuals per m$^2$.

## Changes in communities of benthic macroinvertebrates along a barrage-lake hydrosystem

Taxon richness and Shannon diversity index decreased downstream the hydrosystem (Tab. 3). The abundance showed a similar pattern in the downstream decrease, except for Kaluđerovac Lake, where we recorded higher values than in Kozjak Lake.

Among the investigated substrates, the highest taxa richness was recorded on *Chara* sp. and mosaic substrate sand/leaf litter in Prošće Lake, and the lowest on sand in Kozjak Lake (Tab. 3).

According to the NMDS analyses (Fig. 3), macroinvertebrate communities of each lake grouped together. Macroinvertebrate communities on different substrates in each lake were more similar to each other than macroinvertebrate communities on the same substrates in different lakes.

**Tab. 3.** Benthic macroinvertebrate taxa richness (S), abundance (N) and Shannon diversity index (H') in the four lakes and taxa richness (S) at various substrates in the Plitvice Lakes barrage-system. Abundance is expressed as number of collected individuals during the study.

| Lake | S | N | H' | Substrate | S |
|---|---|---|---|---|---|
| Prošće | 51 | 15762 | 1.81 | *Chara* sp. | 46 |
| | | | | Sand/Leaf litter | 40 |
| Ciginovac | 38 | 4783 | 1.59 | Cobbles | 34 |
| | | | | Leaf litter | 33 |
| Kozjak | 33 | 2306 | 1.40 | *Chara* sp. | 24 |
| | | | | Leaf litter | 24 |
| | | | | Sand | 9 |
| Kaluđerovac | 32 | 3231 | 1.36 | Cobbles/Leaf litter | 32 |

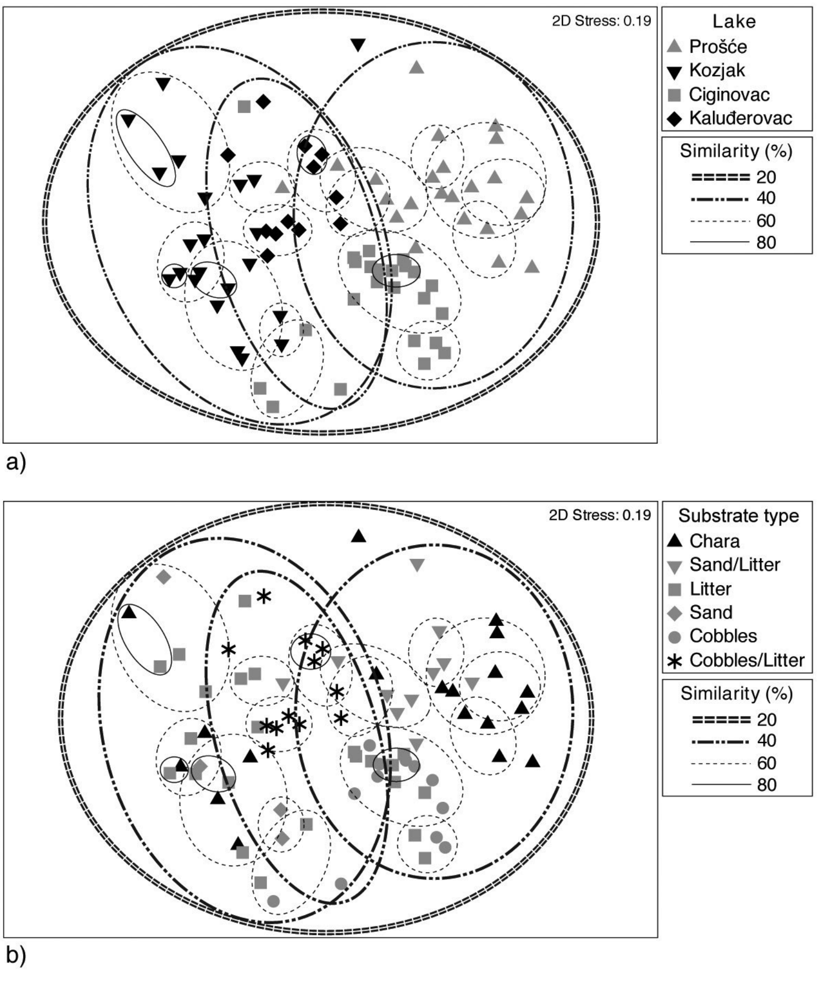


**Fig. 3.** NMDS analysis of the monthly macroinvertebrate samples at different substrate types in four lakes in the Plitvice Lakes barrage-system based on: a) each lake and b) substrate type.

## DISCUSSION

The chemistry of carbonate deposition in freshwater habitats is relatively well understood, yet the biological factors included in this process are still intriguing and a subject of research (e.g. Bayari & Kurttas, 1997; Drysdale, 1999; Pentecost & Zhang, 2000; Bellinzoni *et al.*, 2003; Golubić *et al.*, 2008). Our study confirmed the results of previous studies, which reported a wide range of organisms associated with harsh environment in tufa-depositing habitats (Pentecost, 2005). Of all freshwater invertebrates, the insects are generally the most diverse, and tufa-depositing systems like the Plitvice Lakes are no exception (Pentecost, 2005). As expected, Diptera dominated in all four investigated lakes (Minckley, 1963; Humphreys *et al.*, 1995; Carthew *et al.*, 2003) due to their wide ecological preferences in terms of feeding behaviour, habitat and microhabitat selection as well as their tolerance to the environmental factors (Malmqvist *et al.*, 1999; Edwards & Usher, 1985; Shimada *et al.*, 1991; Ivković & Pont, 2016). High taxa richness of Megaloptera recorded in the Plitvice Lakes was previously reported from carbonate-depositing ecosystems (Leonard, 1939), where they contribute to the maintenance of the populations structure as predators (Diehl, 1995). On the other hand, rather low taxa richness of predatory Odonata could be a result of a limitations of a sampling methodology used, as the sampling net collects their relatively large nymphs from a rather small surface area (e.g. Horning & Pollard, 1978). Trichoptera larvae represent a popular subject in studies focused on tufa diagenesis (Durrenfeldt, 1978; Drysdale, 1999; Paprocki *et al.*, 2003; Habdija *et al.*, 2004) as their biological structures are often found fossilized within tufa (Pentecost, 2005). In the Plitvice Lakes hydrosystem, Trichoptera were abundant only in the area of tufa barriers and water suppliers (Previšić *et al.*, 2007; Šemnički *et al.*, 2012), characterized by high water flow, compared to the lentic conditions in lakes. Although infrequent in lakes, their rather high taxa richness was not surprising, since the Balkan Peninsula was already recognized as an important evolutionary centre for a number of trichopteran genera (e.g. Kumanski & Malicky, 1999; Kučinić *et al.*, 2015; Previšić *et al.*, 2014; Vitecek *et al.*, 2015). As the majority of mayfly species prefer rhithral sections of lotic habitats (Bauernfeind & Soldán, 2012), relatively low diversity was recorded in the studied lakes. The presence of species such as *Caenis horaria* is generally believed to be an important environmental indicator of oligotrophic to mesotrophic conditions (Bauernfeind & Moog, 2000). Although the lakes' trophic state is important feature for Ephemeroptera assemblages, presence of rare species like *Leptophlebia vespertina* (Linnaeus, 1758) and *Paraleptophlebia werneri* Ulmer, 1920 (Vilenica *et al.*, 2015) seem to depend more on special conditions in the context of carbonate depositing area than on trophic state (e.g. Menetrey *et al.*, 2008). Very low abundance of Plecoptera is not surprising as majority of species prefer headwaters of lotic habitats (Graf *et al.*, 2002; 2009; 2023).

A substantial decrease of organic matter downstream the Plitvice Lakes barrage system (Obelić *et al.*, 2005; Horvatinčić *et al.*, 2006; Miliša *et al.*, 2006, Iveković, 1971) is most probably the reason for restricted distribution of Heteroptera along this hydrosystem due to the food availability. As majority of species are gatherers/collectors or predators (Zettel, 1995; Schmedtje & Colling, 1996), the highest amount of sedimented fine particulate organic matter in the Prošće Lake, and consequently highest abundance of some other macroinvertebrates, such as mayflies, could have provided optimal food resources for these insects. Regarding the other recorded macroinvertebrates, it is important to mention that Mollusca and Oligochaeta were present and abundant in all four lakes due to their wide ecological tolerance and/or preference for lentic habitats (Hörner *et al.*, 1995; Nesemann & Reischütz, 1995). Surprisingly, Isopoda, which are usually common in a typical benthic-lake macrofauna and have already been recorded in tufa-depositing systems (e.g. Minckley, 1963), were collected only in the Ciginovac Lake. Absence of the Isopoda species in the studied lakes is probably consequence of geological and climatological history of this area which was, and still is, because of the tufa deposition, transforming from the stream-river to the lake system (Kostić-Brnek & Brnek-Kostić, 1974). Finally, a decrease in abundance of other macroinvertebrates most probably caused decrease in abundance of predatory and parasitic Hirudinea downstream the hydrosystem (Nesemann & Moog, 1995; Schmedtje & Colling, 1996).

Development of tufa dams along a river profile creates a series of lakes and waterfalls. When the pooled waterbodies in the barrage system are formed, they become effective traps of eroded material (Golubić, 1969). Water behind the tufa dams accumulates in the form of lakes containing their own plankton, benthos and littoral communities (Golubić *et al.*, 2008). Accordingly, NMDS analyses showed that macroinvertebrate composition in the Plitvice Lakes hydrosystem was specific for each lake, regardless of the substrate type. Thus, differences in abundance and composition of benthic macroinvertebrate communities formed differences between the lakes. Dynamics of the physico-chemical environment, which in barrage-lake systems could be a consequence of the damming process, surely controls the biodiversity at relevant scales, and should also affect the community composition (Huston, 1994). In the case of the Plitvice Lakes, physico-chemical fluctuations did not explain the biological patterns that were observed. On the contrary, although the physical stream continuum has been disturbed by the development of tufa barriers (Habdija *et al.*, 1994), lakes in the barrage system can be taken as a continuum of physical and chemical conditions. These results corroborate results of previous a study where effects of the dams were not evident from examination of water quality variables (Nichols *et al.*, 2006). It seems that position of the lakes within the system plays a crucial role in the explanation of the observed patterns in benthic macroinvertebrates. Therefore, our results suggest that observed biodiversity patterns are, together with biology of individual taxa, also a consequence of the geomorphology of the Plitvice Lakes. Prošće Lake is the first lake in the barrage system, acting like a filter for organic matter, sediments and even fauna (Iveković, 1971), which explains a higher diversity observed there than in the other three lakes. All food and sediment particles coming with the inflowing water from the two main springs are first being retained in the Prošće Lake. Due to that process, the progressive filling with sediment and aquatic vegetation, like *Chara* sp., has been recorded there (Iveković, 1971). Therefore, we assume that lakes in barrage systems are not just effective traps of eroded material but also "small filtering screens". Similar to lakes that are inserted into river systems, these lakes in the cascade probably also function as sediment sinks (e.g. Arp *et al.*, 2007). They retain organic matter and faunal components like benthic macroinvertebrates (Miliša *et al.*, 2014), the distribution of which in the Plitvice Lakes does not correspond to the river continuum concept (RCC) hypothesis (Habdija *et al.*, 1994; Šemnički *et al.*, 2012; Vilenica *et al.*, 2017). Furthermore, as a result of the retention effect in barrage systems, organisms should show specific quantitative and qualitative patterns. Indeed, taxa richness and diversity showed a decreasing trend downstream the Plitvice Lakes. This trend was partially related to the abundance, which decreased in the upper section, where Prošće, Ciginovac and Kozjak lakes are placed. It is possible that Rječica Stream, a tributary that flows into the Kozjak Lake, represents a disturbance (e.g. Katano *et al.*, 2009), which caused a reduction in total macroinvertebrate abundance in the Kozjak Lake (e.g. Obelić *et al*., 2005). This observation could additionally be explained by habitat characteristics. The substrates sampled in Kaluđerovac Lake were stable microhabitats, while there was dynamics of appearance and disappearance of sampled substrates in Kozjak Lake. Substrate heterogeneity is also an interesting consideration in barrage systems. If we consider a barrage system as a set of spatial discontinuities then, according to the serial discontinuity concept (SDC), environmental heterogeneity exhibits a pattern along the stream profile that is similar to biotic diversity (Ward & Stanford, 1983). Such a conclusion must, however, remain highly speculative at this time, since further studies are necessary.

Generally, the observed decreasing trend of macroinvertebrate components should also be discussed and further studied in the context of tufa deposition, which has an increasing trend downstream the Plitvice Lakes (Srdoč *et al*., 1985). In this study, we also measured conductivity, which can be used as a surrogate measure of $Ca^{2+}$ concentration (Drysdale *et al*., 2002; Chen *et al*., 2004; Liu *et al*., 2006). Thus, according to the results, tufa formation was pronounced downstream and followed by a significantly decreasing diversity and abundance of organisms. Furthermore, several studies have suggested that deposition of carbonates has negative effects on macroinvertebrate communities (Minckley, 1963; Carter & Marks, 2007). Specifically, Rundio (2009) showed that taxa richness was lower at sites with tufa in comparison to the non-tufa sites.

## CONCLUSION

The barrage-lake system is a model of spatial discontinuities, where retention effects and tufa deposition cause notable alterations in ecosystem patterns, such as changes in taxon richness and the composition and structure of communities. These spatial discontinuities constitute sediment sinks, where lakes retain and accumulate organic matter and fauna. Therefore, each lake acts as a filtering screen and consequently appears to be a small ecosystem. Moreover, each lake has its own community characteristics, regardless of the fact that water flows from one lake to the next, connecting them and resulting in similar abiotic conditions in each lake along the system.

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**Appendix 1.** Benthic macroinvertebrate composition on different substrate types in the Plitvice Lakes barrage-system from April 2007 to March 2008. (P = Prošće, C = Ciginovac, Ko = Kozjak, Ka = Kaluđerovac, Ch = *Chara* sp., Co = cobbles, L = leaf litter, Sa = sand, Co/L = cobbles/leaf litter, Sa/L = sand/leaf litter). Within each macroinvertebrate group, taxa are presented in alphabetical order.

| Taxa | Sampled lakes | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | P | | C | | Ko | | | Ka |
| | Ch | Sa/L | Co | L | Ch | L | Sa | Co/L |
| TURBELLARIA | 17 | 39 | 36 | 28 | 33 | 7 | 12 | 13 |
| MOLLUSCA | | | | | | | | |
| *Bithynia tentaculata* (Linnaeus, 1758) | 65 | 5 | 12 | 19 | 29 | 12 | 2 | 30 |
| *Gyraulus crista* (Linnaeus, 1758) | | | 7 | | | | | |
| *Pisidium* sp. | 691 | 173 | 259 | 254 | 10 | 21 | 17 | 151 |
| *Sadleriana* sp. | | | | 1 | | | | |
| *Sphaerium* sp. | 21 | 1 | | | 7 | 7 | | 1 |
| *Valvata* sp. | 62 | 3 | 1 | | | | | |
| OLIGOCHAETA | 358 | 663 | 87 | 117 | 86 | 588 | 137 | 985 |
| HIRUDINEA | 57 | 8 | 6 | 3 | | 1 | | |
| ARACHNIDA | 21 | 25 | 24 | 23 | | 2 | | 1 |
| CRUSTACEA | | | | | | | | |
| *Asellus aquaticus* (Linnaeus, 1758) | | | 278 | 162 | | | | |
| *Gammarus* sp. | | 3 | | 1 | | | | 2 |
| EPHEMEROPTERA | | | | | | | | |
| *Caenis horaria* (Linnaeus, 1758) | 3373 | 480 | 101 | 97 | 1 | 2 | | 14 |
| *Centroptilum luteolum* (Müller, 1776) | 150 | 33 | 10 | 7 | | | | 4 |
| *Ephemera danica* Müller, 1764 | | 14 | 12 | 7 | 3 | | | 10 |
| *Habrophlebia lauta* Eaton, 1884 | | 18 | | | | | | |
| *Leptophlebia vespertina* (Linnaeus, 1758) | 200 | 14 | | | | | | |
| Leptophlebidae non det. | 36 | | | | | 1 | | |
| *Paraleptophlebia* sp. | 40 | 2 | | | | | | |
| *Paraleptophlebia werneri* Ulmer, 1920 | 13 | 58 | | | | | | |
| ODONATA | | | | | | | | |
| *Anax imperator* Leach 1815 | | | | | | 1 | | |
| *Coenagrion* sp. | 4 | | | | | 1 | 1 | |
| *Coenagrion pulchellum* (Vander Linden, 1825) | 17 | | | 3 | | | | |
| Gomphidae non det. | | | | | | | | 2 |
| *Ischnura elegans* (Vander Linden, 1820) | 4 | 1 | | | 1 | | | |
| *Lestes* sp. | | | | | 1 | 4 | 1 | |
| *Libellula fulva* Müller, 1764 | 21 | 7 | | | | | | |
| *Onychogomphus forcipatus* (Linnaeus, 1758) | 1 | | | | 5 | 1 | | |
| *Platycnemis pennipes* (Pallas, 1771) | | | 31 | 31 | | 4 | 1 | 11 |
| *Pyrrhosoma nymphula* (Sulzer, 1776) | 1 | | | | | | | |
| PLECOPTERA | 2 | 2 | | | 8 | | | 8 |
| COLEOPTERA | | | | | | | | |
| *Elmis aenea / rioloides* | 7 | 8 | | | 5 | | | |
| *Haliplus* sp. | 77 | 15 | 10 | 3 | | | | |
| *Riolus cupreus / subviolaceus* | 77 | 349 | 216 | 66 | 16 | 27 | | 3 |
| *Limnius volckmari* / sp. | | 21 | | | 1 | 11 | | |
| lar. Scirtidae non det. | | | | | | | | 15 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| MEGALOPTERA | | | | | | | | |
| *Sialis fuliginosa* Pictet, 1836 | 2 | 7 | 3 | | | 1 | | 13 |
| *Sialis lutaria* (Linnaeus, 1758) | 17 | 5 | 1 | 4 | | | | 3 |
| *Sialis morio* Klingstedt, 1932 | 13 | 1 | 2 | 5 | | | | 1 |
| *Sialis sordida* Klingstedt, 1932 | 26 | 8 | 4 | 11 | 1 | 2 | | 5 |
| TRICHOPTERA | | | | | | | | |
| *Agrypnia varia* (Fabricius, 1973) | | | | | 1 | | | 9 |
| *Athripsodes* sp. | 39 | 3 | 29 | 17 | | | | |
| *Ceraclea* sp. | 18 | | 1 | 1 | | | | |
| *Cyrnus trimaculatus* (Curtis, 1834) | 2 | | 1 | 3 | | | | 49 |
| *Hydropsyche instabilis* (Curtis, 1834) | | | | | 10 | | | 1 |
| *Hydropsyche saxonica* McLachlan, 1884 | | | | | 5 | | | 1 |
| *Hydropsyche* sp. | | | | | 5 | | | |
| *Hydroptila* sp. | 5 | | | | | | | |
| *Limnephilus* sp. | 1 | 1 | 1 | 1 | | | | |
| *Mystacides* sp. | 2 | | 3 | 5 | | | | 20 |
| *Notidobia ciliaris* Linnaeus, 1761 | 1 | 3 | | 17 | | | | |
| *Oecetis testacea* (Curtis, 1834) | 1 | | 5 | 5 | 4 | 4 | | 7 |
| Hydroptilidae non det. | 1 | 1 | | | | | | |
| *Philopotamus* sp. | 1 | 2 | | | | | | |
| *Rhyacophila* sp. | | | 2 | | | 1 | | |
| *Tinodes* sp. | 1 | 1 | 4 | 2 | | | | |
| DIPTERA | | | | | | | | |
| Ceratopogonidae | 102 | 63 | 4 | 6 | 15 | 11 | 9 | 105 |
| Chironomidae | 5586 | 1713 | 1829 | 1078 | 269 | 589 | 305 | 1740 |
| Empididae | 2 | | | | | | | 4 |
| Limoniidae | | | | | 1 | | | |
| *Tipula* sp. | | | | | | | | 3 |
| Simuliidae | | | 12 | | 18 | 1 | | 8 |
| HETEROPTERA | 137 | 501 | 2 | 3 | | | | |
| COLLEMBOLA | 1 | 1 | 1 | 1 | | 2 | | 4 |
| NEMATODA | 11 | 12 | 3 | 5 | | | | 7 |
| Total number of collected individuals | 11284 | 4264 | 2997 | 1986 | 535 | 1301 | 485 | 3230 |
| Taxa richness | 46 | 40 | 34 | 33 | 24 | 24 | 9 | 32 |